COOKE, F., & R. HARMSEN. 1983. Does sex ratio vary with egg sequence in Lesser Snow Geese? Auk 100: 215–217.

EDWARDS, T. C., JR., & M. W. COLLOPY. 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. Auk 100: 630–635.

———, & M. N. KOCHERT. 1986. Use of body weight and length of footpad as predictors of sex in Golden Eagles. J. Field Ornithol. 57: 317–319.

GARGETT, V. 1977. Sibling aggression in the Black Eagle in the Matapos, Rhodesia. Ostrich 49: 57–63.

MOCK, D. W. 1984. Infanticide, siblicide, and avian nestling mortality. Pp. 3–30 in Infanticide: comparative and evolutionary perspectives (G. Hausfauter and S. B. Hrdy, Eds.). New York, Aldine.

———. 1985. Siblicidal brood reduction: the prey size hypothesis. Am. Nat. 125: 327–343.

NEWTON, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo Books.

RYDER, J. P., & B. M. TERMAAT. 1987. Secondary sex ratios and egg sequence in Herring Gulls. Auk 104: 526–528.

SAFRIEL, U. N. 1981. Social hierarchy among siblings in broods of the Oystercatcher Haematopus ostralegus. Behav. Ecol. Sociobiol. 9: 59–63.

SMITH, G. W., & N. C. NYDEGGER. 1985. A spotlight line-transect method for surveying jack rabbits. J. Wildl. Manage. 49: 699–702.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry, 2nd ed. New York, W. H. Freeman and Co.

SPELLERBERG, I. F. 1971. Breeding behaviour of the McCormick Skua Catharacta macccormicki in Antarctica. Ardea 59: 189–230.

STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pp. 157–170 in Raptor management techniques manual (B. A. Giron Pendelton, B. A. Millsap, K. W. Kline, and D. M. Bird, Eds.). Washington, D.C., Nat. Wildl. Fed.

———, & M. N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. J. Wildl. Manage. 46: 885–893.

———, ———, & J. H. DOREMUS. 1983. Nesting of subadult Golden Eagles in southwestern Idaho. Auk 100: 743–747.

U.S. DEPARTMENT OF INTERIOR. 1979. Snake River birds of prey special research report. Bureau of Land Manage. Boise District, Idaho.

WERSCHKUL, D. F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. Auk 96: 116–130.

WILLIAMS, D. A. 1976. Improved likelihood ratio tests for complete contingency tables. Biometrika 63: 33–37.

Soil Analyses and ¹³C/¹²C Ratios Identify Sites of Deserted Rockhopper Penguin Colonies

P. J. MOORS,[1] T. W. SPEIR,[2] AND G. L. LYON[3]

[1]Science Directorate, Department of Conservation, P.O. Box 10-420, Wellington, New Zealand,
[2]New Zealand Soil Bureau, Private Bag, Lower Hutt, New Zealand, and
[3]Institute of Nuclear Sciences, Department of Scientific and Industrial Research,
Private Bag, Lower Hutt, New Zealand

During the 1940s the breeding population of Rockhopper Penguins (*Eudyptes chrysocome*) at Campbell Island (52°33′S, 169°09′E), in the Australasian quadrant of the Southern Ocean, probably exceeded a million birds (Bailey and Sorensen 1962, Moors 1986). Since then, numbers have fallen dramatically. Breeding colonies have been deserted and the remainder are now greatly reduced in area and numbers of occupants (Moors 1986). Seas around the island have warmed over the past 40 years (Moors unpubl. data), and the consequent change in food availability is the most likely cause of the decline.

Comparisons of present numbers with field observations and photographs taken intermittently between 1941 and the early 1950s were used to assess the extent of this decline. Such evidence is, however, inadequate or absent for several colonies. We investigated the use of chemical analyses of soil to identify deserted breeding sites of the Rockhopper Penguin.

Rockhopper colonies on Campbell Island are generally on rocky slopes close to the sea. The same breeding locations are used each year, and birds are present from mid-October through the end of April. A breeding Rockhopper Penguin produces 4.3–36.3 g dry wt of guano each day. The excreta contain high concentrations of nitrogen, phosphorus, calcium, and other elements (Burger et al. 1978). Colonies often contain thousands of breeding birds and the underlying soil becomes heavily enriched by their guano. Lower amounts of nutrients are also deposited from molted feathers and the decomposed remains of eggs, dead birds, and food (Williams and Berruti 1978, Siegfried et al. 1978, Williams et al. 1978).

Rockhopper Penguins feed entirely at sea, and the

deposited nutrients are derived ultimately from marine food chains. Marine organisms, and animals that feed on them, generally have higher $^{13}C/^{12}C$ ratios in the organic carbon of their tissues than organisms from terrestrial food chains (Fry and Sherr 1984, Rounick and Winterbourn 1986). Low $^{13}C/^{12}C$ ratios are particularly evident in food chains based on land plants which exploit the C_3 or Calvin photosynthetic cycle of carbon fixation. As far as is known, all grasses, herbs and shrubs at Campbell Island belong to the C_3 group of plants. Soil in penguin colonies should therefore be enriched with ^{13}C compared with nearby soil and peat never occupied by penguins. We analyzed and compared the C, N, and P concentrations and the $^{13}C/^{12}C$ ratios of samples from (1) sites presumed never to have been occupied by Rockhopper Penguins, (2) deserted and occupied colonies, and (3) Rockhopper Penguin guano. We also examined the $^{13}C/^{12}C$ ratios of plants growing near colonies.

Five groups of samples were collected in January 1986 on the west coast of Campbell Island at Penguin Bay, where about 4,600 pairs of Rockhopper Penguins were still breeding. Soil was collected from 4 sites in deserted colonies identified from photographs taken when penguins still bred there and chosen to give a sequence of times since desertion. Each site was probably deserted only a few years after the date of its photograph. Four samples (depths 5–15 cm) were collected at 2 sites still occupied in 1951 (1951 sites); 2 samples (depths 5–10 cm) were collected from a site active in 1974 (1974 site); and 4 samples (depths 5–20 cm) were taken from a site still occupied in 1979 (1979 site). Soil was collected from 5 locations (depths 1–5 cm) in 2 colonies where rockhoppers continued to nest. Two samples (depths 15–25 cm) were taken from each of 3 control sites more than 100 m from, and about 20 m above, the closest known rockhopper colony. These sites had the same aspect and exposure as the rockhopper colonies, but were on steep vegetated slopes. This habitat was not used by Rockhopper Penguins at Campbell Island. We collected fresh guano from 6 adult Rockhopper Penguins, 3 samples of vegetation from the margins of an active colony and 2 samples from the 1974 site.

Shallow soil in the active colonies and varying thickness of peat at other sites prevented our collection of samples at constant depths. Because C, N, and P decline proportionally with soil depth, ratios of these elements were likely to be less affected by variability in sampling depth. C/N and C/P ratios were the main basis for comparison of soil elements.

Soil and peat samples were stored in a field-moist condition for several weeks at about 4° C. They were then sieved, the ≤2 mm material was air-dried and finely ground and the >2 mm material (primarily stones) was discarded. Liquid guano was collected in a large plastic bag strapped around each bird and then run onto a glass-fiber filter paper. Three filter papers were used, each receiving guano from 2 birds. The

papers were dried by gentle heating and finely ground. The vegetation samples were refrigerated for 2 weeks and dried at about 65°C before being finely ground in a plant mill.

We analyzed $^{13}C/^{12}C$ by sealed-tube combustion of subsamples that contained 1–3 mg C. The released CO_2 was analyzed by mass spectrometry (Rounick et al. 1982). Analytical precision was 0.3‰ (parts per thousand). Results are reported as deviations ($\delta^{13}C$) relative to the international limestone standard known as PDB, which has an arbitrary value of zero, where:

$$\delta^{13}C_{PDB} = 1{,}000 \times \left[\frac{(^{13}C/^{12}C)_{sample} - (^{13}C/^{12}C)_{PDB}}{(^{13}C/^{12}C)_{PDB}} \right].$$

$\delta^{13}C$ is usually a negative number and becomes increasingly negative as the $^{13}C/^{12}C$ ratio of the sample declines.

Organic C was measured with a Leco induction furnace after soil acidification to remove carbonate C. After Kjeldahl digestion (Cu catalyst), total N was measured as NH_4^+-N by autoanalyzer and total P as phosphate P by colorimetry (Motomizu et al. 1983). Results are expressed as percent composition of oven-dry (105°C) wt of soil (Blakemore et al. 1987). Single classification analyses of variance and Kolmogorov-Smirnov two-sample tests were used to examine differences among samples in C, N, P, and $\delta^{13}C$, and Kolmogorov-Smirnov tests for differences in C/N and C/P ratios (Sokal and Rohlf 1981).

Guano contained the largest proportions of C and N (Table 1). Total P was considerably more abundant in guano and soil from colonies than in control samples. Guano N and P composition was similar to that for Rockhopper Penguins on Marion Island (Burger et al. 1978).

There were significant differences between control sites, occupied colonies, and combined deserted colonies in the percentage concentrations of C ($F_{2,18} = 5.74$; $P < 0.02$) and P ($F_{2,18} = 31.9$; $P < 0.001$), but not N ($F_{2,18} = 0.48$; $P > 0.5$). C and N did not accumulate in colony soil at Penguin Bay, despite fresh guano being especially rich in these elements. The average concentrations of C and N in soil from active colonies were only a fraction of those in guano, and were much lower at the oldest abandoned site than at the more recently abandoned one (Table 1; Kolmogorov-Smirnov $D_{4,4} = 16.00$; $P < 0.05$). Organic C and N from guano are rapidly mineralized and lost as CO_2 and NH_3^+ and NO_3^-, particularly in Campbell Island's moist climate (mean annual rainfall, 1,377 mm).

The average percentage of P was greater in soil from occupied colonies than in guano (Table 1), but this difference was not significant ($F_{1,6} = 1.00$; $P > 0.25$). Total P in soil from occupied colonies was significantly higher than in deserted colonies ($F_{1,13} = 13.42$; $P < 0.005$). Usually P is strongly retained by soil, but run-off from the acidic peat and soils on the

TABLE 1. Average concentrations of C, N, P and ^{13}C in soil, vegetation, and penguin guano from Campbell Island, with particular reference to occupied and deserted colonies of Rockhopper Penguins. SDs in parentheses.

Sample type	n	Total C %	Total N %	C/N ratio	Total P %	C/P ratio	δ^{13}C ‰
Guano	3	27.0 (0.9)	18.6 (3.6)	1.5 (0.36)	3.0 (0.65)	9.2 (1.9)	−18.0 (1.2)
Occupied colonies	5	5.5 (2.9)	1.1 (0.40)	4.8 (1.2)	3.6 (0.83)	1.5 (0.58)	−23.2 (0.7)
Deserted colonies:							
1979 site	4	5.2 (1.9)	1.0 (0.47)	5.3 (0.54)	2.5 (0.51)	2.1 (0.39)	−21.8 (0.61)
1974 site	2	7.8 (0.57)	1.4 (0.13)	5.8 (0.14)	2.0 (0.30)	3.9 (0.28)	−22.5 (1.1)
1951 sites	4	2.4 (1.0)	0.39 (0.18)	6.2 (1.2)	2.2 (0.74)	2.0 (1.1)	−22.4 (0.50)
Total	10	4.6 (2.5)	0.84 (0.50)	5.8 (0.9)	2.3 (0.56)	2.0 (1.1)	−22.2 (0.7)
Control sites	6	12.6 (7.9)	0.91 (0.60)	14.0 (1.4)	0.85 (0.22)	15.1 (10.1)	−24.8 (0.4)
Vegetation	5	—	—	—	—	—	−27.2 (2.1)

island (Campbell 1981) was probably responsible for its gradual removal from the deserted colonies.

Soil samples from both active and abandoned penguin colonies were separated from control samples by C/N and C/P ratios (Table 1). The ratios for colony sites were significantly less than those for control sites (Kolmogorov-Smirnov tests; all $P < 0.025$). The C/N and C/P ratios from the 3 deserted sites were not significantly different from the corresponding ratios for occupied colonies (both $D_{10,5} = 20.0; P > 0.1$). The C/N ratio tended to increase with time since the colonies were deserted (Table 1). δ^{13}C also differed among samples (Table 1), with significant differences between past and present rockhopper colonies and control sites ($F_{2,18} = 21.25; P < 0.001$). The 3 deserted colonies did not differ significantly ($F_{2,7} = 1.15; P > 0.2$), nor was there a significant difference between the occupied colonies and combined deserted colonies ($D_{10,5} = 30.0; P > 0.1$). However, there was a highly significant difference between the deserted colonies and control sites ($D_{10,6} = 60.0; P = 0.001$). The correlation between δ^{13}C values and C/N ratios for active, abandoned, and control sites was highly significant ($r = -0.82; n = 21; P < 0.001$). As expected, the values of δ^{13}C were highest in guano and lowest in vegetation. The δ^{13}C values for these samples were similar to those previously reported for marine organisms (Fry and Sherr 1984) and C$_3$ plants (Bender 1971). Campbell (1981) noted that the high concentrations of nutrients such as N, P, and K in soils near active albatross nests on Campbell Island were leached away once the nests were deserted. Similarly, Speir and Cowling (1984) reported gradual losses of C, N,

and P from soil in Adélie Penguin (*Pygoscelis adeliae*) colonies in Antarctica. However, these elements did not decline consistently with time since desertion in the Rockhopper Penguin colonies at Campbell Island (Table 1).

Total P was most abundant in colony soils at Penguin Bay, but even the control samples contained relatively high levels compared with Campbell's (1981) analyses and the normal range of 0.01–0.3% P in New Zealand topsoils (Saunders 1968). The elevated P most likely came from seabirds, probably Sooty Shearwaters (*Puffinus griseus*). They once bred in very large numbers on Campbell Island (Bailey and Sorensen 1962), and favored steep tussocky coastal slopes, like those at the control sites, for their nesting burrows. This interpretation is supported by a much lower P concentration of 0.06% in soil (C/N ratio 29.8, C/P ratio 845) which we collected in February 1987 from a flat ridge-top about 750 m away from the rockhopper colonies, where shearwaters and other seabirds are unlikely ever to have nested.

We believe that deserted Rockhopper Penguin colonies can be readily identified by soil characteristics, even when abandoned for more than 30 years. The most useful soil indicators are the C/N and C/P ratios and the δ^{13}C value. The C/N ratio is preferable for most purposes because it can be determined with simple analytical techniques. Investigation of the annual rate of change of these indicators, using sites for which the dates of abandonment are known, may enable the time since desertion to be estimated for other colonies. These methods are applicable to studies of the past breeding distribution and abundance of colonial

seabirds, and are likely to be most successful with species nesting in dense aggregations on the surface or in burrows.

LITERATURE CITED

BAILEY, A. M., & J. H. SORENSEN. 1962. Subantarctic Campbell Island. Denver, Denver Mus. Nat. Hist.

BENDER, M. M. 1971. Variations in the $^{13}C/^{12}C$ ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. Phytochemistry 10: 1239–1244.

BLAKEMORE, L. C., P. L. SEARLE, & B. K. DALY. 1987. Methods for chemical analysis of soils. New Zealand Soil Bureau Sci. Rep. 80. Lower Hutt, New Zealand, Dep. Sci. Industrial Res.

BURGER, A. E., H. J. LINDEBOOM, & A. J. WILLIAMS. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. South African J. Antarct. Res. 8: 59–70.

CAMPBELL, I. B. 1981. Soil pattern of Campbell Island. New Zealand J. Sci. 24: 111–135.

FRY, B., & E. B. SHERR. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27: 13–47.

MOORS, P. J. 1986. Decline in numbers of rockhopper penguins at Campbell Island. Polar Rec. 23: 69–73.

MOTOMIZU, S., T. WAKIMOTO, & K. TOEI. 1983. Spectrophotometric determination of phosphate in river waters with molybdate and malachite green. Analyst 108: 361–367.

ROUNICK, J. S., & M. J. WINTERBOURN. 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36: 171–177.

———, ———, & G. L. LYON. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. Oikos 39: 191–198.

SAUNDERS, W. M. H. 1968. Phosphorus. Pp. 95–103 in Soils of New Zealand, part 2. New Zealand Soil Bureau Bull. 26.

SIEGFRIED, W. R., A. J. WILLIAMS, A. E. BURGER, & A. BERRUTI. 1978. Mineral and energy contributions of eggs of selected species of seabirds to the Marion Island terrestrial ecosystem. South African J. Antarct. Res. 8: 75–87.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry, second ed. San Francisco, W. H. Freeman & Co.

SPEIR, T. W., & J. C. COWLING. 1984. Ornithogenic soils of the Cape Bird Adélie penguin rookeries, Antarctica. I. Chemical properties. Polar Biol. 2: 199–205.

WILLIAMS, A. J., & A. BERRUTI. 1978. Mineral and energy contributions of feathers moulted by penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. South African J. Antarct. Res. 8: 70–73.

———, A. E. BURGER, & A. BERRUTI. 1978. Mineral and energy contributions of carcasses of selected species of seabirds to the Marion Island terrestrial ecosystem. South African J. Antarct. Res. 8: 53–59.

Food Supplement Effects on Breeding Time and Harem Size in the Red-winged Blackbird (*Agelaius phoeniceus*)

PETER H. WIMBERGER[1]
Washington State Museum, University of Washington, Seattle, Washington 98195 USA

Some bird species (e.g. *Parus major*, Källander 1974; *Corvus corone*, Yom-Tov 1974; *Falco tinnunculus*, Cavé 1968; and *Melospiza melodius*, Smith et al. 1980) advance the onset of breeding in response to increased food resources during the pre-laying season, whereas others (e.g. *Pica pica*, Högstedt 1981) do not. Ewald and Rohwer (1982) report advancing the onset of breeding in Red-winged Blackbirds (*Agelaius phoeniceus*) by feeding. Their study, however, used whole lakes as experimental units, as opposed to territories or groups of territories within lakes. Ponds differ in surrounding vegetation, topography, substrate and productivity (Orians 1980), factors that may affect upland foraging success during the early breeding season, and relative timing of insect emergence later in the season. These latter factors may affect timing of breeding. One could therefore argue that the advancement that Ewald and Rohwer observed was due to intrinsic differences between marshes rather than

[1] Present address: Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853-2701 USA.