The relationship between the floristic composition of rain forests and the abundance of folivorous marsupials in north-east Queensland.

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Summary

1. Three species of folivorous ringtail possums (Marsupialia: Pseudocheiridae) inhabit higher elevation rain forests on the Atherton Tablelands, north-east Queensland, Australia. Each possum is thought to specialise on a restricted suite of host plants. It has been hypothesised that the absence of the possums from lowland forests may reflect the absence or "inappropriate combination" of their host plants in lowland forests.

2. We test this 'floristics hypothesis' using data from published dietary studies, herbarium records and field surveys. Studies of the possums' diets show that each possum eats a wide variety of plant species. However, the majority of each possum's diet comes from a few genera or families of plants and there is considerable dietary partitioning between the possums. These data are consistent with the hypothesis that the possums are specialists on a restricted suite of plant taxa.

3. The altitudinal ranges of plants known to be important in the diets of the ringtail possums were compiled from herbarium records. Several plant species eaten by the possums are absent from lowland forests, but all genera and families of plants important in the possums' diets occur in lowland forests.

4. The relationship between the floristic composition of forests and the abundance of the ringtail possums was examined at 16 sites on the Atherton Tablelands. The floristic composition of forests varied primarily with geology and secondarily with altitude. This was true whether the entire plant assemblage was considered, or just those families known to be important in each possum's diet. Possum abundance varied primarily with altitude and secondarily, for two species, with geology. There was no correlation between the abundance of ringtail possums and the floristic composition of forests,

whether the entire plant assemblage was considered, or just those families known to be important in each possum's diet.

5. Altitudinal variation in the abundance of ringtail possums in north Queensland does not appear to be a response to variation in the floristic composition of those forests.

Key-words: arboreal mammal, dietary specialisation, oligophagy, Pseudocheiridae, tropical forest.

Introduction

Narrow host specialisation is as uncommon amongst arboreal folivorous mammals as it is the rule amongst phytophagous insects (Crawley 1983). Exceptions include the koala *Phascolarctos cinereus* Goldfuss and the greater glider *Petauroides volans* Kerr, both specialists on *Eucalyptus*, and *Hapalemur spp.* Geoffroy, specialists on bamboo (Kavanagh & Lambert 1990; Tan 1999). Unlike generalist folivores, whose distributions are primarily determined by the nutrient content of foliage (Oates *et al.* 1990; Ganzhorn 1992; Peres 1997), specialist folivores are constrained by the distribution and abundance of suitable host plants. For example, the koala is restricted to *Eucalyptus* forest and woodland (Hindell & Lee 1991). The koala does not inhabit rain forest within its range, even though rain forest trees tend to have more nutrient-rich foliage than *Eucalyptus* (Braithwaite 1996; Cork 1996).

Narrow specialisation is untenable for most arboreal folivores inhabiting rain forest, because the majority of plants in rain forest are represented by few individuals at the scale of a folivore's home range (Eisenberg 1983). Consequently, rain forest folivores tend to be generalists and the alpha diversity of folivores in rain forest is usually low – typically, no more than three folivores occur sympatrically at sites in Africa, Asia and the neotropics (Eisenberg 1978; Oates *et al.* 1990). However, moderately diverse assemblages of arboreal folivores have evolved in Madagascar, New Guinea and Australia. Six species of folivorous lemurs may occur at some sites in Madagascar (Ganzhorn 1992). Five species of folivorous marsupials are sympatric at sites in northern Australia, and as many as nine species in New Guinea (Flannery 1994; Flannery, Martin & Szalay 1996).

There appears to be considerable dietary partitioning amongst sympatric folivores in the Malagasy and Australian assemblages (the New Guinean fauna is poorly known). Some of this partitioning is attributable to differences in body size and digestive physiology between folivores. For example, large folivores can persist on less nutritious foliage than smaller taxa (Demment & van Soest 1985; Cork & Foley 1991). However, there is evidence that some of the smaller folivores may specialise on suites of plants characterised by particular phytochemicals ('oligophagy', *sensu* Crawley 1983). For example, in Madagascar, Ganzhorn (1988) reported that *Lepilemur mustelinus* Geoffroy fed on plants rich in alkaloids, whereas *Avahi laniger* Gmelin avoided alkaloidal plants and consumed foliage rich in condensed tannins. In northern Australia, Goudberg (1990) found that the diets of three ringtail possums (*Hemibelideus lemuroides* Collett, *Pseudochirulus herbertensis* Collett and *Pseudochirops archeri* Collett) were largely comprised of different genera and even families of plants. While the basis of this partitioning has not been established, some plants important in the diets of *H. lemuroides*, *P. herbertensis* and *P. archeri* are rich in alkaloids, saponins and terpenes, respectively (Webb 1949; Simes *et al.* 1959). Partitioning along phylogenetic lines is consistent with oligophagy (Crawley 1983; Bernays & Chapman 1994).

Assuming the ringtail possums are oligophagous, then it follows that their distributions may be constrained by the distribution of suitable host plants. Using just this argument, Laurance (1990) suggested that the absence of ringtail possums from lowland rain forests in northern Australia may be a consequence of the scarcity or "inappropriate combination" of host plants in lowland forests. In this paper, we test the 'floristics hypothesis' of Laurance (1990). First, we examine the evidence for dietary specialisation in the ringtail possums. Second, we use herbarium records to determine whether known host plants for the possums are absent from lowland forests. Third, we

examine whether there is a correlation between the floristic composition of forests and the abundance of ringtail possums at sites within their range.

Materials and methods

DIETS OF THE RINGTAIL POSSUMS

Information on the diets of the possums was obtained from Goudberg (1990), who studied *H. lemuroides*, *P. herbertensis* and *P. archeri* at Longlands Gap State Forest, and Procter-Gray (1984), who studied *P. archeri* at Curtain Fig State Forest. These are the only published studies of the possums' diets. Both studies were conducted on the Atherton Tablelands (17° - 18^oS, $145^o25'$ - $145^o45'$ E), an elevated plateau (700 – 1300 m a.s.l.) in north Queensland, Australia.

DISTRIBUTION OF PLANTS IMPORTANT IN THE DIETS OF THE RINGTAIL POSSUMS

Plants were considered important in the possums' diets if they contributed at least 5% of feeding records in either Goudberg (1990) or Procter-Gray (1984). Data on the altitudinal distribution of plants found in rain forest in the vicinity of the Atherton Tablelands and adjacent lowland forests were obtained from recently published herbarium records (Hyland *et al.* 2003).

RELATIONSHIP BETWEEN THE FLORISTIC COMPOSITION OF FORESTS AND POSSUM ABUNDANCE

The relationship between the floristic composition of forests and possum abundance was examined at 16 sites on the Atherton Tablelands. Sites were stratified by altitude and geology. Eight sites were in upland forests (400 - 800 m) and eight in highland forests (800 - 1200 m). Within each altitudinal stratum, four sites were located on

nutrient-rich soils derived from basalts and four sites on nutrient-poor soils derived from acid igneous or metamorphic rocks. Sites were located on ridges or upper slopes. Mean annual rainfall at the sites ranged from 1800 to 3200 mm.

At each site, all species of trees and vines were recorded on a single 100 m x 5 m plot. Possum abundance was estimated by spotlight survey at 15 of the 16 sites. Surveys were conducted on foot along roads or the forest edge, using a 30 W spotlight, between 1900 and 0100 hours. Transects were 0.5 – 1.5 km long and located adjacent to the floristic plots. Each transect was surveyed on three to six occasions between 1995 and 1999, with sites subjected to similar levels of total survey effort. To control for differences in the detectability of possums between sites, only observations within 10 m of the transect were counted. Abundance data at the remaining site were determined from long-term observations of a 4 ha plot.

The response of possum abundance to altitude and geology was analysed using generalised linear models. Both attributes were treated as fixed factors with two levels: i.e., (i) upland and highland; and (ii) basalt and acid igneous/ metamorphic parent materials, respectively. Models exhibited extra-Poisson variation and were rescaled following Crawley (1993).

Multivariate methods were used to examine the relationship between possum abundance and the floristic composition of sites. Abundance data were $\ln(x+1)$ transformed prior to analyses. The association between sites in terms of possum abundance was measured with the Gower metric, which treats joint absences as informative. The floristic similarity of sites was measured with the Czekanowski metric, based on the presence of 259 species of trees and vines recorded at two or more sites in the survey. The Czekanowski metric disregards the joint absence of taxa when

comparing two sites; in species-rich forests at this scale of survey, joint absence often reflects sampling limitations (Williams *et al.* 1973).

The relative contributions of altitude and geology in determining variation in the multivariate datasets were calculated using a non-parametric MANOVA procedure (Anderson 2001). Other multivariate analyses were run on PATN (Belbin 1993). The relationship between the floristic composition of the 16 sites and the abundance of ringtail possums was quantified using a Mantel test. To illustrate the results, sites were classified using an unweighted pair-group mean average (UPGMA) fusion method.

Analyses of the floristic composition of sites were conducted in two stages: first, considering only plant families known to be important in the diet of each possum; and second, considering the entire floristic assemblage. The latter analysis was conducted because our knowledge of plants important in the possums' diets is almost certainly incomplete.

Results

DIETS OF THE RINGTAIL POSSUMS

The ringtail possums are not narrow specialists. At the sites they have been studied, each possum has been recorded eating 19 – 77 species of plants from 12 – 21 families (Table 1). Nevertheless, each possum obtains most of its diet from a small number of higher taxa, eating most of the species in those taxa present at a site. For example, at Longlands Gap, *H. lemuroides* obtained 71% of its diet from the Elaeocarpaceae, Lauraceae and Rutaceae, eating 32 of the 34 species in these families recorded at the site; while *P. herbertensis* obtained 68% of its diet from the Elaeocarpaceae, Myrtaceae and Rhamnaceae, eating 12 of the 14 species recorded at the site. However, the limited available data show that, at least for *P. archeri*, diet may vary considerably between sites. For example, only two of the six plant families important in the diet of *P. archeri* at Curtain Fig were also important in its diet at Longlands Gap.

DISTRIBUTION OF PLANTS IMPORTANT IN THE DIETS OF THE RINGTAIL POSSUMS

Several plant species known to be important in the possums' diets are absent from lowland forests. These include two of the eight species known to be important in the diet of *H. lemuroides*, two of the three species important in the diet of *P. herbertensis*, and two of the twelve species important in the diet of *P. archeri*. However, all genera and families of plants known to be important in the diets of the ringtail possums occur in lowland forests. For example, *Flindersia*, the most important genera in the diet of *H. lemuroides* at the site studied by Goudberg (1990), is represented by seven species in both lowland and highland forests. *Elaeocarpus*, important in the diets of both *H.*

lemuroides and *P. herbertensis* at the same site, has nine species in lowland forests and 14 in highland forests; while *Ficus*, important in the diet of *P. archeri*, has 23 species in lowland forests and 14 species in highland forests. Collectively, these taxa are represented by at least as many species in lowland as in highland forests (Fig. 1).

THE FLORISTIC COMPOSITION OF RAIN FORESTS ON THE ATHERTON TABLELANDS

In total, 279 species of trees and 54 species of vines, from 69 families, were recorded in the floristic survey of the 16 sites on the Atherton Tablelands (an average of 86 species per site, range 55 to 118). The floristic composition of these sites surveyed varied primarily with geology and secondarily with altitude (non-parametric MANOVA, altitude $F_{1,12} = 3.36$, $P = 0.004$; geology $F_{1,12} = 4.83$, $P = 0.0002$, interaction $F_{1,12} = 1.29$, $P = 0.19$). The same trends were evident when the analysis was restricted to species in families known to be important in each possum's diet (distribution of plants important in the diet of: (i) *H. lemuroides*, altitude $F_{1,12} = 2.46$, geology $F_{1,12} = 5.30$; (ii) *P. herbertensis*, altitude $F_{1,12} = 3.72$, geology $F_{1,12} = 7.13$; (iii) *P. archeri*, altitude $F_{1,12} = 2.49$, geology $F_{1,12} = 3.97$; main effects $P < 0.05$ in all cases; interaction $P > 0.1$ in all cases). The relative importance of geology in determining floristic composition is evident in a classification of sites, where the primary division is between forests on basalt and forests on acid igneous or metamorphic lithologies (Fig. 2).

VARIATION IN THE ABUNDANCE OF RINGTAIL POSSUMS

All three species of ringtail possum present in the study area were much more abundant in highland than upland forests (Table 2). Abundance also varied with geology for two species: *P. herbertensis* was more abundant in forests on basalt than acid igneous and

metamorphic lithologies, whereas *H. lemuroides* was also more abundant on basalt sites, but only in upland forests. At an assemblage level, altitude was associated with significantly greater variation in the abundance of ringtail possums than was geology (non-parametric MANOVA, altitude $F_{1,12} = 28.25$, $P = 0.0006$; geology $F_{1,12} = 2.92$, $P = 0.097$; interaction $F_{1,12} = 1.12$, $P = 0.29$). The relative importance of altitude in determining possum abundance is evident in a classification of sites (Fig. 2). Two main groups were formed: the first comprising all highland sites and two upland sites where the possums were relatively abundant; the second comprising the remaining upland sites, where the possums were uncommon.

RELATIONSHIP BETWEEN THE FLORISTIC COMPOSITION OF FORESTS AND THE ABUNDANCE OF RINGTAIL POSSUMS

There was no correlation between the floristic composition of sites and the abundance of ringtail possums detected at those sites. This was the case whether the analysis was restricted to each possum and plants from families known to be important in its diet (*H. lemuroides*, $r = 0.12$, $P = 0.10$; *P. herbertensis*, $r = 0.060$, $P = 0.26$; *P. archeri*, $r = 0.029$, $P = 0.38$), or between each possum and the entire floristic assemblage (*H. lemuroides*, $r = 0.12$, $P = 0.087$; *P. herbertensis*, $r = 0.071$, $P = 0.21$; *P. archeri*, $r = -0.060$, $P = 0.74$).

Discussion

THE 'FLORISTICS HYPOTHESIS'

The results of this study do not support the hypothesis of Laurance (1990) that the absence of ringtail possums from lowland forests in north Queensland is a consequence of the absence or "inappropriate combination" of their host plants in lowland forests. Although some plant species eaten by the possums are absent from lowland forests, the possums are manifestly not specialists on individual plant species. The available dietary data show that, at best, the possums specialise on certain genera, families or otherwise phytochemically-related higher plant taxa. However, all genera and families of plants known to be important in the possums' diets occur in lowland forests and many are characteristic of lowland forest types (Tracey 1982; Webb, Tracey & Williams 1984; Williams & Tracey 1984).

The notion that the possums are absent from the lowlands because of an "inappropriate combination" of their host plants is more difficult to test, not least because what constitutes the "correct combination" of host plants for the possums has not been established. Nevertheless, we argue that if the floristic composition of forests is an important determinant of possum abundance, then this should be evident at sites within the possums' range, particularly where sites differ in floristic composition. However, we found no correlation between possum abundance and the floristic composition of sites on the Atherton Tablelands. The possums are relatively common in all highland forests, regardless of the considerable floristic differences between forests on basalt and forests on acid igneous lithologies; whereas they are uncommon in most upland forests, despite the floristic similarities between upland and highland sites.

While the results of this study do not support the 'floristics hypothesis' as an explanation for the restricted altitudinal distribution of the ringtail possums, the limited evidence available does suggest that the possums may specialise on a restricted suite of host plants. Indeed, it is difficult to explain sympatry between the ringtail possums without reference to host specialisation, as the possums are similar in size and gut physiology (Goudberg 1990; Crowe & Hume 1997) and would be expected to compete for foliage of a similar nutrient quality (Cork & Foley 1991). Further studies are required to characterise the degree of specialisation in the possums and the factors underlying dietary partitioning. These might include observations in a wider range of forest types than studied to date or feeding trials, provided the possums could be maintained in captivity.

ALTITUDINAL VARIATION IN THE ABUNDANCE OF RINGTAIL POSSUMS

Not only the ringtail possums endemic to the rain forests of north Queensland, but seven of the nine species of ringtail possums in New Guinea are restricted to higher elevation forests (Flannery 1994). The cause of this phenomenon is unknown. The ringtail possums have no competitors in lowland forests in north Queensland. In New Guinea, various species of cuscus (*Phalanger* Storr, *Spilocuscus* Gray) inhabit lowland forests, but most are relatively generalised herbivores and, in any case, are sympatric with ringtail possums in higher elevations forests (Flannery 1994). There is no evidence that predation on the possums is more intense at lower elevations, at least in north Queensland (Kanowski 1998). Other possible explanations for the phenomenon, besides the 'floristics hypothesis', include an intolerance by the possums of the hot lowland climate (the 'climate hypothesis': Winter 1997) and altitudinal variation in the nutritional quality of foliage (Braithwaite 1996). The relative merits of these

possibilities are discussed elsewhere (Kanowski 1999; Kanowski *et al.* 2001): briefly,

the climate hypothesis seems most plausible.

Acknowledgements

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Table 1. Diets of ringtail possums in north Queensland. Data are the proportion of feeding records contributed by each plant family to the diets of *H. lemuroides* (*Hl*), *P. herbertensis* (*Ph*) and *P. archeri* (*Pa*) at Longlands Gap (LG) and Curtain Fig (CF) State Forests, and the number of species eaten in each family (in brackets). Only families comprising at least 5% of the diets of the possums are listed. Data compiled from Goudberg (1990) and Procter-Gray (1984).

Plant family	*Hl* (LG)	*Ph* (LG)	*Pa* (LG)	*Pa* (CF)
Araliaceae		5% (4)		
Cunoniaceae	5% (1)			
Elaeocarpaceae	26% (6)	11% (4)		
Elaeagnaceae				12% (1)
Euphorbiaceae				26% (1)
Lauraceae	20% (18)		34% (4)	9% (3)
Moraceae			35% (4)	11% (3)
Myrtaceae		14% (7)		
Proteaceae	6% (7)		11% (5)	
Rhamnaceae		43% (1)		
Rutaceae	25% (8)	5% (4)		
Sapindaceae	6% (3)	5% (5)		
Sterculiaceae				17% (2)
Urticaceae				19% (2)
Vitaceae			11% (2)	
Species eaten:	77	50	22	19
Total records:	1358	285	118	141

Table 2. Mean abundance (± SE) of ringtail possums ha^{-1} at 16 sites stratified by altitude and geology in rain forests of the Atherton Tablelands, north Queensland.
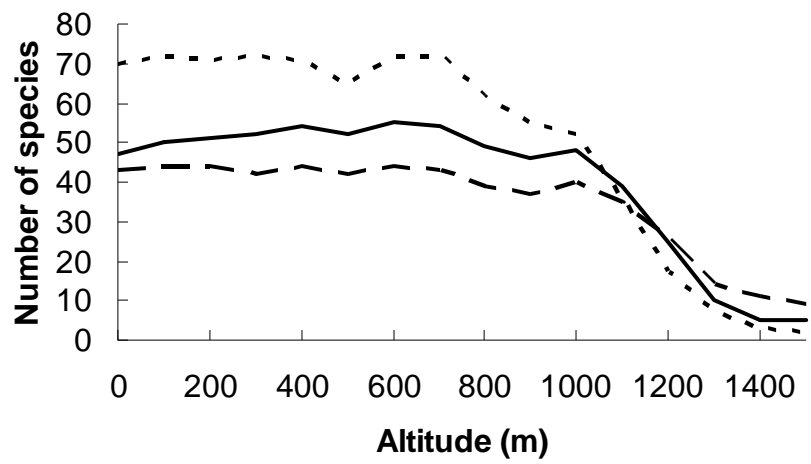
Forest type	*Hemibelideus lemuroides*	*Pseudochirulus herbertensis*	*Pseudochirops archeri*
Highland basalt	3.1 ± 0.3	1.1 ± 0.2	0.5 ± 0.2
Highland acid igneous	2.9 ± 0.4	0.7 ± 0.1	0.6 ± 0.2
Upland basalt	1.3 ± 0.6	0.2 ± 0.1	0.2 ± 0.1
Upland acid igneous/ metamorphic	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
[a] Altitude	***	***	*
Geology		**	
Interaction	*		

[a] Statistical significance of altitude, geology and their interaction as predictors of the abundance of the ringtail possums. * $0.01<p<0.05$; ** $0.001<p<0.01$; *** $p<0.001$
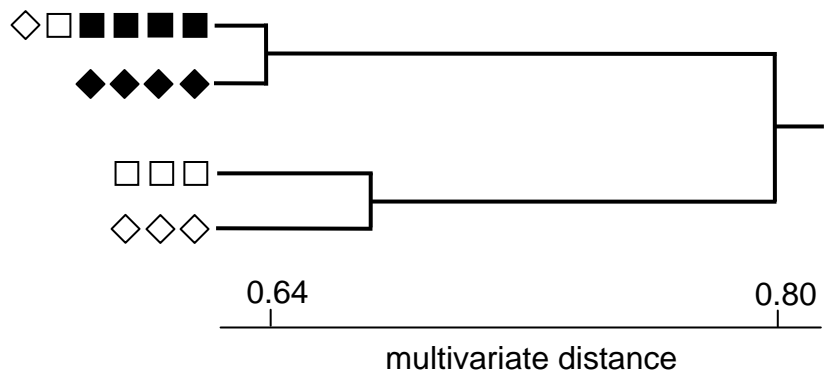
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Fig. 1. Altitudinal variation in species richness of plant genera important in the diets of ringtail possums on the Atherton Tablelands, north Queensland (solid line, *H. lemuroides*; dashed line, *P. herbertensis*; dotted line, *P. archeri*). Dietary information from Procter-Gray (1984) and Goudberg (1990). Plant distributions from Hyland *et al.* (2003). The possums are restricted to elevations above 300 – 500 m.

Fig. 2. Classification of 16 sites in rain forests on the Atherton Tablelands, north Queensland, in terms of: (i) floristic composition; (ii) abundance of ringtail possums (*H. lemuroides*, *P. herbertensis*, *P. archeri*). Forest types: highland 800–1200 m (squares), upland 400-800 m (diamonds); basalt (black), acid igneous or metamorphic (open).

(i) Floritic composition

multivariate distance

(ii) Possum abundance

multivariate distance