The feeding ecology and field energetics of the Pedra Branca skink (*Niveoscincus palfreymani*)

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Abstract.   The diet and food requirements of free-living Pedra Branca skinks (*Niveoscincus palfreymani*) were studied on Pedra Branca Island, the only known location for this vulnerable, endemic species. While discarded fish remains and regurgitate from seabirds are utilised as food by the skinks during summer, invertebrates represent the most important prey. Isotope turnover rates indicate that feeding is negligible over winter and that significant amounts of non-food water are turned over during summer, either by drinking rainwater or as pulmo-cutaneous water exchange. An assessment is made of the seasonal and annual food requirements of individual skinks and the population.

Introduction

Niveoscincus palfreymani is an endemic skink with a distribution that is confined to Pedra Branca, a small (2.5 ha, 55 m elevation) rocky island located 26 km off the south-east coast of Tasmania (43°52′S, 146°56′E). This skink is Australia's southernmost, wholly terrestrial vertebrate, and is the only reptile species inhabiting the island.

During the austral summer, the island is the breeding site of about 7000 pairs of Australian gannets (*Sula serrator*), 250 pairs of shy albatross (*Thalassarche cauta*), 50 pairs of silver gull (*Larus novaehollandiae*), and low numbers of kelp gulls (*L. dominicanus*), Pacific gulls (*L. pacificus*), black-faced shags (*Phalacrocorax fuscescans*) and fairy prions (*Pachyptila turtur*) (Brothers *et al.* 2001, pp. 506–509). During the seabird breeding season the young birds are regularly provisioned with food, which is regurgitated by their parents. During this process substantial amounts of food are inadvertently dropped or pirated by non-breeding birds, and dropped fish are scattered around the island. Australian fur seals (*Arctocephalus pusillus dorifererus*) use the island as a regular haul-out site, with up to 500 seals being present when sea conditions permit. The only terrestrial plant on the island is a low, sparsely distributed samphire (*Sarcocornia quinqueflora*), and suitable habitat for *N. palfreymani* is restricted to six small areas (totalling 1400 m^2) of weathered catacomb and boulder sandstone, some of which is often inundated by seawater and spray.

Niveoscincus is a predominantly Tasmanian genus: seven of the eight species occur in Tasmania and six of these are endemic (Hutchinson and Schwaner 1991). *N. palfreymani* is the largest skink within the genus: adult males and females are similar in size with a mean snout–vent length of 88 mm and a mean mass of 17.7 g (N. Brothers, unpublished data). The population of *N. palfreymani* has been isolated from the Tasmanian mainland for at least 19 000 years, but possibly as long as 100 000 years (Banks 1993). In 1986 the skink population was estimated to contain 560 individuals, but declined to 290 by 1996 before recovering to an estimated 470 individuals in 2000 (Anon. 2001). In view of the small population size and its restricted distribution, the species is regarded as Vulnerable and is proposed for listing as Endangered.

Prior to this study, the diet of *N. palfreymani* was known only from direct observations made by research personnel monitoring seabird and skink populations. These observations suggested that the flesh of dead jack mackerel (*Trachurus declivis*), regurgitated by gannets and albatrosses during chick feeding, was the major food source for the skinks (Rounsevell *et al.* 1985). These authors also noted that a terrestrial isopod, *Ligia australiensis*, was very abundant on the lower slopes of Pedra Branca and could serve as prey for skinks with more limited access to fish detritus.

A better understanding of the diet and energy requirements of *N. palfreymani* was considered to be vital to

the future management of this highly vulnerable species, particularly in the event of any major ecological disturbances to the seabird populations on Pedra Branca.

Materials and Methods

Diet

Whole scats were collected from four sub-sites (Main, West Cliff, South-east and Rockpile) regularly between July 1992 and March 2000 during regular population surveys. Where time and weather conditions allowed, all visible scats were collected. The scats were stored dry in individual glass vials until analysed. In the laboratory, individual scats were soaked in 70% ethanol for up to 48 h before being sorted under a microscope. All hard parts were given a reference number, stored in 70% ethanol and subsequently identified to species wherever possible. Where possible, the number of individuals of a particular species per scat was determined. Characteristic body parts (e.g. isopod mandible, amphipod propodus, diptera wing) were used to calculate the maximum/minimum number of individuals present in each scat.

Composition of food materials

Some representative fish, seabird regurgitate and invertebrates were analysed for water and energy content to enable estimates of food consumption rates to be derived. These materials were weighed fresh and after complete drying in a fan-forced oven at 60°C, using an electro-balance. All dried samples were ground in a Wiley mill, after which weighed subsamples were combusted in a Gallenkamp ballistic bomb calorimeter, using benzoic acid as a standard. All calorimetric weighings were made to the nearest milligram.

Energetics and food consumption

Isotope turnover studies were commenced in February 1986. The skinks were captured by dangling a lure (raw fish meat tied onto a string) at the entrance to a rock crevice occupied by one or several of the lizards. An animal would invariably attack the lure, whereupon the lizard could be easily noosed with a light line, and transferred to a cotton bag. The animals were maintained in the cotton bags while they were processed, after which they were released at their respective points of capture.

Each animal was weighed with a spring balance (to the nearest 0.5 g) and identified by toe-clip marks. If an animal was not previously marked it was given an individual toe-clip using sharp, fine scissors. Each of 43 animals was then given an intra-peritoneal injection (50 μL) of tritiated water (containing 10 MBq activity) to allow the determination of total body water and water flux rates (Nagy and Costa 1980). In addition to tritiated water, 30 individuals were given an injection of 95% atoms excess ^{18}O water (50 μL) to allow the measurement of field metabolic rate (FMR) (Lifson and MacClintock 1966; Nagy 1980). After injection, the animals were maintained overnight and bled the following morning just prior to release. About 100 μL of whole blood was obtained from the caudal vein via 25-gauge syringe needles and the blood samples transferred to individual, screw-capped plastic vials. To prevent the immediate recapture of injected animals, released lizards were given a small paint dot on the dorsal surface for easy recognition.

Of the injected lizards, 21 were recaptured in April 1986, 46–49 days after release. They were re-weighed and bled as before, but not re-injected with isotope before being re-released. A subsequent recapture exercise was carried out about 200 days later (in October 1986), when further body weights and blood samples were obtained from 14 of the animals recaptured in April.

In October 1986, 38 animals were injected with both tritiated water and ^{18}O water, but none of these animals were subsequently recaptured the following March. Thus FMRs and water fluxes could not be estimated for the spring/summer of 1986/87.

Blood samples were kept as cool as possible on the island, and transferred to a freezer as soon as possible (usually within 4 days of collection). For isotope analysis the blood samples were thawed and transferred to modified Pasteur pipettes and heat-distilled under vacuum (Nagy 1983). The extracted water was subjected to isotope analysis; for ^{18}O, 50 μL sub-samples were subjected to Urey exchange with standard charges of CO_2 (Green *et al.* 1991), after which the equilibrated CO_2 was drawn off and 46 : 44 ratios measured in an Isotope Ratio Mass Spectrometer (VG Isogas 903). For tritium, 10 μL subsamples were added to 3 mL of scintillation cocktail (PCS, Amersham) and counted in a Beckman 2800 Liquid Scintillation Counter.

Body water pools were calculated by comparing tritium activities at equilibration with standard dilutions of injected tritium. It was assumed that there were no changes in mass-specific pool sizes during the release periods, and that any changes in body mass and water pool were linear. Rates of water flux and CO_2 production were calculated following Lifson and McClintock (1966) and Nagy (1980). Since *N. palfreymani* is carnivorous, a thermal equivalent of 25.7 kJ L^{-1} CO_2 was assumed in calculating energy expenditure (Nagy 1983).

Zimmerman and Tracy (1989) have reviewed digestive efficiency in a range of reptiles; for 10 species of carnivorous lizard feeding on crickets or mealworm larvae, a mean energy assimilation of 85.2 ± 5.1% was found. Since 9% of assimilated energy is excreted as urinary waste (Andrews and Asato 1977), 78% of total prey energy is available to a carnivorous lizard as metabolisable energy (ME). The free water content of potential food items was derived from the fresh and dry weights of food materials, and the potential metabolic water (MW) content of food was calculated as 0.028 mL kJ^{-1} ME (Schmidt-Nielsen 1975).

All mean values are provided with standard deviations. Seasonal dietary comparisons were made by Chi-square analysis. Comparisons of water-influx rates between genders and sub-sites of the population were made by ANOVA, and subsequent *t*-tests if warranted. Probability values of <0.05 were taken to indicate statistical significance.

Results

Diet

The scat samples were not evenly distributed between the sub-sites, reflecting the different numbers of skinks inhabiting the sites, the timing of collection trips and the absence of intact scats at some sites due to inundation by heavy sea spray. In total, 254 intact scats were collected and analysed for prey remains. The locations and times of collection of skink scats are shown in Table 1, while the composition and frequency of occurrence of food items is shown in Table 2.

Prey taxa identified during the entire sampling period indicate that the diet of *N. palfreymani* includes three Orders of Insecta, two Orders of Crustacea, one Order of Araneae and fish remains (Table 2). Of the identifiable prey, isopods occurred most frequently (present in 65% of scats), with the larger of the two species, *Ligia australiensis*, predominating (present in 48% of scats). The smaller species, *Deto marina*, occurred in 5.5% of scats. There was a significant seasonal influence on the occurrence of *L. australiensis* in the diet, fewer being present than expected in March, and more than expected in May, November and December (χ^2 = 21.3, d.f. = 4, *P* < 0.01).

Table 1.   Scat samples collected for analysis of the diet of *N. palfreymani*

Date of collection	Sub-site location				Monthly total
	Main	West Cliff	South-east	Rockpile	
March 1994				25	
March 1996	5	20	10	15	
March 1997		14	4	12	175 (68.8%)
March 1998			10	6	
March 2000		26	7	21	
May 1998				12	12 (4.7%)
July 1992				11	11 (4.3%)
November 1998				19	19 (7.5%)
December 1994			5	16	37 (14.6%)
December 1997				16	
Total	5 (2.0%)	60 (23.6%)	36 (14.2%)	153 (60.2%)	254

Table 2.   Prey species in *N. palfreymani* scat samples

		Frequency of occurrence		Numerical abundance		Number per scat when present	
		n	%	*n*	%	Mean	Range
Isopoda	All isopods	165	65.0	195	27.9		
	Ligiidae – *Ligia australiensis*	122	48.0	174	24.9	1.4	1–4
	Scyphacidae – *Deto marina*	14	5.5	21	3.0	1.5	1–4
Diptera	All Diptera	100	39.4	433	61.9		
	Coelopidae	89	35.0	354	50.6	3.9	1–20
	Tipulidae – *Molophillus* sp.	19	7.5	73	10.4	3.8	1–17
	Unidentified pupa	6	2.4	6	0.9		
Amphipoda	Talitridae – *Orchestia australis*	41	16.1	46	6.6	1.1	1–3
Araneae	All Araneae	14	5.5	14	2.0		
	Anyphaenidae – *Amaurobiodes maritima*	9	3.5	9	1.3	1	1
	Segesriidae – *Segestria* sp.	3	1.2	3	0.4	1	1
Hymenoptera	Proctotrupoidae	9	3.5	9	1.3	1	1
Coleoptera	Coccinellidae – *Coccinella undecimpuctata*	1	0.4	1	0.1	1	1
	Unidentified sp.	2	0.8	2	0.3	1	1
Fish	Unidentified sp.	8	3.1				

Dipteran remains were the second most represented identifiable prey item, occurring in 100 scats (39.4%). Two species were identified: a kelp fly (family Coelopidae) and a crane fly (family Tipulidae). The kelp fly was present in scats from all four sub-sites, whereas crane flies were recorded only in scats from the South-east and Rock-pile sub-sites. Kelp flies were found in scats in March only.

Amphipods were the third most common item in scats, represented by a single species (*Orchestia australis*); it was present in 16% of scats and was almost exclusively confined to scats collected in March ($\chi^2 = 13.7$, d.f. $= 3$, $P < 0.01$).

Remains of Araneae were present in 5.5% of scats, and were evenly represented with respect to site and season.

Dipterans were taken in larger numbers (62%) than isopods (28%). This is reflected in the large number of flies (up to 20) present in an individual scat.

Fish remains (scales, otoliths, vertebrae or lenses) were identified in only 3.1% of scats. However, the composition of four other scats probably consisted of fish remains; they had a soft consistency and contained very few of the invertebrate remains that are characteristic of most scats. Thus a probable frequency of occurrence for fish in the diet is 4.7%, and fish were only ever recorded in scat samples collected in March.

No remains of the terrestrial plant *Sarcocornia quinqueflora* were detected and only one scat contained a small amount of an unidentified seaweed species. Other items identified in the scats were regarded as being non-dietary: seal hair, feathers and mites. These items could have been accidentally ingested or may have become attached to fresh scats before collection.

It is clear that invertebrate prey constitute a major part of the diet *N. palfreymani*, especially outside of the summer, sea-bird breeding season.

Composition of food materials

The free water and total energy contents of a range of food materials is shown in Table 3. The free water contents of all potential food items for carnivores are relatively high and uniform, while there is a greater degree of variation in the energy contents. The mean water content of prey was 69.7 ±

Table 3.   Free water, energy and total water content of representative prey and food materials

Species		n	Free water (%)	kJ g^{-1} fresh	Total water (%)
Crustacea	*Ligia australiensis*[A]		64.8	3.69	73.1
	Orchestia australis[A]		71.5	4.91	82.5
Araneae	Huntsman spider	6	70.0 ± 1.6	7.09 ± 0.63	85.9
Fish	Trachurus declivus	6	69.0 ± 3.6	7.53 ± 1.37	85.8
	Neopilchardus sp.	4	74.7 ± 0.6	5.13 ± 0.21	86.2
Regurgitate	From *Thalassarche cauta*	8	66.8 ± 9.5	6.68 ± 2.05	81.8
	From *Eudyptula minor*	8	71.3 ± 4.4	6.18 ± 1.05	85.1
Mean ± s.d.		7	69.7 ± 3.26	5.89 ± 1.37	82.9 ± 4.7

[A]Pooled sample.

Table 4.   Water influx and FMR in *N. palfreymani* and other skinks in summer

	Niveoscincus palfreymani	*Mabuya striata*	*Chalcides sexlineatus*
Mass (g)	16.7 ± 3.3	19.5 ± 4.8	7.8
TBW (%)	77.9 ± 5.5	66.0 ± 3.1	63.3
FMR (mL CO$_2$ day^{-1})	52 ± 10	111 ± 33	–
(kJ day^{-1})	1.33 ± 0.26	2.9 ± 0.9	0.72
(kJ kg^{-1} day^{-1})	78 ± 15	149 ± 46	90.5
(kJ kg$^{0.95}$ day^{-1})	91.7	172.6	102.3
Water influx (mL day^{-1})	1.01 ± 0.20	0.64 ± 0.24	0.10
(mL kg^{-1} day^{-1})	59.2 ± 12.1	32.8 ± 10.8	12.5
(mL kg$^{0.95}$ day^{-1})	69.7	38.1	14.2
WEI (mL kJ^{-1})	0.76	0.22	0.14

3.3% of fresh mass, while the mean energy content was 5.89 ± 1.37 kJ g^{-1} fresh mass (equivalent to a ME content of 4.71 kJ g^{-1} fresh). The metabolism of this amount of energy would generate 0.13 mL MW g^{-1} fresh food, giving a total water content (free and metabolic water combined) of 0.83 mL g^{-1} fresh food.

Body mass

The mean initial body mass of animals that returned isotope turnover data was 16.7 ± 3.3 g ($n = 22$), and there was no significant difference between the sexes. During the summer release period (February–April) most animals maintained, or increased, body mass (as much as 16% in one case), although eight animals lost body mass (the greatest loss being 18% for a female that was in advanced pregnancy at initial capture). However, during the Apri–October period (predominantly winter), only one individual gained in mass – the other 13 lost or maintained body mass.

Water pool and isotope turnover

The mean body water pool of the lizards at their initial release was 77.9 ± 5.5% of body mass ($n = 22$). Water influx rates in both summer and winter were mainly obtained from animals that inhabited the main sub-site. The water influx rates in summer were uniform across the sites and no gender differences were discernible, the overall mean water influx being 59.2 ± 12.1 mL kg^{-1} day^{-1} ($n = 22$), equivalent to 1.01

mL day^{-1} for a 17-g adult (Table 4). Water influx rates in winter were much lower than those of summer: mean = 5.4 ± 2.8 mL kg^{-1} day^{-1} ($n = 14$), equivalent to 0.09 mL day^{-1} for an average adult. Again, there were no significant site or gender differences.

Due to insufficient blood volumes being drawn from most animals at recapture in April, only five determinations of FMR (CO$_2$ production) were derived from doubly-labeled water turnover in summer: mean = 0.127 ± 0.025 mL CO$_2$ g^{-1} h^{-1}, equivalent to the metabolic expenditure of 1.33 kJ day^{-1} for a 17-g skink (78 kJ kg^{-1} day^{-1}).

Discussion

N. palfreymani has often been observed feeding on fish remains, and it has generally been thought that fish, dropped or regurgitated by seabirds, forms an important part of the diet of *N. palfreymani*. This observation is reinforced by the ease of capturing these skinks using fish as bait or fish oil as an attractant. However, faecal analysis suggests that fish remains are present in only about 5% of scats, and then only during summer. If the skinks were to feed predominantly on the flesh of discarded fish, it would be expected that fish remains would be under-represented in faeces. Even so, it is clear that invertebrates contribute substantially to the diet throughout the year, especially outside of the seabird breeding season (spring and summer).

Clearly, isopods, dipterans and amphipods are the dominant invertebrate prey items of *N. palfreymani*. There is a seasonal shift in prey, with dipterans and amphipods being dominant in March and isopods at other times. The large numbers of dipterans in the scats at any one time indicates that they are readily available. Diptera are vulnerable to predation when they are emerging from their pupae, as they need to dry their bodies before they can fly. It is likely that during this emergence period the skinks prey heavily on the dipterans. Dipteran larvae are also avidly consumed but leave no hard parts in the scats. Adult kelp flies have also been observed to be inactive on occasion, again affording skinks the opportunity to prey on them.

On occasion, we have observed adult *N. palfreymani* hunting and preying on neonate skinks, although no remains were found in any of the scats.

Even if fish or regurgitate have a less important role in the direct provisioning of the skink population than previously thought, the indirect importance of fish to the total energy and nutrient status of Pedra Branca cannot be overlooked. The discarded food, guano and faeces that are deposited on the island by chicks and adult sea-birds provide substantial amounts of nutrients for lower-level food-web producers and invertebrate consumers, which are ultimately available as prey to *N. palfreymani*. This dependent relationship of a skink on the nutrients provided by the feeding and excretion of seabirds has also been reported for *Leiolopisma nigriplantare* on the Chatham Islands (Fleming 1939), *L. lichenigera* on Ball's Pyramid (D. Hiscox, personal communication) and *L. smithi* on Poor Knights Islands (Patterson 2000). In addition, the population size of the Fiordland skink (*Leiolopisma acrinasum*) is correlated with the presence of the New Zealand fur seal (*Arctocephalus forsteri*) (Thomas 1985), while population density and breeding success in an iguanian lizard (*Uta palmeri*) is correlated with the density of adjacent sea-bird breeding sites (Hews 1993).

The importance of marine inputs (fish scraps, excretory products, seaweed, etc) to the productivity of islands, particularly smaller islands, is substantial. Polis and Hurd (1996) found that arthropods in the supralittoral zone of islands in the Gulf of California were 85–560 times more abundant than inland, and 2.2 times more abundant on islands with seabird colonies than on those without.

The isotope turnover data for the period between February and mid-April represents late summer and early autumn activity. The mean FMR measured during this period was 1.33 kJ day^{-1} (78 kJ kg^{-1} day^{-1}), about half that predicted (2.40 kJ day^{-1}) for a scleroglossan lizard (by means of the expression 0.163M$^{0.949}$, where M is mass in grams: Nagy *et al.* 1999).

Comparative FMR data are available for only two other skinks. *Chalcides sexlineatus* (Brown *et al.* 1992) also has an FMR (0.72 kJ day^{-1}, 92 kJ kg^{-1} day^{-1}) that is lower than predicted (1.14 kJ day^{-1}, 146 kJ kg^{-1} day^{-1}), whereas *Mabuya striata*, a desert skink that is similar in size to *N. palfreymani*, has an FMR (2.9 kJ day^{-1}, 149 kJ kg^{-1} day^{-1}) close to that predicted (2.73 kJ day^{-1}, 140 kJ kg^{-1} day^{-1}) (Nagy and Knight 1989). The higher FMR of *M. striata* probably reflects the higher environmental temperature profile experienced by this desert species compared with the cooler mesic environments inhabited by *C. sexlineatus* and *N. palfreymani*.

The mean water-influx rate of *N. palfreymani* at this time (1.01 mL day^{-1} for a 17-g animal) is about double the rate predicted (0.51 mL day^{-1}) from the allometric function (0.065M$^{0.726}$, where M is mass in grams) described by Nagy and Peterson (1988) for reptiles in the field.

Again, there are only two other species of skink for which water-influx data are published: 12.5 mL kg^{-1} day^{-1} for *Chalcides sexlineatus* (Brown *et al.* 1992) and 32.8 mL kg^{-1} day^{-1} for *Mabuya striata* (Nagy and Knight 1989). After allometric conversion (mass $^{0.73}$: Nagy and Peterson 1988) both skinks exhibit much lower water-influx rates than *N. palfreymani* (Table 4).

The distinction is also marked when comparing the water economy index (WEI, the ratio of water used to energy metabolised: Nagy and Peterson 1988) of each skink. The WEI value for *N. palfreymani* (0.76) is substantially higher than that of *C. sexlineatus* (0.14) and *M. striata* (0.22), and values reported for other reptiles, which average about 0.2 (Nagy and Peterson 1988). Previously, the highest WEI estimate for a terrestrial lizard was 0.52 for *Lacerta viridis*, which inhabits a mesic environment in late summer (Bradshaw *et al.* 1987). The WEI value for *N. palfreymani* is exceeded only by that of the marine iguana (*Amblyrhynchus cristatus*), which spends much of its time swimming and diving in sea-water (0.81: Shoemaker and Nagy 1984).

The daily energy expenditure of an average 17-g *N. palfreymani* during late summer/early autumn (1.33 kJ) would be balanced by the daily consumption of 0.28 g food (assuming a total energy content of 5.89 kJ g^{-1}, of which 4.71 kJ g^{-1} is metabolisable). This amount of food would, in turn, provide 0.23 mL of water (free and metabolic water combined); only 23% of the recorded total water influx of 1.01 mL day^{-1}.

This large discrepancy indicates that rain-water drinking and/or substantial pulmocutaneous exchange of water may take place within the rock crevices that the skinks inhabit. All sub-sites occupied by skinks are constantly subject to sea spray, and waves occasionally break over the Rockpile colony. Skinks were also observed on occasion swimming through shallow seawater pools, as is done by the Fiordland skink, *L. acrinasum* (Thomas 1985). In addition, meteorological data from nearby Maatsuyker and South Bruny Islands indicate that, on average, it rains on 249 and 210 days, respectively, each year, thereby further increasing the input of water into skink habitat. Unfortunately, there are no data on the microclimate of crevices to help elucidate this

point any further, but it is likely that the rock crevices experience high levels of humidity most of the time, a situation that would promote exchange of water across the lungs and skin of the skinks.

Although skinks have not been observed drinking from rain puddles, it remains a possibility. It is not known whether *N. palfreymani* has any extra-renal mechanism for eliminating excess electrolytes taken up from its highly saline environment, but the absence of such salt-secreting glands would require drinking to allow the renal excretion of electrolytes.

The water-influx data for the period between April and October represents an integration of water intake for late autumn, winter and early spring, and shows that little feeding occurs over this period. This interpretation is supported by the fact that most of the animals lost body mass during this period and presumably were utilising stored energy reserves for metabolism. In addition, very few scats could be collected during May and July.

Assuming that feeding is negligible in the period from May to October and that activity and feeding take place only between November and April, an estimate can be made of the total food required by an individual and the population. If the mean body mass for individuals in the population is 17 g, the total energy metabolised by an average individual over an activity period of 180 days would be 240 kJ. This would require the consumption of 51g of fresh food. Assuming that the population consists of 500 individuals, the total amount of food required for maintaining the population during the active season is 25.5 kg.

The metabolic expenditures of *N. palfreymani* over winter are not known, and there are few data for any other reptiles. Inactive, over-wintering *Varanus rosenbergi* living in a temperate environment have a mean FMR that is only 20% of that measured in summer (Green *et al.* 1991). Assuming a similar proportionality, the winter FMR for an average 17-g *N. palfreymani* is about 0.27 kJ day^{-1}. Thus, an average skink would metabolise about 50 kJ over the 185 days between late autumn and early spring. This energy would be derived from body reserves that are laid down during the active summer season, and equate to the consumption of an additional 11 g of food during the active feeding season. Thus, the total food required annually per individual is about 62 g, and the population would require 30.5 kg per annum of fresh food.

This is a minimal estimate, as the extent of extra energy and food required for growth in the young, and for gestation by females, is not known. However, this minimal estimate of the total food required to sustain the *N. palfreymani* population should prove useful if there is ever a major decline in seabird populations on Pedra Branca that seriously threatens the survival and abundance of skinks. Specific management strategies may need to be developed for the possible implementation of supplementary food provisioning for an interim period.

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