

Home-range Characteristics and Movement Patterns of the Red-legged Pademelon (*Thylogale stigmatica*) in a Fragmented Tropical Rainforest

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Abstract

Home-range characteristics and movement patterns of five male and eight female red-legged pademelons (*Thylogale stigmatica*) were studied in north-eastern Queensland between September 1991 and June 1992 using radio-telemetry. In relation to mean body weight, the home range of *T. stigmatica* was small ($\bar{x} = 2.26$ ha, $n = 9$), individually variable (range 0.82–3.70 ha) and partitioned into spatially distinct diurnal and nocturnal components. The nocturnal range ($\bar{x} = 1.00$ ha, $n = 6$) incorporated forest edge and pasture habitat, and was somewhat smaller than the diurnal range ($\bar{x} = 1.67$ ha, $n = 10$), which was located entirely within the forest. Home-range shape was governed largely by the distance between the diurnal and nocturnal ranges, which in turn was related to physical features within the habitat. Pademelons moved slowly within and quickly between their diurnal and nocturnal ranges. Movement between these areas occurred just after dusk and just prior to dawn. The diurnal rate of movement (m min^{-1}) was generally higher than the nocturnal rate, suggesting that pademelons moved extensively in the forest during the day, and were relatively sedentary whilst on pasture at night.

Introduction

The red-legged pademelon (*Thylogale stigmatica*) is the smallest member of a genus containing six species of small and stocky macropodids that live within the closed forests of eastern Australia and New Guinea. The primary habitat requirement of *T. stigmatica* is dense forest vegetation, usually rainforest; however, it is also found in wet sclerophyll forest and occasionally in dry vine-thickets (Johnson and Vernes 1995). In fragmented rainforest in north Queensland, the diet of *T. stigmatica* is known to consist of both forest browse and pasture grass species (Vernes 1994). The red-legged pademelon is one of the more common and larger rainforest-dwelling mammals in the north Queensland wet tropics, and one of only three rainforest macropodids in the region. Despite this, very little is known of *T. stigmatica* ecology, with past studies restricted to behaviour (Cooke 1979) and diet (Jarman and Phillips 1989) in the south of its range, and reproduction in a captive colony (Johnson and Vernes 1994).

This paper examines home-range characteristics and diel movement patterns of the red-legged pademelon in upland tropical rainforest that has been fragmented by human activities. Using radio-telemetry, we aimed to determine the size, shape and partitioning of home range by *T. stigmatica*, and how the mean rate of movement of radio-tracked animals fluctuate within different parts of their home range and during different periods of the day and night.

Methods

Study Site

The study was conducted at Millaa Millaa Falls (17°29'50''S, 145°36'30''E, elevation 800 m), a 75-ha fragment of complex notophyll vine forest (CNVF) (Tracy and Webb 1975) approximately 1 km from the township of Millaa Millaa on the southern Atherton Tableland in the north Queensland wet tropics. This fragment was established through clear-felling of the surrounding rainforest in 1910 for dairy pastures, which now encircle the site. Selective logging continued within the fragment until 1940 when it was declared a scenic reserve (Pahl 1979).

Rainfall for Millaa Millaa is high (\bar{x} = 2631 mm per year). Approximately 62% of annual rainfall occurs from January to April, with the remainder spread throughout the rest of the year creating a high humidity environment (Australian Bureau of Meteorology records 1914–1992). Due to the elevation of Millaa Millaa Falls, temperatures are lower than is expected for this latitude resulting in a climate that is milder than nearby lowland areas.

Radio-telemetry

In all, 28 pademelons were captured using the drive-fence technique (Vernes 1993) or in baited cage traps. Of these, 13 were fitted with a two-stage radio-transmitter (Type TX1-LD, Bio-telemetry Tracking, Norwood, South Australia) attached to a leather neck-collar. Newly collared animals were given at least two days to become accustomed to this collar before tracking commenced. Animals were tracked on foot using a three-element hand-held Yagi antenna (Bio-telemetry Tracking) and a Custom Electronics CE-12 telemetry receiver. During the day, pademelons were tracked within the forest from three intersecting paths, each marked at 20-m intervals. The approximate diurnal range location used by each radio-collared animal was quickly learned by the tracker, and thus suitable locations from which to obtain fixes could be chosen without disturbing target pademelons. At night, pademelons were tracked near the forest edge from fixed stations located in the surrounding pasture. During each tracking period, six fixes were collected per animal per day at two-hourly intervals, for eight days per month. Ten consecutive tracking periods were sampled. On each day of tracking, collection of fixes began 2 h later than the previous day's tracking, which enabled the full 24-h cycle to be sampled in each tracking period. Due to transmitter-related technical problems, the length of time individual animals were tracked varied considerably.

Positions of animals were obtained by triangulation (Mech 1983), with bearings taken sequentially from at least three locations by one person. Fixes were typically obtained within 3–6 min of taking the first bearing. Fixed-station tracking can be unreliable in dense vegetation on account of signal reflection (Garrott *et al.* 1986; Schmutz and White 1990). Therefore, if signal reflection was considered to be strongly influencing the perceived position of a pademelon, the resulting fix was discarded from the range analyses.

Definition of Terms

The term 'home range' is used in this paper to refer to the estimate generated from 95% of the fixes obtained on an individual pademelon. In addition, separate diurnal and nocturnal ranges were calculated on 95% of diurnal and nocturnal fixes. The sum of these separate range areas was never equal to the home-range estimate since the diurnal and nocturnal range sometimes overlapped, or at other times were separated by an area not included in either the diurnal or nocturnal range (but that was included within the overall home range). Initially, fixes were classified as diurnal (0800–1600 hours), nocturnal (2000–0400 hours), and dusk–dawn (0600 and 1800 hours). However, pademelons were consistently well within the forest at dusk and dawn, so the fixes obtained at these times were treated as diurnal fixes for the range analyses.

Radio-tracked pademelons referred to in the text are denoted by an identification number preceded by either an A for adult, or SA for subadult; and M for male or F for female. Thus, subadult male number 8, for example, is referred to in the text as SAM8.

Data Analysis

All home-range analyses were performed using the radio-tracking analysis computer package RANGES IV (Robert Kenward; Institute of Terrestrial Ecology, Wareham, United Kingdom). Home-range estimates were generated by two techniques: (i) the Harmonic Mean Model (HMM) and (ii) the Minimum Convex Polygon Method (MCP) (for explanation, see Kenward 1987). After exploratory data analysis, the HMM was chosen as the most suitable model for describing the home range of the red-legged pademelon. The suitability of this model lies in its capacity to define home ranges with two centres of activity (see White

and Garrott 1990), as in the case of the diurnal and nocturnal centres characteristic of the *T. stigmatica* ranges examined. The MCP was also used, however, as this technique allows direct comparisons with most previous macropodoid home-range studies.

Incremental Area Analysis (IAA) (Kenward 1990) was performed on the radio-telemetry data to determine the minimum number of fixes required to provide robust estimates of diurnal, nocturnal and home range. IAA provides a plot of the increase in range size with addition of each new fix. The desired number of fixes are achieved when range size reaches an asymptote (Kenward 1990). Diurnal, nocturnal and home-range fixes for each animal were randomly sorted before constructing individual incremental area curves for each range. Ranges were included in the analysis only if their incremental area curve reached an asymptote.

To determine whether the ranges had core areas of activity, the area enclosed by HMM isolines were plotted using increasing percentages of the diurnal, nocturnal and home ranges (Kenward 1990). This provided plots of home-range utilisation. A marked decrease in the slope of a distribution indicates a core area within the isoline where the decrease occurred (Kenward 1990).

The rate of movement of pademelons was taken as the distance between two consecutive radio-telemetry fixes recorded on any one day. Only distances between fixes that were the usual two hours apart were included in the analysis. If a fix were missed during a tracking session, the distance moved by the animal over the four (or more) hours between fixes was excluded from the analysis. The distances were converted to m min^{-1} , and averaged across all animals for each time period to calculate the Mean Rate of Movement (MRM) over the diel cycle.

Results

Incremental Area Analysis

Incremental area analyses indicated that a robust estimate of home-range size of the pademelon was achieved with between 23 and 80 fixes ($\bar{x} = 49$) (Table 1). Diurnal ranges stabilised between 17 and 54 fixes ($\bar{x} = 35$), and nocturnal ranges between 17 and 47 fixes ($\bar{x} = 29$) (Table 1). Three diurnal ranges, seven nocturnal ranges and four home ranges did not stabilise, and were subsequently not used in the range calculations (refer Table 1).

Range Utilisation

No marked decreases occurred in the slope of the distribution for utilisation plots of diurnal, nocturnal and home ranges, indicating that the diurnal, nocturnal and home ranges of *T. stigmatica* were evenly utilised, and were without distinct core areas, or alternatively were composed entirely of a core area.

Home Range

Home-range estimates for radio-tracked *T. stigmatica* at Millaa Millaa Falls using the HMM and MCP are presented in Table 1. A significant difference was detected between the home-range estimates generated using the two techniques (Paired *t*-test: $t = 2.71$, d.f. = 8, $P = 0.027$), the home range generated from the MCP being greater than that from the HMM. Due to the small sample sizes for each sex, it was not possible to formally test for differences in home-range size between males and females.

Home-range shapes for *T. stigmatica* at Millaa Millaa Falls appeared to be governed by two main factors: (1) distance between diurnal and nocturnal ranges and (2) geography of the habitat. The following home-range shapes were encountered in this study (Fig. 1).

Type I. Diurnal range close to nocturnal range; both ranges enclosed by a common 95% isoline. Five home ranges were of this shape (pademelons SAF13, AF16, AF17, AF20 and AM23).

Type II. Diurnal and nocturnal ranges completely separate; each range enclosed within its own 95% isoline. Four home ranges were of this shape (pademelons SAM8, AF12, SAF14 and AF21).

Type III. Diurnal and nocturnal ranges close together due to a creek/waterfall barrier; the range more circular as a result of this barrier. This was evident only in AM15.

Table 1. Intensity of tracking, number of fixes required for range stabilisation and range sizes of 13 *T. stigmatica* radio-tracked at Millaa Millaa Falls between September 1991 and June 1992

| Animal identification | No. of fixes | | (No. required to stabilise) | | Days tracked | Periods tracked | Diurnal range (ha) | | Nocturnal range (ha) | | Home range | |
|-----------------------|---------------|-----------------|-----------------------------|------------|--------------|-----------------|--------------------|-----------------|----------------------|-----------------|-----------------|-----|
| | Diurnal range | Nocturnal range | Nocturnal range | Home range | | | HMM | MCP | HMM | MCP | HMM | MCP |
| SAM8 | 49 (28) | 35 (-) | 84 (65) | 21 | 3 | 2-23 | 2-06 | - | - | 2-13 | 4-95 | |
| AF12 | 115 (35) | 84 (20) | 199 (35) | 42 | 6 | 1-92 | 1-75 | 1-66 | 1-13 | 2-74 | 5-83 | |
| SAF13 | 48 (38) | 47 (37) | 95 (52) | 21 | 3 | 1-12 | 1-18 | 0-57 | 0-55 | 1-91 | 2-38 | |
| SAF14 | 49 (35) | 32 (23) | 81 (32) | 22 | 3 | 2-48 | 2-17 | 0-65 | 0-85 | 2-18 | 5-24 | |
| AM15 | 70 (52) | 43 (29) | 113 (49) | 24 | 4 | 2-08 | 2-36 | 0-77 | 0-83 | 2-32 | 2-35 | |
| AF16 | 32 (17) | 24 (-) | 56 (-) | 15 | 2 | 0-88 | 1-12 | - | - | - | - | |
| AF17 | 36 (24) | 24 (-) | 60 (23) | 15 | 2 | 1-02 | 1-58 | - | - | 1-49 | 1-63 | |
| AF20 | 117 (51) | 73 (47) | 190 (80) | 33 | 5 | 2-34 | 2-07 | 1-45 | 1-00 | 3-05 | 3-33 | |
| AF21 | 24 (20) | 17 (-) | 41 (28) | 7 | 1 | 0-52 | 1-23 | - | - | 0-82 | 2-34 | |
| AM23 | 71 (54) | 48 (17) | 119 (79) | 21 | 3 | 2-09 | 2-46 | 0-91 | 0-46 | 3-70 | 3-57 | |
| SAF18 | 15 (-) | 6 (-) | 21 (-) | 4 | 1 | - | - | - | - | - | - | |
| AM19 | 14 (-) | 6 (-) | 20 (-) | 4 | 1 | - | - | - | - | - | - | |
| AM24 | 8 (-) | 7 (-) | 15 (-) | 3 | 1 | - | - | - | - | - | - | |
| | | | Mean \pm s.e. | | | 1-67 \pm 0-22 | 1-80 \pm 0-16 | 1-00 \pm 0-18 | 0-80 \pm 0-10 | 2-26 \pm 0-28 | 3-51 \pm 0-50 | |
| | | | N | | | 10 | 10 | 6 | 6 | 9 | 9 | |

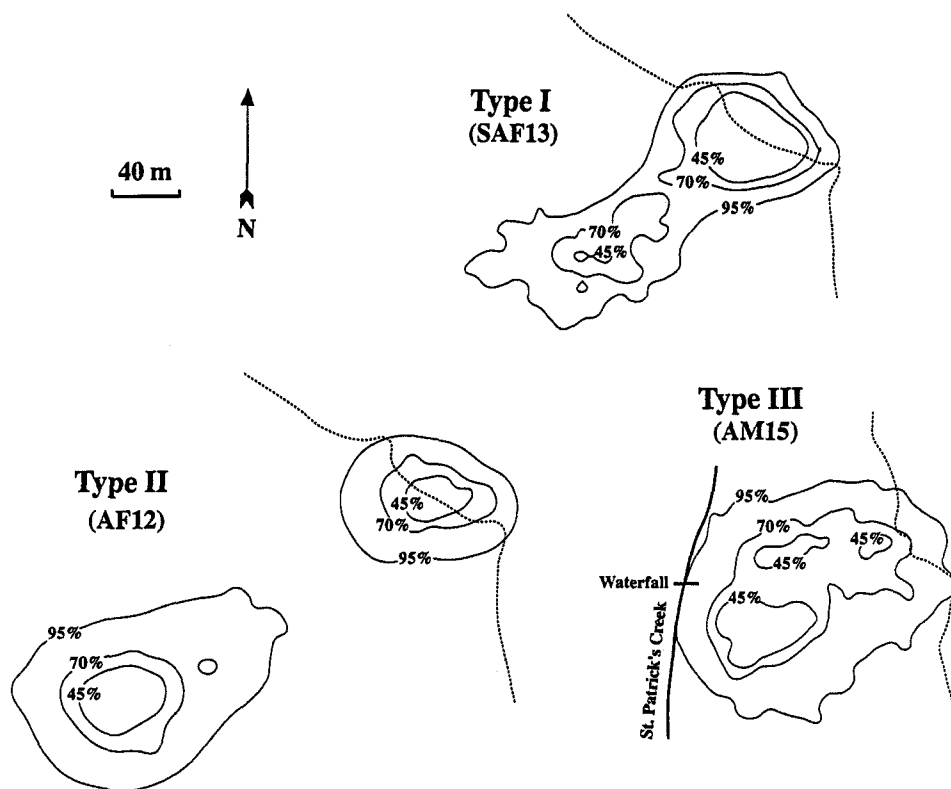


Fig. 1. The three detected types of home-range shape of *T. stigmatica* at Millaa Millaa Falls. In each case pasture lies to the right of the dotted pasture–forest boundary, and rainforest to the left. Home ranges were calculated using the Harmonic Mean Model (HMM).

Diurnal and Nocturnal Ranges

All the radio-tracked *T. stigmatica* exhibited spatially and temporally distinct diurnal and nocturnal ranges (Fig. 2). The diurnal range was always located within the forest and did not encompass any open grassy areas. The nocturnal range was centred on the boundary between the forest and open pasture. An exception was AM15 which utilised two smaller patches of grass within the forest associated with a logging track and a maintained lawn beside a waterfall, in addition to the forest edge.

Pademelons rarely ventured outside the forest edge until after dark, although they were occasionally located by radio, or heard giving alarm thumps just inside the forest boundary in the late afternoon. By dawn the radio-tracked pademelons had always moved off the pasture and returned to the forest.

The mean diurnal range estimate generated using the HMM and MCP (Table 1) was larger than the mean nocturnal range estimate, a difference that approached significance (3-way ANOVA; d.f. = 1, 5, $P = 0.0637$, Table 2); however, there was no significant difference detected between either of the models used to estimate these ranges (3-way ANOVA; d.f. = 1, 5, $P = 0.6255$, Table 2).

There was a significant interaction effect between range type (diurnal and nocturnal) and individual pademelon (3-way ANOVA; d.f. = 5, 5, $P = 0.0423$, Table 2), indicating that range size was highly variable between animals (see Table 1). The small sample sizes precluded formal statistical comparisons between males and females.

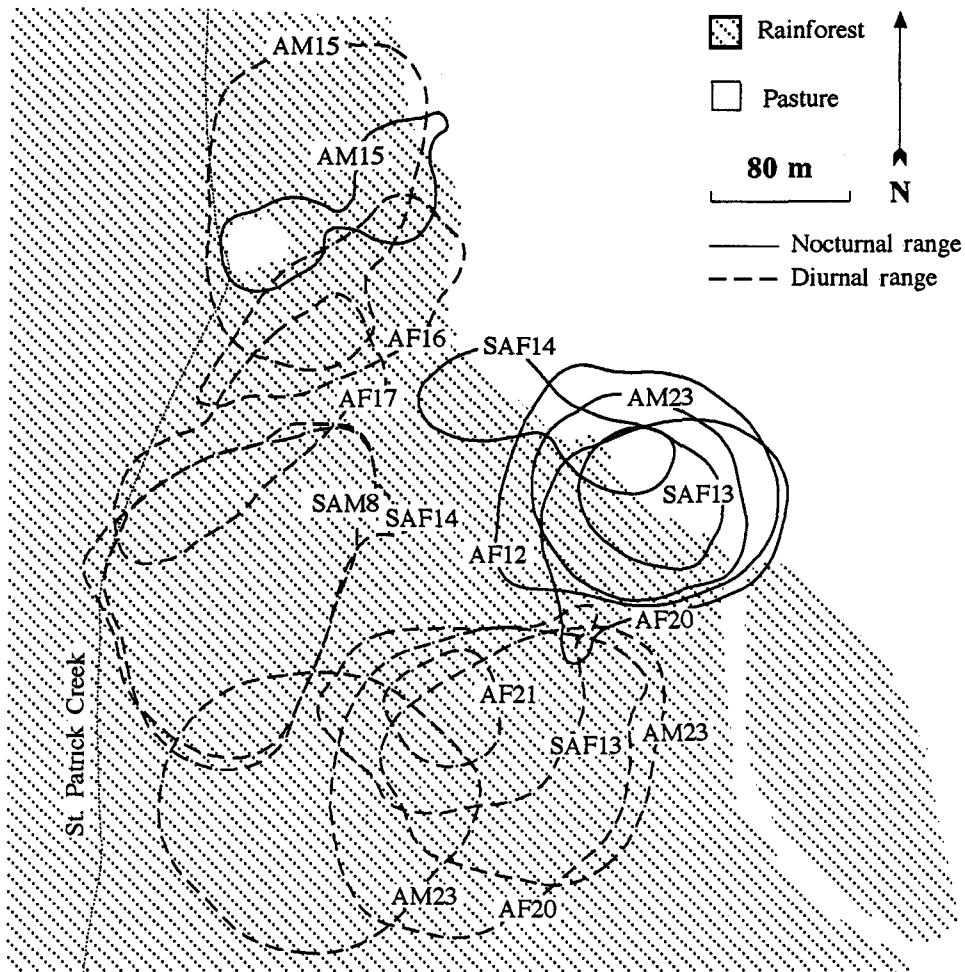


Fig. 2. Nocturnal and diurnal ranges and habitat utilisation of nine *T. stigmatica* at Millaa Millaa Falls. Ranges are displayed using the Harmonic Mean Model (Kenward 1987). Only ranges that stabilised are included (see Table 1). AF, adult female; AM, adult male; SAF, subadult female; SAM, subadult male.

Movement and Activity Over the Diel Cycle

Mean rate of movement of red-legged pademelons throughout the diel cycle followed a consistent pattern of slow movement ($< 1 \text{ m min}^{-1}$ per 2-h period) within diurnal and nocturnal ranges, and rapid movement (up to 2.31 m min^{-1}) between these ranges (Fig. 3).

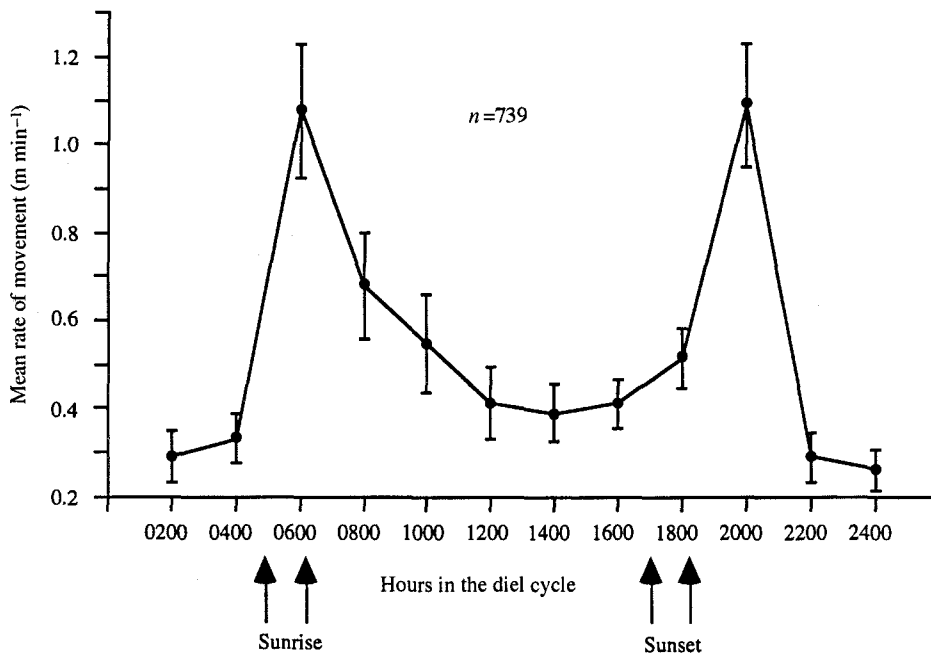
Throughout the night when the pademelons were grazing on pasture, MRM was low. At dawn, MRM was higher as pademelons moved rapidly between the nocturnal and diurnal ranges. Once the animals had returned to the forest (the diurnal range), they continued to be active throughout the morning, moving through the forest browsing leaves and fruit (authors' observation) until about 1200 hours. Between 1200 and 1600 hours (early afternoon), MRM was low, but increased in the late afternoon prior to dusk, before another rapid rate of movement just after dusk (Fig. 3) which brought the pademelons back to the pasture. Movement during the late afternoon was usually in the direction of the forest edge, and was associated with browsing (authors' observation).

Table 2. Results of a three-factor analysis of variance to determine the effects of range type estimation model and individual pademelon on range sizes*, significant at $P < 0.05$

| Source of variance | d.f. | s.s. | F | P |
|--|------|--------|------|---------|
| Range type ^{AC} | 1 | 7.2490 | 5.67 | 0.0637 |
| Estimation model ^{AD} | 1 | 0.0630 | 0.27 | 0.6255 |
| Pademelon ^B | 5 | 1.8544 | — | — |
| Range type × Pademelon ^E | 5 | 1.2782 | 5.50 | 0.0423* |
| Estimation model × Pademelon ^E | 5 | 0.2301 | 0.99 | 0.5043 |
| Range type × Estimation model ^E | 1 | 0.0551 | 0.24 | 0.6400 |
| Residual | 5 | 0.2322 | | |

A Fixed factor. B Random factor. C Tested against Range type × Pademelon.

D Tested against Estimation model × Pademelon. E Tested against Residual.

**Fig. 3.** The mean rate of movement (MRM) ± s.e. throughout the diel cycle of 13 radio-tracked *T. stigmatica*.

The movements of males and females were not compared statistically because of the small number of animals. Individual movement curves, however, generally resembled the composite MRM curve (Fig. 3). No changes were discernible in the diel pattern of rate of movement throughout the ten months of the study.

Discussion

Range Size, Shape and Movements

On the Atherton Tableland, *T. stigmatica* partitions home range into two spatially, temporally and physiognomically distinct areas: rainforest and the forest-pasture boundary. The diurnal range is located within rainforest and is considerably larger than the nocturnal range

centred on the forest–pasture boundary, which is only utilised from after dusk and prior to dawn each night. *T. stigmatica* consumes both rainforest browse and pasture grasses (Vernes 1994), and the larger diurnal range is probably related to the wide variety and patchy distribution of preferred foods available in the rainforest, compared with the grasses found on pasture.

The large diurnal forest range and smaller nocturnal pasture range characteristic of *T. stigmatica* in this study is consistent with the findings of Johnson (1980) on the home range of the red-necked pademelon, *Thylogale thetis*, in northern New South Wales. This pattern is not typical of small-macropodid home ranges (Croft 1989), and indicates that *T. stigmatica*, like *T. thetis*, is unusual in that it is active during a substantial part of the diurnal period and makes extensive movements during such times. Mean rate of movement throughout a given 24-h period supports the home-range data, being higher in the forest during the early morning and late afternoon than it was at any time on pasture at night.

The mean home-range size of *T. stigmatica* is small when compared with most similar-sized macropodids (Table 3). Although positive relationships between body mass and home-range size have been postulated by a number of authors (e.g. McNab 1963; Harestad and Bunnell 1979; Mace and Harvey 1983; Lindstedt *et al.* 1986), other factors such as diet, social organisation, and primary productivity of the habitat are also clearly important (Croft 1989; Norbury *et al.* 1989).

Table 3. Mean body weights and home-range sizes (estimated from Minimum Convex Polygons) for some medium-sized Australian macropodids

Weights are from Strahan (1983) or the cited source; home-range values are from the cited source

| Species | Mean weight | | Mean home-range size (ha) | | Source |
|---------------------------------|-------------|------|---------------------------|------|-------------------------|
| | Female | Male | Female | Male | |
| <i>Thylogale stigmatica</i> | 3.3 | 4.9 | 3.5 | 3.6 | This study |
| <i>Thylogale thetis</i> | 3.8 | 7.0 | 9.1 | 14.8 | Johnson (1980) |
| <i>Onychogalea fraenata</i> | 4.5 | 5.5 | 26.0 | 59.0 | Evans (1992) |
| <i>Dendrolagus lumholtzi</i> | 5.9 | 7.4 | 2.0 | 4.0 | Proctor-Gray (1985) |
| <i>Dendrolagus bennettianus</i> | 9.6 | 12.9 | 5.0 | 21.7 | Martin (1992) |
| <i>Wallabia bicolor</i> | 13.0 | 17.0 | 14.8 | 17.9 | Troy and Coulson (1993) |
| <i>Macropus rufogriseus</i> | 13.8 | 18.6 | 11.8 | 31.6 | Johnson (1987) |

Food abundance and distribution may be a major governing factor in the diurnal, nocturnal and home-range sizes of *T. stigmatica*. Vernes (1994) observed that the diurnal activity of *T. stigmatica* is typically associated with searching for preferred forest food items (chiefly dicots) which are encountered infrequently, whilst nocturnal activity is associated with more sedentary behaviour and intensive grazing at the forest edge. This difference in feeding strategy between day and night matches the large diurnal and small nocturnal range found in this study, and the high MRM recorded during the day compared with that during the night. The abundance of grass available at the forest edge, and the rich abundance and diversity of potential foods typical of north Queensland tropical rainforests may contribute to the small overall home-range size.

Effects of Habitat Fragmentation

Prior to rainforest fragmentation in north Queensland, was *T. stigmatica* chiefly a rainforest or an edge dweller? On the Atherton Tableland, much of the forest habitat available to red-legged pademelons now contains substantial edge zones by way of pasture, roads and powerline corridors that bisect rainforest, and other cleared areas such as those associated with

past logging operations and tin mining activities. Large tracts of rainforest still exist in the region; however, many have been subjected to logging which opens up the forest canopy allowing more grass to exist in association with logging roads and tracks, and other clearings.

Natural edges do exist on the Atherton Tableland, particularly on the western fringe where rainforest grades into wet sclerophyll forest. Additionally, prior to European settlement, open areas of grassy woodland within rainforest were maintained by repeated burning by indigenous inhabitants [e.g. Koombaloo Pocket, approximately 40 km south of the study site (Tracy 1982)]. Johnson (1980) makes mention of comparable fire-induced pockets on the Dorrigo Plateau in New South Wales which would have been available to *T. thetis*. Natural ecotones, however, are relatively rare in the study area compared with the abrupt transition zones created in the last 100 years by human activities.

In the south of its range, *T. stigmatica* rarely leaves the forest and subsists entirely on non-grassy vegetation (Jarman and Phillips 1989). In such circumstances, however, population densities appear to be lower than the sympatric *T. thetis* (Maynes 1977; Redenbach 1982) and lower than densities recorded on the Atherton Tableland (Vernes 1994). *T. stigmatica* has also been recorded in undisturbed rainforest in the north Queensland wet tropics (Cannabullen Plateau; authors' observation) where densities also appeared low. Therefore, prior to European alteration of the landscape *T. stigmatica* in northern Queensland probably occurred throughout its current range, but maintained the highest densities where rainforest was bordered by natural grassy ecotones, such as those associated with the more-open sclerophyllous forests. Furthermore, the home-range sizes of *T. stigmatica* living in deep undisturbed rainforest or along natural ecotones may be larger than those reported in this study, given that high-quality grass would be either unavailable, or patchily distributed and seasonally limited.

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