

# DIET AND BREEDING OF THE RUFOUS SPINY BANDICOOT *ECHYMI-PERA RUFESCENS AUSTRALIS*, IRON RANGE, CAPE YORK PENINSULA

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A population of the rufous spiny bandicoot *Echymipera rufescens australis* was studied for 14 months by live-trapping, and diets were determined by faecal analysis. The population had a high density (approximately 48 individuals on a trapping grid of 2.25 ha). A wide variety of foods were eaten, but fruits and seeds contributed the largest proportion of material to faeces, followed by invertebrates, fungi and dicot plants. *Echymipera rufescens* may potentially be a significant seed disperser for some plants, such as *Pandanus zea*. There was a short breeding season, with births occurring between December and March. Females produced one or two litters per year. Mean litter size was just under three, and litter size increased with the mother's mass. Females produced a mean of 4.9 young per year. We conclude that although *E. rufescens* is a 'typical' bandicoot in that it is omnivorous and has high fecundity, it is more frugivorous and has a somewhat lower reproductive rate than other Australian bandicoots.

Key words: Peroryctinae, Peramelidae, bandicoot ecology, life history, breeding biology

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THE bandicoot genus *Echymipera* contains five species spread across New Guinea and adjacent islands. One of these species, *E. rufescens*, also occurs in Australia on the Cape York Peninsula of north Queensland where it is represented by the sub-species *E. r. australis*. This subspecies occurs in near-coastal regions from the McIlwraith Range to the tip of Cape York Peninsula (Gordon 1995a). Flannery (1995) commented that in New Guinea the species tends to be uncommon and is found in relatively dry habitats; in Australia it is found in a broad range of habitats, but always within or close to large tracts of rainforest, where it may be common (Gordon, *et al.* 1990).

Very little is known of the biology of *E. rufescens*, or of any other members of the bandicoot subfamily Peroryctinae. Like other bandicoots, the *Echymipera* species appear to be omnivorous. They have particularly long snouts, suggesting that they are well-adapted for foraging on invertebrates, although there are anecdotal observations of *E. kaluba* and *E. clara* feeding heavily on fruit and seeds (Flannery 1995). There have been no detailed studies of breeding or demography in any species of *Echymipera* or of any other member of the bandicoot subfamily Peroryctinae (which includes the

genera *Echymipera*, *Peroryctes* and *Microperoryctes*). This paper reports the results of a fifteen-month study of the natural history of *E. r. australis* in the Iron Range National Park of the northern Cape York Peninsula, which aimed to fill this knowledge gap by investigating the seasonal demography and feeding of this species.

## METHODS

### Study site and trapping

The climate of the area is monsoonal, with heavy rain and very humid conditions in the wet season between December and April, and little or no rain (but continuing high humidity) at other times. Mean annual rainfall at Lockhart River is 2 086 mm. Mean monthly maximum temperatures range from 32.5 °C in December to 27.5 °C in July.

A trapping grid was established at Lamond Hill (12° 43.37' S; 143° 17.30' E). This site was on a hillside of metamorphic rocks at an elevation of approximately 140 m. The vegetation was semi-deciduous mesophyll vine forest that had regenerated from a simulated atomic bomb blast in the 1960s and had vegetation characteristics indicating a history of disturbance, in particular a dense layer of *Calamus* and several gaps occupied by

grasses. A more detailed vegetation description can be found in Shevill (1999). This site was chosen on the basis of a larger trapping survey of a range of habitats in the Iron Range National Park which showed Lamond Hill to have a high abundance of *E. rufescens* (Shevill 1999).

Bandicoots were live-trapped using 50 wire cage treadle traps (440 x 200 x 250 mm; constructed by DIS), and baited with a mixture of peanut butter, honey, rolled oats and vanilla essence. Traps were laid on a grid consisting of ten transects set 25 m apart, each with five traps placed at 25 m intervals, and covering an area of 2.25 ha, and were left in position for the duration of the study. The trap grid was operated for three or four days each month from June 1997 to July 1998.

Upon capture, bandicoots were placed into calico bags, and the trap was inspected for scats. Scats samples were stored in 70% alcohol. Individuals were marked by tattooing on the inside of the ear pinna, weighed to the nearest 25 g, and measured for head width and length, and length of head-body, tail, ear, pes, teats and testes. Pouches of females were examined to determine reproductive status. Pouch-young were sexed where possible, and the following measurements taken: head-body length, head width and length, tail length, pes length, ear length and (where possible) weight. Developmental features were noted, following Hall (1990).

### Materials for diet analysis

Attempts to collect faecal samples from trapped animals were often frustrated by heavy rain and the rapid disposal of scats by dung beetles. Faecal samples were collected from 56 *E. rufescens* captures and four *P. nasuta*.

A plant collection, consisting mainly of understory plants and fruit, was made at the study site, and this was used to make an epidermis reference collection for identification of leaf, fruit and fungal matter in faeces. Techniques followed Johnson and McIlwee (1997) and McIlwee and Johnson (1998). Sub-samples were cut into pieces of approximately 20 mm<sup>2</sup> and soaked overnight in 50% alcohol for rehydration, then placed in a 50 ml Erlenmeyer flask with 5 ml of Jeffery's solution and 5 ml of 10% nitric acid. The flask was placed into a hot (90 °C) water bath and swirled regularly until the epidermal and mesophyll layers separated. Ammonia was then added to neutralize the nitric acid, followed by distilled H<sub>2</sub>O. The tissue sample was removed with a spatula and placed into a watch glass containing distilled H<sub>2</sub>O to remove chemical residue, then moved to another watch glass and stained with 1% gentian violet for one minute before being rinsed with distilled H<sub>2</sub>O in another watch glass. The stained sample was then mounted in glycerol jelly on a microscope slide and photographed.

Faecal samples were prepared as follows. Each

sample was placed into a 5 ml plastic vial with 2 ml of 5% KOH, shaken vigorously for one minute, and left to stand for five minutes. Samples were washed with distilled H<sub>2</sub>O through a series of sieves 425 µm and 300 µm in diameter. The remaining material was filtered through filter paper at ~ 65 µm to collect any spores. The fractions retained by each sieve were placed onto watch glasses and stained with Lugol's iodine solution, left for one minute, and returned to the respective sieve and rinsed with distilled H<sub>2</sub>O. These stained samples were transferred to another watch glass and stained with 1% gentian violet, then rinsed as above. Finally, a sub-sample from each fraction was mounted on a microscope slide.

### Diet analysis

All samples were initially scanned at low power using a stereo dissection microscope to find large, identifiable plant or invertebrate fragments. Sieved samples (i.e. those sieved at 425 µm, 300 µm and 65 µm) were scanned at x100 magnification (x200 for the finest fraction). In each of thirty fields of view on a transect over the slide, the proportions of fungi, monocot leaf, dicot leaf, fruit, seed, root, vertebrate, invertebrate and unidentified material were scored into categories of 1 = < 25%, 2 = 25%-50%, 3 = 50%-75%; 4 = >75%. If an item within a food category was identified to a finer level it was scored as a subcategory within that category. To calculate the percentage of different food types on each slide, the sum of each food type was divided by the sum of all scores and multiplied by 100. To obtain a single set of percentages for each faecal sample analysed, the fraction sub-sample results were averaged. Fungal taxa in the diet were identified (from spore characteristics) to genus, by Dr Victoria Gordon of CSIRO Atherton. Invertebrates were identified using Naumann *et al.* (1991) and with help from Dr Fred Ford of JCU.

For analysis of diet seasonality, the following seasons were identified: early dry season (March-July), late dry season (August-October), early wet season (November-January), and late wet season (February - April).

## RESULTS

### Diet

The representation of different food categories in *E. rufescens* faeces throughout the year is shown in Fig. 1. The greatest contribution was from fruit and seeds with a mean total value of 27.12% (n = 56), followed closely by invertebrates (25.56%), then fungi (18.89%) and dicots (18.19%). Other food categories of relatively small importance were roots/soil/other (6.99 %), seeds (3.37%), monocots (2.91%) and vertebrates (2.91%). We tested for seasonal variation in representation for the most common food categories using ANOVA, and found that there was significant variation in the occur-

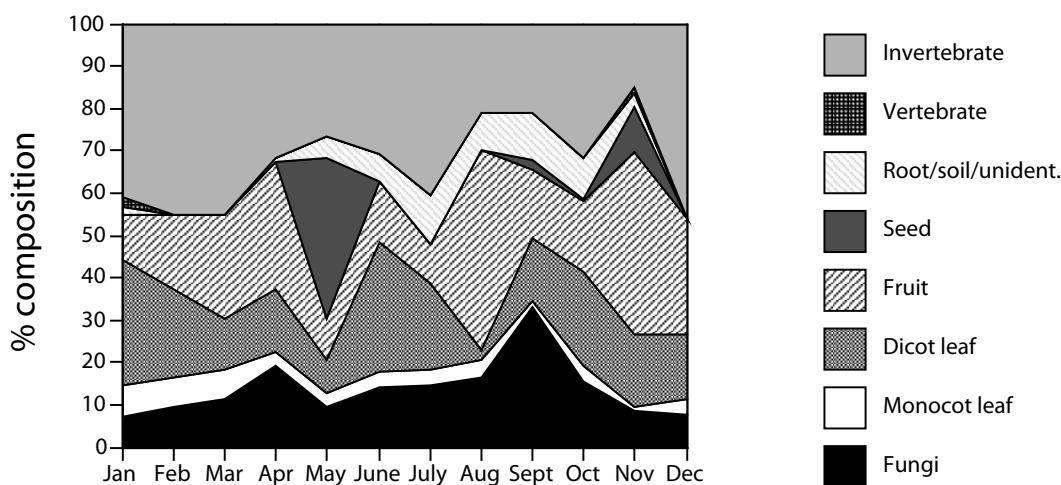


Fig. 1. Seasonal variation in the representation of food categories in faeces of *E. rufescens*.

rence of fungi ( $F_{3,55} = 4.26$ ,  $P < 0.01$ ), invertebrates ( $F_{3,55} = 2.82$ ,  $P < 0.05$ ) and fruit ( $F_{3,55} = 11.56$ ,  $P < 0.01$ ), but not dicots ( $F_{3,55} = 2.00$ , n.s.). Consumption of fungi was evidently high in the late dry season and low in the early wet season; consumption of fruit was low in the early dry season and was higher at other times; while invertebrates were lower in the late dry season than at other times.

Fruit and seed residues were mostly from *Pandanus zea* and *Alpinia caerulea*. One stomach that was examined contained more than 25 *P. zea* seeds, and *P. zea* seeds were found in scats of 34 other bandicoots. Spores of three genera of fungi were identified in *E. rufescens* faeces. These were *Cortinarius*, *Glomus* and *Hysterangium*. These are all mycorrhizal genera; *Cortinarius* fruit bodies are produced above ground and the other two are hypogeous. Spores of *Hysterangium* were comparatively rare and the few that were found were degraded, suggesting that they may possibly have been ingested incidentally with soil. Spores of the other two taxa were in good condition. The invertebrates consisted mostly of Coleoptera (beetles), with Blattodea (cockroaches) and Orthoptera (grasshoppers) also eaten but to a lesser extent. Vascular plant material was predominantly dicot leaf. Few fragments could be identified, but those that were consisted of *Canarium* sp., *Euroschinus falcate*, *Solanum viridifolium* and *Pisonia umbellifera*.

Limited data on the diet of the co-occurring *P. nasuta* suggests that it differed from *E. rufescens* in consuming more invertebrates (41.83%,  $n = 4$ ) and less fruit (2.58%); otherwise, the *P. nasuta* samples contained fungi (26.68%) and dicots (23.43%) along with small proportions of other plant and unidentified material.

## Demography and breeding

Between May 1997 and July 1998, the total trapping effort of 2250 trap-nights resulted in 424 captures of *E. rufescens* (as well as captures of four other mammal species: cinnamon antechinus *Antechinus leo* (2), long-nosed bandicoot *Perameles nasuta* (11), white-tailed rat *Uromys caudimaculatus* (18) and feral pig *Sus scrofa* (2)). Captures of *E. rufescens* consisted of a total of 29 individual males (24 adults and 5 subadults) and 29 individual females (19 adults, 10 subadults), not including pouch young. Calculation of numbers known to be alive (KTBA) for each month suggested a resident population of 48 individuals (25 males, 23 females). Monthly KTBA estimates showed little seasonal variation, although there was a suggestion that the population was slightly larger between September and January than at other times (Fig. 2; the low values for the first two months and the last two months are probably due to incomplete estimation of KTBA). Another 10 individuals (4 males and 6 females) were present for one month or less and were thus classed as transients. Body masses of adults varied from 700 to 2225 g (mean 1265) for males, and 550 to 1200 g (mean 799) for females. Trapability of resident animals was high, at a mean of 77.5% per month, with no significant difference between males and females ( $F_{1,28} = 0.16$ , n.s.).

Females carried pouch young between November and May, and 80 to 100% of females were with pouch young in January, February and March (Fig. 3). This indicates a concentration of births between December and March. Between November 1997 and May 1998, 18 breeding females produced 88 pouch young (4.9 young per female) in 32 litters (1.8 litters per female). Litter

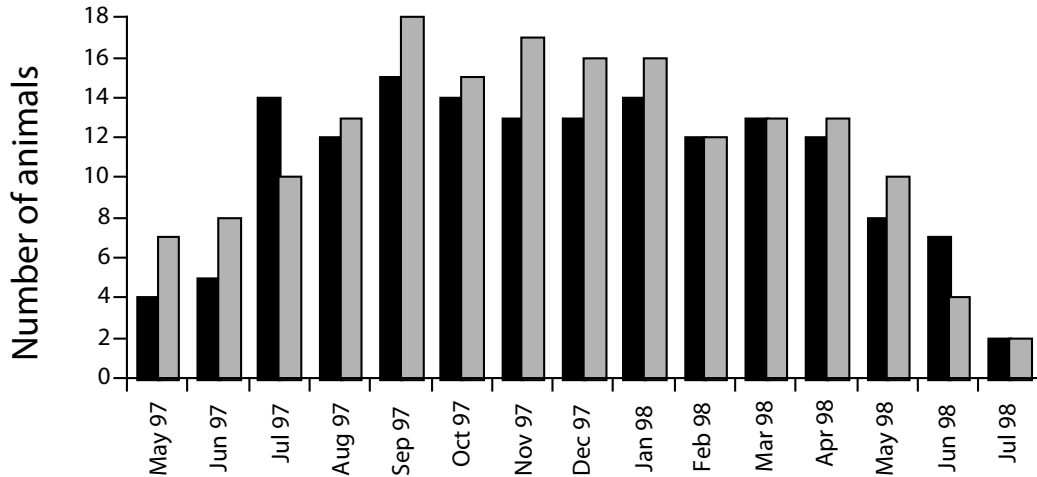


Fig. 2. Number of male (black bars) and female (grey bars) adult and subadult *E. rufescens* known to be alive at the Lamond Hill study area.

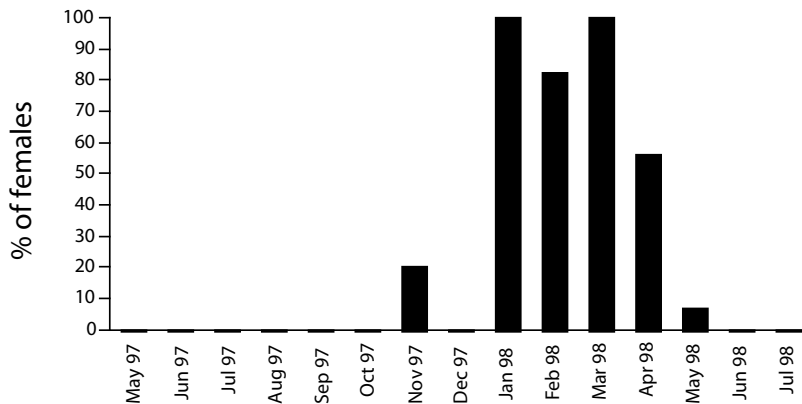


Fig. 3. Percentages of female *E. rufescens* carrying pouch young in different months.

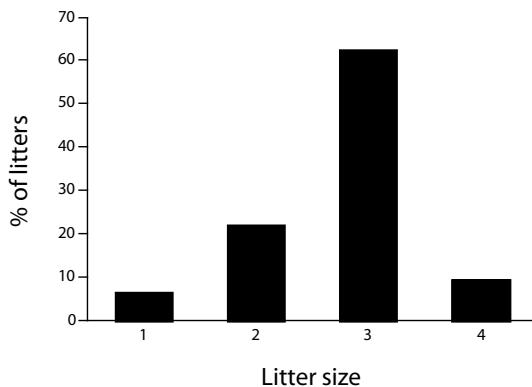


Fig. 4. Variation in litter size of *E. rufescens*.

size ranged from one to four (Fig 4) with a mean of  $2.8 (\pm 0.13)$ . Of all pouch young, 49 were male and 39 were female; this is a non-significant departure from parity ( $\chi^2 = 1.12$ , n.s.). There was a significant positive relationship between female body mass and litter size (Fig 5; by logistic regression,  $\chi^2 = 4.29$ ,  $p < 0.05$ ). The appearance of sub-adults in the trapped population was also seasonal, being greatest around August and September and least from May to July.

Distinct pads or pathways were found throughout the area. Analysis of trap locations suggested that bandicoot home ranges were on the order of one to two ha. *E. rufescens* denned in shallow burrow complexes dug to depths of just over half a metre, typically with at least two openings (up to four) and covering an area of about two to three square metres (Shevill 1999).

## DISCUSSION

This study, the first detailed field study of any of the peroryctine bandicoots, identifies several points of similarity, and some important differences, between the biology of *E. rufescens* and other Australian bandicoots (subfamily Peramelinae).

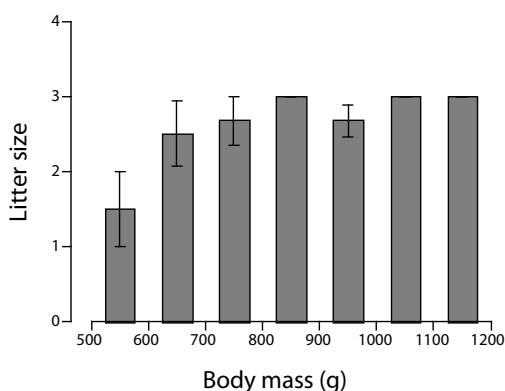


Fig. 5. Differences in litter size (mean with s.e.m.) for female *E. rufescens* in different weight classes.

*Echymipera rufescens* was clearly omnivorous and had a flexible diet, but a large proportion of its food intake consisted of fruit. Fruit consumption by *E. rufescens* appeared to be characterised by opportunism. In particular, fruits and seeds of *Pandanus zea* were occasionally eaten in large quantity, and this probably reflected heavy feeding on dense patches of fallen fruit (assuming that bandicoots were unable to harvest the fruit directly from the plants) which are occasionally produced as a result of strong winds shaking the parent tree. Nonetheless, *E. rufescens* found fruit to eat at all times of the year. Although not quantified, the diversity and abundance of fruit in the study area was high, and this may explain the high local abundance of *E. rufescens*.

Seeds in *E. rufescens* faeces appeared to be in good condition and were probably viable. This suggests that *E. rufescens* may be significant as a seed disperser for plants like *P. zea*, particularly if passage through the digestive tract were to stimulate germination. Faeces also contained fungal spores suggesting that *E. rufescens* may also play a role in dispersal of fungi, as do many other partly mycophagous mammals (Johnson 1996). However, few fungal taxa were found in *E. rufescens* faeces. This is consistent with studies of other bandicoots, in which although consumption of fungi (mainly hypogeous mycorrhizal species) may be significant at some times of the year, the diversity of fungi eaten is much less than in specialist mycophagists such as rat-kangaroos (Potoroidae) (Claridge and May 1994).

Although all other bandicoots are omnivorous, there is considerable variation in diet composition among species. The southern brown bandicoot *I. obesulus* is largely insectivorous, with significant consumption of

fungi at some times of the year; this is also true of *Perameles nasuta* and *P. gunnii* (this study; Claridge *et al.* 1991; Heinsohn 1966; Keiper and Johnson 2004). The northern brown bandicoot also eats invertebrates but with a higher representation of plant material, including grasses (Keiper and Johnson 2004; McIlwee and Johnson 1998). The extinct pig-footed bandicoot *Chaeropus ecaudatus* may have been more herbivorous still (Johnson and Burbidge 1995), while the extinct desert bandicoot *P. eremiana* might have eaten mainly ants and termites (Gordon 1995b). Of all these species, *E. rufescens* is the most frugivorous, and in the Iron Range it ate substantially more fruit than sympatric bandicoot species (Shevill 1999). Although not a specialist, within its limited range in Australia *E. rufescens* appears to play the role of medium-sized terrestrial mammalian frugivore. This is a foraging niche that is occupied by several species in the tropics of South America and Africa, but which has very few representatives in Australia.

Australian bandicoots in general have high reproductive output and rapid development, leading to high population growth rates. In some species these life history traits are linked to occupation of early-successional habitats, such as heath regenerating after fire (Gordon and Hulbert 1989; Stoddart and Braithwaite 1979). *Echymipera rufescens* also has high fecundity, with females producing one or two litters of up to four offspring each during the breeding season. However, reproductive output is constrained by two factors.

First, the breeding season is quite short. In this study females were found in breeding condition between November and May, consistent with the majority of births taking place between December and March. This is a short breeding season that coincides with the peak rainfall of the northern wet season. It is possible that in many years the breeding season is actually shorter than reported here. There was an early start to the 1997/98 wet season, because of unusually warm and wet weather in October 1997, and the season was longer than usual courtesy of a cyclone in March 1998. Because this wet season was unusually prolonged the breeding season of *E. rufescens* might have been extended as well. Other tropical bandicoots also breed seasonally (e.g. *I. macrourus* in North Queensland, Johnson *unpubl.*, Andrew Krockenberger *pers. comm.*) but breeding may be more prolonged in southern populations. For example, in *P. gunnii* and *I. obesulus* in Tasmania, births occur from June to February inclusive.

Second, the rate of development of pouch young may be somewhat slower in *E. rufescens* than in other bandicoots. Successive measurements of a single pouch young gave a regression of head length (mm) on time

(days) of 0.68 (Shevill 1999), compared with 0.90 for *I. macrourus* (Hall 1990). This implies a pouch life of approximately 65 days in *E. rufescens* (Shevill 1999). In *P. gunnii*, *P. nasuta* and *I. macrourus* young leave the pouch at around 50 days (Heinsohn 1966; Stodart 1966; Hall 1990). The difference in development time of young also implies that the interval between successive litters produced by an individual female within the breeding season would be extended by around two weeks in *E. rufescens*.

The shortness of the breeding season combined with the length of time needed for offspring to complete pouch-life means that females produce one or at most two litters per year. Mean litter size is similar to other bandicoots, and smaller females (presumably in their first year of reproduction) tend to produce small litters. The combination of these reproductive traits means that annual reproductive output is limited to around five offspring per female. This a moderate fecundity compared with more southern populations of species of *Isoodon* and *Perameles*, which have prolonged breeding, rapidly-developing young, and litters of up to five or six offspring.

To summarize, although *E. rufescens* is a typical bandicoot in having an omnivorous diet and a fast life-history, it is nonetheless distinguished by being more frugivorous than other bandicoots, and in having a somewhat lower reproductive output. Possibly, these features are a product of the evolutionary history of the species in tropical rainforest, and might also be found to some degree in the other peroryctine bandicoots.

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