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Ecological correlates of folivore abundance in north Queensland rainforests

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Abstract. The ecological factors controlling the distribution and abundance of the folivorous marsupials endemic to the rainforests of northern Australia are not understood. In this study, we surveyed folivore abundance at 40 sites stratified by altitude and geology in rainforests of the Atherton Tableland, north Queensland. All five species of folivore that inhabit the study area were more abundant in highland (800–1200 m) than in upland (400–800 m) forests. Allowing for the effects of altitude, four species of folivore were more abundant in forests on nutrient-rich basalts than in forests on nutrient-poor acid igneous or metamorphic rocks. The abundance of two folivore species also varied inversely with rainfall. Altitudinal variation in folivore abundance in the study area has been attributed to habitat destruction, Aboriginal hunting, the distribution of host plants and climate; however, none of these hypotheses has been tested. Variation in folivore abundance with geology is plausibly explained as a response to the nutritional quality of foliage. Foliage quality may also explain the inverse relationship between two of the folivores and rainfall. The results of this study show that only a relatively small proportion of north Queensland rainforests support abundant populations of the endemic folivorous marsupials.

Introduction

Seven taxa of leaf-eating marsupials are endemic to the rainforests of north Queensland, including two species of tree-kangaroo (*Dendrolagus bennettianus* and *D. lumholtzi*: Macropodidae), four species of ringtail possums (*Hemibelideus lemuroides*, *Pseudocheirops archeri*, *Pseudocheirus cinereus* and *Pseudocheirus herbertensis*: Pseudocheiridae) and a subspecies of brushtail possum (*Trichosurus vulpecula johnstoni*: Phalangeridae) (Flannery 1994; Strahan 1995). After a century of survey and collecting work, the distributions of the folivores across the various rainforest isolates of the region are well established (Lumholtz 1889; Cairn and Grant 1890; Waite 1894; Tate 1952; Winter 1984; Nix and Switzer 1991; Winter *et al.* 1991; Williams *et al.* 1996; Newell 1999a). These regional distribution patterns are thought largely to reflect historical processes, notably the alternate contraction and expansion of suitable rainforest habitat during the Pleistocene (Williams 1997; Winter 1997). No study has examined natural variation in folivore abundance at a finer scale than the entire region,

however, and the ecological determinants of folivore abundance are unknown.

In this study, we surveyed folivore abundance within primary rainforests of the Atherton Tableland, the largest rainforest isolate in north Queensland (Winter 1984; Nix and Switzer 1991). Forests of the study area support five of the seven taxa of folivorous marsupials endemic to the region (Winter 1997). By restricting the survey to a single rainforest isolate, with no internal barriers to dispersal, we aimed to identify ecological (rather than historical or biogeographical) correlates of folivore abundance.

Methods

Study area and survey design

Folivores were surveyed at 40 sites within rainforests of the Atherton Tableland and adjacent ranges, north Queensland (17–18°S, 145°25′–145°45′E) (Fig. 1). Sites were stratified by altitude and geology, important determinants of forest type in the region (Tracey 1982). In all, 23 sites were located in upland forests (400–800 m) and 17 in highland forests (800–1200 m). Forests below 400 m were not sampled, as folivorous marsupials are mostly absent from lowland forests in the study area (Winter 1997). Rainforests above 1200 m are inaccessible by

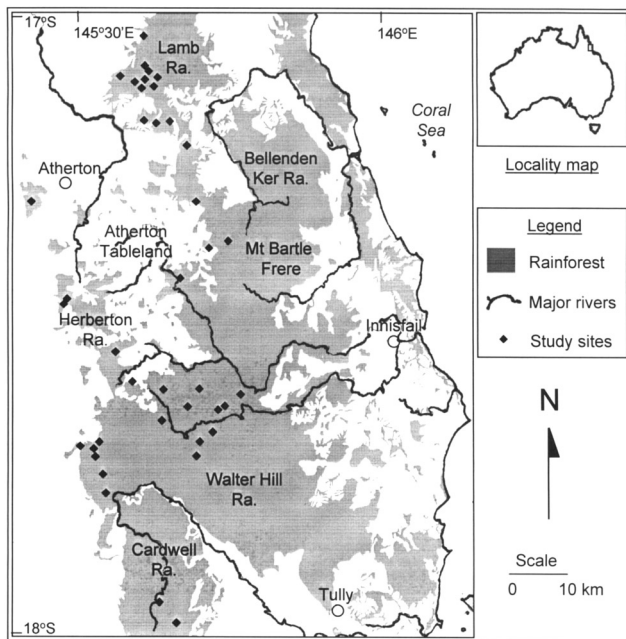


Fig. 1. Location of study sites within the Atherton Tableland.

road and were not surveyed. Within each altitudinal stratum, approximately half the sites were located on nutrient-rich soils derived from basalts and the remaining sites were located on relatively nutrient-poor soils derived from acid igneous or metamorphic rocks (Spain 1990). Mean annual rainfall ranged from approximately 1550 to 3100 mm at the sites (see Acknowledgements).

The location of sites was constrained by three additional factors. Firstly, surveys were restricted to forests alongside roads, as spotlighting within the forest itself is ineffectual (Russell 1980). Secondly, sites were located along ridges or upper slopes, where possible, to conserve the dichotomy between nutrient-rich and nutrient-poor soils (e.g. Landsberg and Gillieson 1995). Thirdly, sites were located within large areas of forest (>1000 ha) to avoid any confounding effects that forest fragmentation may have on folivore abundance (Pahl *et al.* 1988; Laurance 1990a). Within these constraints, sites were located across the full geographical extent of the study area. The mean distance between adjacent sites was 3.3 km (range 0.4–18 km). Closely adjacent sites were located at different altitudes or on different parent materials. No attempt was made to control for logging history. Forests at all sites surveyed in the study had been selectively logged prior to the declaration of the Wet Tropics World Heritage Area in 1988.

Survey methods

Folivores were surveyed on foot, using a 30-W spotlight, along marked transects at each site. Transects were 0.5–1.5 km in length, depending on local conditions, with 32 of 40 transects being 0.95–1.1 km in length. Thirty-seven of the transects were located on roads bisecting the forest while the remaining three transects were located on roads along the forest edge. To standardise search effort, surveys of the forest edge were walked at twice the pace of transects through the forest interior (1 km h⁻¹ in the latter case). All surveys were conducted by the same observer (JK).

Surveys were conducted between March 1995 and August 1997. One, two or, occasionally, three sites were surveyed in an evening. Conditions that may adversely affect the detectability of the folivores, including bright moonlight, rain and dense fog were avoided (Laurance

1990b; Williams 1995). The folivores were most commonly detected by their eyeshine, although one-third of the records of *D. lumholtzi* were obtained from aural cues (the distinctive noise made by this species leaping to the ground).

To control for temporal variation in the detectability of folivores and to increase survey effort, each site was surveyed on several occasions. Most transects were surveyed on four occasions but, to standardise effort, shorter transects were surveyed on 5–6 occasions and longer transects on three occasions. At each site, the time of evening that the survey was conducted and the direction of transit were varied for at least one replicate survey. While the survey schedule was determined haphazardly by weather conditions and access to sites, there was no temporal bias in the allocation of effort across environmental strata.

To control for differences in the detectability of folivores between sites, only individuals observed within 10 m of the transect were included in abundance estimates (e.g. Kavanagh 1984). A strip-transect approach was used, rather than an alternative such as line-transect methodology, because the density of the rainforest vegetation greatly reduces the detectability of arboreal animals away from the transect. For example, over 90% of all observations of folivore species in this study were within 10 m of the transect and fewer than 1% of observations were beyond 20 m of the transect. Such highly skewed data are problematical for line-transect methodology (Buckland *et al.* 1993; Struhsaker 1997). Abundance estimates were standardised as the number of individuals observed per hectare of strip transect. Animals identified as juveniles were not included in abundance estimates.

Statistical analyses

Generalised linear models were used to analyse variation in the abundance of each species in response to environmental factors. Altitude and rainfall were treated as continuous variables. Geology was treated as a fixed factor with two levels: (1) nutrient-rich basalt and (2) nutrient-poor acid igneous and metamorphic sites. A quadratic term for altitude was included in models to examine apparent departures from linearity in the response of species to altitude. This term was retained only if it significantly improved the fit of a model ($\alpha = 0.05$).

The distributions of the abundance data were highly skewed, with a modal value near zero for all species. These data were assumed to exhibit extra-Poisson variation, with the scaling factor relating the variance to the mean estimated from the data following Crawley (1993). A log link was specified for all models. The statistical significance of each explanatory variable was assessed by removal from a model containing all terms.

To determine whether folivores responded similarly to environmental factors, or displayed mutually exclusive distributions, we examined the rank correlation between the abundances of folivores. This analysis was restricted to highland sites to remove the potentially confounding effects of altitude on folivore abundance.

Results

Overview of survey results

In total, 858 observations were made of the five species of folivorous marsupials. The ringtail possums *H. lemuroides*, *P. herbertensis* and *P. archeri* were detected at most of the sites, while *T. v. johnstoni* and *D. lumholtzi* were detected at just 15 and 11 of the 40 sites surveyed, respectively (Table 1). On average, *H. lemuroides* was the most abundant folivore at the sites surveyed, while *P. archeri* and *D. lumholtzi* were the least frequently encountered species. Estimates of abundance were more precise for common than for rare species: the mean coefficient of variation of the abundance

Table 1. Folivore abundance at 40 sites in rainforests of the Atherton Tableland

Folivore	Body mass ^A (kg)	Number of sites detected	Mean (\pm s.e.) abundance ^B (individuals ha ⁻¹)	Maximum abundance (individuals ha ⁻¹)
<i>H. lemuroides</i>	1.0	29	1.90 \pm 0.24	4.8
<i>P. herbertensis</i>	1.1	34	0.55 \pm 0.076	1.6
<i>P. archeri</i>	1.1	33	0.36 \pm 0.050	1.3
<i>T. v. johnstoni</i>	1.7	15	0.68 \pm 0.17	2.2
<i>D. lumholtzi</i>	7.8	11	0.40 \pm 0.078	1.0

^ASources: Flannery (1994), Strahan (1995), Newell (1999b).

^BCalculated only from sites where the species was detected.

estimates (calculated from repeated surveys of each transect) ranged from 70% for *H. lemuroides* to 144% for *P. archeri*.

Variation in the abundance of folivores with altitude, geology and rainfall

Folivore abundance varied strikingly with altitude (Fig. 2). All five folivore species present in the study area were relatively abundant at most highland sites but were uncommon at most upland sites. Altitude was a highly significant predictor of the abundance of all folivore species in generalised linear models of the data (Table 2). With the

exception of *P. archeri*, altitude accounted for about half of the total deviance in these models.

Allowing for the effects of altitude, geology was a significant predictor of the abundance of four of the five species of folivore in the study area (*H. lemuroides*, *P. herbertensis*, *T. v. johnstoni* and *D. lumholtzi*). At high-altitude sites, these folivores were, on average, nearly twice as abundant in forests on nutrient-rich basalt soils than in forests on acid igneous or metamorphic rocks (Fig. 2). Additionally, there were significant inverse relationships between rainfall and the abundances of *T. v. johnstoni* and

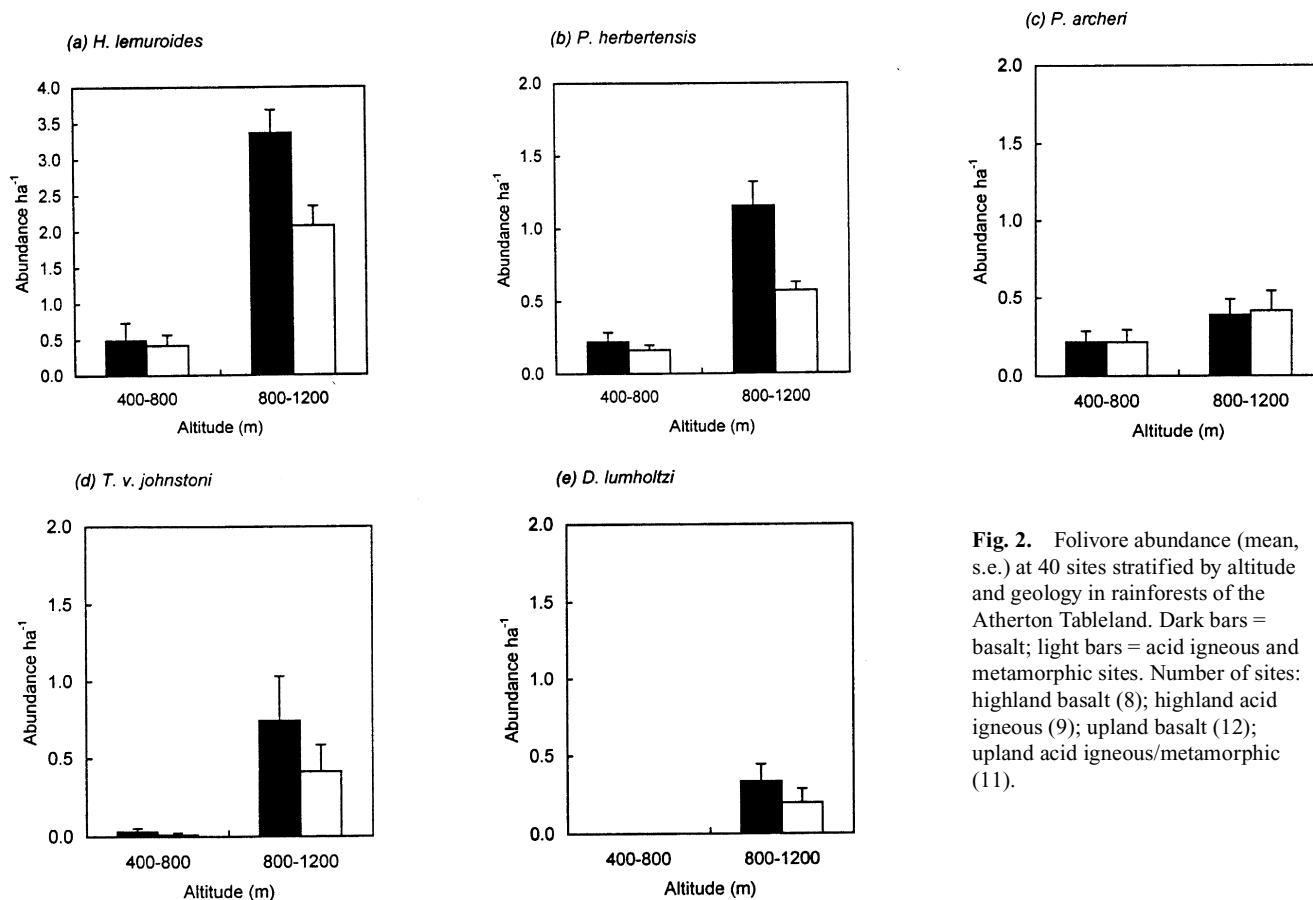


Fig. 2. Folivore abundance (mean, s.e.) at 40 sites stratified by altitude and geology in rainforests of the Atherton Tableland. Dark bars = basalt; light bars = acid igneous and metamorphic sites. Number of sites: highland basalt (8); highland acid igneous (9); upland basalt (12); upland acid igneous/metamorphic (11).

Table 2. Analysis of deviance table showing the statistical significance of relationships between folivore abundance and environmental factors at 40 sites in rainforests of the Atherton Tableland

Models for *H. lemuroides*, *P. herbertensis*, *T. v. johnstoni* and *D. lumholtzi* include a quadratic term for altitude; the change of deviance in these cases is distributed as χ^2 with 2 d.f. For all other variables, the change of deviance is distributed as χ^2 with 1 d.f. Significant values ($P < 0.05$) are shown in bold

Folivore	Change in deviance (P) associated with each environmental factor		
	Altitude	Geology	Rainfall
<i>H. lemuroides</i>	52.8 ($P < 0.001$)	7.29 ($P = 0.007$)	1.11 ($P = 0.29$)
<i>P. herbertensis</i>	26.3 ($P < 0.001$)	8.41 ($P = 0.004$)	0.59 ($P = 0.44$)
<i>P. archeri</i>	6.74 ($P = 0.009$)	0.026 ($P = 0.87$)	0.081 ($P = 0.78$)
<i>T. v. johnstoni</i>	51.7 ($P < 0.001$)	8.18 ($P = 0.004$)	6.56 ($P = 0.010$)
<i>D. lumholtzi</i>	43.8 ($P < 0.001$)	5.10 ($P = 0.024$)	5.30 ($P = 0.021$)

Table 3. Rank correlations (r_s , P) between the abundance of folivores at 17 sites in highland rainforests (>800 m above sea level) of the Atherton Tableland
Significant values ($P < 0.05$) are shown in bold

Folivore	<i>D. lumholtzi</i>	<i>T. v. johnstoni</i>	<i>P. archeri</i>	<i>P. herbertensis</i>
<i>H. lemuroides</i>	$r_s = 0.10$ ($P = 0.70$)	$r_s = 0.29$ ($P = 0.26$)	$r_s = -0.30$ ($P = 0.24$)	$r_s = 0.74$ ($P = 0.001$)
<i>P. herbertensis</i>	$r_s = 0.22$ ($P = 0.40$)	$r_s = 0.34$ ($P = 0.19$)	$r_s = -0.06$ ($P = 0.81$)	
<i>P. archeri</i>	$r_s = 0.20$ ($P = 0.44$)	$r_s = 0.05$ ($P = 0.85$)		
<i>T. v. johnstoni</i>	$r_s = 0.78$ ($P < 0.001$)			

D. lumholtzi. Most records of *T. v. johnstoni* and *D. lumholtzi* were obtained from sites in the Herberton Range, on the drier, western margin of rainforest in the study area, and few from sites in the relatively wet Lamb Range.

Association between folivores

At highland sites, there were positive correlations between the abundances of *H. lemuroides* and *P. herbertensis*, and between *T. v. johnstoni* and *D. lumholtzi* (Table 3). There were no negative correlations between any pair of folivore species in the study area.

Discussion

Precision of the abundance estimates

Precise estimates of the abundance of arboreal mammals in rainforest are difficult to obtain from transect-based surveys, and previous studies have frequently expended considerable effort, as many as 10 or 20 replicate surveys per site, to estimate abundance with acceptable precision (Whitesides *et al.* 1988; Laurance 1990a; Ganzhorn 1992; Williams 1995; Laurance and Laurance 1996; Struhsaker 1997). However, these studies have typically surveyed a small number of sites. In this study, we accepted a lower level of precision as the trade-off for surveying a relatively large number of sites.

More confidence can be placed in models of the abundance of commonly encountered species such as *H. lemuroides* than of rare or cryptic species such as *P. archeri*. For example, the apparent lack of a response of *P. archeri* to geology may reflect the imprecision of the abundance estimates for this species.

Generality of the survey results

This survey was restricted to forests alongside roads. Roadside vegetation, which is characterised by a relative abundance of pioneer species and is well-illuminated from canopy to ground-level, might be expected to be nutritionally superior to undisturbed vegetation in the forest interior (Coley 1983; Ganzhorn 1995). As folivores are considered sensitive to foliage quality (Cork and Foley 1991; Oates 1996), folivore abundance may be elevated at the survey sites relative to undisturbed sites elsewhere in the study area. This bias should not seriously affect comparisons of the relative abundance of folivores across the environmental gradients examined in this study.

Variation in folivore abundance with altitude

It has long been established that most of the folivorous marsupials endemic to the rainforests of north Queensland

are restricted to higher-elevation forests (Lumholtz 1889; Cairn and Grant 1890; Waite 1894; Winter 1984; Winter *et al.* 1991; Williams *et al.* 1996). In the vicinity of the Atherton Tableland, the ringtail possums are rarely recorded in forests below 300–500 m elevation, while *T. v. johnstoni* has not been recorded below 600 m (Winter 1997). No previous study has rigorously demonstrated the great disparity in folivore abundance between upland and highland forests in the region, although altitudinal variation in folivore abundance has been noted by several authors (Laurance 1990a; Trenerry and Werren 1993; Laurance and Laurance 1999).

Altitudinal variation in abundance is widely reported for folivorous marsupials inhabiting other ecosystems. In particular, almost all the diverse radiation of ringtail possums and tree-kangaroos in New Guinea are restricted to mid-elevation and montane rainforests (Flannery 1994; Flannery *et al.* 1996). Arboreal folivores do occur in lowland rainforests in New Guinea, but the assemblages are dominated by phalangerids (cuscus) that are absent from north Queensland, except in Cape York (Flannery 1994). Several folivorous marsupials that inhabit eucalypt forests in Australia also display marked altitudinal variation in abundance, although not all species show a trend to maximum abundance at higher altitudes (Braithwaite 1983; Bennett *et al.* 1991; Kavanagh and Bamkin 1995; Kavanagh *et al.* 1995). Of particular relevance to this study, two of the folivores that inhabit eucalypt forests in north Queensland, the greater glider (*Petauroides volans*) and the common ringtail possum (*Pseudocheirus peregrinus*), are also largely absent from lowland forests in the Wet Tropics region (Williams *et al.* 1996; Winter 1997).

Various hypotheses have been proposed to account for the restriction of folivores to higher-elevation forests in north Queensland. For example, Johnson (1995) and Crome (1991) have suggested that habitat destruction in the lowlands is at least partly responsible for the contemporary distribution of *D. lumholtzi*. However, historical accounts indicate a predominantly montane distribution for *D. lumholtzi* (and other folivores in the Atherton region) prior to clearing (Lumholtz 1889; Cairn and Grant 1890). Furthermore, most clearing in the lowlands has occurred on the coastal plain (Winter *et al.* 1987), and this study clearly shows that all folivores in the study area decline in abundance at mid-elevations. Other suggested explanations for altitudinal variation in the abundance of the folivores include intense Aboriginal hunting pressure in lowland forests (Flannery *et al.* 1996; Newell 1999a), the distribution of plants eaten by the folivores (Laurance 1990b) and an intolerance of high temperatures by the folivores (Winter 1997).

There has been no serious attempt to test any of these hypotheses. Goudberg (1990) provided some evidence in support of the climate hypothesis, finding that both

H. lemuroides and *P. herbertensis* exhibited high rates of water turnover in the field, an indication that these folivores, at least, were adapted to a cool, moist (i.e. montane) climate. Conversely, Laurance (1990b) presented data that he claimed contradicted the climate hypothesis, finding that fewer individuals of *H. lemuroides*, *P. herbertensis* and *T. v. johnstoni* were observed in spotlight surveys conducted on cool compared with warm nights. However, the warmest evenings recorded by Laurance (1990b) (c. 25°C) fall well below the high temperatures commonly experienced in lowland forests. For example, temperatures exceed 30°C on one day in three, on average, at Cairns in the lowlands (Bureau of Meteorology 2000).

The restriction of ringtail possums and tree-kangaroos to higher-elevation rainforests throughout the tropics suggests that a general explanation should be sought for the phenomenon. The climate hypothesis is one such possibility. An alternative general hypothesis, proposed by Braithwaite (1996), is that foliage may be more nutritious at higher altitudes because the respiration costs of plants are reduced in montane climates. Neither hypothesis has yet been tested.

Variation in abundance with geology and rainfall

This study found that *H. lemuroides*, *P. herbertensis*, *T. v. johnstoni* and *D. lumholtzi* were more abundant in forests on nutrient-rich basalts than in forests on nutrient-poor acid igneous or metamorphic rocks. Variation in the abundance of rainforest-dwelling marsupial folivores with soil fertility has not previously been reported. However, numerous studies in other ecosystems have found that arboreal folivores tend to be most abundant on nutrient-rich soils (McKey *et al.* 1978; Braithwaite *et al.* 1984; Waterman *et al.* 1988; Peres 1997). This pattern is usually interpreted as a response by folivores to foliage quality, as fertile soils tend to support forests with relatively high concentrations of foliar nutrients and low levels of carbon-based secondary compounds (Gartlan *et al.* 1980; Braithwaite *et al.* 1983, 1984; Cork 1992; although see Oates *et al.* 1990). A positive correlation between soil fertility, foliage quality and folivore abundance has been demonstrated for the study area (Kanowski 1999).

The inverse relationship between the abundance of *T. v. johnstoni* and *D. lumholtzi* and rainfall may also be driven by foliage quality, as rainforest soils tend to be more leached (less fertile) in wet compared with seasonally dry climates (Laffan 1988; Clinebell *et al.* 1995). A decline in foliage quality with increasing rainfall has been reported for rainforests in the study area (Brasell *et al.* 1980; Brasell 1981) and for tropical forests in Madagascar (Ganzhorn 1992). If this interpretation is correct, the results of this study suggest that *T. v. johnstoni* and *D. lumholtzi* may be more sensitive to foliage quality than are the ringtail possums, because variation in soil fertility with rainfall in the study area tends to be relatively modest compared with the

variation between soils developed on different parent materials (Laffan 1988).

Interspecific variation in folivore abundance

Previous surveys of primary forests in the Atherton Tableland have reported similar trends in the relative abundance of folivores to that reported here (*H. lemuroides* most abundant, *P. herbertensis* and *T. v. johnstoni* intermediate, *P. archeri* and *D. lumholtzi* least abundant) (Preen 1981; Pahl *et al.* 1988; Laurance 1990a; Laurance and Laurance 1996). These interspecific differences in abundance partly reflect differences in detectability, as *H. lemuroides*, *P. herbertensis* and *T. v. johnstoni* have brighter eyeshine than either *D. lumholtzi* or the cryptically coloured *P. archeri* (Smith and Winter 1984; Laurance and Laurance 1996). However, the observed trends in abundance are also broadly consistent with the predicted resource requirements of the folivores. On the basis of body size, the relatively small ringtail possums would be expected to be the most abundant of the folivores and *D. lumholtzi* the least, with *T. v. johnstoni* occupying an intermediate position (Harestad and Bunnell 1979; Nagy 1987). These predicted trends in abundance are observed, except that amongst the ringtail possums, *P. herbertensis* and *P. archeri* are much less common than *H. lemuroides*.

Dietary specialisation amongst the ringtail possums may explain the relative scarcity of *P. herbertensis* and *P. archeri* compared with *H. lemuroides* in primary forests. Feeding records indicate considerable dietary partitioning between all folivores on the Atherton Tableland, at the generic and even family levels (Procter-Gray 1985; Goudberg 1990; J. Winter unpublished data). Many of the taxa eaten by *H. lemuroides* are characteristic of the later stages of forest succession; whereas *P. herbertensis* obtains much of its diet from plants favoured by disturbance and *P. archeri* from figs (*Ficus* spp.). That is, in comparison with *H. lemuroides*, both *P. herbertensis* and *P. archeri* appear to occupy relatively specialised niches within primary forests.

Associations between folivores

This study found positive associations between the abundances of *H. lemuroides* and *P. herbertensis*, and between *T. v. johnstoni* and *D. lumholtzi*, at highland sites. Similar results for both pairs of species were reported by Laurance (1996) for sites within fragments and continuous forest on the Atherton Tableland. The positive correlation between *T. v. johnstoni* and *D. lumholtzi* reflects the relative abundance of both species in the drier, western margin of the study area. The positive correlation between *H. lemuroides* and *P. herbertensis* is perhaps more surprising, given that these possums are thought to specialise on primary and secondary forest species, respectively (see above). However, all sites surveyed in this study were located within relatively intact, primary forests. Within primary forests, both *H. lemuroides* and *P. herbertensis* may respond similarly to

potentially limiting factors such as foliage quality or the availability of dens.

The absence of any negative correlation between the endemic folivores suggests that their distributions within rainforests of the study area are not determined by interspecific competition. At a regional scale, however, the allopatric distributions of the congeners *D. lumholtzi* and *D. bennettianus* may well be maintained by competitive exclusion (Winter 1997; Newell 1999a). The absence of the common ringtail possum (*Pseudocheirus peregrinus*) from rainforests of the study area may also be due to competitive exclusion by *P. herbertensis* (Winter 1997). *P. peregrinus* occurs in sclerophyll forests immediately to the west of rainforests in the study area and elsewhere in the Wet Tropics, yet it inhabits rainforests only in the Paluma Range, in the extreme south, from which *P. herbertensis* is absent (Winter 1984).

Conservation implications

The conservation status of the endemic rainforest possums was reviewed by Winter (1984). He argued that the endemic possums were secure, because forests within the altitudinal range of the possums occupied 1450–3000 km² on the Atherton Tablelands, some one to two orders of magnitude larger than the size of natural rainforest isolates that support a full complement of species. Similarly, Flannery *et al.* (1996) and Newell (1999a) estimated that *D. lumholtzi* occupied some 5500 km² throughout the Wet Tropics region.

These assessments assume that all rainforest within the altitudinal range of the folivores constitute viable habitat for the folivores. This assumption may be optimistic. The results of this survey indicate that, within continuous primary forests of the Atherton Tableland, abundant populations of all folivore species are restricted to highland forests, well above lower altitudinal limits at which the folivores have been recorded. The relative scarcity of folivores in upland forests implies that habitat quality declines (for whatever reason) from highland to upland forests. It is possible, for example, that folivore populations at lower elevations are maintained by immigration from source populations in highland forests.

In short, while extensive tracts of rainforest in the vicinity of the Atherton Tableland are conserved as the Wet Tropics World Heritage Area, only the relatively small proportion of those forests at high altitudes support abundant populations of folivorous marsupials. Additionally, as a consequence of clearing for agriculture, most of the remaining highland forests are located on infertile soils (Tracey 1982; Winter *et al.* 1987). Nevertheless, the total area of highland rainforests in the Atherton Tableland (some 650 km²) is well above the size of natural rainforest isolates that Winter (1984) has argued appear adequate for the long-term survival of the folivores.

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