ELSEVIER

Biological Conservation 91 (1999) 231–239

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals

Susan G. Laurance [a,b,*], William F. Laurance [b,c]

[a]Department of Ecosystem Management, University of New England, Armidale, NSW 2350, Australia
[b]Biological Dynamics of Forest Fragments Project, National Institute for Research in the Amazon (INPA), CP 478, Manaus, AM 69011-970, Brazil
[c]Biodiversity Program, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA

Abstract

In fragmented landscapes, linear forest remnants have the potential to provide habitat and movement corridors for wildlife. We used systematic spotlighting surveys to sample arboreal mammals in 36 linear rainforest remnants in tropical Queensland, Australia. The effects of corridor width, height, isolation, elevation, and floristic composition on mammals were assessed with multiple regression models. Six species were recorded during 108 surveys. The most vulnerable species, the lemuroid ringtail possum (*Hemibelideus lemuroides*), was found only in remnants comprised of primary rainforest that were linked to large tracts of continuous forest. Two other species, the Herbert River ringtail possum (*Pseudochirulus herbertensis*) and striped possum (*Dactylopsila trivirgata*), also favored corridors that were linked to forest tracts or fragments, with the former favoring high-diversity forest (primary forest or mixed regrowth) over low-diversity (*Acacia*) regrowth. Three other species, the coppery brushtail possum (*Trichosurus vulpecula*), green ringtail possum (*Pseudochirops archeri*), and Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*), occurred in both isolated and non-isolated remnants and both primary forest and regrowth. Our findings suggest that linear forest remnants that are floristically diverse (not *Acacia*-dominated regrowth) and at least 30–40 m width can function as habitat and probably movement corridors for most arboreal mammals in this region. The lemuroid ringtail, however, apparently requires corridors of primary rainforest of at least 200 m in width. Because the lemuroid ringtail is highly vulnerable to forest fragmentation, faunal corridors in this region should be designed wherever possible to meet its ecological requirements.

Keywords: Arboreal mammals; Australia; Habitat fragmentation; Marsupials; North Queensland; Rainforest; Tropical forest; Wildlife corridors

1. Introduction

Wildlife corridors have been widely advocated in conservation planning as a way to help reduce effects of habitat fragmentation (Harris, 1984; Forman and Godron, 1986; Noss, 1987; Bennett, 1990; Saunders and Hobbs, 1991; Laurance and Laurance, 1999). The design of faunal corridors is still in its infancy, however, especially in tropical forests, which are being cleared and fragmented faster than any other biome (Whitmore, 1997).

There are few published studies on use of potential corridors by tropical wildlife. Lovejoy et al. (1986) described how army ant-following birds in Amazonia disappeared from a 100-ha forest fragment soon after a corridor linking it to primary forest was removed. Newmark (1993) discussed the use of a forest corridor by elephants in Tanzania, while Lima and Gascon (1999) showed that Amazonian frog and small mammal assemblages in linear remnants did not differ significantly from those in primary forest. In northern Queensland, studies on birds (Crome et al., 1995), mammals (Laurance, 1990, 1991a), and insects (Hill, 1995) have shown that a substantial proportion of rainforest species can use linear forest remnants, at least as habitat. None of these studies examined more than a few remnants, however, and hence their implications for corridor design are limited.

It is not yet known whether corridor-design principles developed for other habitat types, such as temperate or open forests (e.g. Saunders and Hobbs, 1991; Lindenmayer et al., 1993), can be applied to tropical rainforests. Tropical rainforests have unique structural, floristic, and microclimatic characteristics, and support more species with specialized habitat and dietary requirements than temperate forests (Laurance and Bierregaard, 1997). For these reasons, tropical species

* Corresponding author at Biological Dynamics of Forest Fragments Project, INPA Ecologia, CP 478, Manaus, AM 69011-970, Brazil. Fax: +55-92-642-2050.

E-mail address: sgl@inpa.gov.br (S.G. Laurance)

0006-3207/99/$ - see front matter
PII: S0006-3207(99)00077-4

may be particularly sensitive to edge-induced habitat changes, and thus could require wider corridors than their temperate forest counterparts.

Arboreal mammals in north Queensland rainforests are an ideal group for assessing the utility of potential faunal corridors. They are diverse, readily censused, and being locally endemic are of high conservation significance. They also are strongly associated with forest vegetation and exhibit varied responses to land uses such as forest fragmentation (Pahl et al., 1988; Laurance, 1990, 1991a) and logging (Preen, 1981; Laurance and Laurance, 1996).

In this study we assess the use of linear forest remnants by possums and tree-kangaroos in tropical Queensland. By sampling 36 remnants that varied greatly in terms of connectivity, floristic composition, and structure, we developed a good understanding of the habitat tolerances of these species. Here, we present these findings and consider their implications for the design of tropical faunal corridors.

2. Methods

2.1. Study area

The study area (Fig. 1) encompassed most of the Atherton Tableland (17° 18′ S, 145° 29′ E to 17° 36′ S, 145° 44′ E), a mid-elevation (600–900 m) plateau spanning ca. 900 km^2 in the wet tropics of northeastern Queensland. The Tableland is flanked by mountains of up to 1600 m high to the east, south, and south-west. Annual rainfall ranges from 1800–2800 mm with a pronounced wet season from January to April. Basalt is the most prevalent soil parent-material on the Tableland but granitic and metamorphic substrates are not uncommon (Wilmott and Stephenson, 1989).

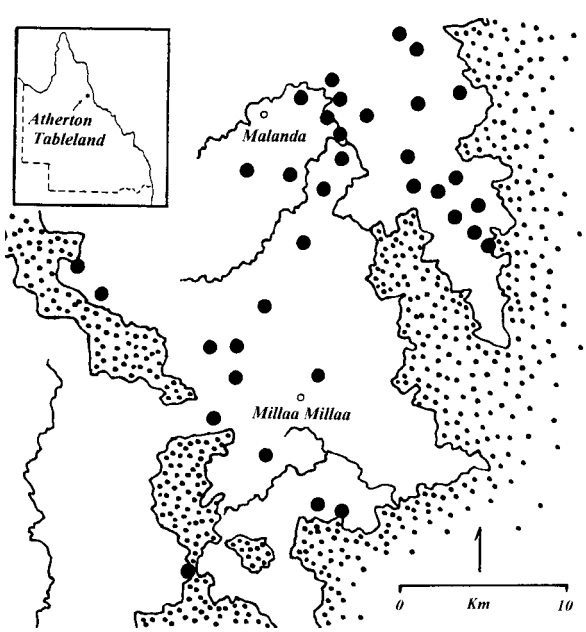

Fig. 1. Map of the study area in tropical Queensland, Australia. ● = study sites. Stippled areas are rainforest while unstippled areas are mostly cattle pastures. Dark, wavy lines indicate rivers.

Prior to this century, the Tableland was mostly covered by dense upland rainforest. Deforestation for cattle pastures and crops commenced in the early 1900s and proceeded rapidly for the next few decades (Frawley, 1983). By 1983, > 76,000 ha of forest had been removed (Winter et al., 1987), leaving numerous forest remnants ranging from 1 to 600 ha in area (Laurance, 1991a). Linear strips of relict primary or regrowth forest are also common, especially along streams. Large (> 3000 ha) forest tracts survive only on steeper mountainsides.

Three types of linear forest remnant are common on the Tableland: (1) Relict primary rainforest occurs in areas that were never completely deforested, typically along stream gullies. Most primary remnants contain a core of mature rainforest trees bordered by some secondary vegetation. Lianas, climbing rattans (*Calamus* spp.), and weedy plants are often abundant, probably because of recurring wind-disturbance (Laurance, 1991b) and lateral light penetration. (2) Mixed-regrowth forest occurs where primary vegetation has been completely cleared and allowed to regenerate. Species diversity of plants in mixed regrowth can be quite high, especially on richer basaltic soils (Tracey, 1982). (3) *Acacia* regrowth also regenerates in cleared areas but is most prevalent on infertile metamorphic soils and in lower rainfall areas (Tracey, 1982). Plant diversity in *Acacia* regrowth is generally lower than in mixed regrowth and the forest is more homogeneous structurally (S.G. Laurance, 1996).

Linear remnants on the Tableland also exhibit three levels of connectivity: (1) completely isolated from other forest by cattle pastures or crops; (2) linked to isolated fragments of primary forest (> 5 ha in area); and (3) linked to the large (> 3000 ha) rainforest tracts that fringe the Tableland.

2.2. Arboreal mammals

The rainforests of the Atherton Uplands support Australia's most diverse assemblage of sympatric, leaf-eating marsupials (Fig. 2). This guild includes the coppery brushtail possum (*Trichosurus vulpecula johnstoni*); three species of tropical ringtail possum, the green ringtail (*Pseudochirops archeri*), Herbert River ringtail (*Pseudochirulus herbertensis*), and lemuroid ringtail (*Hemibelideus lemuroides*); and the Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*). The ringtails and tree-kangaroo are all endemic to north Queensland, while the coppery brushtail is a locally endemic subspecies. The four possums are all upland specialists with

highly restricted ranges and minimum elevational limits ranging from 300 to 600 m (Winter et al., 1984). A sixth species, the insectivorous striped possum (*Dactylopsila trivirgata*), occurs in rainforests of northern Queensland and New Guinea (Strahan, 1995).

2.3. Study design

During a 13-month period in 1994–1995, arboreal marsupials were sampled at 36 linear remnants by spotlighting at night. Samples were usually conducted by a single observer (S.G.L.) using a 30-watt spotlight powered by gel-cell batteries carried in a backpack. Arboreal mammals in the study area are distinctive in appearance and were identified by coloration, size, and eyeshine, using binoculars. Each site was sampled three times by spotlighting along one side of the corridor, typically at 3–4 month intervals. Samples were timed to the nearest minute and were used to generate abundance estimates (mean no. animals/h) for each species and site.

A balanced factorial study design (Green, 1979) was used to select study sites. Nine treatment combinations were distinguished (3 forest types×3 levels of isolation, as described above), each represented by four replicates, yielding 36 sites altogether. Some combinations were uncommon on the Tableland (e.g. *Acacia* remnants linked to rainforest tracts) and it was necessary to survey >100 sites before all replicates could be located. Selected remnants (Table 1) had continuous canopy cover and ranged from 9 to 490 m in mean width and 250–1250 m in length. Most (89%) occurred on basaltic soils and many (69%) bordered streams.

2.4. Remnant attributes

Several floristic, structural, and landscape attributes were recorded for each remnant. Floristic composition was assessed using a sample of 60 canopy trees from each site, stratified on the length and width of the remnant. To select trees, each remnant was divided into six equal-length segments. At the midpoint of each segment, a target tree and its four nearest neighbors (all canopy trees or above ⩾10 cm diameter-at-breast height) were selected on both the edge and interior of the remnant. Sterile or fertile material was collected for unknown trees and identified by taxonomic experts (A.J. Irvine, N. Tucker, R. Jensen, personal communication). Remnant floristic composition was assessed by performing an ordination analysis on the commonest tree species (see below).

Structural features (Table 1) included the mean width and mean height of vegetation at each remnant (recorded at the six midpoints described above). Landscape features were remnant elevation (recorded from 1:50,000 maps), isolation (linear distance to the nearest large [>3000 ha] tract of forest), and a quantitative index of remnant connectivity (1 = isolated; 2 = linked to >5 ha forest fragment; 3 = linked to >3000 ha forest tract). Three metrics (width, altitude, isolation) were log-transformed to improve normality and the linear fit to data on species abundances.

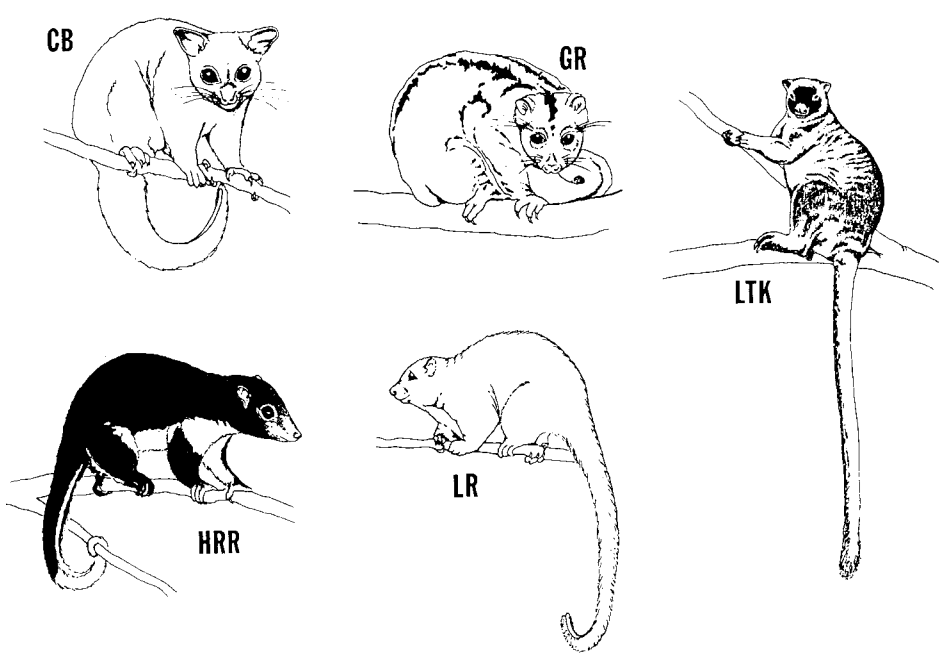

Fig. 2. Arboreal mammals encountered in north Queensland rainforests: CB, coppery brushtail possum (*Trichosurus vulpecula johnstoni*); GR, green ringtail possum (*Pseudochirops archeri*); HRR, Herbert River ringtail possum (*Pseudochirulus herbertensis*); LR, lemuroid ringtail possum (*Hemibelideus lemuroides*); LTK, Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*). Not shown is the striped possum (*Dactylopsila trivirgata*).

Table 1
Attributes of 36 linear forest remnants studied in tropical Queensland

Site no.	Mean width[a]	Length[a]	Mean height[a]	Elevation[a]	Isolation[a]	Connectivity[b]	Tree spp.[c]	Soil[d]	Topography
Primary rainforest sites									
1	35	600	17.4	680	50	1	34	Ba	Slope
2	25	420	16.8	820	10	1	25	Ba	Stream
3	44	400	17.0	750	1300	1	20	Ba	Stream
4	35	325	16.4	720	3500	1	29	Ba	Ridge
5	27	400	16.3	770	2500	2	24	Ba	Stream
6	26	350	19.2	740	2500	2	27	Ba	Slope
7	16	370	16.8	980	20	2	31	Ba	Ridge
8	36	620	15.3	800	0	2	30	Gr	Stream
9	88	1250	21.2	750	0	3	29	Ba	Stream
10	320	700	16.3	700	0	3	29	Ba	Slope
11	200	840	20.0	780	0	3	32	Ba	Stream
12	490	720	18.8	1000	0	3	32	Ba	Slope
Mixed-regrowth sites									
13	34	350	10.8	720	5500	1	24	Ba	Stream
14	37	360	12.5	720	2200	1	22	Ba	Stream
15	22	655	11.3	800	4200	1	15	Ba	Stream
16	23	500	11.5	780	2700	1	21	Ba	Stream
17	24	280	13.8	700	300	2	26	Ba	Stream
18	24	733	13.2	720	1200	2	22	Ba	Stream
19	29	250	11.7	1000	1000	2	24	Ba	Slope
20	18	460	10.2	700	3800	2	23	Ba	Stream
21	52	330	14.3	680	0	3	31	Ba	Stream
22	29	300	9.0	750	0	3	21	Ba	Stream
23	10	920	16.2	840	0	3	23	Gr	Stream
24	14	380	7.0	950	0	3	20	Ba	Slope
Acacia-*regrowth sites*									
25	24	250	13.6	740	3000	1	14	Met	Stream
26	26	335	10.0	750	4200	1	13	Ba	Stream
27	18	390	11.8	700	3000	1	22	Ba	Stream
28	14	460	11.3	780	1700	1	16	Ba	Stream
29	17	470	15.0	700	5000	2	14	Ba	Stream
30	32	400	15.0	710	4000	2	17	Ba	Stream
31	22	425	14.0	740	5500	2	19	Ba	Slope
32	9	310	10.2	700	4500	2	15	Ba	Stream
33	19	600	11.6	720	0	3	18	Met	Stream
34	44	380	11.0	770	0	3	18	Ba	Stream
35	40	350	17.0	720	0	3	25	Met	Slope
36	124	400	14.5	770	0	3	17	Ba	Ridge

[a] All measurements in meters.
[b] 1, isolated; 2, linked to >5 ha forest fragment; 3, linked to >3000 ha forest tract.
[c] Out of a sample of 60 canopy trees.
[d] Abbreviations of soil types: Ba, basalt; Gr, granite; Met, metamorphic.

2.5. Data analysis

A robust ordination method, nonmetric multidimensional scaling (Minchin, 1987), was used to describe floristic gradients in the study area. Because ordinations can be distorted by rare species, we used only relatively common tree species (detected at $\geqslant 10$ sites). The ordination was performed on PC-ORD with the Sorensen dissimilarity index and all default options, as recommended (McCune and Mefford, 1995).

As potential predictors of arboreal mammal abundances, we used three ordination axes describing floristic gradients plus the five landscape variables described above (remnant width, height, elevation, isolation, connectivity). With the exception of the isolation and connectivity measures, which were moderately correlated ($R^2 = 62\%$), none of the predictors were strongly intercorrelated ($R^2 < 30\%$).

Responses of mammals to the predictors were assessed with multiple regression analyses, using Best Subsets Regression to select significant predictors. Care was taken to examine relationships between predictors and response variables to ensure approximate linearity and to guard against outliers. Residuals from each regression were plotted against the fitted (predicted) values and each predictor, to ensure that residuals exhibited no

strong, systematic relationship (e.g. a fan-shaped pattern) that could violate assumptions of the regression models (cf. Crawley, 1993). Mammal abundance data were log $(X+1)$-transformed prior to the analysis. Analyses were run on Statistix (Analytical Software, 1991).

3. Results

3.1. Remnant floristics

Of 180 tree species detected in the study area, only 24 were recorded at 10 or more sites. Ordination of these 24 common species revealed three floristic gradients. Axis 1 described a gradient between lower-diversity sites with many *Acacia aulacocarpa* and *Alphitonia petriei*, and higher-diversity sites with numerous *Neolitsea dealbata* and *Amoora ferruginea*. Axis 2 mainly discriminated sites with varying amounts of *Guoia lasioneura*, an early successional treelet common on forest edges. Axis 3 described a gradient between sites having many *Rhodomyrtus pervagata* and those with dense *A. aulacocarpa* and *Flindersia brayleana* ($r>0.5$, $P<0.002$, for all correlations between species and ordination axes).

The *Acacia* regrowth and primary rainforest sites were completely separate in ordination space (Fig. 3), suggesting that they were distinctive floristically. Mixed-regrowth remnants overlapped with both rainforest and *Acacia* sites (especially the former), suggesting they were intermediate but variable in composition.

The floristic diversity of each remnant was substantially influenced by remnant age, with older remnants (primary forest and older regrowth) having more species. This is reflected in the fact that species richness of trees was strongly and positively related to mean forest height, a reasonable index of remnant age ($F_{1,34}=20.43$, $R^2=37.5\%$, $P<0.0001$).

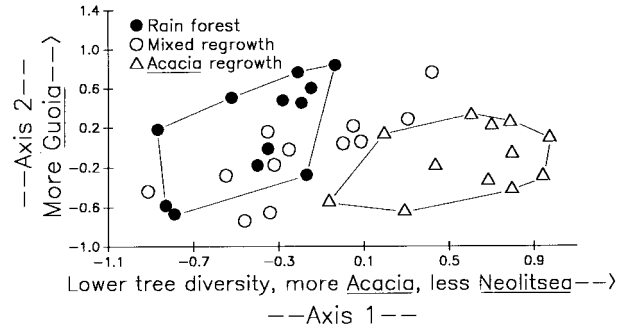

Fig. 3. Ordination of common tree species in 36 linear rainforest remnants in tropical Queensland, using nonmetric multidimensional scaling. Axis lengths are proportional to the amount of variation captured by each axis.

3.2. Mammal populations

In 108 samples we recorded 443 detections of six arboreal mammal species. These were, in order of decreasing abundance, the coppery brushtail possum ($n=254$), green ringtail possum ($n=59$), Lumholtz's tree-kangaroo ($n=52$), Herbert River ringtail possum ($n=43$), lemuroid ringtail possum ($n=32$), and striped possum ($n=3$). Ten additional sightings could not be positively identified.

Coppery brushtail possums were detected at 81% of the sites. The multiple regression model suggested that coppery brushtails were positively associated with sites that were isolated (far from primary forest) and at higher elevations. Remnant connectivity was also a positive predictor, which probably reflects the fact that brushtails achieved their highest abundances in remnants that were linked to forest fragments. The model was highly significant ($P<0.0001$), explaining 56% of the variation in brushtail abundance (Table 2).

Herbert River ringtails were detected at 39% of the sites. The multiple regression model suggested that Herbert River ringtails preferred tall, high-diversity forest (rainforest and mature mixed-regrowth; low

Table 2
Muliple regression models used to assess effects of floristic, structural and landscape predictors on arboreal mammals in linear rainforest remnants

Variable[a]	Predictors	Slope	Predictor importance (%)[b]	Regression statistics		
				R^2 (%)	F	P
Coppery brushtail possum	Isolation	+	39.4	55.6	13.36	< 0.0001
	Elevation	+	8.6			
	Connectivity	+	7.6			
Green ringtail possum	–					
Herbert River ringtail possum	Axis 1	–	40.3	64.7	19.58	< 0.0001
	Elevation	+	14.4			
	Forest height	+	10.0			
Lumholtz's tree-kangaroo	Isolation	+	11.4	11.4	4.39	0.044
Species richness	Forest height	+	20.4	35.2	8.97	0.0008
	Elevation	+	14.8			

[a] Abundance data were $\log_{10}(X+1)$-transformed prior to analysis.
[b] Percentage of variation in mammal abundance explained by each predictor.

values of Axis 1) at higher elevations. The model was highly significant ($P < 0.0001$), explaining 65% of the variation in Herbert River ringtail abundance (Table 2).

Lemuroid ringtails were detected at only three sites (8% frequency), all remnants of primary forest that were directly linked to large forest tracts. They were moderately abundant (2–4.7 animals/h) at these three sites. A regression model was not generated given their low frequency, but they clearly avoided remnants that were isolated, narrow (< 200 m width), or comprised of regrowth forest.

Green ringtails were detected at 67% of the sites, and appeared little influenced by remnant features. There were no significant predictors of its abundance (Table 2).

Tree-kangaroos were detected at 56% of the sites. The multiple regression model suggested they preferred more-isolated sites, although the model explained only 11% of the variation in tree-kangaroo abundance (Table 2).

Striped possums were detected at only three sites, each represented by a single animal. All were linked to large forest tracts; one remnant was primary rainforest while the other two were *Acacia* regrowth.

3.3. Mammal communities

A multiple regression model suggested that arboreal mammal richness was positively associated with forest height and elevation. The model was highly significant ($P = 0.0008$), explaining 35% of the variation in mammal richness (Table 2).

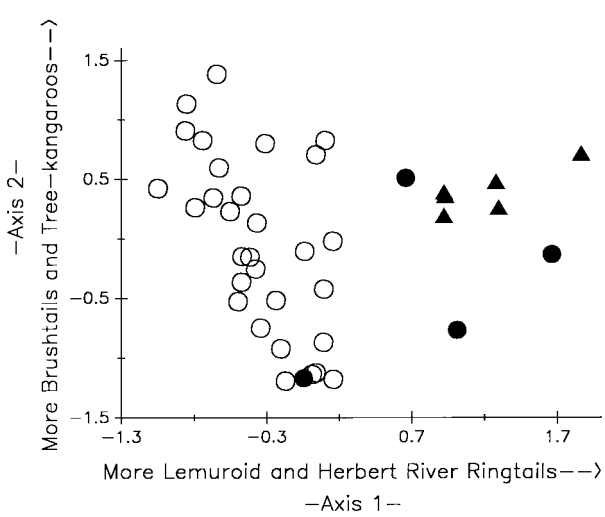

Fig. 4. Ordination of arboreal mammal assemblages in 34 linear forest remnants (two remnants had no animals detected) and six large rainforest tracts on the Atherton Tableland, using nonmetric multidimensional scaling. ▲, Large rainforest tracts; ●, remnants comprised of primary rainforest that are linked to large rainforest tracts; ○, all other remnants. Axis lengths are proportional to the amount of variation captured by each axis (significant correlations with ordination axes: axis 1: lemuroid ringtails, $r = 0.90$; Herbert River ringtails, $r = 0.76$; axis 2: coppery brushtails, $r = 0.94$; tree-kangaroos, $r = 0.62$; $P < 0.0001$ in all cases).

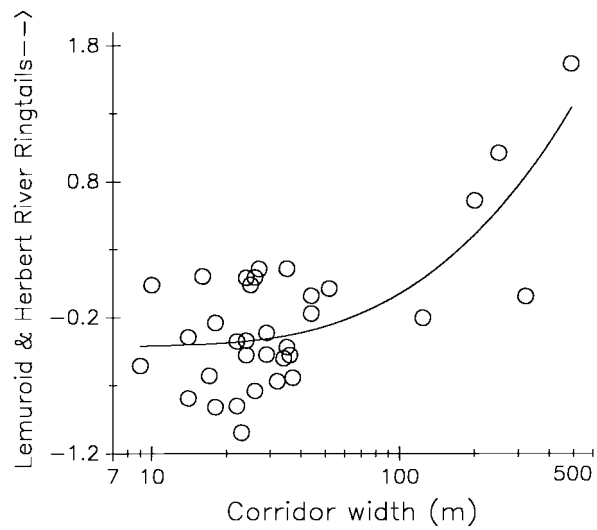

Fig. 5. Relationship between NMDS axis 1, which describes a gradient in abundance of rainforest-dependent possums, and the widths of linear remnants. The curve was fitted by polynomial regression.

An ordination analysis, using abundance data for the five most abundant species, revealed that only a few linear remnants had arboreal mammal assemblages similar to those in continuous forest (Fig. 4), based on comparisons with six sites in large (> 3000 ha) forest tracts on the southern Atherton Tableland (8–9 spotlighting samples/site) surveyed in the late 1980s (Laurance, 1990). Many remnants had comparable numbers of coppery brushtail possums, green ringtail possums, and tree-kangaroos, but only three had similar abundances of lemuroid and Herbert River ringtail possums. These three remnants were all composed of primary forest and directly linked to large forest tracts.

Significantly, axis 1, which described a gradient in abundance of the two most forest-dependent species (lemuroid and Herbert River ringtails) appeared to be strongly influenced by corridor width (Fig. 5). The three remnants that contained lemuroid ringtails ranged from 200 to 490 m in width.

4. Discussion

4.1. Mammal ecology

Arboreal mammals in north Queensland rainforests vary greatly in their ability to use linear forest remnants. Three species, the coppery brushtail possum, green ringtail possum, and Lumholtz's tree-kangaroo, occur in both isolated and non-isolated remnants and appear little influenced by forest type. A fourth, the Herbert River ringtail possum, favors taller, more diverse forests

(primary rainforest or mature mixed-regrowth) over lower-diversity *Acacia* regrowth. Two others, the lemuroid ringtail possum and striped possum, were detected only in remnants linked to large tracts of continuous forest, and the lemuroid ringtail apparently uses only primary rainforest.

The habitat tolerances of arboreal mammals are determined by traits such as their diet, denning requirements, and degree of arboreality (Laurance, 1990). Most linear remnants on the Atherton Tableland are comprised of regrowth, and even those that contain primary rainforest are often heavily disturbed and bordered by successional vegetation. Species that can feed on successional trees or vines, such as the coppery brushtail, green ringtail, Herbert River ringtail, and Lumholtz's tree-kangaroo, are better adapted for using linear remnants than those like the lemuroid ringtail, which are mainly dependent on primary-forest trees (Procter-Gray, 1984; Winter and Atherton, 1984; Goudberg, 1990).

Mammals that do not require hollow tree cavities for daytime sleeping have an advantage in linear remnants, because trees large enough to form natural cavities are rare in regrowth. Both the green ringtail and tree-kangaroo sleep on branches, with the former being effectively camouflaged by its green coloration. Coppery brushtails use a wide range of dens, while Herbert River ringtails can make temporary nests out of epiphytes. The lemuroid ringtail, however, requires a hollow cavity high in a tree, to which it exhibits very strong fidelity (Goudberg, 1990).

Finally, mammals that can cross open ground should be better able to colonize and use linear remnants, especially those isolated from other forest. The coppery brushtail and tree-kangaroo cross open areas quite readily (Pahl et al., 1988; Laurance, 1990), apparently for distances of up to a few hundred meters, although tree-kangaroos appear vulnerable to dog predation while on the ground (Newell, 1998, 1999). The green ringtail can also cross open areas for limited distances (S.G. and W.F. Laurance, personal observations; J.W. Winter, personal communication). However, the Herbert River ringtail appears much more strongly arboreal, while the lemuroid ringtail is strictly arboreal, with most of its foraging activity confined to the middle and upper canopy layers (Laurance, 1990). Little is known about the ground-crossing abilities of the striped possum, but its presence in some forest fragments and a road-killed animal found in 1987 suggest it may cross open areas on occasion (W.F. Laurance, unpublished data).

4.2. Matrix-tolerance and extinction proneness

In fragmented landscapes, linear forest remnants are often retained or regenerate along streamlines. These remnants comprise an important part of the modified matrix surrounding fragments, and are used by a number of nominally forest-dependent animals (Laurance, 1990, 1991a; Crome et al., 1995). In general, vertebrates that tolerate or exploit the matrix often persist in forest fragments, while those that avoid these habitats frequently decline or disappear (Laurance, 1990, 1991a, 1994, 1997; Malcolm, 1991; Gascon et al., 1999). Because matrix-tolerant species can move among forest blocks, the deleterious effects of small population size may be greatly reduced (Brown and Kodric-Brown, 1977). Such species may also be tolerant of edge effects in fragments (Laurance, 1991b; Gascon et al., 1999) and may even use the matrix for breeding habitat (S.G. Laurance, 1996).

Among the arboreal species in this study, the matrix-avoiding lemuroid ringtail possum is by far the most vulnerable to fragmentation, having disappeared from most fragments on the Atherton Tableland under 600 ha in area (Laurance, 1990). The Herbert River ringtail and tree-kangaroo apparently decline in smaller (<20 ha) fragments, while green ringtail and coppery brushtail possums remain stable or increase in fragments (Pahl et al., 1988; Laurance, 1990). Other species, such as rodents and terrestrial marsupials, also exhibit a strong correlation between matrix-tolerance and vulnerability in fragmented landscapes (Laurance, 1991a, 1994).

Because the matrix plays such an important role in the dynamics of faunal communities, the conservation value of reserves and forest remnants will be determined not only by intrinsic factors such as fragment size and shape, but also by the surrounding matrix, which determines their connectivity to other forest areas. Conservation initiatives that focus only on forest reserves, while ignoring the matrix, will often have limited success. In rapidly developing areas such as the Amazon Basin, the retention of strips of primary forest along streams and rivers could play a key role in helping to maintain some ecosystem connectivity in human-dominated landscapes (Laurance and Gascon, 1997; Lima and Gascon, 1999).

4.3. Design of tropical faunal corridors

In north Queensland, at least four attributes of linear remnants affect their suitability for arboreal mammals. The first is floristic composition. Primary forest is clearly most favorable, supporting all six arboreal species. This is followed by mature mixed-regrowth and then *Acacia*-dominated regrowth (Fig. 4), the latter of which usually contained only mammals insensitive to fragmentation (coppery brushtail, green ringtail). Floristic composition is related to forest age, with taller forests (primary rainforest and mature regrowth) having higher tree diversity than shorter forests (young mixed-regrowth and *Acacia* regrowth). Clearly, faunal

corridors composed of primary forest are likely to be the most suitable for strongly forest-dependent species, which are usually the most vulnerable to fragmentation.

The second factor is physical connectivity. Linear remnants isolated from forest tracts or fragments rarely supported Herbert River ringtails and never contained lemuroid ringtails, the two most vulnerable species. Moreover, on the Atherton Tableland, forest patches linked to mainland forest by continuous riparian strips supported higher arboreal mammal richness than did similar-sized patches that lacked such linkages (Laurance, 1990). For completely arboreal species like the lemuroid ringtail, even narrow breaks in canopy cover, such as from a paved highway, may render a corridor impassable. Strictly arboreal species are a common feature of tropical forests (Eisenberg, 1981), and other tropical animals, such as certain understory birds (Bierregaard and Stouffer, 1997; S.G. Laurance, 1999), bats (Crome and Richards, 1988), small mammals, and amphibians (Goosem, 1997), also avoid narrow (10–80 m) forest clearings, suggesting that corridor continuity will be crucial for some species.

Remnant elevation was also important. All five of the folivorous (leaf-eating) mammals we studied are most abundant at higher elevations (Winter et al., 1984; Laurance, 1990; Newell, 1998), while the insectivorous striped possum is most common in the lowlands (< 300 m). Our results and other studies in the region (Winter et al., 1984; Laurance, 1990; Laurance and Laurance, 1996) suggest that corridors above ca. 750 m elevation are likely to be most effective. Many tropical species exhibit pronounced elevational zonation (Winter et al. 1984; Fjeldsa and Rahbek, 1997), and thus in some areas elevation could be an important feature of corridor design.

The final factor is corridor width (Fig. 5). Linear remnants of moderate width (20–80 m) were used by five of the six species. The lemuroid ringtail, however, which is highly sensitive to fragmentation, occurred only in remnants of 200–490 m width that were linked to nearby continuous forest. This suggests that corridors of at least 200 m width are needed by this species [although we could locate only two suitable remnants of intermediate (88–124 m) widths on the Atherton Tableland, neither of which supported lemuroid ringtails]. Studies in the Amazon have yielded comparable results: Laurance and Gascon (1997) suggested that 300 m-wide corridors would retain core habitat that was only moderately influenced by edge-related changes in forest dynamics and microclimate, while Lima and Gascon (1999) found that assemblages of small mammals and litter-dwelling frogs in 140–190 m-wide corridors did not differ significantly from those in nearby continuous forest. Thus, for smaller (< 20 kg) tropical vertebrates, corridors of at least 200–300 m width could be sufficient for many forest species, at least for corridors of limited length (< 3 km). This conclusion must remain tentative, however, given the current paucity of research on faunal corridors in the tropics. Future studies should focus explicitly on species known to be highly vulnerable to forest fragmentation, for which wildlife corridors will be most crucial.

Acknowledgements

We thank Denis Saunders, Andrew Bennett, Tony Norton, and two anonymous referees for comments on the manuscript. This project was undertaken as part of an M.Nat.Res. degree by the first author, who gratefully acknowledges the help and encouragement of her thesis supervisor, Peter Jarman. John Winter provided important feedback, Steven McKenna and Damien Milner assisted with field work, and Tony Irvine, Nigel Tucker, and Rigel Jensen identified many plant specimens. Support was provided by the Queensland Department of Environment, Winifred Violet Scott Trust, and Wet Tropics Management Authority. This is publication number 245 in the Biological Dynamics of Forest Fragments Project Technical Series.

References

Analytical Software, 1991. Statistix, Version 3.5. Analytical Software, St. Paul, MN.

Bierregaard, R.O., Stouffer, P., 1997. Understory birds and dynamic habitat mosaics in Amazonian rainforests. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 138–155.

Bennett, A.F., 1990. Habitat Corridors: Their Role in Wildlife Management and Conservation. Department of Conservation and Environment, Melbourne.

Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58, 445–449.

Crawley, M.J., 1993. GLIM for Ecologists. Blackwell Scientific, London.

Crome, F.H.J., Richards, G.C., 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. Ecology 69, 1960–1969.

Crome, F.H.J., Isaacs, J., Moore, L.A., 1995. The utility to wildlife of remnant riparian vegetation and associated windbreaks in the tropical Queensland uplands. Pacific Conservation Biology 2, 328–343.

Eisenberg, J.F., 1981. The Mammalian Radiations. University of Chicago Press, Chicago.

Fjeldsa, J., Rahbek, C., 1997. Species richness and endemism in South American birds: Implications for the design of networks of nature reserves. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 466–482.

Forman, R.T.T., Godron, M., 1986. Landscape Ecology. John Wiley, New York.

Frawley, K.J., 1983. A history of forest and land management in Queensland, with particular reference to the north Queensland rainforest. Report to Rainforest Conservation Society of Queensland, Brisbane.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B.,

Tocher, M., Borges, S., 1999. Matrix habitat and species persistence in tropical forest remnants. Biological Conservation.

Goosem, M., 1997. Internal fragmentation: The effects of roads, highways, and powerline clearings on movements and mortality of rainforest vertebrates. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 241–255.

Goudberg, N., 1990. The feeding ecology of three species of north Queensland upland rainforest ringtail possums, *Hemibelideus lemuroides*, *Pseudocheirus herbertensis*, and *P. archeri* (Marsupialia: Petauridae). Ph.D. thesis, James Cook University, Townsville, Australia.

Green, R.H., 1979. Sampling Design and Statistical Methods for Environmental Biologists. Wiley-Interscience, New York.

Harris, L.D., 1984. The Fragmented Forest: Island Biogeographic Theory and the Conservation of Biotic Diversity. University of Chicago Press, Chicago.

Hill, C.J., 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. Conservation Biology 9, 1559–1566.

Laurance, S.G., 1996. Utilisation of linear rainforest remnants by arboreal marsupials in north Queensland. M.Nat.Res. thesis, University of New England, Armidale, Australia.

Laurance, S.G., 1999. Effects of roads on movements and composition of understory birds in the central Amazon. Published abstract, 1999 Annual Meeting of the Ecological Society of America, Spokane, Washington.

Laurance, S.G., Laurance, W.F., in press. Bandages for wounded landscapes: Faunal corridors and their roles in wildlife conservation in the Americas. In: Bradshaw, G., Marquet, P. (Eds.), Landscape Alteration in the Americas, Columbia University Press, New York.

Laurance, W.F., 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. Journal of Mammalogy 71, 641–653.

Laurance, W.F., 1991a. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5, 79–89.

Laurance, W.F., 1991b. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. Biological Conservation 57, 205–219.

Laurance, W.F., 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biological Conservation 69, 23–32.

Laurance, W.F., 1997. Responses of mammals to rainforest fragmentation in tropical Queensland: a review and synthesis. Wildlife Research 24, 603–612.

Laurance, W.F., Bierregaard, R.O. (Eds.), 1997. Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago.

Laurance, W.F., Gascon, C., 1997. How to creatively fragment a landscape. Conservation Biology 11, 577–579.

Laurance, W.F., Laurance, S.G., 1996. Responses of five arboreal marsupials to recent selective logging in tropical Australia. Biotropica 28, 310–322.

Lima, M., Gascon, C., 1999. The conservation value of linear forest remnants in central Amazonia. Biological Conservation 91, 241–247.

Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., 1993. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia, IV. The presence and abundances of arboreal marsupials in retained linear habitats (wildlife corridors) within logged forest. Biological Conservation 66, 207–221.

Lovejoy, T.E., Bierregaard, R.O. Jr., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S. Jr., Powell, A.H., Powell, G.V.N., Schubart, H.O.R., Hays, M., 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soule, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates Inc, Sunderland, Massachusetts, pp. 257–285.

Malcolm, J.R., 1991. The Small Mammals of Amazonian Forest fragments: Pattern and Process. Ph.D. thesis, University of Florida, Gainesville.

McCune, B., Mefford, M., 1995. PC-ORD: Multivariate Analysis of Ecological Data. MJM Software Design, Gleneden Beach, OR.

Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89–107.

Newell, G.R., 1998. Australia's tree kangaroos: current issues in their conservation. Biological Conservation 87, 1–12.

Newell, G.R., 1999. Responses of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) to loss of habitat within a tropical rainforest fragment. Biological Conservation 91, 181–189.

Newmark, W.D., 1993. The role and design of wildlife corridors with examples from Tanzania. Ambio 22, 500–504.

Noss, R.F., 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1, 159–164.

Pahl, L.I., Winter, J.W., Heinsohn, G., 1988. Variation in responses of arboreal marsupials to fragmentation of tropical rainforest in north-eastern Australia. Biological Conservation 46, 71–82.

Preen, A.R., 1981. The Effects of Selective Logging on the Vertebrate Fauna of a Tropical Rainforest in North-east Queensland. B.Sc. honors thesis, James Cook University, Townsville, Australia.

Procter-Gray, E., 1984. Dietary ecology of the coppery brushtail possum, green ringtail possum and Lumholtz's tree-kangaroo in north Queensland. In: Smith, A.H., Hume, I.D. (Eds.), Possums and Gliders. Australian Mammal Society, Sydney, pp. 115–128.

Saunders, D.S., Hobbs, R.J. (Eds.), 1991. Nature Conservation 2: The Role of Corridors. Surrey Beatty, Chipping Norton, Australia.

Strahan, R. (Ed.), 1995. The Australian Museum Complete Book of the Mammals of Australia, Second Edition. Reed Books, Chatswood, Australia.

Tracey, J.G., 1982. The Vegetation of the Humid Tropical Region of North Queensland. CSIRO, Melbourne.

Whitmore, T.C., 1997. Rainforest disturbance, disappearance, and species loss. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 3–12.

Wilmott, W.F., Stephenson, P., 1989. Rocks and Landscapes of the Cairns District. Queensland Department of Mines, Brisbane.

Winter, J.W., Atherton, R.G., 1984. Social group size in north Queensland ringtail possums of the genera *Pseudocheirus* and *Hemibelideus*. In: Smith, A.H., Hume, I.D. (Eds.), Possums and Gliders. Australian Mammal Society, Sydney, pp. 311–319.

Winter, J.W., Bell, F., Pahl, L., Atherton, R., 1984. The specific habitat requirements of selected rainforest mammals of north-eastern Australia. Report to World Wildlife Fund-Australia, Sydney.

Winter, J.W., Bell, F., Pahl, L., Atherton, R., 1987. Rainforest clearfelling in northeastern Australia. Proceedings of the Ecological Society of Queensland 98, 41–57.