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Aspects of the ecology of the kalubu bandicoot (*Echymipera kalubu*) and observations on Raffray's bandicoot (*Peroryctes raffrayanus*), Eastern Highlands Province, Papua New Guinea

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Abstract. Bandicoots in the family Peroryctidae in New Guinea are widespread and relatively abundant, but little is known of their ecology. We present the first detailed study on the ecology of the kalubu bandicoot (*Echymipera kalubu*) and observations on Raffray's bandicoot (*Peroryctes raffrayanus*), from mid-montane forest in Papua New Guinea. Both species were primarily nocturnal and utilised a range of habitats including those modified by human activity, although Raffray's bandicoot was more frequently encountered in less disturbed areas. Male kalubu bandicoots were larger than females, with larger animals having larger short-term home ranges and evidence for intrasexual territoriality. Mean short-term home-range size was 2.8 ha (MCP, $n = 10$), with an estimated population density of ~85 animals km^{-2} in the study area. Female kalubu bandicoots attained sexual maturity at ~400 g and 67% of mature females were reproductively active with an average of 1.5 young per litter. Both species were hunted, but their density, rate of reproduction and use of modified habitats suggest that they were able to withstand current hunting levels.

Additional keywords: conservation, hunting, intrasexual territoriality, Peroryctidae.

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Introduction

Bandicoots belonging to the family Peroryctidae are one of the most widespread and common groups of marsupial mammals in New Guinea, where four genera and at least 11 species are recognised (George and Maynes 1990; Flannery 1995; Aplin *et al*. 2010). New Guinea's bandicoots are terrestrial and omnivorous and most are small to medium-sized with adult masses of ~2 kg (Seebeck *et al*. 1990). The exceptions to this are the Papuan bandicoot (*Microperoryctes papuensis*) and the giant bandicoot (*Peroryctes broadbenti*), which range in mass from ~180 g to >4 kg, respectively (Aplin and Woolley 1993; Aplin *et al*. 2010). As well as being widely distributed across most habitats in New Guinea, from subalpine grassland, rainforest and lowland savannah (Flannery 1995), bandicoots are also one of the most commonly hunted and favoured game species in the region (van Deusen and Keith 1966; Pangau-Adam *et al*. 2012), forming as much as 50% of captures in several hunting studies (Hide *et al*. 1984; Morren 1986) and comprising, on average, 26% of captures from a review of nine hunting studies in Papua New Guinea (Cuthbert 2010).

Unlike many of the Australian species of bandicoots, in the family Peramelidae, which have been extensively studied (e.g. Seebeck *et al*. 1990 and references therein; Scott *et al*. 1999; Richards and Short 2003), the ecology and behaviour of the Peroryctidae of New Guinea is almost unknown. To date, published studies on the ecology of New Guinea's bandicoots consist of information on hunting returns (e.g. Dwyer 1985; Hide *et al*. 1984), spool-and-line tracking (Anderson *et al*. 1988), and data on reproductive status, natural history and distribution (Hughes *et al*. 1990; Aplin and Woolley 1993; Flannery 1995). Knowledge of some of New Guinea's rarest and most elusive mammals such as the long-beaked echidna (*Zaglossus bruijnii*) (Opiang 2009) currently exceeds that available for the region's widespread and common bandicoots.

Both genera *Echymipera* and *Peroryctes* are centred in New Guinea, with three and four species, respectively. In this paper we present new information on the ecology of the kalubu bandicoot (*Echymipera kalubu*) and Raffray's bandicoot (*Peroryctes raffrayanus*) from a village area in mid-montane rainforest of Papua New Guinea.

Materials and methods

Study site

The study was undertaken during March–May 2002 and May–June 2004, within the Crater Mountain Wildlife Management Area in Eastern Highlands Province, Papua New Guinea. Fieldwork was undertaken around the village of Herowana (6.652°S, 145.194°E) at 1650 m in mid-montane rainforest.

The village and surrounding area were mapped at a scale of 1 : 1000 through a combination of on-the-ground measurements and GPS locations. Six major habitat types were recognised. These were: closed-canopy secondary forest (canopy 10–20 m with leaf litter covering the ground), open-canopy secondary forest (canopy 10–15 m and forbs ground cover), coffee gardens (planted with coffee and several species of shade-trees, with forbs ground cover), old gardens (consisting of a few large trees with invading scrub, grasses and herbaceous areas), new gardens (cleared land with a few large unfelled trees, planted with a variety of fruits and vegetables), and pit-pit grass (*Saccharum edule*/ *Saccharum robustum*). Village areas containing houses with fenced surroundings and paths and a grass airstrip were also present; however, village areas covered only 1% of the study site and no radio-tracking locations were recorded within the village or on the airstrip.

Fieldwork methods

Bandicoots were captured in metal wire Tomahawk traps or in locally made wooden traps. Traps were baited with ripe banana or a mixture of banana and peanut butter, and set within areas of active coffee garden, old gardens and secondary forest. Traps were positioned close to areas of bandicoot foraging signs (conical rooting holes in the soil: Scott *et al*. 1999) or alongside favoured food plants, including fruiting *Zingziber* or *Ficus* trees (Flannery 1995). Traps were set for 1–3 weeks and remained set in the same location after each trap's initial capture. All traps were set in the late afternoon (16:00–18 : 00 hours) before animals became active, and were checked at dawn. All live animals captured were weighed and measured (body, tail, hind foot and ear length) and their sex recorded. Bandicoots were classified as adult or immature according to the presence or absence of pouch young or enlarged nipples in female animals, or large developed (length and width >16 mm) and external testes for males. Additional information from bandicoots hunted by local people in the area were collected during the period of fieldwork (2002 and 2004) as well as during March–May 2003, when bandicoot skulls were collected as part of a hunting study (Cuthbert 2010), and included data on body mass, size, sex and reproductive status. Information on the site and habitat of all live captures and all hunting captures was also collected.

All live-captured animals were fitted with 2.5-g two-stage radio-transmitters (Holohill, Canada) with a real-time variable-pulse activity sensor ('tip-switch') and were tracked using a Telonics TR4 hand-held receiver and Yagi antenna. Transmitters were attached to the tails of animals using Leukoplast adhesive tape (Moseby and O'Donnell 2003). Animals were not anaesthetised during tag attachment and were held in a cloth bag for the attachment procedure. Tag attachment, weighing and measurements took ~4–5 min for each animal. After attachment, all animals were immediately released at the capture site and tracking commenced after 24 h. Radio-tracking was undertaken during the day and night. During daylight hours (06:00–18 : 00 hours), when bandicoots were generally inactive, one location fix was obtained for each animal per day. At night (when animals were active), 1–4 fixes were obtained for each animal, a minimum of 2 h apart to reduce autocorrelation in location. Nocturnal locations were estimated from triangulation from known mapped positions on the ground (White and Garrott 1990). Diurnal locations were either obtained from triangulation, or the animal's position on the ground was located to the nearest 4–6 m by approaching the site on foot. The exact position and location of daytime den sites was not determined, as approaching close to (<4 m) den sites resulted in animals flushing, changing their normal behaviour. Following radio-tracking, all bearings and tracking locations were transferred to the large-scale map of the study area and error areas were measured on the map from the size of each location's triangulation area. Locations were, on average, 137 ± 87 m ($n = 751$) (± 1 standard deviation) from the animal, with an estimated average error area of $19.7 \pm 27.2\ m^2$ ($n = 190$) (equivalent to an error diameter of 5.0 m, assuming a circular error area). For each fix we recorded whether the animal was active or inactive, based on listening to each transmitter for >1 min and determining whether the transmitter's pulse rate was changing (indicating activity from the transmitter's tip-switch) or constant (inactivity). Additional activity fixes (without a corresponding location) were obtained at 2-hourly intervals over the course of the day and night to determine daily activity patterns.

Analysis

Because of the limited number of independent locations available for each animal (range 10–31), home-range area was estimated by the minimum convex polygon (MCP) method (White and Garrott 1990) using GIS software MapInfo 7.5 (PBBI, Troy, NY, USA) after excluding all locations with a large (>100 m^2) error area. Examination of cumulative home-range area against days and number of independent locations indicated that areas stabilised after 8–10 days (ranges 91 ± 8% revealed after 10 days) or with more than 18–20 fixes (ranges 92 ± 9% revealed with 20 fixes) and estimates of short-term home range are reported for bandicoots that met either criteria. The area of each of the six main habitat types was calculated for each animal's home range and habitat selection by individual animals was determined from the actual and expected frequency of fix locations within each habitat and resulting Chi-square test (excluding habitat types with ≤ 3 foraging locations). Preference for individual habitats was assessed using the Vanderploeg and Scavia electivity index (E^*_i) (Lechowicz 1982), which produces an index ranging from –1 (avoidance) to +1 (selection) with a score of 0 being equivalent to no selection. To evaluate whether kalubu bandicoots were selecting certain habitats we calculated E^*_i for each individual and each habitat, and then for each habitat type we tested whether the mean E^*_i from all animals was significantly different from zero (utilising a two-tailed *t*-test between the population mean and a hypothesised mean of 0). Because the whole study site was not completely mapped, the habitat types within the home range of one animal (male M3) were unknown for part of this animal's range. Consequently, for this individual we assessed only habitat selection and preference for tracking locations that fell within the mapped area. To evaluate whether animals were reusing the same daytime nest sites or localities we calculated for each individual the linear distance between all daytime locations (for fixes with an error area <100 m^2) and recorded the number of locations within 10 m of each other (twice the mean error diameter). We also calculated, for each individual and for all animals, the mean distance between successive daily localities. All statistics are presented as means ± 1 standard deviation, all tests are two-tailed and significant if $P < 0.05$.

Results

Body size and breeding

The kalubu bandicoot was the most commonly encountered species in the study, comprising 20 of the 21 animals live-trapped for radio-telemetry and 73 of 83 animals captured by local hunters, an overall proportion of 89% (93 of 104 bandicoots). Raffray's bandicoot comprised all other captures within the study area, with one individual captured for radio-tracking and 10 killed by local hunters. Male kalubu bandicoots were heavier and larger than females, for all measurements with the exception of tail length (Table 1). Body mass and body length were strongly correlated ($r^2 = 0.954$, $n = 51$, $P < 0.001$). Limited morphometric data were available for Raffray's bandicoot, which suggest that males were larger and heavier than females (Table 1) but small sample size reduced the power of statistical tests. Raffray's bandicoot was generally larger and with a longer tail than the kalubu bandicoot (Table 1).

Of 21 female kalubu bandicoots examined, where body measurements were available, 15 animals of >400 g in mass were carrying pouch young or had previously bred, one animal of 380 g had a single pouch young, one animal of 390 g had not bred, and four <375 g mass had not bred. All male kalubu bandicoots examined ($n = 30$) had developed external testes, including the two smallest individuals of 275 g. Kalubu bandicoots had an average of 1.53 ± 0.51 pouch young ($n = 19$, range = 1–2 young), with 10 of 15 (67%) adult females (>400 g) carrying young at the time of capture. Pouch young varied in size from 8 to 91 mm in crown–rump length (average = 46 ± 35 mm, $n = 6$ litters), ranging from naked early-stage embryos to large, haired and near-independent-age young. Neither of the two female Raffray's bandicoots were carrying young; one animal (mass 880 g) had previously bred whereas the other (220 g) had not.

Activity patterns

Radio-transmitters were attached to 17 kalubu bandicoots and one Raffray's bandicoot. Excluding tagged animals that were killed by hunters ($n = 2$) or a hunter's dog (1) or where the transmitter failed (1), tags remained attached for an average of 11 days (range = 4–19 days, $n = 14$ tags), with 10–31 independent locations (mean = 20.9 ± 6.4 locations) obtained for each animal (excluding locations with a large error area >100 m^2). In total, 447 independent activity fixes were obtained from 13 kalubu bandicoots. There were no significant differences between the sexes in the proportion of active fixes during daylight (log-likelihood $G'_1 = 0.58$, $P = 0.45$) or night-time hours (log-likelihood $G'_1 = 0.71$, $P = 0.40$), so data for both sexes were pooled. Kalubu bandicoots were primarily nocturnal, with 75% (149 of 199) of night-time fixes indicating activity versus 14% (33 of 239) activity during the day (log-likelihood $G'_1 = 73.63$, $P < 0.001$). Animals became active from 18 : 00 to 20 : 00 hours, with activity peaking from 20 : 00 to 02 : 00 hours, before dropping to low levels of activity between 04 : 00 and 06 : 00 hours and throughout the day (Fig. 1). Kalubu bandicoots were unaffected by rain, with all nocturnal locations during periods of rain ($n = 15$) indicating activity. Limited information from a single tracked Raffrey's bandicoot showed a similar pattern of activity, with all fixes from 19 : 00 to 02 : 00 hours indicating activity ($n = 10$) and with most daylight fixes showing no activity (8 of 10 inactive).

Estimated linear movements between successive radio-telemetry locations indicated that kalubu bandicoots moved an average linear distance of 29 ± 18 m h^{-1} during the night. Consecutive daytime locations indicated that individual animals moved an average of 93 ± 103 m ($n = 43$) between their daytime nest sites; however, there was considerable variation between

Table 1. Morphometric measurements of reproductively active female and male kalubu bandicoots and Raffray's bandicoot

Data shown are mean ± standard deviation (with sample size shown in parentheses). The results of *t*-tests (*t* statistic and probability) for testing between the sexes are also shown

	Female	Male	*t*	*P*
Kalubu bandicoot (*Echymipera kalubu*)				
Body mass (g)	592 ± 113 ($n = 16$)	1008 ± 425 ($n = 30$)	3.82	<0.001
Tail (mm)	70.0 ± 7.0 ($n = 14$)	80.8 ± 16.2 ($n = 27$)	1.71	0.095
Head–body (mm)	303 ± 25 ($n = 16$)	356 ± 63 ($n = 30$)	3.23	<0.01
Hind foot (mm)	55.9 ± 2.9 ($n = 12$)	68.5 ± 9.4 ($n = 24$)	4.51	<0.001
Ear length (mm)	21.2 ± 1.6 ($n = 9$)	24.1 ± 2.5 ($n = 23$)	3.19	<0.01
Raffray's bandicoot (*Peroryctes raffrayanus*)				
Body mass (g)	550 ± 467 ($n = 2$)	1038 ± 235 ($n = 5$)	1.97	0.106
Tail (mm)	132 ± 50 ($n = 2$)	152 ± 34 ($n = 6$)	0.67	0.528
Head–body (mm)	290 ± 118 ($n = 2$)	392 ± 31 ($n = 6$)	2.25	0.065
Hind foot (mm)	73 ± 5 ($n = 2$)	80 ± 4 ($n = 6$)	2.19	0.072
Ear length (mm)	23 ± 3 ($n = 2$)	27 ± 4 ($n = 6$)	1.21	0.269

individuals (Table 2). Kalubu bandicoots were tracked to the same (<10 m) daytime location on 8% of occasions (6 of 76 locations) and this ranging behaviour was spread among all individuals (Table 2). Three tags were recovered from daytime sites, two underneath large and deep piles of leaves on the forest floor and the other within a hollow tree stump. Exact information on the location of den/nest sites was not obtained to avoid disturbance; however, the above three locations appeared typical, with animals in the day being found in areas with deep piles of leaf litter, tree stumps, or areas of thick grass. Daytime locations of the single Raffray's bandicoot revealed successive daily movements of 87 ± 72 m ($n = 5$) and indicated that this animal reused the same daytime location on 2 of 9 occasions.

Home range

Short-term home ranges were estimated for 10 kalubu bandicoots (six males, four females). Home-range area varied from 0.9 to 7.3 ha (mean $= 2.79 \pm 2.05$ ha, $n = 10$) and increased with increasing body mass (linear regression, $F_{1,9} = 104.8$, $R^2 = 0.93$, $P < 0.001$) (Fig. 2). While there was an indication that males may have larger home ranges than females (male: 3.46 ± 2.43 ha, $n = 6$; female: 1.80 ± 0.56 ha, $n = 4$) the limited sample sizes meant that this was not statistically significant (t-test, $t = 1.30$, $P = 0.230$). Home-ranges of kalubu bandicoots suggest that intrasexual territoriality was occurring, with adjoining ranges of two male animals in 2002 and two males in 2004 both showing little overlap, and a similar pattern of little overlap for two females in 2002 (Fig. 3). In contrast, the ranges of two females were encompassed within a single male's range in 2002, and two males' ranges were completely and partially overlapped by a female's range in 2004 (Fig. 3). Based on the mean home-range size of male and female animals and assuming no overlap within the sexes and complete overlap between sexes, then population density of the kalubu bandicoot in the vicinity of the study site is estimated to be ~85 ± 31 animals km^{-2}. A single male adult Raffray's bandicoot (mass 1000 g) was tracked for a total of 19 days, with 21 independent tracking locations being obtained. The MCP estimate of home range of this animal was 2.7 ha.

Habitat use

Based on 88 capture locations, kalubu bandicoots were recorded from range of habitats, with captures occurring in open- and

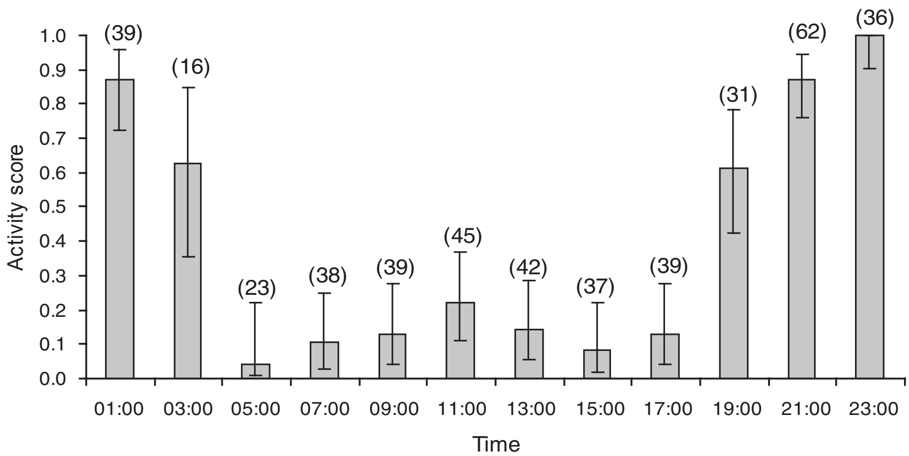

Fig. 1. Mean proportion of active fixes for radio-tracked kalubu bandicoots over a 24-h period. Times represent the midpoint of each 2-h block, numbers in parentheses are the number of independent observations, and error bars are upper and lower 95% binomial confidence limits about the mean.

Table 2. Details of tracking information for kalubu bandicoots
Home-range size could not be estimated for a further seven bandicoots in which 14 or fewer fixes were obtained

Year	Sex (no.)	Mass (g)	No. of fixes (night-time)	No. of days tracked	MCP home-range size (ha)	Distance between daytime locations (m)
2002	F (1)	375	17 (10)	8	1.46	–
2002	F (2)	620	20 (9)	12	2.59	51 ± 19
2002	F (3)	515	27 (22)	10	0.91	–
2004	F (7)	720	24 (12)	11	2.23	49 ± 34
2002	M (2)	1070	21 (10)	16	4.81	78 ± 32
2002	M (3)	1500	29 (13)	12	7.25	161 ± 162
2004	M (5)	520	18 (10)	9	1.56	75 ± 33
2004	M (6)	610	23 (12)	13	1.60	239 ± 231
2004	M (7)	930	26 (11)	14	4.36	103 ± 78
2004	M (9)	620	31 (15)	18	1.15	42 ± 32

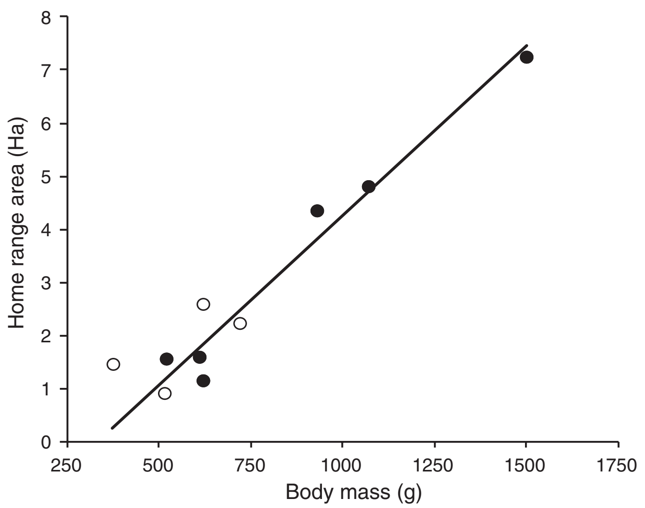

Fig. 2. Relationship between body mass and home-range area of kalubu bandicoots. Females are indicated by open circles and males by filled circles.

closed-canopy secondary forest (38%), new gardens (19%), old gardens (16%), coffee gardens (13%), primary forest (7%) and also from along paths and within village areas (8%). Radio-tracking data indicated similar results, with bandicoots recorded within all available habitat types (Fig. 3), apart from village areas or on the grass airstrip. However, the short-term home range of one animal in 2004 (female F7) indicates that it was crossing the airstrip and village areas (Fig. 3), despite no tracking locations being recorded from these habitats. Chi-square tests for each animal within each habitat type indicated no habitat selection for 12 of the 13 tracked animals, with the remaining bandicoot (male M2) being encountered more frequently in open-canopy secondary forest than expected ($\chi^2 = 20.7$, $P < 0.001$). Mean values of the electivity index (E^*_i) for each habitat type were not significantly different from zero (*t*-tests, $P > 0.05$ in all instances), indicating no overall preference for any particular habitat.

A single Raffray's bandicoot was captured and tracked in areas adjoining an old garden bordering mature secondary forest and primary forest. Of eight Raffray's bandicoots captured (including hunting records) where information on the capture site was available, six were caught in mature secondary forest and two from old gardens.

Discussion

The kalubu bandicoot was the most commonly encountered bandicoot in the study, comprising almost 90% of captures. Records from capture locations and radio-tracking of this species confirm the spool-and-line tracking work of Anderson *et al.* (1988) and observations of Flannery (1995), with this species being found in a diverse range of habitats, including gardens, pit-pit grass and areas of coffee plantation and secondary forest. By contrast, Raffray's bandicoot was less common and captures of this species and radio-tracking data for one individual suggest that it is more commonly encountered in more mature areas of secondary forest and old gardens. Flannery (1995) suggests that Raffray's bandicoot is primarily found in undisturbed forest; however, our results indicate that it will also use secondary forest and old gardens. These results confirm previous studies indicating that kalubu bandicoots are among the most abundant game species encountered in New Guinea (Hide *et al.* 1984; Flannery 1995) and are able to exploit a wider range of often disturbed habitats (Anderson *et al.* 1988) than Raffray's or Clara's bandicoot (*Echymipera clara*) (van Deusen and Keith 1966; Flannery 1995). While habitat use by the kalubu bandicoot and Raffray's bandicoot were different to some degree, their behaviour was broadly similar, with animals being almost exclusively active at night and resting in hollow tree stumps, piles of leaves or thick vegetation during the day, as previously reported (Anderson *et al.* 1988).

The average number of pouch young carried by female kalubu bandicoots found in our study (mean = 1.53, range = 1–2, $n = 19$) is similar to other studies of this species, where reported average litter sizes are 1.64 (range = 1–3, $n = 56$: Hide *et al.* 1984) and 1.70 (range = 1–3, $n = 10$: Hughes *et al.* 1990). As previously noted (Flannery 1995), kalubu bandicoots are very fecund and the proportion of females carrying pouch young in our study (67%, 10 of 15 animals) is consistent with the results of Hide *et al.* (1984) (66%, 56 of 85 animals) and Hughes *et al.* (1990) (71%, 10 of 14 animals). Females were breeding during both periods of our study (March–May 2002 and May–June 2004), and the size of pouch young varied from very small to large haired near-independent young. Hughes *et al.* (1990) reports a similar range in size of pouch young from several years, suggesting that breeding occurs throughout the year (Flannery 1995). Our records of mass and reproduction substantiate Flannery's (1995) observations that females breed at a young age, with sexual maturity occurring at a body mass of ~375–400 g. In contrast to Lidicker and Ziegler (1968), who reported that testes reach mature size in animals weighing 300–500 g, we found that all males captured in our study had large external testes, including animals as small as 275 g. Both *Perameles* and *Isoodon* species of the Peramelidae are reported to reach sexual maturity at 3–5 months and 4–8 months, respectively (Gemmell 1986; Short *et al.* 1998), and it is plausible that kalubu bandicoots reach maturity at a similar age. The kalubu bandicoot (Anderson *et al.* 1988; Flannery 1995) and other bandicoots (Flannery 1995) are reported to utilise daytime nest or den sites, a result confirmed by our study. However, radio-tracking of kalubu bandicoots and the single Raffray's bandicoot indicates that animals were not restricted to a few nest sites, but on most occasions (>90% for the kalubu bandicoot) were using a different site from one day to the next. Other than hollow tree stumps or logs (Anderson *et al.* 1988) or shallow burrows (Flannery 1995), our impression was that bandicoots were simply utilising deep piles of leaf litter or thick vegetation during the daytime, rather than having specific nest sites.

Limited tracking data were obtained for the bandicoots in this study, with an average attachment period of just 11 days (range = 4–19). This tracking period is similar to that found in a study of *Isoodon obesulus* and *Perameles nasuta* in New South Wales (Hope 2012), where transmitters attached in the same manner remained on for 2–21 days, but contrasts with a study of greater bilby (*Macrotis lagotis*) in northern South Australia, where animals were tracked for 16–91 days (mean = 52 days) using the same attachment method (Moseby and O'Donnell

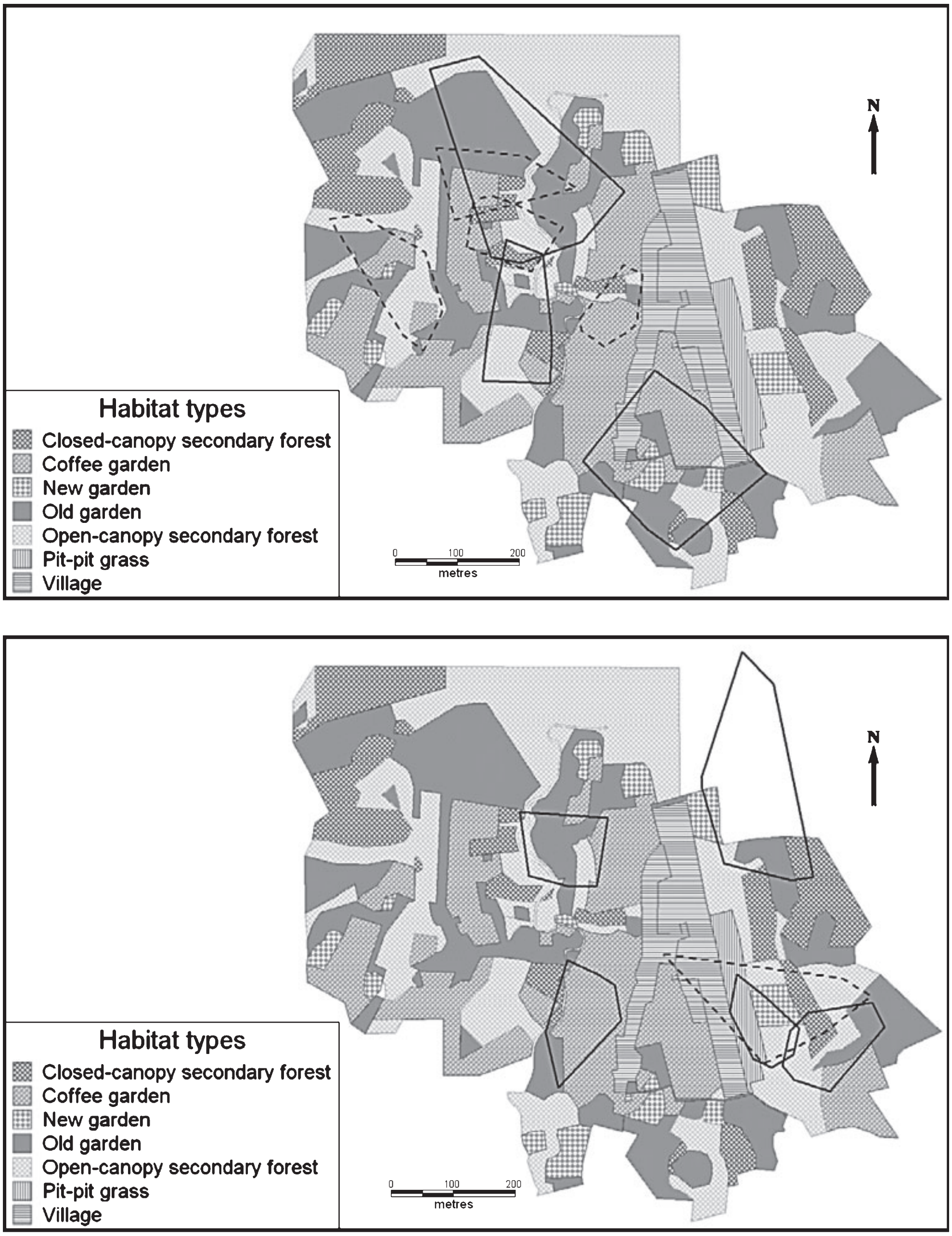

Fig. 3. Minimum Convex Polygon estimates of home ranges of male (solid lines) and female (dashed lines) kalubu bandicoots radio-tracked in 2002 (upper figure) and 2004 (lower figure) overlaid onto a habitat map of the study site. Habitats did not change between study years.

2003). Hope (2012) reports that rainfall reduced the attachment period of transmitters, and the high rainfall and humidity encountered in our study, and the smaller overall size and tail of bandicoots (cf. the greater bilby) may be responsible for the short tracking period. Other attachment methods would be worth considering in any further tracking study, although harnesses and collars present a risk of entanglement in thick vegetation. MCP estimates of short-term home-range size indicated an average home range for the kalubu bandicoot of 2.8 ha and a single estimate for Raffray's bandicoot of 2.7 ha. The robustness of MCP estimates of home-range size are known to be limited and potentially biased (Börger *et al*. 2006); however, the short period of attachment and consequent limited number of locations restricted more complex analysis such as kernel density estimates. Despite these limitations, our estimates of home-range size are broadly comparable with those recorded for bandicoots in the Peramelidae, where MCP home ranges of *Perameles nasuta* are reported as 1.8–2.0 ha (Scott *et al*. 1999) and 4.0–4.2 ha (Hope 2012), and of *Perameles gunni* as 1.6 ha (Dufty 1994). Our estimates of short-term home range also appear plausible in comparison with results from spool-and-line tracking, where night-time ranges of five males ranged from 0.34 to 0.64 ha and males covered an average distance of 344 m (Anderson *et al*. 1988). Short-term home ranges in our study varied from 1 to 7 ha and increased in relation to bandicoot size, with larger ranges belonging to larger male animals. Such a relationship may be a consequence of larger-sized animals requiring, and being able to defend, a greater area in order to meet their foraging requirements. Alternatively, larger-sized ranges may be due to males ranging over larger areas in search of mating opportunities. These two hypotheses are not mutually exclusive, but some support for the latter was the apparent presence of non-overlapping intrasexual territories in kalubu bandicoots observed in this study. The kalubu bandicoot is reported to be pugnacious to its own kind (Anderson *et al*. 1988; Flannery 1995) and it is plausible that they could defend exclusive intrasexual territories. In support of this, despite continued live trapping no further animals were captured within the ranges of animals tracked during our study. While this appears to be the case in our study, Anderson *et al*. (1988) reported that ranges of male kalubu bandicoots overlapped and radio-tracking studies of the long-nosed bandicoot (*Perameles nasuta*) indicate that females had overlapping ranges throughout the year, whereas males displayed territorial behaviour to other males in non-breeding months but ranges overlapped during the breeding season (Scott *et al*. 1999). Further studies at a range of sites and species, ideally utilising kernel density estimates of home range rather than MCP estimates, as the latter are often of limited utility in assessing temporal or spatial overlap between animals (Laver and Kelly 2008), will be necessary to determine whether intrasexual territoriality, as suggested by our study, is the norm for New Guinea's peroryctids.

If the home-range estimates and territorial behaviour of kalubu bandicoots in our study are representative then the maximum population density of the species is estimated to be ~85 animals km^{-2} in our study area and potentially in other areas of New Guinea with a similar mosaic of habitat types. No other density estimates from tracking studies are available for peroryctids in New Guinea; however, allometric relationships between body size and population density for frugivorous/ omnivorous marsupial mammals estimate a population density for bandicoots of ~57 animals km^{-2} (Cuthbert 2010). The relatively high population density of the kalubu bandicoot and high rates of reproduction of bandicoot species (Cuthbert 2010) suggests that the species should be able to withstand relatively high levels of hunting pressure and its continued presence in areas with high hunting pressure indicates that this is the case (Hide *et al*. 1984; Pangau-Adam *et al*. 2012). Less is known of the potential population density of Raffray's bandicoot and its capacity to withstand hunting. However, it is widespread and relatively common (Flannery 1995), and its more restricted use of undisturbed forest, secondary forest and old gardens may place it less at risk from hunting than the kalubu bandicoot, which is frequently encountered and killed as people work in new gardens and areas close to villages (Mack and West 2005; R. J Cuthbert, unpubl. data). While the kalubu bandicoot and Raffray's bandicoot remain widespread and relatively abundant, it should not be assumed that all bandicoot species can withstand high hunting pressure. Both the smallest (*Microperoryctes papuensis*) and largest (*Peroryctes broadbenti*) species of bandicoot, and several other bandicoot species, are known from only a few specimens and restricted sites, and are considered threatened (George and Maynes 1990; Flannery 1995). Studies of the ecology of these species in comparison to the kalubu bandicoot and Raffray's bandicoot would help to elucidate why these species are so rare and restricted in distribution and potentially allow prescriptions for management and protection to be implemented.

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