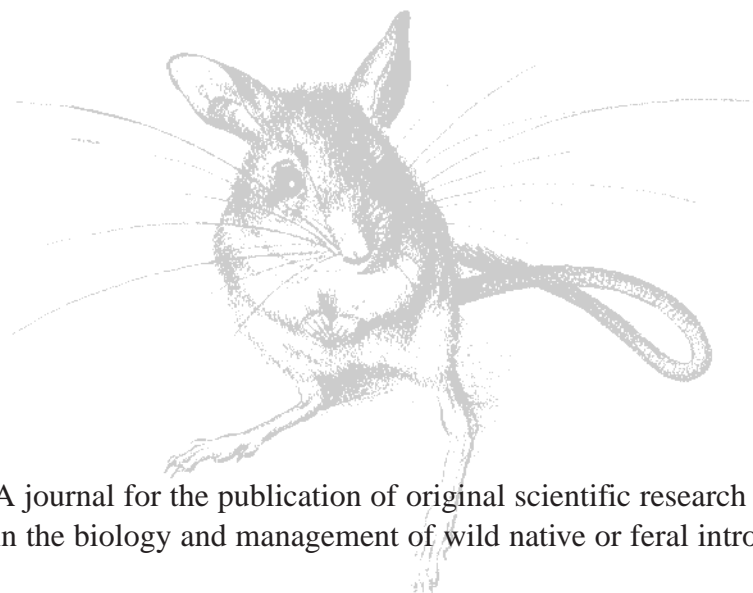

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Ecology and population biology of long-nosed bandicoots (*Perameles nasuta*) at North Head, Sydney Harbour National Park

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Abstract

The population biology, habitat utilisation and diet of a small, isolated population of long-nosed bandicoots (*Perameles nasuta*) was studied over a 22-month period at North Head in Sydney Harbour National Park, New South Wales. Reproductive output in this urban environment was high, with a mean litter size of 2.3 and production of up to four litters per year. The peak of reproductive activity was in late spring and early summer, with a cessation of breeding in late autumn or early winter. The main causes of death were identified as road trauma (58% – probably an overestimate because of the ease of finding road deaths) and predation by cats and foxes (37% – probably an underestimate because of the difficulty of locating carcasses unless radio-collared). Bandicoots utilised all macrohabitats (open grassed areas, heath, forest, swamp and scrub), but extensively used open grassed areas for foraging. Males had larger home ranges (4.4 ± 0.8 ha) than females (1.7 ± 0.2 ha). The largest home ranges of males coincided with the peak of the breeding season (September–November). Throughout the year *P. nasuta* fed primarily on beetles, invertebrate larvae and ants, but also on other invertebrates and on plant and fungal material. Some vertebrate and human-derived material (birdseed, vegetable scraps, plastic, twine) was also eaten. Although remarkably adaptable in its reproductive and dietary strategies, this population of long-nosed bandicoots is likely to follow other urban bandicoot populations toward extinction unless there is active management to reduce the high rate of mortality from motor vehicles and introduced predators.

Introduction

Although the long-nosed bandicoot (*Perameles nasuta*) is relatively common along Australia's eastern coastline, it has become locally extinct in areas of excessive disturbance due to habitat clearance throughout its range. It is becoming increasingly rare in urban and suburban Sydney, with one of the few populations of any significant number being confined to North Head, in Sydney Harbour National Park, and adjacent areas of the suburb of Manly (Chambers 1991). The total area used by this small population is approximately 300 ha.

Like other bandicoots, *P. nasuta* is polyoestrous, and capable of producing several offspring per litter and several litters per year (Lyne 1990). Reproductive output may vary between locations and years, depending on rainfall. This flexible reproductive strategy is matched by a digestive system that is capable of processing foods as different as invertebrate larvae, plant roots and fungi (Moyle *et al.* 1995).

Although its reproductive flexibility and digestive capacity have been documented, and its use of suburban gardens is well known (Stodart 1995), little is known about habitat use by the long-nosed bandicoot in more natural areas. It is clear that future conservation efforts with the species must be based on more extensive information on patterns of habitat use and population dynamics in patches of remnant habitat. To this end we studied the population ecology of long-nosed bandicoots at North Head over a period of 22 months in order to provide a data base for the development of a management plan to assist in the conservation of remaining bandicoot populations in urban environments.

Materials and Methods

Study site

The natural vegetation of the North Head section of Sydney Harbour National Park, an area of 200 ha, is dominated by *Leptospermum* scrub, dry heath and dry sclerophyll forest communities, but has been modified by developments that include a Water Board Treatment Plant, a School of Artillery, a Police College and an historic Quarantine Station (Fig. 1). These developments, especially the Quarantine Station, include expanses of open grassed areas. Chambers (1991) identified five macrohabitats at North Head, viz. open grassed areas, heath, forest, swamp and scrub, and these were used to specify habitats in the current study. The grassed areas provide long-nosed bandicoots with important foraging habitat, while adjacent dense natural vegetation provides diurnal and nocturnal refugia.

Rabbits (*Oryctolagus cuniculus*) also forage on the grassed areas. Other mammals that occur on North Head include common brushtail possums (*Trichosurus vulpecula*), common ringtail possums (*Pseudocheirus peregrinus*), black rats (*Rattus rattus*), brown rats (*R. norvegicus*), dogs (*Canis familiaris*), cats (*Felis catus*), and occasionally foxes (*Vulpes vulpes*).

North Head is within the temperate zone of the central coast of New South Wales. The average monthly maximum temperature in February (summer) is 26°C and the average monthly minimum temperature in July (winter) is 8°C (Bureau of Meteorology 1991). The annual average rainfall exceeds 1200 mm, with rain falling in all months of the year but with a peak in autumn.

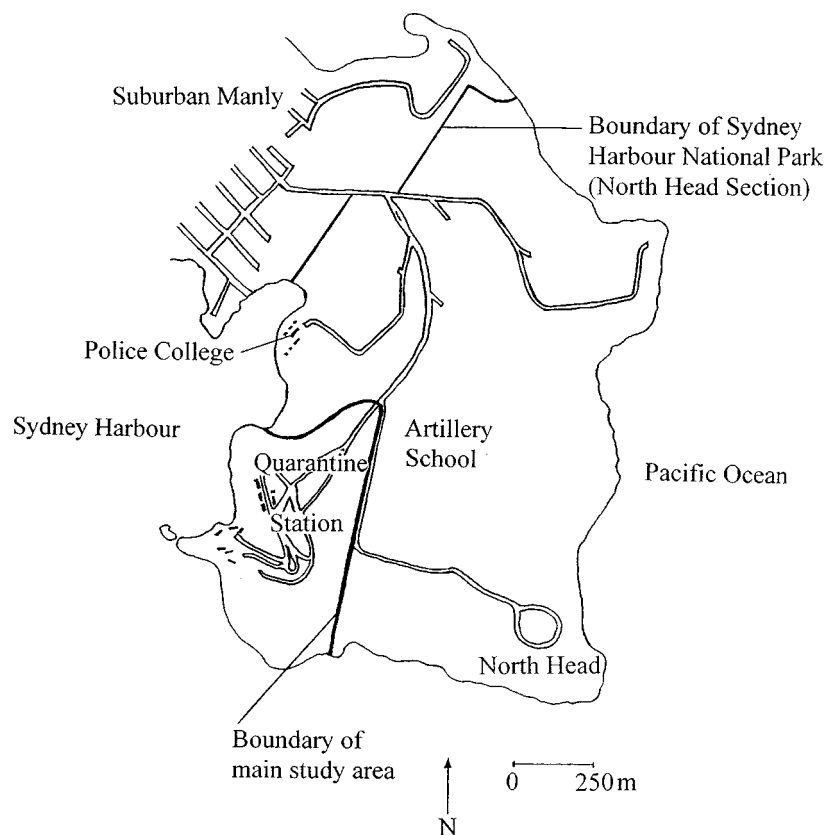


Fig. 1. The study site at North Head, Sydney Harbour National Park.

Population biology

Bandicoots were trapped approximately once per week on the Quarantine Station between November 1992 and August 1994 (a total of 101 nights). Traps were initially set at the Artillery School and Police College as well, to determine whether bandicoots used these areas, but low trapping success led us to abandon these sites. Between 15 and 30 wire cage traps (20 cm by 20 cm by 60 cm long) baited with bread and peanut butter were set during each trapping session. Traps were set just before sunset in open grassed areas where bandicoots had previously been observed or where there was evidence of foraging (conical digging holes); this was often close to dense natural vegetation. Traps were checked several times during the first 1–4 h after dark, and were removed at the final check.

At first capture, all animals were sexed, numbered by tattooing the right ear (females) or left ear (males), and weighed. The pouches of females were examined for enlarged nipples or young, and all offspring were counted and their head length measured. Enlarged nipples (larger than others on the same female) were gently squeezed; if milk was expressed the animal was recorded as lactating (breeding); if no milk was expressed the animal was recorded as non-breeding. Date, capture location and ambient temperature were recorded before animals were released at the point of capture. Any faeces on the floor of the trap were collected and sealed in plastic bags, then stored frozen for later analysis.

Maximum longevity could not be established over the relatively short term of this study. The sex, age class and likely cause of mortality were recorded for all bandicoots found dead over a 12-month period in 1993/94. Age class of females was based on body mass: the smallest reproducing female captured was 545 g, thus females heavier than 500 g were considered adult. Age class of males was based on scrotal size: young males have small scrotums prior to their first breeding season. Adult males were heavier than 600 g. Independent animals weighing less than adults were recorded as subadults. Dead bandicoots were located during radio-tracking sessions and also while conducting other aspects of the study. If cause of death could not be determined at time of collection, a necropsy was carried out as soon as possible thereafter. Carcasses found on or next to roads and with no puncture wounds or torn body cavities were placed in the category 'road trauma'. Those found in dense vegetation with the body cavity torn open, and sometimes with organs missing, were placed in the category 'predator'. One radio-collar with a pile of bandicoot fur and internal organs but no carcass was also placed in this category. It was assumed that carcasses found in dense vegetation were not bandicoots that had been injured on a road but had subsequently died in the dense vegetation and then been scavenged by a cat, fox or other predator. All cat and fox scats encountered were collected and frozen for later analysis. No dog scats were found during the study.

Home-range size

Between two and five adult bandicoots of each sex were selected at random and fitted with a collar-mounted radio-transmitter in autumn (March–May), winter (June–August) and spring (September–November) of 1993 and summer (December–February) of 1993/94. Animals were trapped while they foraged at night in open grassed areas. Only females with small pouch young or none at all were radio-collared. The leather collar with buckle carried a single-stage transmitter sealed in epoxy resin and attached to a vertical whip antenna (Bio-Telemetry Tracking, Adelaide, South Australia). Reflective tape was attached to the collar to facilitate identification in a spotlight beam at night. The collars weighed 14–17 g, less than the recommended maximum load of 5% of the animal's body weight (Cochran 1980). The collar was lined with lamb skin with the fleece side in contact with the bandicoot in order to prevent chafing. The fit of the collar was snug (necessary because of the stream-lined head and neck shape of bandicoots and lack of protruding jaw bones), but loose enough so that the collar could be rotated around the neck. Radio-collared animals were trapped every two weeks and collars and transmitters checked for condition and fit.

Although transmitter batteries had an operating life of up to 4 months, radio-collars remained on the animals for only 6–8 weeks. Transmitter range was up to 500 m. Animals were located with an H-Adcock antenna attached to a Telonics receiver. Locations were confirmed visually using natural and artificial features of the habitat and plotted on an aerial photograph of the study site. If an animal was not sighted because of dense vegetation its approximate location was determined by triangulation based on bearings to the collared bandicoot from three points of the compass. Each bandicoot was radio-tracked for approximately 8 nights during the 6–8-week period, and at least four fixes per night were obtained for each animal. Locations of occupied nests were established during the day at least once per week. Radio-locations of each individual were established at least 1 h apart. Bandicoots frequently crossed their home range within an hour, so hourly radio-fixes should not have been highly autocorrelated (Swihart and Slade 1985). Direct observations of bandicoot behaviour and social interactions were recorded whenever possible. Telemetry sessions were not concurrent with the trapping sessions described under 'Population biology' above.

Home-range size was determined by the minimum convex polygon method (MCP; Southwood 1978) for ease of comparison with previous studies of *P. nasuta* (Chambers 1991) and the closely related eastern barred bandicoot (*P. gunnii*) (Heinsohn 1966; Dufty 1991, 1994). The MCP method is also least affected by autocorrelation among several methods for determining home-range size (Swihart and Slade 1985). However, MCP usually overestimates the size of home range as it includes areas that are never visited (Harris *et al.* 1990).

Although differences in home-range size between years could not be tested statistically because of small sample sizes, no difference was apparent, and so tracking periods were pooled. Differences between means for males and females were tested by Student's *t*-test (Snedecor and Cochran 1965), recognising that, if data were sufficient, two-way analysis of variance to test for differences in home-range size due to year and sex would be more appropriate.

In order to determine the minimum number of observations required to define the home range of a bandicoot by the MCP method, three individual animals with 35 or more radio-locations were selected. Their home ranges were calculated using the full data set, as well as with reduced data sets of 15, 20 and 25 randomly chosen locations. The relationship between home-range size and the number of locational fixes was plotted to estimate by eye the point beyond which additional locations resulted in negligible increases in home-range size (Harris *et al.* 1990). Home-range size reached an asymptote at 15–20 locational fixes (Fig. 2). Therefore estimates of home-range size were based on a minimum of 20 fixes.

Diet and invertebrate availability

Faecal analysis was used to estimate diet, as it allowed multiple sampling from the same population of bandicoots without undue interference. Stored faecal samples were dried at 80°C in a forced-draft oven to constant weight, then homogenised by careful manual crushing in a plastic bag. Many faecal samples consisted of more than one pellet; all pellets were used. Dried faeces were reconstituted in water and then separated into three size classes by washing through a nest of Endecott (London, U.K.) sieves of 1200, 600, 150 and 75 µm mesh sizes. Sieved fractions were transferred to filter paper in a Buchner funnel, then the large (600–1200 µm) and medium (150–600 µm) particles examined under a dissecting microscope, and the small (75–150 µm) particles under a compound microscope.

The large particles were classified into broad categories of invertebrate, plant, fungal, vertebrate and human-derived material, and the volume occupied by each category, as a proportion of the total faecal sample, was estimated visually. The two smaller size classes were examined primarily for fungal spores and earthworm chaetae. Invertebrates were identified to order, by comparison with reference specimens collected from pitfall traps (see below) and from leaf litter searches on the study site. Minimum numbers of invertebrates from each order were recorded in each faecal sample examined, following the procedures of Churchfield (1982), Fox and Archer (1984) and Green (1989). The plant fraction was first divided into monocot and dicot material using the dissecting microscope, then into leaf, stem, seed, bud and root based on examination of epidermal characters, and each component expressed as a proportion of the total faecal

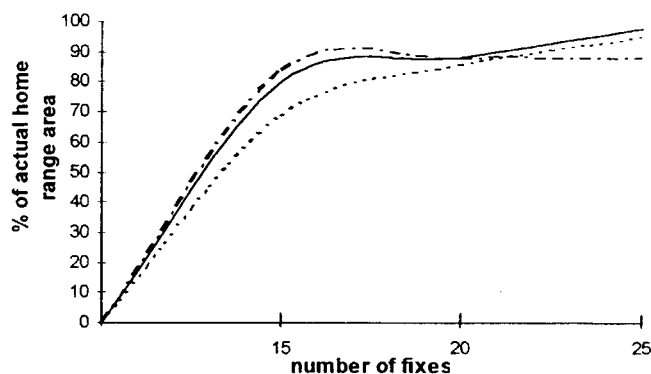


Fig. 2. Relationship between percentage of calculated home-range area and the number of radio-locations for three individual *Perameles nasuta* at North Head.

sample. In order to confirm that an adequate number of faecal samples was analysed to characterise the diet, the cumulative number of dietary items identified was plotted against the cumulative number of faecal samples examined (Hurtubia 1973), and the minimum sample size required was estimated to be 12. All food items were ranked according to constancy (proportion of scats containing each item). In addition, the invertebrate orders identified were ranked by average relative abundance (minimum number per gram of dry faecal matter) (Moyle 1992).

A sampling site for invertebrates, measuring 60 m by 30 m, was located randomly within each of the five macrohabitat types defined by Chambers (1991). Sampling sites were separated by a minimum of 100 m. An index of invertebrate activity, and therefore of their availability, was obtained from pitfall traps (Dickman 1991) set in grids of 20 plastic specimen jars at each site. Pitfall traps containing 50 mL of 3% formalin solution were set four times over a 12-month period in order to compare prey availability between seasons. Traps were placed randomly within each sampling site in each macrohabitat each time to ensure independence of samples, and were left for 7–10 days. Captured invertebrates were transferred to 70% ethanol and classified to order, then oven-dried to constant weight in order to estimate total dry biomass. Numbers of individuals per order were recorded for each trap. After the first collection (in autumn, 1993), the cumulative frequency of invertebrates was plotted against number of pitfall traps. This suggested that 20 traps were adequate to reliably estimate the diversity of invertebrates in each macrohabitat. Although two indices of invertebrate availability were computed (dry-weight biomass and numbers of individuals), only total numbers per order per pitfall trap were used in statistical analyses.

Statistical analyses

The data for both food items and invertebrate availability were transformed ($x^1 = x^{0.25}$) in order to eliminate any large differences in scale among variables (Clarke 1993). Multivariate analyses were used to compare dietary composition among seasons, and the composition and abundance of available invertebrates among seasons within and among macrohabitats. Similarities were calculated between samples using the Bray–Curtis similarity index (Bray and Curtis 1957). This results in a symmetric triangular matrix of similarity values. A two-dimensional ordination of the samples was produced using non-parametric multidimensional scaling (MDS) (Clarke and Green 1988). MDS relies on rank order of similarities between samples, and thus there are no restrictive assumptions of normality or equality of variances or covariances among variables (Anderson and Underwood 1994). The difference between the rank-order distances between samples in the original similarity matrix and the rank-order distances represented by the two-dimensional MDS of those samples is expressed by a stress coefficient. MDS produces a visual representation of the data, and stress values of less than 0.20 generally lead to an interpretable MDS pattern (Clarke 1993).

Analysis of similarities (ANOSIM) was used to test spatial and temporal differences in the composition and abundance of available invertebrates and seasonal differences in diet. An ANOSIM test establishes biological differences between sites (or scats) and includes a non-parametric randomisation test for use with site–species arrays (Clarke and Green 1988). All multivariate analyses were carried out with the PRIMER v3.1 computer program .

Results

Population biology

Over 1492 trap-nights, 48 individual bandicoots were trapped (22 females, 26 males). Overall, there was a total of 420 captures during the 22-month trapping period. The maximum time an individual remained in the trapping records was 18 months. There appeared to be a general decline in trapping success over time despite consistent trapping effort (Fig. 3).

The mean (\pm s.e.) weight of adult females at first capture was 706 \pm 40 g (range 520–880 g), while adult males averaged 897 \pm 43 g (range 670–1330 g). There were no apparent seasonal effects on body weights, although no statistical analysis was conducted. The smallest female captured at North Head with pouch young weighed 545 g, including the pouch young. The mean weight at first capture of subadults born during the 1992/93 breeding period was 467 \pm 40 g (n = 7) for males and 280 \pm 37 g (n = 5) for females; and for the 1993/94 breeding period was 403 \pm 59 g (n = 5) for males. A single subadult female was trapped from the 1993/94 breeding period; she weighed 490 g. The smallest independent bandicoot trapped at North Head weighed 180 g.

Reproduction was strongly seasonal (Fig. 4). Females were first observed carrying pouch young in late July in 1993 and in early August in 1994. Females did not breed between March and June in 1993, and between May and July in 1994.

Mean (\pm s.e.) litter size during the study period was 2.3 ± 0.1 (range 1–4; $n = 38$). Litters of 2 and 3 pouch young contributed $76 \pm 5\%$ of the total number of young produced (Table 1).

Four breeding females were trapped regularly for the complete 1993/94 reproductive period. Each of these females weaned 6–9 offspring, with an average of 8.0 ± 0.7 young for the season; taken together, they reared a total of 32 young (Table 2). The two older females (nos 4, 63) each produced one litter more than the younger females, but with the same number of young in each litter.

Of 19 dead bandicoots collected as fresh carcasses during a 12-month period, seven adults, two subadults and two large, almost weaned pouch young were victims of road trauma, four adults and three pouch young were apparently taken by introduced predators (cat, fox), and one adult was parasitised by lung worm (*Filostrongylus peramelis*) (H. Collins, personal communication). Of 19 cat and fox scats collected from North Head during the study period, 68% contained hair of rabbit, 26% bandicoot, 16% common ringtail possum, 11% rodent and

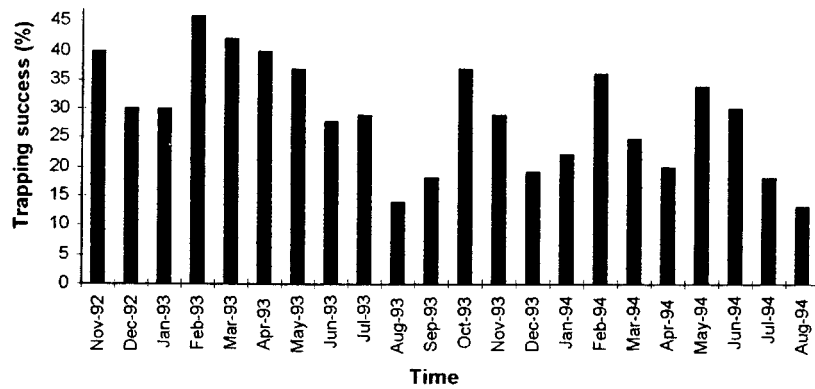


Fig. 3. Numbers of bandicoots captured, expressed as a percentage of trap-nights, over 22 months at North Head.

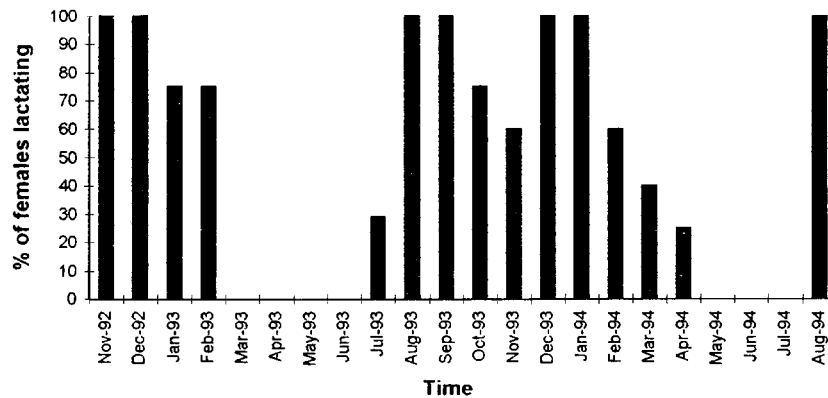


Fig. 4. Percentage of adult female bandicoots lactating on a monthly basis at North Head.

5% common brushtail possum; 5% also contained scales of reptiles (G. M. McKay, personal communication).

Home-range sizes

The mean home-range sizes of radio-tracked bandicoots during each tracking period are shown in Table 3. Overall mean home-range size (\pm s.e.) for males was 4.4 ± 0.8 ha, which was significantly greater than the 1.7 ± 0.2 ha for females ($t = 3.24$, $P < 0.05$). Home ranges of females tended to be larger during the non-breeding months than at other times of the year, while those of males tended to be smallest at this time, although sample sizes were insufficient to test this statistically. The largest home ranges of males appeared to coincide with the peak of the breeding season (September–November).

Table 1. Litter sizes and total production of young by female *Perameles nasuta* over 22 months at North Head

Litter size	No. of litters	No. of young	% of total no. of young
1	5	5	5.6
2	19	38	42.7
3	10	30	33.7
4	4	16	18.0
Total	38	89	100.0

Table 2. Breeding performance of four female *Perameles nasuta* trapped regularly throughout the 1993/94 reproductive season at North Head

Female	Pre-breeding weight (g)	No. of litters	No. of young	Mean litter size (\pm s.e.)	Post-breeding weight (g)
4	755	4	9	2.3 ± 0.7	755
5 ^A	540	3	6	2.0 ± 0.6	790
8 ^A	575	3	8	2.7 ± 0.5	745
63	780	4	9	2.3 ± 0.5	820

^AIndicates first reproductive season

Table 3. Home-range areas calculated for male and female *Perameles nasuta* at North Head during four times of the year

	<i>n</i>	Male Mean \pm s.e. (ha)	Range (ha)	<i>n</i>	Female Mean \pm s.e. (ha)	Range (ha)
Apr–May ^A	3	2.3 ± 0.5	13–3.1	4	2.0 ± 0.1	1.7–2.2
June–Aug	2	3.5 ± 2.0	13–5.5	3	1.4 ± 0.3	0.9–2.0
Sept–Nov	3	7.2 ± 2.1	4.9–11.5	3	1.8 ± 0.2	1.5–2.2
Jan–Mar	5	4.4 ± 1.3	1.8–9.3	3	1.2 ± 0.4	0.7–2.1

^AIndicates non-breeding period.

Throughout the year, females frequently had overlapping home ranges. In contrast, males appeared to avoid other males during non-breeding months, but displayed considerable overlap in home ranges during the breeding season. Home ranges commonly included several of the five macrohabitats at North Head, but only the largest home ranges of some adult males included all macrohabitats. Most animals utilised large areas of open grassed habitat for nocturnal foraging, as illustrated for one period (September–November) in Fig. 5. Diurnal nests were cryptic, commonly made of dry grass twigs and leaf litter, and were often concealed in dense undergrowth. They were found in all vegetation types, including open grassed areas where the grass was tall and dense, and at the base of large trees where the vegetation was relatively undisturbed. Nests were frequently found near the perimeter of the animal's home range. More than half (62%) of the bandicoots that were radio-tracked used more than one nest site during any tracking period. The mean (\pm s.e.) number of nest sites located per animal was 2.1 ± 0.3 (range 1–4, $n = 13$) for males and 2.3 ± 0.4 (range 1–5, $n = 13$) for females.

Diet and the availability of invertebrates

Sites in which the bandicoots foraged were identified by the characteristic conical holes, as deep as 21 cm, excavated in search of underground food items such as plant roots, hypogeal

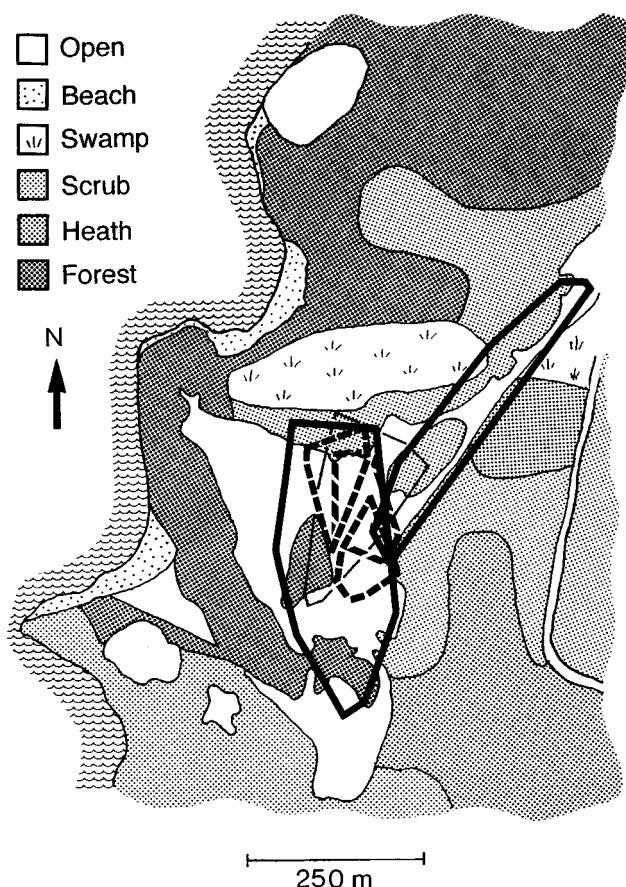


Fig. 5. Home ranges of radio-tracked bandicoots at North Head during September–November 1993. Solid lines = males; broken lines = females.

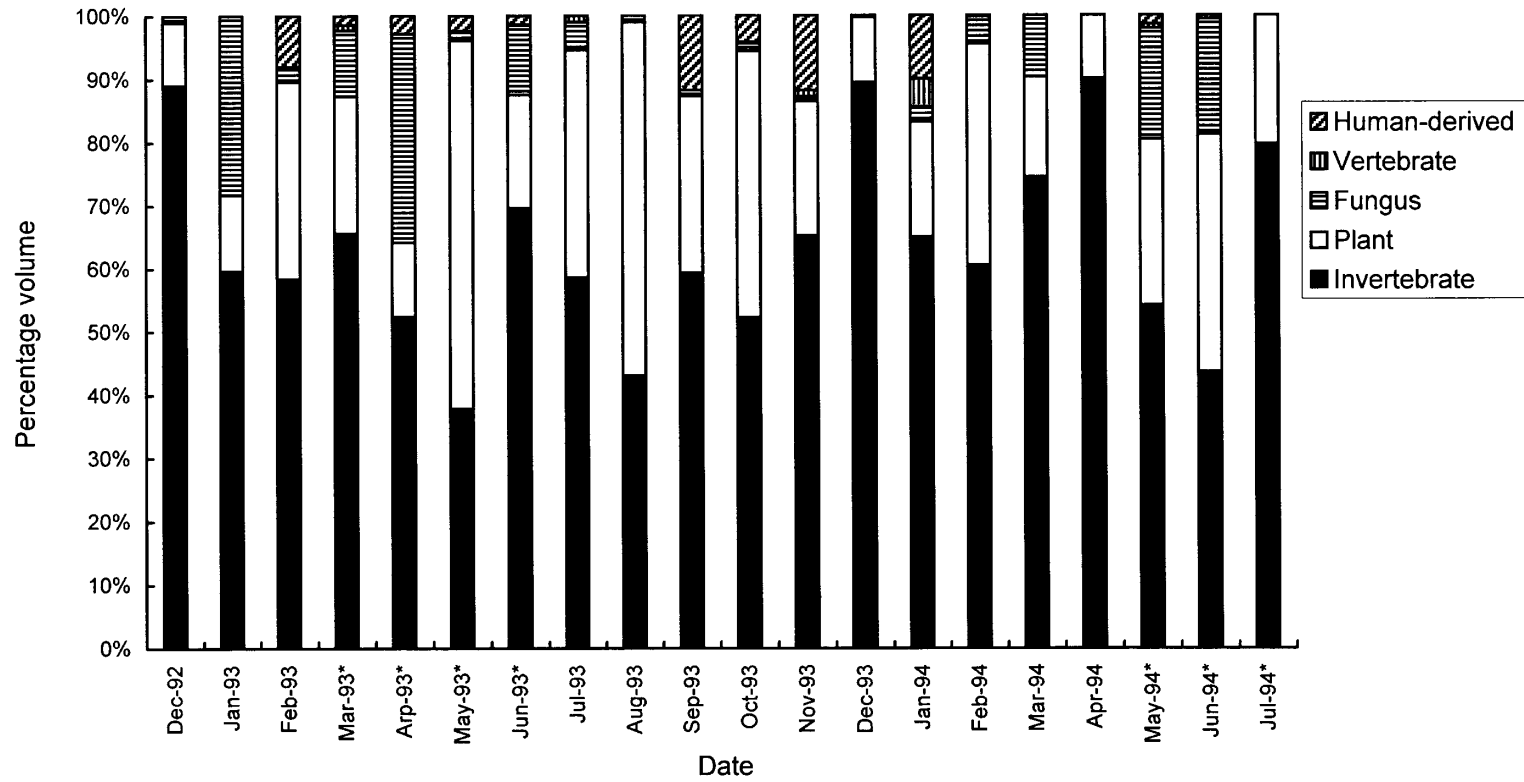


Fig. 6. Percentage volume for five main dietary categories in faecal samples of *Perameles nasuta* over 20 months at North Head. Non-breeding months indicated by asterisks.

fungi and invertebrate larvae. However, *P. nasuta* was more commonly observed capturing adult terrestrial invertebrates on the soil surface. Bandicoots appeared to rely mainly on their sense of smell for locating food items, which is consistent with previous findings (Heinsohn 1966; Stodart 1977; Quin 1988). Once located, prey were captured quickly and eaten. Large invertebrates were often manipulated with the forepaws, while smaller items were grasped primarily in the mouth or licked up off the ground.

Five main dietary categories (invertebrate, plant, fungus, vertebrate and human-derived material) were identified from 82 faecal samples. Their estimated percentage volume in scats collected over a 20-month period is shown in Fig. 6. Scats frequently contained large quantities of sand; this was assumed to have been ingested accidentally while bandicoots foraged for underground food, and so is not included as a dietary category. The representations of the main dietary categories did not differ significantly among seasons (ANOSIM, $P > 0.05$).

Invertebrates were the predominant food category, constituting more than 50% of the volume of scats (excluding sand) in 16 of the 20 months. Plant material was consumed in varying proportions (10–60% of scat volume) throughout the study period. Fungi were consumed in 17 of the 20 months sampled; peak volumes were recorded in the wetter months of summer 1993 (28%) and late autumn and early winter 1994 (18%). Vertebrate material (adult skinks (Scincidae), skink eggs, and bird feathers) was a minor component of the diet, being present in scats during 10 of the 20 months, and reaching only 4% of scat volume. Human-derived material was also consumed in half the months sampled, at up to 14% of scat volume, and included birdseed, vegetable scraps, plastic, twine, and in one scat, a metal staple.

All 27 dietary categories are ranked according to constancy (percentage occurrence in scats) in Table 4. The relative abundances of invertebrate groups are also included. There were no significant differences (ANOSIM, $P > 0.05$) in the proportion or abundance of invertebrate groups among seasons. Coleoptera (beetles), Hymenoptera (mainly ants), and insect larvae (mainly beetles) were the most common invertebrate groups and overall food items identified in terms of both constancy (83–98%) and average relative abundance (2.6–5.0 g⁻¹). Ticks (*Ixodes holocyclus*) (S. Pope, personal communication) and mites (Acarina) were presumably ingested from the fur while grooming.

Table 4. Ranking of 27 diet categories by constancy (percentage occurrence in faeces), and average relative abundance of 14 categories of invertebrates (minimum number per gram of dry faeces), for *Perameles nasuta* at North Head

Diet category	Constancy (%)	Mean relative abundance (g ⁻¹)	Diet category	Constancy (%)
Invertebrates			Other	
Coleoptera	97.5	2.6	Monocot leaf	76.8
Larvae	89.0	3.0	Monocot stem	76.8
Hymenoptera	82.9	5.0	Fungi	63.4
Hemiptera	37.8	1.2	Monocot and dicot root	46.3
Orthoptera	34.1	1.0	Monocot seed	37.8
Dermaptera	32.9	1.1	Dicot stem	30.5
Acarina	31.7	2.0	Bud	28.0
Pupa/Egg case	20.7	2.3	Skink	17.1
Isopoda	18.3	1.0	Human-derived	13.4
Araneae	17.1	1.1	Dicot seed	9.8
Blattodea	7.3	1.3	Aves	7.3
Unknown invertebrate	4.9	1.5	Dicot leaf	4.9
Millipede	4.9	0.7	Resin	3.7
Lepidoptera	1.2	1.2		

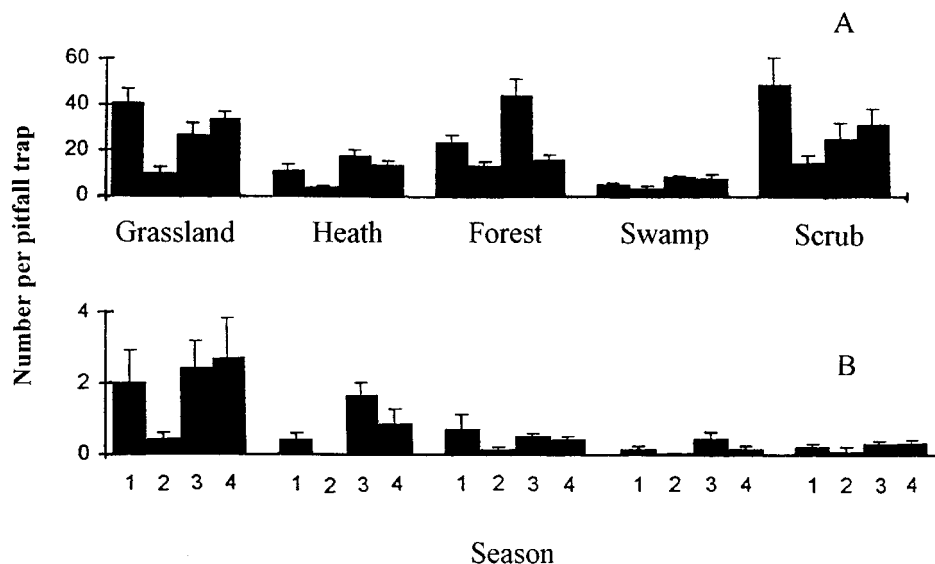


Fig. 7. Availabilities of (A) invertebrates, and (B) coleopterans (both total number of individuals per pitfall trap) in five macrohabitats in four seasons at North Head. Season 1 = autumn, 2 = winter, 3 = spring and 4 = summer.

Monocot (mostly grass) leaf and stem were the plant items most frequently encountered (both in 77% of scats), followed by roots (both monocot and dicot), monocot seed and dicot stem (in 30–46% of scats). Most fungi consumed were hypogaeal (underground) species, thought to form symbiotic mycorrhizal associations with plant roots (Claridge 1993). Most fungi were from the family Zygomycetes, the most commonly occurring species in scats being *Glomus fuegianum*.

The availabilities of invertebrates were distinctly different among macrohabitats (ANOSIM, $P < 0.005$ in 32 of 40 pairwise comparisons between macrohabitats (10 per season)) regardless of season (Fig. 7A). Swamp and heath consistently had low invertebrate availabilities. The high availability of invertebrates in the open grassy areas was due partly to the high representation of Coleoptera (a preferred prey item) (Fig. 7B).

Total invertebrate availability was highest in spring and lowest in winter in all macrohabitats except heath, in which there were no significant differences among seasons (ANOSIM, $P < 0.008$ in 17 of 30 pairwise comparisons between seasons).

Discussion

Population biology

Significant features of the population biology of long-nosed bandicoots at North Head include the strong seasonality of breeding, with females ceasing lactation by late autumn or early winter, after a peak in production of pouch young in late spring or early summer. Although *P. nasuta* will breed throughout the year in captivity (Lyne 1964; Close 1977), the generally seasonal reproductive pattern of this bandicoot in the wild (Stodart 1995) suggests that increased thermoregulatory demands in winter, in conjunction with a lower abundance of invertebrates, may compete with and curtail reproduction. Reproduction recommenced in late winter or early spring in both years of the study, and production of pouch young peaked in late spring or early summer. Thus peak lactation (Fig. 4) would have coincided with reduced thermoregulatory

demands and increased availability of invertebrates (Fig. 7), the long-nosed bandicoot's preferred food (Fig. 6).

The autumn cessation of breeding by *P. nasuta* at North Head is confirmed by Chambers' (1991) failure to trap lactating females at the same location during a three-month period in autumn. In spring, the association of peak lactation and weaning with a peak in food availability favours the selection of apparently synchronous oestrus and mating in *P. nasuta* (Braithwaite and Lee 1979) in late winter. This could explain the relatively low numbers of lactating females found during October and November in 1993 (Fig. 4); most of these animals were probably gestating for the second time in that breeding period. At North Head, a strategy of synchronous oestrus and mating in late winter would allow the first litters of the season to reach independence and reproduce in the same breeding period as their birth. This is probably a major contributor to the high annual reproductive output that is characteristic of *P. nasuta* and other bandicoots in seasonal environments.

The large difference in body weights of pre- and post-breeding females during their first breeding period (Table 2) indicates that females start to breed before they are fully grown, and continue to grow while reproducing. However, the energetic costs of reproduction and growth apparently restrict the number of litters produced in the first breeding period. The greater production of young by females in their second breeding period seems to be due to the production of one extra litter rather than of larger litters (Table 2).

Despite the high fecundity of *P. nasuta*, only a few subadult animals were trapped at North Head, suggesting a high rate of mortality. Of all pouch young produced during the 1993/94 breeding season, less than 10% survived to subadulthood. Furthermore, of those young that survived to subadulthood, over 70% vanished from the study area after two months. Unfortunately, the dispersal ecology of most peramelids is poorly known (Stoddart and Braithwaite 1979).

The main cause of death in this urban population was apparently road trauma (58%), but this is probably an overestimate because of the relative ease with which road deaths are detected. Conversely, the 37% taken by cats and foxes is likely to be an underestimate as the only dead animals discovered were all radio-collared individuals. Bandicoots comprised 26% by volume of 19 scats deposited by foxes and cats in the study area, and 28% by volume of 20 cat stomach content and scat samples collected from North Head in 1990/91 (Dickman 1996). Also of concern was the 50% of bandicoots trapped during the present study that disappeared or were found dead within two months of their initial capture. Traps were set randomly in areas of conspicuous bandicoot foraging activity rather than in lines or grids, and results may mainly reflect variations in density at these particular areas of the study site. Results must therefore be interpreted with caution. The isolated nature of the North Head population of long-nosed bandicoots, together with its apparently small size, high incidence of road deaths and high predation pressure, resulted in the listing of the population as an endangered population under the Threatened Species Conservation Act of New South Wales (NSW Scientific Committee 1997). One consequence of the listing is a requirement for the development of a recovery plan for the population; this is currently being prepared by the National Parks and Wildlife Service of New South Wales.

Home-range sizes

Home ranges calculated by the minimum convex polygon (MCP) method for *P. nasuta* in the urban environment of North Head (4.4 ha for males, 1.7 ha for females) were similar to estimates derived using the same approach for the closely related *P. gunnii* (eastern barred bandicoot) in another urban environment, at Hamilton, Victoria (4.0 ha and 1.6 ha) (Dufty 1994). At North Head, there was a concentration of bandicoot foraging activity in the vicinity of residential buildings, occupants of which fed the wildlife both directly by leaving out food scraps and indirectly via compost heaps and unsealed rubbish bins. While this provided additional food resources for bandicoots, it may also have enticed introduced predators to the area.

Food supplementation tends to result in smaller home ranges (Boutin 1990), as was demonstrated with *Isoodon obesulus* (southern brown bandicoot) by Broughton and Dickman (1991). Thus, the home ranges of *P. nasuta* at North Head may be smaller than those of animals living in more natural environments, but the latter have not been measured. Home ranges estimated by the MCP method for *I. obesulus* in agricultural habitat in Tasmania were slightly larger (5.3 ha and 2.3 ha) (Heinsohn 1966).

The larger home ranges of males than of females at North Head have been observed commonly in other bandicoot species (Heinsohn 1966; Lobert 1990; Broughton and Dickman 1991; Dufty 1994). In this study, males increased the size of their home ranges to a mean maximum of 7.2 ha in spring, the height of the breeding season (Table 3), presumably to improve their mating opportunities (Morris 1988). Although home ranges of males did not overlap with one another in the non-breeding season, there was considerable overlap both within and between sexes during the breeding season. Males probably defend territories that include parts of the home ranges of several females, and mate polygynously or promiscuously (Lee and Cockburn 1985) in order to monopolise this defendable resource (Ostfeld 1990). This is suggested by displays of territoriality observed between males during the present study: on more than one occasion, a male bandicoot was observed in a bipedal stance with hind limbs and tail in contact with the ground while hissing at another male. Apparent scent marking by males was also observed on three occasions. Scent marking during aggressive interactions is probably an attempt to match owner's scent to territory (Kruuk 1992); urine marks may contain olfactory cues that are used in intraspecific communication (Mallick 1992). Agonistic encounters between males were most evident during the first half of the breeding season, indicating a relationship between reproductive activity and aggressive behaviour. Males were often observed with large scratches and bare patches during this time. In contrast, females showed a marked tendency to remain in the same general locality throughout the year, and lived in close proximity to each other without overt displays of territoriality or dominance. Maintenance of the same territory with established nest sites may provide a temporary safe haven for young bandicoots immediately after vacating the pouch.

Diet and availability of invertebrates

Although faecal analysis is a convenient way to estimate the diet of free-living animals with minimal disturbance, it suffers from a number of disadvantages. These include the fact that some invertebrate parts may be more easily identified than others, while predators may also regurgitate some hard invertebrate parts. Underestimation of soft-bodied prey items may also occur because of differential digestion (Putman 1984; Dickman and Huang 1988; Reynolds and Aebischer 1991). Some authors (e.g. Putman 1984) have suggested that correction factors can be established in order to estimate the actual number of prey items ingested, but these are usually unreliable in practice (Dickman and Huang 1988). Expressing dietary items in terms of constancy (the frequency of occurrence) reduces some of the potential sources of bias in faecal analysis (Quin 1988; Dickman and Huang 1988).

There is little other information available on the diet of the long-nosed bandicoot, but our results from North Head are in agreement with other dietary studies on this species, both at North Head (Moyle 1992) and in south-eastern New South Wales (Claridge *et al.* 1991; Claridge 1993). They are also similar to those from several other peramelid species (e.g. Heinsohn 1966; Quin 1988; Claridge *et al.* 1991; Bradshaw *et al.* 1994). Long-nosed bandicoots at North Head consumed foods from a broad spectrum, but appeared to be primarily insectivorous; in 17 of the 20 months sampled, their scats consisted of more than 50% by volume of invertebrates, despite mean availability of invertebrates varying between 4 and 50 individuals per pitfall trap across all macrohabitats. Our findings of high constancy and average relative abundance of coleopterans (beetles) and hymenopterans (ants) in the faeces of long-nosed bandicoots at North Head (Table 4) concur with those of Moyle (1992) on the same population. Together, they are consistent with our observation that bandicoots most commonly obtained invertebrates directly from the soil

surface or from within leaf litter. However, they also ingested considerable amounts of plant and fungal material, much of which was obtained through digging activities. Unfortunately, assessment of the availability of food was limited to sampling of invertebrates due to the inherent difficulties associated with sampling fungal and plant material. It is likely that long-nosed bandicoots prefer to forage in open habitats where beetles and other invertebrates are more abundant and also are more accessible to bandicoots because of the lack of leaf litter.

The small amounts of vertebrate material recorded in the diet of *P. nasuta* at North Head are likely to be underestimates. For instance, one animal was observed digging up a nest containing freshly laid water dragon (*Physignathus lesueurii*) eggs, which it masticated to obtain the yolky contents before discarding the shell (L. K. Scott, personal observation); this food item would not be detected by faecal analysis. Similarly, golden bandicoots (*I. auratus*) on Barrow Island are considered to be major predators of green turtle (*Chelonia mydas*) eggs (Morris 1987).

The importance of plant and fungal material in the diet of bandicoots is often ignored. Moyle *et al.* (1995) suggested that both invertebrate larvae and some plant roots are potentially rich sources of digestible energy. In our study, up to 60% of the volume of scats was plant material (both monocot stem and root); the amount of plant material was particularly high during the non-breeding months (Fig. 6). Similarly, fungal material was consumed by North Head bandicoots throughout the year, with the greatest intake during the wetter months (Fogel 1976). Similar findings have been reported for *P. nasuta* around Sydney by McGee and Baczocha (1994) and in south-eastern New South Wales by Claridge *et al.* (1991) and Claridge (1993), and for *I. obesulus* in Tasmania by Quin (1988). Fungal species are often rich sources of lipids, crude protein and carbohydrates (Hume 1999), and additionally contain a variety of vitamins and minerals (Claridge and May 1994). Bandicoots and other ground-dwelling small mammals may play an important role in the dispersal of fungal spores through their deposition in faeces (Claridge 1993; Comport and Hume 1998).

Management implications

One of the impacts of urbanisation is the availability of human-derived material to wildlife. At North Head this material was consumed by bandicoots, but probably provided them with little nutritional benefit. Additionally, this food source is a potential problem because it may attract cats and foxes, thereby contributing to high mortality of bandicoots due to predation.

Another impact of urbanisation on bandicoots is a reduction in the availability of a mosaic of open foraging areas and dense refuge sites. Historically, this mosaic was probably maintained by wildfire (T. F. Flannery, personal communication). At North Head the main areas of foraging habitat are now the mown lawns of the Quarantine Station. Both adult and larval coleopterans, preferred food items, were found in high numbers in open grassed areas in spring, summer and autumn (Fig. 7b). Any reduction in expanse of these grassy areas will therefore limit the availability of food for the bandicoots. This, together with the high rate of mortality from motor vehicles and introduced predators, would threaten the long-term viability of this small urban bandicoot population. The contraction of *P. nasuta* in the Sydney metropolitan region to only a few localised areas appears alarmingly similar to the decline of the closely related mainland form of the eastern barred bandicoot (*P. gunnii*) in Victoria, which, in 1990, had been reduced to one population at Hamilton (Seebeck *et al.* 1990); this population continues to decline in numbers of bandicoots (J. H. Seebeck, personal communication).

Any management plan for the future conservation of the endangered population of long-nosed bandicoots at North Head must therefore include either the maintenance or increase of open foraging areas with associated dense refuge sites, the control of motor vehicles, and the removal of introduced predators. These elements should be addressed not only within the limits of the Quarantine Station, but also in other sections of Sydney Harbour National Park at North Head, and adjacent areas of residential Manly. The education and involvement of the public, especially residents in the vicinity of the National Park, is a key element of any management strategy in such an urban setting.

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