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Research Article

Corridors and connectivity: when use and function do not equate

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Abstract

Connectivity, or the integration of populations into a single demographic unit, is an often desired, but largely untested aspect of wildlife corridors. Using a corridor system that was established at least 85 years prior, we investigated the extent of connectivity provided. This was undertaken using a combined ecological and genetic approach with connectivity estimated by gene flow. Vegetation within the corridor was found to be comparable in physical structure and species composition to that within the connected patches and the two target species (*Melomys cervinipes* and *Uromys caudimaculatus*) were shown to occur along the corridor but not within the surrounding matrix. These factors indicated that the corridor was suitable for use as a model system. The population structure (weights of individuals, sex ratios and the percentage of juveniles) of both species were also similar within the corridor and the connected patches suggesting that the corridor provided the resources necessary to sustain breeding populations along its length. Despite this, populations in patches linked by the corridor were found to show the same significant levels of genetic differentiation as those in isolated habitats. *M. cervinipes*, but not *U. caudimaculatus*, also showed population differentiation within the continuous habitat. Although based on only one corridor system, these results clearly demonstrate that connectivity between connected populations will not always be achieved by the construction or retention of a corridor and that connectivity cannot be inferred solely from the presence of individuals, or breeding populations, within the corridor.

Introduction

Genetic theory suggests that the isolation of habitat patches as a result of fragmentation will; reduce effective population size and levels of genetic diversity (Amos and Harwood 1998; Lindenmayer and Peakall 2000), increase inbreeding levels (Frankham and Ralls 1998; Soulé and Mills 1998) and may eventually compromise adaptive potential and influence long term population persistence (McCaughley 1993; Saccheri et al. 1998). These disruptions arise from a reduction of, or more likely, a cessation to dispersal which leads to reduced levels of gene flow (Burgman and Lindenmayer 1998). Further, conservation biology theory suggests that construction or retention of a wildlife corridor between two otherwise isolated habitat patches may increase or at least maintain the levels of inter-patch dispersal (Kozakiewicz 1993; Primack 1993; MacMahon and Holl 2001). This can translate into gene flow among

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populations within the habitats, which can in turn lead to elevated levels of genetic diversity, and a general homogenization of their genetic composition. This has the potential to balance any potentially negative effects of isolation (Harris and Scheck 1991; Merriam 1991; Bolen and Robinson 1995).

Despite the potential increase in gene flow being stated as a major aim of wildlife corridors in most theoretical papers (e.g. Harris and Scheck 1991; Simberloff et al. 1992; Rosenberg et al. 1998; Bolger et al. 2001), very few corridor studies, conducted at a landscape scale, have included a genetic component (but see Leung et al. 1993; Mech and Hallett 2001). Instead, the majority of research has employed mark-recapture techniques to investigate corridor use as additional habitat or for movement, and in some instances to provide the basis for comment on the potential for gene flow (Bennett 1990).

Although well established within the literature as a means for detecting gene flow, direct methods (i.e. trapping) are actually indicators of dispersal or habitat occupation and their use as an indicator of gene flow is potentially constrained by an inability to detect all dispersal events or to determine whether dispersal events actually translate into gene flow (Slatkin 1994). Dispersers may not be tolerated by conspecifics and they may not integrate into the recipient population if individuals have moved into populations experiencing shortages of space or resources, as may occur in the remnant patches created by habitat fragmentation. Use of the corridor by a non-breeding subset of the population, or a sex-biased cohort, may also prevent gene flow. Extrapolation of trapping data to estimates of effective gene flow can therefore be erroneous in both directions (Lidicker and Patton 1987; Whitlock and McCaughley 1999). By contrast, indirect methods of estimation (i.e. the use of genetic markers) assess the cumulative contribution to the recipient population of only effective dispersal events while not discriminating between the spatial and temporal manner via which gene flow occurred (Slatkin 1994; Mech and Hallett 2001; Neigel 2002). Hence, as gene flow requires integration of an individual into the recipient breeding population, it usually cannot be estimated by use of ecological methods alone (Mech and Hallett 2001). Exceptions to this statement exist when demographic data exist for populations pre- and post-corridor construction and changes to population structure indicate an increase in gene flow (Mansergh and Scotts 1989).

Increasing the level of connectivity [the integration of sub-populations of organisms into a functional unit (*sensu* Merriam 1984)] between otherwise isolated populations is often the desired function of a wildlife corridor and as gene flow depends on the successful integration of individuals or their genes into an alternate population, it provides a means for quantifying the extent of connectivity. Where gene flow, and hence connectivity is demonstrated, the use of genetic methods alone may provide an adequate understanding of the processes that are operating within the corridor system. In instances where gene flow via a corridor is shown to be absent or minimal however, the use of ecological techniques may provide an indication of the factor responsible for the lack of connectivity. Lindenmayer (1994) and Bierregaard *et al*. (1997) called for wildlife corridor studies to adopt an integrated approach, yet this combined use of ecological and genetic methods has generally been ignored. The current study used such a combined approach to assess the effectiveness of a corridor in providing connectivity. In particular, the issue of whether the 'use' of the corridor as habitat translated into the 'function' of increasing connectivity was examined.

Methods

Study sites

The study system was located on the Atherton Tablelands of tropical northern Queensland, Australia (Figure 1). The area was originally covered by complex notophyll and mesophyll rainforest (Tracey and Webb 1975) however, extensive clearing in the early 1900s (Frawley 1983) created a highly modified landscape mosaic consisting of agricultural land and remnant rainforest patches. The region is of conservation significance due to its high levels of species richness and endemism (Rainforest Society of Queensland 1986; Winter 1991).

Sites were categorized according to their degree of physical connectedness (*sensu* Baudry and Merriam 1988) to other habitats of similar vegetation type and included: (i) *connected* sites consisting of

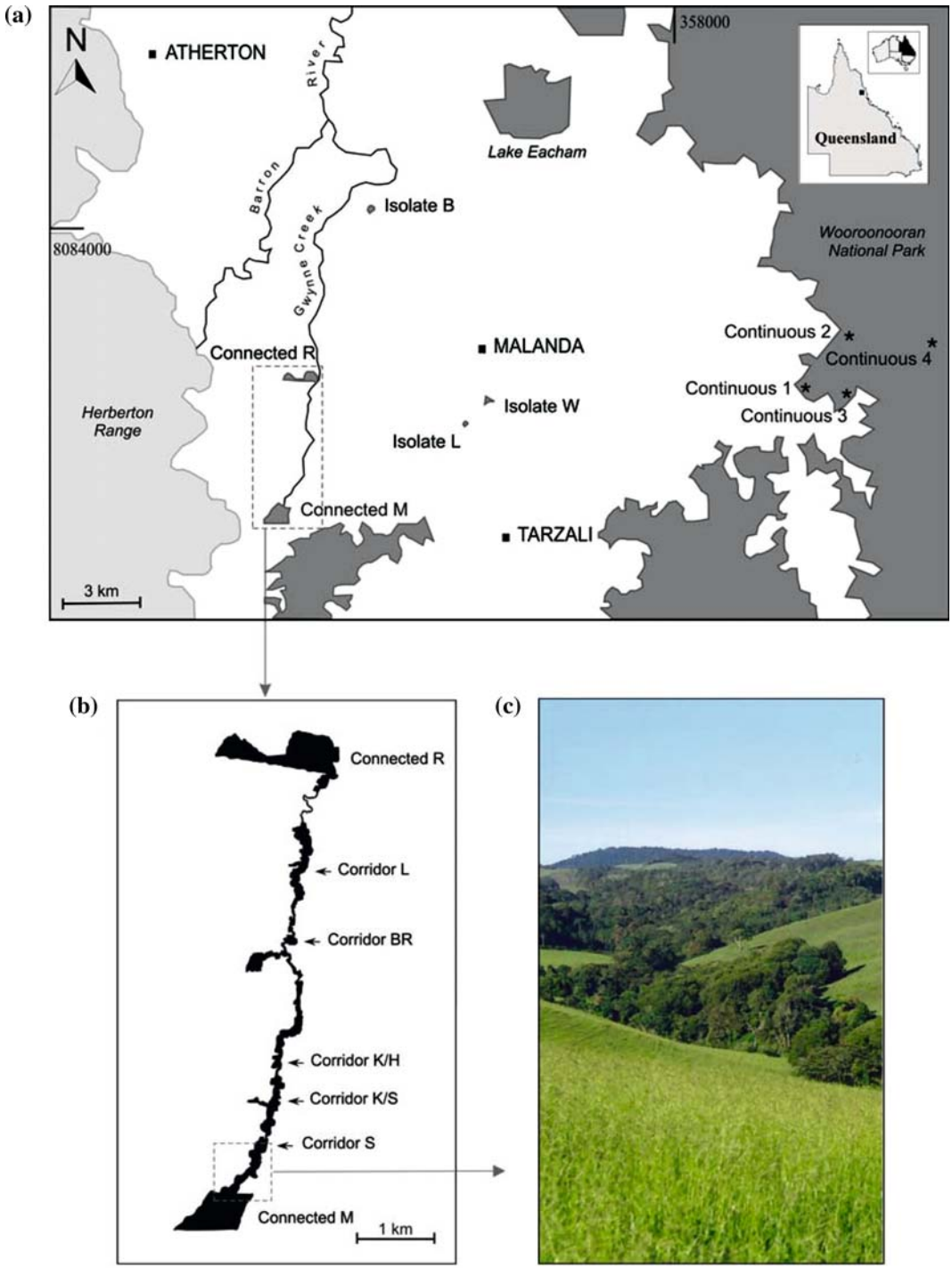

Figure 1. Location of the study system: (a) regional map of the Atherton Tablelands (Australian Map Grid Zone 55, WGD'66) indicating 'connected', 'isolate' and 'continuous' study sites. ▫ = sclerophyll forest, ■ = rainforest, (b) detailed map of the corridor system showing 'corridor' sites, (c) photograph of the corridor system highlighting the difference in the vegetation of the corridor and matrix.

remnant rainforest habitat surrounded by a pasture matrix but connected to another rainforest habitat by a corridor, (ii) *corridor* sites located within the corridor, (iii) *isolate* sites of remnant rainforest habitat completely surrounded by a pasture matrix, (iv) *continuous* sites within a large tract of rainforest habitat and (v) *matrix* sites within the pasture surrounding the corridor/patch.

The corridor system (i.e. the connected patches and the corridor) in which this study was conducted consists of original riparian vegetation linking two rainforest remnants within an extensive matrix of short, heavily grazed cattle pasture. The corridor consists primarily of rainforest species but also includes some exotics. The conversion of rainforest to pasture was completed prior to 1918 leaving the ~4.5 km corridor as the only linkage between remnant patches for at least 85 years (landowner, pers. comm.) thus providing an ideal opportunity to assess the effectiveness of an 'original' corridor over an extended time frame.

To increase comparative power, the distance between pairs of 'continuous' and 'isolate' control sites was matched to the length of the corridor as closely as possible. Further, to ensure that the geographic and effective distance were equivalent, the selected isolate sites were surrounded by a matrix habitat similar to that surrounding the corridor system and two of the three sites were located on a creekbank, therefore containing riparian vegetation. This design ensured that any differences in gene flow among sites could be attributed solely to the level of site connectedness.

Study species

Species were selected on the basis that they (i) were likely to be present in all forested sites, (ii) were not likely to utilize the matrix to any great extent, (iii) were sufficiently abundant to obtain adequate sample sizes for genetic analysis and (iv) had a short generation time to enable the detection of any disruption to gene flow post-fragmentation.

Two closely related species of native rodent were selected for study, *Melomys cervinipes* (35–150 g, Watts and Aslin 1981) and *Uromys caudimaculatus* (665–1000 g, Watts and Aslin 1981). The two species have very similar life-history strategies in that females become reproductively mature in their first year and have gestation periods of 38–40 days (Watts and Aslin 1981) suggesting a minimum of 85 generations since fragmentation. The species differ however, in their movement and dispersal capabilities with respect to distance. The average observed range length estimates for *M. cervinipes* reached a maximum value of 75 m (Wood 1971) and the average distance between successive captures for males of the species was 71.5 m (Smith 1984) while *U. caudimaculatus* individuals are known to move up to 1 km in a 2-day period (Goosem 2001). Thus, the smaller species is likely to rely upon 'generational' movement whereby the offspring of individuals (or generations subsequent), rather than the original dispersing individuals themselves immigrate into the destination patch (Bennett 1999). Alternatively, *U. caudimaculatus* individuals have a greater chance of dispersing directly between the connected patches.

U. caudimaculatus has recently been recorded as living in habitats other than rainforest, including *Allocasuarina* woodlands and wet-sclerophyll forests (Vernes 2003), and is even known to make short forays into open areas (Crome et al. 1994; Harrington et al. 2001). These forays however, are often associated with man-made structures such as dairies and farmhouses and do not involve travel in short pasture over the distance of kilometres, as would be required to move between connected patches by means other than the corridor.

Genetics

Tissue was obtained from ear biopsies and genomic DNA extracted using a phenol/chloroform procedure (modified from Fuller et al. 1997). Polymerase chain reaction (PCR) was used to amplify a 414 base pair sequence of the D-loop region of the mitochondrial DNA (mtDNA) using the MT15996L (created by M.S. Elphinstone, Southern Cross University) and MT16498H (Meyer et al. 1990) primers. PCR was also used to amplify five microsatellite loci (Mc1K, Mc2B, Mc2E, Mc2O and Mc2P; D. Paetkau pers. comm.) for *M. cervinipes* and six microsatellite loci (UVC19, UVC232, UVC238, UVC245, UVC432, UVC452; Chand et al. 2005) for *U. caudimaculatus*.

MtDNA PCR products were screened for variability using temperature gradient gel electrophoresis (TGGE) (Rosenbaum and Reissner 1987) with haplotypes visualized via silver staining.

Individuals of the congeners *M. burtoni* and *U. hadrourus* were used as outgroup species for the TGGE analysis (Campbell et al. 1995). This not only allowed greater resolution of similar haplotypes in the target species but it also enabled the identification of individuals from morphologically cryptic congeners which may have been sampled inadvertently.

Microsatellite allelic variation was screened via gel electrophoresis using a Gel-Scan 2000 (Corbett Research). Digital images were scored using One-DScan (Scanalytics Inc.) with all output also checked manually. To increase scoring accuracy, and to allow comparisons among gels, reference individuals were run on all microsatellite and TGGE gels.

MtDNA data was checked for neutrality using Tajima's (1989) test while pairwise comparisons of population differentiation were conducted using F_{ST} (Weir and Cockerham 1984) and Raymond and Rousset's (1995) analogue to Fisher's exact test. Given the contemporary nature of the landscape modification, haplotype frequencies, rather than sequence variation, were analyzed (Aars et al. 1998).

nDNA data from each microsatellite loci pair were checked for linkage disequilibrium using an extension of Fisher's exact test (Slatkin 1994). Pairwise tests of population differentiation were conducted using F_{ST} (Wright 1978) and a log-likelihood (G) based exact test (Goudet et al. 1996). Where multiple comparisons were made, α values were adjusted according to the sequential Bonferroni correction technique (Rice 1989). This was performed separately for each genetic marker. All pair-wise comparisons of nDNA involving the connected sites were conducted in two ways: (i) including all samples taken for each species within the connected patch and (ii) including only those samples collected from the trapping grid at the patch/corridor boundary (Connected R1 & M1) where all individuals are assumed to have direct access to the corridor.

Vegetation assessment

Although once part of the same continuous tract of rainforest, vegetation within the corridor and connected patches were compared to ensure that the corridor had remained as suitable habitat for use by the target species. This was conducted to eliminate habitat type as a possible cause of any population structuring that may be detected among populations at either end of the corridor. Structural and floristic attributes of the vegetation were assessed at five sites along the corridor and five random sites along the creek within each of the connected patches. Creek-banks at each corridor site were divided into 5×50 m parallel strata based on distance from the creek (0–5, 5–10, 10–15, 15–20 and >20 m). The number of strata sampled per site within the corridor varied according to corridor width and whether landowner permission allowed sampling on both creek-banks. Sampling sites within the connected patches were stratified in a similar manner but consisted of six strata so that the forest interior was sampled adequately (0–5, 5–10, 10–15, 15–20, 20–30 and 30–50 m).

Ground, vertical and canopy cover were determined at five random locations along each transect (i.e. 50 m $\times$ stratum width) per site. To determine ground cover, a digital photo of the ground was taken from a height of 1.5 m. The image was overlaid with a grid of 100 points and the percent ground cover calculated by scoring the number of grid intersects covered with vegetation. Vertical cover at ground level was determined by photographing a 1 m^2 board placed vertically, onto which 100 grid intersects were marked. Photographs were taken through vegetation from a constant distance so that the board filled the image and the percent cover was determined as the number of grid intersects covered by vegetation. Percent foliage cover (PFC) was estimated as [(1 – visible sky) * 100] from an image taken with a fish-eye lens. The visible sky value was obtained using the canopy analysis software HemiView 2.1 (1999).

Diversity and abundance of plant species present within the corridor were estimated at one random location within each transect. All fruit and seeds present in the leaf litter and the O horizon of the soil within a 0.5 m×0.5 m quadrat were collected during August 2002 which coincides with the period of peak fleshy fruit abundance (D. Elmouttie pers. comm.).

The point-centre quarter technique (Krebs 1989) and diameter at breast height (DBH) were used to determine stem density (as per Pollard 1971) and basal area in three height classes (1–4, 4–10 and

>10 m). For these variables, the original sampling area was divided in half such that each of the two new transects within the corridor was 50 m × 1/2 corridor width. Measurements were taken at five random locations within each transect. Absolute stem density was calculated using the same data but considering the nearest tree (>1 m) in each quadrant regardless of height category. Absolute basal area was calculated as absolute stem density × mean basal area of all height classes. Sampling of these variables within the connected patches was performed at 5 random locations within each of two transects that consisted of strata 1–3 and 4–6 combined.

Vegetation assessment was only undertaken in the connected and corridor sites as its sole purpose was to determine whether the corridor offered similar habitats as the remnant patches or whether it presented a potential barrier to dispersal and/or residency of the target species. Any difference in vegetation structure or composition between these two site types would introduce an additional variable that may present a barrier to gene flow and confound the interpretation of data assessing connectivity levels.

Trapping

Trapping was undertaken every three months from February 2002 until March 2003 within the connected patches at the point of intersection with the corridor and at three sites along the corridor. An additional two corridor sites and four sites within the matrix were added to the final four trapping sessions from May 2002. Trapping was undertaken to ensure that the corridor was used by suitable individuals of each species and that gene flow was not likely to be impeded by demographic factors such as use of the corridor by immature individuals only.

Trapping within the connected patches was conducted on a 7×6 trapping grid with grid intervals of 25 m. One cage trap (20 cm × 20 cm × 56 cm; Mascot wireworks) and one box trap (30 cm × 9cm × 10cm; Elliot Scientific) were placed at each grid point. To maximize trap encounter, an extra box trap was placed between each cage/box pair on grid lines running in an east-west direction. Trapping within the corridor and matrix consisted of 190 m transects with one cage trap and one box trap placed at each of 20 points located 10 m apart. Traplines within the matrix were located 50 m from the corridor/matrix boundary. On each occasion, trapping was undertaken over eight consecutive nights within the connected patches and corridor and over six consecutive nights within the matrix resulting in a total of 8991 trapnights within patches, 7360 within the corridor and 3800 within the matrix. All results were corrected for trap effort where applicable.

Traps were baited with linseed oil soaked cardboard and checked for captures each morning. Upon capture, individuals of the target species were marked with a uniquely numbered microchip (Compliance no. ISO 11794, Veterinary Marketing Network) and the following data were recorded: trap location, weight, sex and sexual condition [recorded as mature female (perforate), reproducing female (extended nipples or other visible signs of pregnancy), immature female, mature male (scrotal testes) or immature male]. Similar to the assessment of vegetation, the collection of this demographic data was only undertaken within the connected and corridor sites. This data was solely intended to demonstrate whether individuals were present within the corridor and if so, whether they were capable of contributing in a positive manner to the process of connectivity between the connected patches. As all components of the system were once connected, and individuals of both species still persist at all sites, it was not deemed necessary to conduct a demographic study of populations from within continuous and isolated sites.

Additional trapping sessions were conducted within the continuous and isolated habitats and at additional locations within the connected patches (Connected R for *U. caudimaculatus* only) on an *ad-hoc* basis to obtain additional samples for genetic analyses. Samples were obtained from a similar spatial area within each site regardless of total patch size.

Results

Population differentiation

Following sequential Bonferroni α correction, no populations of either species displayed a significant deviation from neutrality for the mtDNA marker. All five microsatellite loci (nDNA) used for

M. cervinipes were also shown to be suitable for use as independent markers with no linkage between loci pairs evident. In contrast, two of the six loci analysed for *U. caudimaculatus* were found to be highly and significantly linked in all populations ($p < 0.0001$) (UVC19 and UVC245). Locus UVC19 was therefore eliminated from all further analyses. While some significant linkage disequilibrium was evident in the remaining comparisons, no consistent pattern was evident in other pairs of loci so all remaining loci were retained. All loci were polymorphic with 13–25 alleles and 15–19 alleles per locus present in the sampled individuals for *M. cervinipes* and *U. caudimaculatus* respectively.

Significant population differentiation was detected among *M. cervinipes* populations in isolated sites for both mtDNA and nDNA (Table 1). Similarly, both markers indicates significant structuring between populations in the patches connected by the corridor. Divergent results were obtained for comparisons between *M. cervinipes* populations within the continuous control with microsatellites suggesting restricted or no gene flow and mtDNA markers showing no population differentiation.

Significant differences were detected in the genetic structure of the *U. caudimaculatus* populations between Connected R and both of the isolated sites for both genetic markers (Table 1). Congruent results were also obtained for the markers within the continuous habitat where no structuring was detected among populations. Divergent results were obtained for comparisons between the two connected patches with mtDNA indicating similar population composition and nDNA revealing significant differentiation (Table 1).

Vegetation

Moderate within-site variation was detected in several structural attributes of the vegetation in the three components of the corridor system (Table 2). Discriminate function analysis identified three

Table 1. Summary table of the pair-wise differentiation of (panel a) *M. cervinipes* and (panel b) *U. caudimaculatus* populations at a landscape scale.

Sites (sample size)	mtDNA		nDNA	
	Exact *p*	F_{ST}	Exact *p*	F_{ST}
(Panel a) *M. cervinipes*				
Connected				
Connected R1 (29)/Connected M1 (31)	$< 0.001^{*}$	0.20	$< 0.001^{*}$	0.05
Connected R – all (72)/Connected M – all (129)	$< 0.001^{*}$	0.09	$< 0.001^{*}$	0.03
Isolates				
Connected R1 (29)/Isolate B (49)	$< 0.001^{*}$	0.20	$< 0.001^{*}$	0.05
Connected R1 (29)/Isolate L (30)	$< 0.001^{*}$	0.23	$< 0.001^{*}$	0.08
Connected R1 (29)/Isolate W (31)	$< 0.001^{*}$	0.18	$< 0.001^{*}$	0.05
Connected R – all (72)/Isolate B (49)	$< 0.001^{*}$	0.15	$< 0.001^{*}$	0.05
Connected R – all (72)/Isolate L (30)	$< 0.001^{*}$	0.13	$< 0.001^{*}$	0.07
Connected R – all (72)/Isolate W (31)	$< 0.001^{*}$	0.13	$< 0.001^{*}$	0.05
Continuous				
Continuous 1 (30)/Continuous 2 (33)	0.475	< 0.01	0.02^{*}	0.01
Continuous 3 (11)/Continuous 4 (20)	0.765	< 0.01	0.04^{*}	0.02
(Panel b) *U. caudimaculatus*				
Connected				
Connected R1 (32)/Connected M1 (30)	0.07	0.13	$< 0.001^{*}$	0.05
Connected R – all (43)/Connected M1 (30)	0.17	< 0.01	$< 0.001^{*}$	0.05
Isolates				
Connected R1 (32)/Isolate B (38)	$<0.001^{*}$	0.19	$< 0.001^{*}$	0.05
Connected R1 (32)/Isolate W (28)	0.003^{*}	0.06	$< 0.001^{*}$	0.05
Connected R – all (43)/Isolate B (38)	$<0.001^{*}$	0.20	$< 0.001^{*}$	0.04
Connected R – all (43)/Isolate W (28)	0.003^{*}	0.06	$< 0.001^{*}$	0.05
Continuous				
Continuous 1 (28)/Continuous 2 (21)	0.86	< 0.01	0.31	0.01

* denotes significant *p*-values after sequential Bonferroni correction.

Table 2. Variation in structural attributes of the vegetation within the three components ($n = 5$ for each system component) of the corridor system. Mean (±s.e.) per site with maximum and minimum values in parentheses.

	Connected M	Connected R	Corridor	F, p
Ground cover (%)	17.2 ± 2.1 (11.3–24.1)	21.8 ± 1.9 (17.7–28.5)	31.5 ± 6.4 (11.0–44.8)	2.91, 0.09
Vertical structure 0–1 m (%)	14.6 ± 2.9 (9.1–25.2)	25.5 ± 3.0 (16.3–24.8)	27.9 ± 5.5 (12.0–44.0)	3.39, 0.07
P.F.C. (%)	98.0 ± 0.3 (97.3–99.1)	97.5 ± 0.3 (96.5–98.5)	91.5 ± 2.8 (82.5–97.3)	4.14, 0.04
% density 1–4 m	57.3 ± 3.5 (50.0–69.0)	63.6 ± 3.4 (52.4–70.8)	58.5 ± 6.0 (42.9–76.8)	0.55, 0.59
% density >10 m	16.9 ± 2.0 (13.0–24.5)	19.6 ± 1.3 (15.8–23.1)	19.2 ± 3.9 (9.2–30.8)	0.30, 0.75
Absolute density *100 (No./100 m^2)	43.8 ± 3.5 (31.2–51.0)	36.4 ± 2.2 (32.1–38.4)	31.4 ± 10.3 (6.3–62.7)	0.95, 0.41
Absolute basal area (cm/m^2)	32.2 ± 10.0 (12.5–70.2)	51.4 ± 13.7 (20.6–92.7)	46.0 ± 11.9 (10.9–84.1)	0.69, 0.52

variables capable of distinguishing among the three system components (Wilks $\lambda = 0.34$, $F = 2.4$, $p = 0.06$) (Table 2). These variables were arcsin percent foliage cover (PFC) (partial $\lambda = 0.65$, $p = 0.12$), arcsin vertical structure 0–1 m (partial $\lambda = 0.64$, $p = 0.10$) and total basal area (partial $\lambda = 0.81$, $p = 0.34$). However only arcsin PFC showed any significant differences when compared between system components with ANOVA ($F_{(2,12)} = 4.14$, $p = 0.04$) (Table 2). Tukey's *post-hoc* tests showed PFC in the corridor to differ from that of Connected M but not Connected R. Yet, with a mean PFC of 93%, the sites within the corridor retain a dense canopy cover.

Fifty-five species of plant were identified from the sampling locations within the corridor system, all of which were known rainforest species (Hyland et al. 1999; Williams 1999). Twenty-two species were found within Connected R (6–12 species per site), 33 in Connected M (6–14) and 30 from within the corridor (1–16), with 16 species (29%) present in both the corridor and at least one of the connected patches. Neither the total number of seeds/fruit per site, nor the total species richness per site, varied among the system components (No. fruit: $F_{(2,12)} = 1.32$, $p = 0.30$; species richness: $F_{(2,12)} = 0.16$, $p = 0.86$).

Two sampling locations within Connected R showed highly disproportionate numbers of fruit due to the presence of fruiting *Aleurites molucanna* trees. After removal of this one species from the dataset, Renyi's diversity index showed no substantial differences between the system components (Figure 2). The intersection of all three curves indicates that species diversity within the corridor is similar to that within both connected patches (Southwood and Henderson 2000).

Population structure

Trapping within the corridor system resulted in the capture of 220 *M. cervinipes* individuals (trapped on 508 occasions) and 86 *U. caudimaculatus* individuals (trapped on 137 occasions). Both species were found at all sites within the corridor system (Figure 3) however, as expected from their known habitat preferences, neither *U. caudimaculatus* nor *M. cervinipes* were trapped in the matrix habitat over 3800 trapnights.

The total number of unique individuals trapped per system component (Connected R, Connected M and Corridor) differed for both species (*M. cervinipes*: $\chi^2_{(2)} = 6.47$, $p = 0.039$, *U. caudimaculatus*: $\chi^2_{(2)} = 15.7$, $p < 0.001$). *M. cervinipes* had greater numbers than expected in the corridor relative to Connected M, while *U. caudimaculatus* had more individuals then expected in Connected R compared to Connected M. However, when the two connected sites were pooled, there was no differential habitat use between the connected patches and the corridor (*M. cervinipes*: $\chi^2_{(1)} = 3.69$, $p = 0.06$, *U. caudimaculatus*: $\chi^2_{(1)} = 1.56$, $p = 0.22$). The two species also showed different use of sites within the corridor (*M. cervinipes*: $\chi^2_{(4)} = 40.38$, $p < 0.001$, *U. caudimaculatus*: $\chi^2_{(4)} = 20.01$,

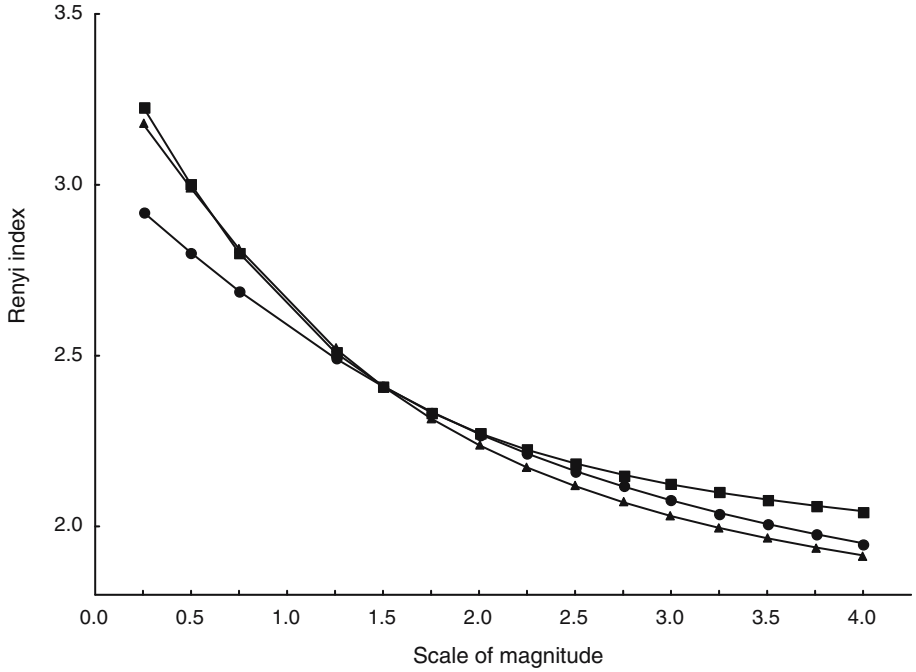

Figure 2. Species diversity per system component as measured by the Renyi index. ● = Connected R, ■ = Connected M, ▲ = Corridor.

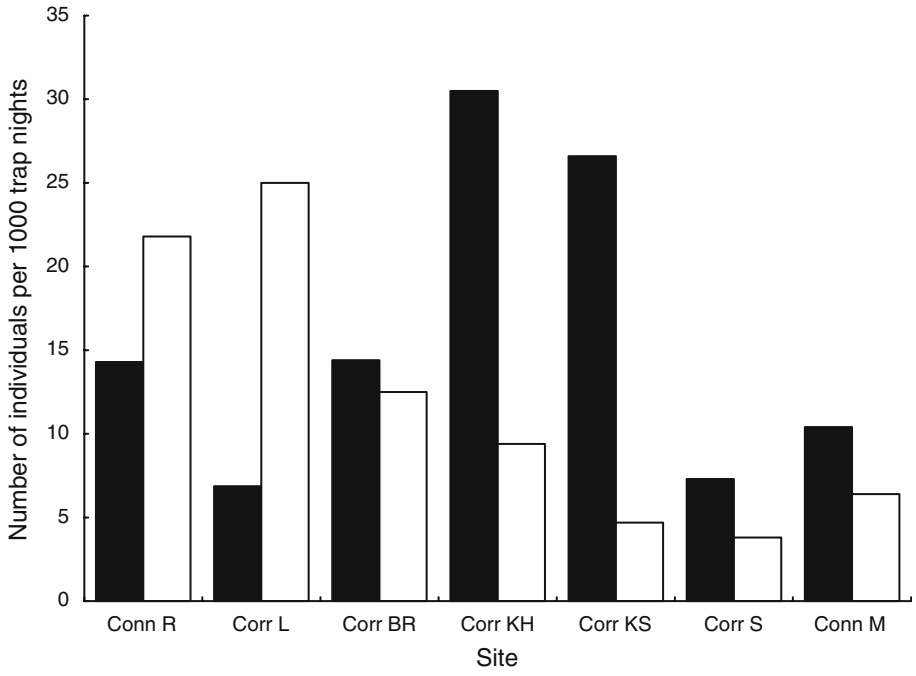

Figure 3. Number of individuals (per 1000 trap nights) per site [*M. cervinipes* (■) and *U. caudimaculatus* (□)].

$p = 0.005$). No relationship was evident between the number of individuals of each species per site ($r^2_{(1,5)} = 0.11$, $p = 0.47$) when corrected for trap success. This suggests that the presence of one species had little impact on numbers of the other species at any given site.

Despite the variation in the number of animals per system component, the structure of all populations were similar. Sex ratios were consistent between the corridor and connected patches when sites were pooled across the entire study. Males were more abundant for *M. cervinipes* but proportions were near equal (n_{corridor} = 69♂, 46♀; $n_{\text{connected patches}}$ = 62♂, 47♀: $\chi^2_{(1)} = 0.15$, $p = 0.69$). Conversely, both sexes of *U. caudimaculatus* were trapped in approximately equal numbers within each system component (n_{corridor} = 21♂, 20♀; $n_{\text{connected patches}}$ = 20♂, 25♀: $\chi^2_{(1)} = 0.19$, $p = 0.67$).

Similarly, no significant differences were detected when sex ratios [expressed as the proportion of males in the population (arcsin transformed)] were compared for each trapping session on a per site basis for *M. cervinipes* (mean ± s.e.: 0.55 ± 0.05) (site: $F_{(6,\ 21)} = 1.96$, $p = 0.12$, month: $F_{(4,\ 21)} = 1.28$, $p = 0.31$). *U. caudimaculatus* showed minimal variation between two corridor sites (S and KH) (mean ± s.e.: 0.45 ± 0.07) (site: $F_{(6,18)} = 2.72$, $p = 0.046$, month: $F_{(4,\ 18)} = 0.56$, $p = 0.69$). This latter result was due to Corridor S having a maximum of a single individual per trip.

Individuals in reproductive condition (pregnant or lactating) of both species were found in the corridor and the connected patches with the breeding season for *M. cervinipes* (November to March) consistent between the two habitat types. Pregnant individuals of *U. caudimaculatus* were not caught in sufficient numbers within any component to determine a distinct breeding season. As expected, given these similarities, the proportion of juveniles per trip was found not to differ between the corridor and connected patches for either species (*M. cervinipes*: $t_{\text{paired }(4)} = 2.19$, $p = 0.09$; *U. caudimaculatus*: $t_{\text{paired }(4)} = 0.85$, $p = 0.40$) with juveniles present in all sites except Corridor S (Figure 4).

Finally, the mean weight of individuals did not differ between connected patches and the corridor for either sex of both species (Figure 5) (*U. caudimaculatus*: male, $F_{(1,\ 38)} = 0.012$, $p = 0.91$; female, $F_{(1,\ 44)} = 0.003$, $p = 0.96$) (*M. cervinipes*: male, $F_{(1,\ 129)} = 1.71$, $p = 0.19$; female, $F_{(1,\ 91)} = 0.60$, $p = 0.44$). These results are based on the individual being the unit of replication such that each data point represents the mean weight if individuals were caught on more than a single trip.

Discussion

The provision of a wildlife corridor, and the corresponding increase in landscape connectedness, is expected to result in increased levels of gene flow between populations in remnant patches. The genetic results from this study, however, did not support this expectation with both genetic markers indicating that populations within remnant patches connected by the corridor were as dissimilar to each other as those in patches isolated completely by a hostile matrix. This high degree of differentiation among *M. cervinipes* populations indicates that limited, if any, gene flow occurs among populations within remnant patches regardless of whether or not they are linked by a corridor.

Similar results were found for *U. caudimaculatus* despite mtDNA results appearing to initially suggest gene flow via the corridor. It is highly likely that the mtDNA results were confounded by a severe reduction in mtDNA diversity. A maximum of four haplotypes were found per site (compared with an average of eight per site within the continuous forest: unpublished data), and 78% of all individuals from the two isolated and two connected sites were of the same haplotype (unpublished data). Alternatively, the nuclear DNA, which retained greater allelic diversity (unpublished data), clearly indicated a lack of gene flow between all remnant patches, regardless of their degree of isolation. While discordant results between mtDNA and nDNA markers are not unusual, it is usually mtDNA data that indicates structuring to a greater extent due to the smaller effective population size and female philopatry (Moritz et al. 1987). For these reasons, greater emphasis is placed here on the *U. caudimaculatus* results obtained for nDNA data that strongly indicate a lack of gene flow between remnant habitats regardless of their degree of isolation. Results for *M. cervinipes* and *U. caudimaculatus* contrast with those of Mech and Hallett (2001) who showed populations of *Clethrionomys gapperi* in habitat linked by corridors to be more genetically similar than those sites separated over the same distance by an alternate habitat.

The extent of genetic differentiation among populations within the continuous forest varied between the two species as may be expected given their different dispersal abilities. No significant

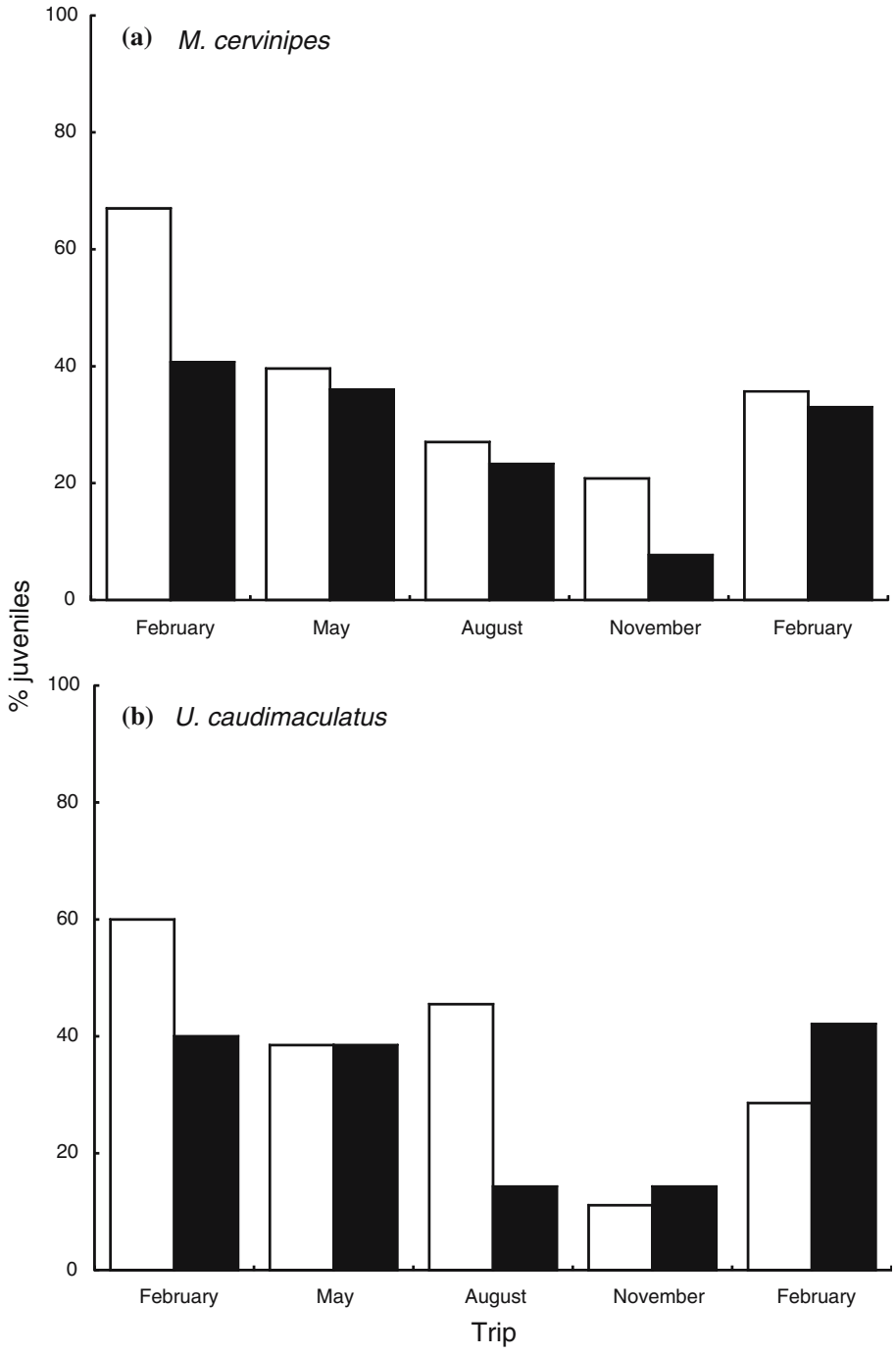

Figure 4. Percent of juveniles per trip per habitat type (corridor □, connected patch ■).

differences were found between populations of the larger *U. caudimaculatus*, with results being consistent for both genetic markers, while nDNA but not mtDNA suggested population structuring for *M. cervinipes*. For both species, the pattern of genetic structuring among populations within the connected patches more closely resembled that of populations in completely isolated remnants rather

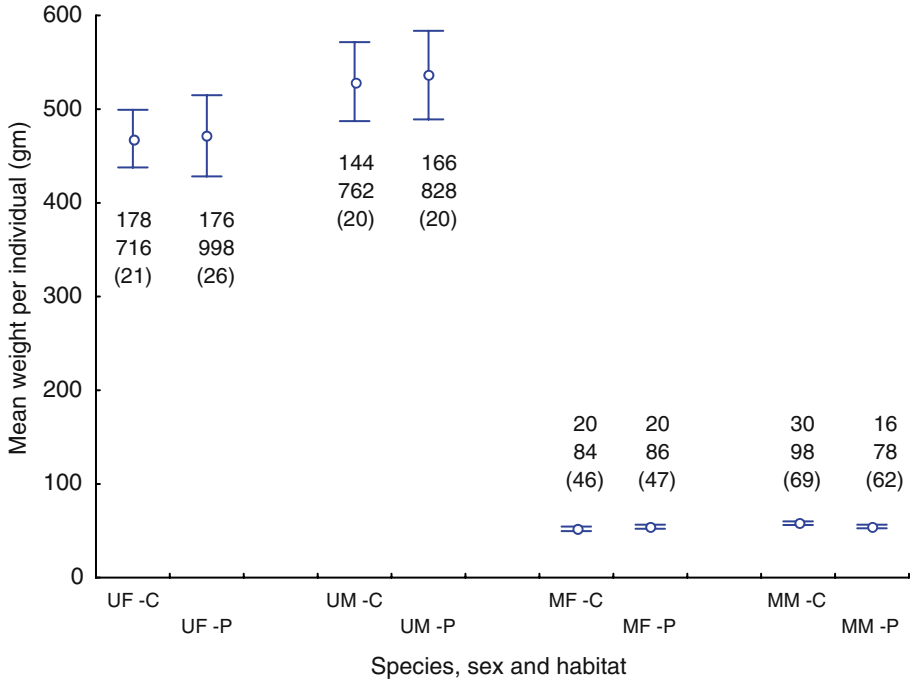

Figure 5. Mean weight (± s.e.) of individuals per sex and habitat type. Numbers immediately under or above bars represent the minimum/maximum weight recorded. Figures in parentheses denote sample size. Labels on *x*-axis: U/M = species, F/M = sex, P/C = habitat (connected patch/corridor) e.g. UF-C = *U. caudimaculatus* (female) from the corridor.

than those within the continuous forest. This suggests that within this study system, the target species are not experiencing the expected increase in gene flow as a result of enhanced dispersal potential via the corridor.

The comparative assessment of physical structure and plant species composition between the corridor and the connected patches did not provide any explanation for the lack of gene flow via the corridor. As was expected, the vegetation within the corridor was representative of that present in the connected patches. Sampling locations within Connected R, Connected M and the corridor all showed some within-site variation suggesting that while the vegetation within the linear linkage may have been affected by factors such as edge effects and the intrusion of exotic species, the connected patches also display a degree of heterogeneity. The similarity in vegetation composition between the components of the corridor system suggested that the corridor should be suitable for use as a path for transit, by both rodent species, between the connected patches or for the provision of additional habitat for residency.

Investigation into the structure of populations within the corridor also failed to provide an explanation for the lack of gene flow. Soulé and Gilpin (1991) suggested that in general, individuals entering a corridor often represent a non-random subset of individuals present within the connected patches. In instances where corridors contain only displaced aged animals, surplus individuals who may be socially excluded, or a sex-biased cohort, gene flow is unlikely. To date, very little attention has been paid to the age or sex ratios of individuals within corridors relative to those within the connected remnant patches and how this may impact upon the likely effectiveness of the corridor under investigation (but see Downes et al. 1997a, b who found male-biased sex ratios and significantly lighter individuals within the corridor for *Antechinus stuartii*). In this current study, age and sex ratios were consistent between the corridor and the connected patches indicating that breeding should occur there. Accordingly, juveniles and pregnant females were present within the corridor at locations unlikely to be reached via direct dispersal from a connected patch. Furthermore, weights of individuals within the corridor were

similar to those within the remnants suggesting that the corridor provides adequate resources and that animals within the corridor do not represent a cohort consisting fully of subordinate or unhealthy individuals. A similar suite of results were found for *U. caudimaculatus* within the corridor system. Hence, although direct dispersal is the most likely mode of movement for this larger species, the presence of breeding individuals within the corridor provides a second possible means of connectivity via generational gene flow. Thus the ecological requirements for connectivity were met for both species.

This observed discrepancy between the ecological and genetic data raises two interesting points. Firstly, it highlights how the combined use of two discrete disciplines (ecology and genetics) can enhance our understanding of a wildlife corridor system and thus supports the call by Lindenmayer (1994) and Bierregaard et al. (1997) for more studies to adopt an integrated approach. If only ecological techniques had been employed in this study to assess the effectiveness of the corridor in providing connectivity, a favourable conclusion would most likely have been drawn.

Secondly, it raises the question as to why the corridor did not increase gene flow, given that it provided suitable ecological conditions? We propose that complex interactions between habitat heterogeneity and rodent social behaviour is the potential reason why use of the corridor as habitat apparently failed to translate into effective gene flow. If hostile interactions such as the active defence of territory, mates or food resources occur between social groups, gene flow may be affected. The extent of population differentiation for *M. cervinipes* within the continuous habitat, as detected by nDNA, suggests that social factors affecting connectivity may be a common attribute of the species whereas the linear nature of the corridor could alter social interactions for *U. caudimaculatus*, resulting in a disruption to gene flow. If this hypothesis is true, the lack of gene flow, and hence connectivity, could be seen as a resulting from the life-history traits of the individual species rather than being due to any physical characteristic of the corridor itself.

While this study demonstrates the benefits of incorporating population genetic methods into an ecological study of connectivity, the technique does have the disadvantage of not being suitable for use in all scenarios. Its use depends on land clearing or corridor construction having existed for sufficient time to allow genetic attributes of a population to have been affected by the habitat change. How much time must pass after modification of the landscape before it is appropriate to use indirect methods will vary and will depend on the individual life-history traits of the target organism.

Assessment of wildlife corridor effectiveness can easily be confounded by differences in meaning of the terms 'use' and 'function', and the implications that these terms can have for data interpretation. While 'function' implies an operation or fulfilment of a task, 'use' simply refers to utilization. Where the specific aim of a corridor is to provide additional habitat, the terms are interchangeable. Should the desired aim of the corridor be however, to provide interaction among populations within connected patches, in either a demographic or genetic sense i.e. connectivity (Merriam 1984), the terms have very different implications. While the results from this one study system cannot be extrapolated to all scenarios, the data obtained show how misleading conclusions can be drawn about the capacity of a wildlife corridor to facilitate connectivity when there has been no specific investigation into this function.

An increase in connectivity after provision of a wildlife corridor has been clearly demonstrated previously (Mansergh and Scotts 1989) and as such, the assertion that corridors have the potential to be of benefit to populations of small mammals cannot be challenged. Merriam (1995) however, suggested that 'connectivity requires more than just corridors'. The data presented here clearly support this comment and indicate that an increase in connectivity cannot be assumed to result simply from provision or retention of a corridor even when habitat use by the target species is shown to occur.

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References

Aars J., Ims R.A., Liu H-P., Mulvey M. and Smith M.H. 1998. Bank voles in linear habitats show restricted gene flow as revealed by mitochondrial DNA (mtDNA). Mol. Ecol. 7: 1383–1389.

Amos W. and Harwood J. 1988. Factors affecting levels of genetic diversity in natural populations. Philos. Trans. Roy. Soc. Lond. B 353: 177–186.

Baudry J. and Merriam G. 1988. Connectivity and connectedness: functional vs structural patterns in landscapes. In: Schreiber K.F. (ed.), Connectivity in Landscape Ecology. Proceedings of the 2nd seminar of the International Association for Landscape Ecology, Munster, pp. 23–28.

Bierregaard R.O. Jr., Laurance W.F., Sites J. W., Lynam A.J., Didham R.K., Anderson M., Gascon C., Tocher M.D., Smith A.P., Viana V.M., Lovejoy T.E., Sieving K.E., Kramer E.A., Restrepo C. and Moritz C. 1997. Key priorities for the study of fragmented tropical ecosystems. In: Laurance W.F. and Bierregaard R.O. (eds), Tropical Forest Remnants. Ecology, Management and Conservation of Fragmented Communities. The University of Chicago Press, Chicago, pp. 515–525.

Bennett A.F. 1990. Habitat corridors and the conservation of small mammals in a fragmented forest environment. Landscape Ecol. 4: 109–122.

Bennett A.F. 1999. Linkages in the Landscape. The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland.

Bolen E.G. and Robinson W.L. 1995. Wildlife Ecology and Management. Prentice-Hall, New Jersey.

Bolger D.T., Scott T.A. and Rotenberry J.T. 2001. Use of corridor-like landscape structures by bird and small mammal species. Biol. Conserv. 102: 213–224.

Burgman M.A. and Lindenmayer D.B. 1998. Conservation Biology for the Australian Environment. Surrey Beatty and Sons, Chipping Norton, NSW.

Campbell N.J.H., Harriss M.S., Elphinstone M.S. and Baverstock P.R. 1995. Outgroup heteroduplex analysis using temperature gradient gel electrophoresis: high resolution, large scale, screening of DNA variation in the mitochondrial control region. Mol. Ecol. 4: 407–418.

Chand V., Streatfeild C.A., Wilson J.C. and Mather P.B. (2005) Isolation and characterization of 11 polymorphic microsatellite loci in the giant white-tailed rat (*Uromys caudimaculatus*). Mol. Ecol. Notes 5(2):352

Crome F., Isaacs J. and Moore L. 1994. The utility to birds and mammals of remnant riparian vegetation and associated windbreaks in the tropical Queensland uplands. Pacific Conserv. Biol. 1: 328–343.

Downes S.J., Handasyde K.A. and Elgar M.A. 1997a. The use of corridors by mammals in fragmented Australian eucalypt forests. Conserv. Biol. 11: 718–726.

Downes S.J., Handasyde K.A. and Elgar M.A. 1997b. Variation in the use of corridors by introduced and native rodents in south-eastern Australia. Biol. Conserv. 82: 379–383.

Frankham R. and Ralls K. 1998. Inbreeding leads to extinction. Nature 392: 441–442.

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

Fuller S.J., Wilson J.C. and Mather P.B. 1997. Patterns of differentiation among wild rabbit populations *Oryctolagus cuniculus* L. in arid and semiarid ecosystems of north-eastern Australia. Mol. Ecol. 6: 145–153.

Goosem M. 2001. Effects of tropical rainforest roads on small mammals: inhibition of crossing movements. Wildlife Res. 28(4): 351–364.

Goudet J., Raymond M., De Meeüs T. and Rousset F. 1996. Testing differentiation in diploid populations. Genetics 144: 1933–1940.

Harrington G.N., Freeman A.N.D. and Crome F.H.J. 2001. The effects of fragmentation of an Australian tropical rain forest on populations and assemblages of small mammals. J. Trop. Ecol. 17: 225–240.

Harris L.D. and Scheck J. 1991. From implications to applications: the dispersal corridor principle applied to conservation of biological diversity. In: Saunders D.A. and Hobbs R.J. (eds), Nature Conservation. Surrey Beatty and Sons Pty Ltd, Sydney, pp. 189–220.

Hemiview 2.1 1999. Canopy Analysis Software. Delta-T Devices Ltd.

Hyland B.P.M., Whiffin T., Christophel D.C., Gray B. and Elick R.W. 1999. Australian Tropical Rain Forest Trees and Shrubs. CSIRO Publishing, Melbourne.

Kozakiewicz M. 1993. Habitat isolation and ecological barriers – the effect on small mammal populations and communities. Acta Theriol. 38: 1–30.

Krebs C.J. 1989. Ecol. Methodol. Harper Collins Publishers, New York.

Leung L.K., Dickman C.R. and Moore L.A. 1993. Genetic variation in fragmented populations of an Australian rainforest rodent, *Melomys cervinipes*. Pacific Conserv. Biol. 1: 58–65.

Lidicker W.Z. Jr. and Patton J.L. 1987. Patterns of dispersal and genetic structure in populations of small rodents. In: Chepko-Sade B.D. and Halpin Z.T. (eds), Mammalian Dispersal Patterns. The Effects of Social Structure on Population Genetics. The University of Chicago Press, Chicago, pp. 144–161.

Lindenmayer D.B. 1994. Wildlife corridors and the mitigation of logging impacts on fauna in wood-production forests in south-eastern Australia. Wildlife Res. 21: 323–340.

Lindenmayer D. and Peakall R. 2000. The Tumut experiment – integrating demographic and genetic studies to unravel fragmentation effects: a case study of the native bush rat. In: Young A.G. and Clarke G.M. (eds), Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge, pp. 173–201.

MacMahon J.A. and Holl K.D. 2001. Ecological restoration. A key to conservation biology's future. In: Soule M.E. and Orians G.H. (eds), Conservation Biology. Research Priorities for the Next Decade. Island Press, Washington, pp. 245–264.

Mansergh I.M. and Scotts D.J. 1989. Habitat continuity and social organization of the mountain pygmy-possum restored by tunnel. J. Wildlife Manage. 53: 701–707.

McCaughley D.E. 1993. Genetic consequences of extinction and recolonization in fragmented habitats. In: Kareiva P.M., Kingsolver J.G. and Huey R.B. (eds), Biotic Interactions and Global Change. Sinauer Associates, MA, pp. 217–233.

Mech S.G. and Hallett J.G. 2001. Evaluating the effectiveness of corridors: a genetic approach. Conserv. Biol. 15(2): 467–474.

Merriam G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. In: Brandt J. and Agger P.A. (eds), Proceedings of the First International Seminar on Methodology in Landscape Ecological Research and Planning. Rosskilde University Centre, Rosskilde, Denmark, pp. 5–15.

Merriam G. 1991. Corridors and connectivity: animal populations in heterogeneous environments. In: Saunders D.A. and Hobbs R.J. (eds), Nature Conservation 2: The Role of Corridors. Surrey Beatty and Sons Pty Ltd, Sydney, pp. 133–142.

Merriam G. 1995. Movement in spatially divided populations: responses to landscape structure. In: Lidicker W.Z. Jr. (ed.), Landscape Approaches in Mammalian Ecology and Conservation. University of Minnesota Press, Minneapolis, pp. 64–77.

Meyer A., Kocher T.D., Basasibwaki P. and Wilson A.C. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature 347: 550–553.

Moritz C., Dowling T.E. and Brown W.M. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. Annu. Rev. Ecol. Systemat. 18: 269–292.

Neigel J. 2002. Is F_{ST} obsolete? Conserv. Genet. 3: 167–173.

Pollard J.H. 1971. On distance estimators of density in randomly distributed forests. Biometrics 27: 991–1002.

Primack R.B. 1993. Essentials of Conservation Biology. Sinauer Associates, Inc., Massachusetts.

Rainforest Conservation Society of Queensland 1986. Tropical Rainforests of North Queensland: their Conservation Significance. Australian Government Publishing Service, Canberra.

Raymond M. and Rousset F. 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Heredity 86: 248–249.

Rice W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Rosenbaum V. and Reissner D. 1987. Temperature gradient gel electrophoresis: thermodynamic analysis of nucleic acids and proteins in purified form and in cellular extracts. Biophys. Chem. 26: 235–246.

Rosenberg D.K., Noon B.R., Megahan J.W. and Meslow E.C. 1998. Compensatory behaviour of *Ensatina eschscholtzii* in biological corridors: a field experiment. Can. J. Zool. 76: 117–133.

Saccheri I., Kuussaari M., Kankare M., Vikman P., Fortelius W. and Hanski I. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392: 491–494.

Simberloff D, Farr J.A., Cox J. and Mehlman D.W. 1992. Movement corridors: conservation bargains or poor investments? Conserv. Biol. 6: 493–504.

Slatkin M. 1994. Gene flow and population structure. In: Real L.A. (ed.), Ecological Genetics. Princeton University Press, Princeton, pp. 3–17.

Smith G.C. 1984. Biology and habitat usage of sympatric populations of the fawn-footed melomys (*Melomys cervinipes*) and the grassland melomys (*M. burtoni)* (Rodentia: Muridae). Aust. Zool. 21: 551–563.

Soulé M.E. and Gilpin M.E. 1991. The theory of wildlife corridor capability. In: Saunders D.A. and Hobbs R.J. (eds), Nature Conservation 2: The Role of Corridors. Surrey Beatty and Sons Pty Ltd, Sydney, pp. 3–8.

Soulé M.E. and Mills L.S. 1998. No need to isolate genetics. Science 282: 1658–1659.

Southwood T.R.E. and Henderson P.A. 2000. Ecological Methods. Blackwell Science Ltd, Oxford.

Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123: 585–595.

Tracey J.G. and Webb L.J. 1975. Vegetation of the Humid Tropical Region of North Queensland (15 Maps at 1:100 000 Scale Plus Key). CSIRO, Long Pocket Labs, Indooroopilly.

Vernes K. 2003. Fine-scale habitat preferences and habitat partitioning by three mycophagous mammals in tropical wet sclerophyll forest, north-eastern Australia. Aust. Ecol. 28: 471–479.

Watts C.H.S. and Aslin H.J. 1981. The Rodents of Australia. Angus and Robertson, Sydney.

Weir B.S. and Cockerham C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38: 1358–1370.

Whitlock M.C. and McCaughley D.E. 1999. Indirect measures of gene flow and migration: $F_{ST} = /1/(4Nm + 1)$. Heredity 82: 117–125.

Williams K.A.W. 1999. Native Plants of Queensland. K.A.W. Williams, North Ipswich, Queensland.

Winter J.W. 1991. Northeastern Queensland: some conservation issues highlighted by forest mammals. In: Lunney D. (ed.), Conservation of Australia's Forest Fauna. Royal Zoological Society of NSW, Mosman, pp. 113–118.

Wood D.H. 1971. The ecology of *Rattus fuscipes* and *Melomys cervinipes* (Rodentia: Muridae) in a south-east Queensland rain forest. Aust. J. Zool. 19: 371–392.

Wright S. 1978. Evolution and the Genetics of Populations, Vol. 4. Variability within and among Natural Populations. University of Chicago Press, Chicago.