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Research, part of a Special Feature on Effects of Roads and Traffic on Wildlife Populations and Landscape Function

Can Road-Crossing Structures Improve Population Viability of an Urban Gliding Mammal?

Brendan D. Taylor [1,2] *and Ross L. Goldingay* [1]

ABSTRACT. Tree-dwelling mammals are potentially highly vulnerable to discontinuities in habitat created by roads. We used population modeling to assess the viability of a metapopulation of Australia's largest gliding marsupial, the greater glider (*Petauroides volans*), occurring in forest remnants in the fastest-urbanizing region of Australia, where habitat is dissected by major roads. Crossing structures for arboreal mammals (consisting of a land bridge with wooden poles for gliding and adjacent rope canopy bridges) have been installed over an arterial road that separates two of these remnants (one large, one small). It is currently unknown whether this species will use the crossing structures, but available tree height and spacing do not allow a glide crossing, and fences with metal flashing prevent access to the road by terrestrial and arboreal mammals. Our modeling reveals that even a relatively low rate of dispersal facilitated by these structures would substantially reduce the probability of extinction of the smaller subpopulation. This rate of dispersal is plausible given the small distance involved (about 55 m). The inclusion of wildfire as a catastrophe in our model suggests that these two remnants may encounter an undesirable level of extinction risk. This can be reduced to an acceptable level by including inter-patch movement via dispersal among other forest remnants. However, this requires connection to a very large remnant 8 km away, through a set of remnants that straddle two motorways. These motorways create discontinuities in forest cover that are beyond the gliding ability of this species. Crossing structures will be required to enable inter-patch movement. A priority for future research should be whether the greater glider will use road-crossing structures. Loss of habitat and habitat connections is continuing in this landscape and is likely to have dire consequences for wildlife if land managers are unable to retain appropriate habitat cover with corridors and install effective wildlife road-crossing structures where large roads intersect wildlife habitat.

Key Words: *crossing structures; gliding mammals; modeling; motorways; population viability analysis*

INTRODUCTION

Roads are a major cause of habitat fragmentation and can disrupt the population processes of some wildlife species (Forman et al. 2003, Riley et al. 2006). Understanding and mitigating the impact of roads on wildlife has attracted increasing global interest in the last decade (e.g., Vos and Chardon 1998, Taylor and Goldingay 2003, 2004, Clevenger and Waltho 2005, Laurance et al. 2006). Foremost in efforts to reduce the fragmentation effects of roads on wildlife has been the installation of crossing structures. Such engineered solutions are designed to assist animals to cross safely either over the road (e.g., land bridges, rope or wooden canopy bridges) or under the road (e.g., underpasses, culverts, ecopipes). Consequently, crossing structures have become a common feature of new road projects in developed countries (see Gloyne and Clevenger 2001, Mata et al. 2005, Bond and Jones 2008).

Research into the impact of roads on wildlife populations and the effectiveness of crossing structures in enhancing population processes is still in its infancy (see McDonald and St. Clair 2004, Clevenger 2005). Much attention has been given to assessing whether structures are being used by different wildlife species, which is a necessary first step. However, little attention has been given to population processes and understanding whether the viability of populations is enhanced by crossing

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structures or indeed compromised by roads in the absence of crossing structures (see van der Ree et al. 2007). Population viability analysis (PVA) provides a way of determining how populations are affected by roads, and whether they might benefit from crossing structures. Population viability analysis is a method of using computer simulation of population processes to assess population behavior to specific scenarios (Boyce 1992). It allows the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival (Miller and Lacey 2005). Only a small number of studies have used this approach to understand road impacts (e.g., Ramp and Ben-Ami 2006), but this approach is well suited to understanding road impacts and modeling scenarios in which crossing structures may create corridors to link habitat fragmented by roads.

Arboreal mammals are one group of wildlife species that may be particularly affected by the impact of roads in disrupting dispersal and gene flow. Some arboreal species may spend time on the ground in their usual activities (e.g., red squirrel, *Tamiasciurus hudsonicus*; Australian brushtail possum, *Trichosurus vulpecula*), and so may show no reluctance to cross over roads along the ground and even be frequent victims of road kill (e.g., Clevenger et al. 2003, Taylor and Goldingay 2004). In contrast, there are arboreal mammal species that infrequently venture to the ground (e.g., Australian lemuroid ringtail possum, *Hemibelideus lemuroides*; Wilson et al. 2007) and may be very reluctant to use underpasses or even overpasses. Gliding mammals are one example of this because they are more likely to use tree cover to move through a landscape (van der Ree et al. 2003, Selonen and Hanski 2003, 2004, 2006, Ball and Goldingay 2008).

An Australian arboreal mammal that may be particularly sensitive to fragmentation by roads is the greater glider (*Petauroides volans*). It is Australia's largest gliding marsupial, weighing approximately 900–1700 g (Comport et al. 1996). It is known to be very clumsy when moving along the ground and highly vulnerable to terrestrial predators (Fleay 1947). It is distributed throughout forests and woodlands of eastern Australia from temperate eastern Victoria to tropical northeast Queensland (Eyre 2004, Kavanagh 2004, van der Ree et al. 2004, Winter et al. 2004). Greater gliders feed almost exclusively on eucalypt foliage (Kavanagh and Lambert 1990). They use gliding locomotion to move between trees and are dependent on tree cover for movement through their home ranges, which are commonly in the order of 1–3 ha (Kehl and Borsboom 1984, Comport et al. 1996, Cunningham et al. 2004, Kavanagh and Wheeler 2004) but may reach up to 11 ha in hollow-limited environments (Smith et al. 2007). Density estimates range from 0.1 to 3.8 individuals/ha (Henry 1984, Kehl and Borsboom 1984, Comport et al. 1996, Smith et al. 2007).

The greater glider is sensitive to habitat disturbance associated with timber production (Tyndale-Biscoe and Smith 1969a, Kavanagh and Wheeler 2004) and has often been treated as a focus of forest management (e.g., Kavanagh 1991, Possingham et al. 1994). It is also likely to be sensitive to wildfire, which is a common element of dry forests in Australia (Whelan 1995, Bradstock et al. 2002). Albeit, little is known about the impact wildfire has on greater glider population processes (see Possingham et al. 1994, Lindenmayer et al. 2008). One isolated population in New South Wales has been listed as endangered due to concern about its inability to disperse through open habitat (NSW Scientific Committee 2007). In southeast Queensland, the greater glider is present within forest remnants that are surrounded by urban development and concern for its survival has led to two remnants being dedicated as conservation reserves for this species. Despite this, there is currently little information available to guide the conservation of this species in this region where natural habitats are highly fragmented and often subjected to wildfires. Moreover, many forest remnants are now surrounded by roads, which may create barriers to dispersal.

This study used population modeling to examine the impact of habitat fragmentation, wildfire, and potential road barriers on a metapopulation of the greater glider. We hypothesize that, in the absence of dispersal among remnants, this metapopulation will have a high risk of extinction. In our study area, road-crossing structures specifically for arboreal mammals have been installed between two forest remnants. These consist of three rope bridges that link the tree canopy on each side of the road, as well as wooden poles on a wildlife land bridge to specifically facilitate the movements of gliding mammals (Goldingay et al. 2006). Wooden poles have been shown recently to facilitate the movement between habitat patches of another species of gliding mammal in Australia (Ball and Goldingay 2008). We used PVA to assess changes to

population viability if the arboreal mammal crossing structures allow inter-patch movement by greater gliders.

METHODS

Study Area

The study area was located in the eastern Australian city of Brisbane (27.48°S 153.03°E) at an elevation of ~40–90 m ASL. Brisbane has a population of approximately 1.9 million people and experiences a subtropical climate with an average annual temperature range of 15–25°C and an average annual rainfall of 1149 mm (Bureau of Meteorology 2008). This study was focused on a series of forest-remnants that are embedded in a landscape containing a rapidly developing urban matrix (Fig. 1). Vegetation in these remnants is predominantly dry sclerophyll open forest and woodland with a heath understory (Bond and Jones 2008). The study area has been declared an area of bioregional importance due to the significance of the habitat and biodiversity it contains (Veage and Jones 2007).

We conducted field surveys for the greater glider in two forest remnants, Karawatha Forest Reserve (~950 ha) and Kuraby Bushland Reserve (~140 ha), that are managed by Brisbane City Council (BCC). These remnants are separated by Compton Road, a busy arterial road (average annual daily traffic ~26 000 vehicles) that was developed from a two-lane road to a four-lane road in 2004 (Bond and Jones 2008). The width of the road between the forest edges is approximately 55–65 m. When the road was expanded, BCC installed a number of wildlife crossing structures, including a 15–20 m wide land bridge with wooden poles for gliding mammals and three rope canopy bridges (Figs. 2 and 3). The gliding-pole array consists of eight, 6–7 m high hardwood poles (~30 cm diameter) spaced 10–12 m apart across the middle of the land bridge (Figs. 2 and 3). Each pole includes two wooden crossbars (~ 240 cm x 10 cm x 10 cm) mounted at ~30 cm and ~70 cm from the top of the pole. The rope canopy bridges were installed specifically for use by non-volant possums, but volant species may also use them. Rope canopy bridges are known to be used by non-volant possums in north Queensland, Australia (Goosem et al. 2005), but it remains unknown whether gliding mammals will use a canopy bridge to cross a road. Monitoring of the canopy bridges by remote camera has so far been unsuccessful due to continued technical problems.

Karawatha Forest is bordered on its western side by the Gateway Motorway which joins the Logan Motorway at the southwest corner of Karawatha (Fig. 1). The two motorways have been in existence since the early 1980s. To the west of Karawatha is contiguous forest in the form of a series of small remnants that include Drewvale (90 ha), Parkinson (400 ha), and Heathwood (250 ha). These contiguous remnants link to the much larger Greenbank Reserve (4450 ha) (Fig. 1). The remnants are separated by a number of major roads and a railway line. The composition of the habitat in all these remnants is similar, but the quality of the habitat due to tree size and the abundance of tree hollows varies considerably.

There are tenuous connections among the southwest remnants. The Gateway Motorway has two bridges that allow connections under the roadway across to Drewvale (Fig. 1). The northern one contains a creek and broad-leaved paperbarks (*Melaleuca quinquenervia*) that may facilitate movement by gliders. The southern one is an unpaved road underpass, requiring movement along the ground. A small number of trees ca. 25–30 m tall are present along the sides of the remnants bordered by the Logan Motorway where gliding movement may occur across to enable dispersal among the Drewvale and Parkinson forest remnants.

Population Census—Spotlighting

The sizes of the subpopulations of greater gliders in each remnant were estimated based on spotlight transect surveys undertaken in Karawatha Forest on five occasions between May 2006 and March 2008. Transect spotlighting is a method of detecting arboreal animals by their eye-shine or movement with a handheld spotlight (see Kavanagh 1984, Lindenmayer et al. 2000). We placed 26 transects (each 200 m long) across the whole remnant and spaced transects at least 200 m apart to ensure independence of the observations. To locate these transects, we stratified the remnant according to 10 forest vegetation alliances (based on Kordas et al. 1993) and allowed the proportional representation of each to determine how many transects were placed in each alliance. Spotlighting was conducted over 3 nights during fine weather conditions. All

Fig. 1. Aerial photograph of the study area landscape showing six forest remnants and the location of the Compton Road land bridge. Source: Google Earth.

traverses were completed in the first half of the night. Transects were spotlighted at a slow pace (approx 500 m/h or approx 25 min/transect) by a single operator with a 50 W spotlight. These data were used to estimate greater glider density (see below).

Population Viability Modeling

PVA software

We used the VORTEX (version 9.73) program (Lacy et al. 2007) to conduct the PVA. VORTEX is a Monte Carlo simulation of the effects of deterministic forces (e.g., habitat clearing) as well as demographic, environmental, and genetic stochasticity and catastrophes (e.g., bushfire) on the dynamics of wildlife populations (Miller and Lacy 2005). Population dynamics (e.g., births, mortality, catastrophes, etc.) are modeled as discrete, sequential events that occur according to defined probabilities (Lindenmayer and Lacy 1995). The model is repeated many times to reveal the distribution of fates that the populations might experience under a given set of input conditions (Miller and Lacy 2005). A detailed description of VORTEX and its features is provided in Lacy (2000) and Miller and Lacy (2005).

VORTEX has been used in numerous studies investigating the viability of free-ranging mammalian populations and to evaluate management strategies. Focal species have included ocelots (*Leopardus pardalis*) (Haines et al. 2005), koalas (*Phascolarctos cinereus*) (Lunney et al. 2002), mountain brushtail possums (*Trichosurus caninus)* (Lindenmayer and Lacy 1995), greater glider (Lindenmayer et al. 1999, 2000), and swamp wallabies (*Wallabia bicolour*) (Ramp and Ben-Ami 2006). The software is appropriate for the greater glider because it is designed to model populations with low fecundity and small local populations (Lacy 2000).

Fig. 2. An aerial view of the land bridge over Compton Road, connecting Karawatha Forest (below) to Kuraby Bushland (above). Three rope canopy bridges spanning the road can be seen as thin white lines. The canopy gap created by the four-lane road is approximately 50 m. Source: Google Earth.

PVA life-history data input

The greater glider has been the subject of a number of detailed field studies. Many of these have examined its dietary and den-tree requirements, and its movement with respect to estimating home-range size. Few studies have been able to collect detailed information on its demography because it is a species that has never been captured in traps. The most detailed demographic study is that by Tyndale-Biscoe and Smith (1969a, b), in which animals were captured as they were displaced from their tree hollows during logging operations over a 4-year period and another sample of animals was collected by shooting during an 18-month period. The two sampling methods produced 1466 observations.

The social system of the greater glider has been examined in a number of studies, and ranged from monogamy through to polygyny (Henry 1984, Kehl and Borsboom 1984, Comport et al. 1996). This has been based on the number of female home ranges that males overlap with. Tyndale-Biscoe and Smith (1969b) observed a skewed sex ratio among adults (38% male), which suggests a polygynous social system in that population. Therefore, we have used polygyny as the baseline setting.

Most females and males appear not to breed until 2 years of age (Smith 1969, Tyndale-Biscoe and Smith 1969b). Based on a very large sample size (348 breeding females), it is clear that only a single young is produced (Tyndale-Biscoe and Smith 1969b). Tyndale-Biscoe and Smith (1969b) found that 25%–40% of adult females were non-breeding but they were uncertain whether this represented failure to breed or might result from females having lost a pouch young some time earlier that they could not recognize. Based on this, we have set the percentage of females producing one young to 70%.

Fig. 3. Land bridge with gliding poles taken 1 month after installation. Photo: B.Taylor.

Tyndale-Biscoe and Smith (1969b) estimated mortality at the end of the first year to average 20% for males and females together. This was based on the assumption that during sampling of the population, any difference between the number of juveniles recorded and the number of females scored in breeding condition (n = 348) should represent juvenile mortality. For other age classes, mortality of males and females was set at 25% based on the estimate of Tyndale-Biscoe and Smith (1969b). They suggested this mortality may allow some individuals to live for 15 years.

A key element of modeling the behavior of a metapopulation is the inclusion of migration among subpopulations in the form of dispersal. Tyndale-Biscoe and Smith (1969a) reported on the number of tagged greater gliders that were recaptured after being displaced from their home ranges during logging. This enforced displacement is not the same as dispersal but the data provide some insight into possible rates of dispersal. For animals tagged and released over a 4-year period, 1.7% of juveniles (n = 232) and 8.3% of immature and adult greater gliders (n = 517) were recaptured after one or more years. The sex ratio of those recaptured did not differ from that of the original sample. These survival values are likely to be conservative because displacement occurred during the day and many individuals were known to have fallen prey to

diurnal birds of prey. The reproductive condition of most recaptured individuals had advanced and their weight increased, which suggested they had become established as breeding residents (Tyndale-Biscoe and Smith 1969b). We have used values of 0.1% and 0.5% to allow a small rate of dispersal among remnants. Tyndale-Biscoe and Smith (1969a) reported dispersal distances of 0.2 to 3.2 km by displaced gliders. A genetic study of greater gliders from this same area, but living in forest remnants surrounded by exotic pine plantations, described dispersal distances of 1–7 km (Taylor et al. 2007). Of 80 animals sampled within these remnants, five (6.3%) were argued to have been immigrants based on assignment tests (Taylor et al. 2007), one of which was recorded by radio-tracking to have dispersed 1 km from its natal patch (Pope et al. 2004). The five individuals comprised two males and three females, and at the time of sampling two were subadults and three were adults. Taylor et al. (2007) suggest that the observed level of genetic diversity in the remnant forest that had been surrounded by exotic pine plantations for 35 years was the result of immigration. Thus, it is reasonable to infer that individuals migrating between patches in our study system can become established and breed, and that there is no sex bias to dispersal.

The input parameters and values used in building the basic model are shown in Table 1.

Population estimates

We estimated the size of the greater glider population in each remnant based on the estimated density within Karawatha Forest. We derived a Karawatha Forest density estimate by calculating the mean of the number of spotlight observations of greater gliders within 40 m either side of the spotlight transect line. Our data showed that the rate of detection of greater gliders beyond 40 m fell markedly, which has been reported for other spotlighting studies in eucalypt forests (see Kavanagh 1984). This provided an effective transect survey area of 1.6 ha (80 m width x 200 m transect length) divided by the number of individuals observed. Overall density was based on the mean of all 26 transects across the five surveys. This density estimate was then used to extrapolate from for the other remnants. This approach has been shown to be a reliable and valid method of estimating the population abundance of arboreal marsupials, such as the greater glider, within a forest remnant (Lindenmayer et al. 2000).

The overall density estimate for Karawatha was 0.36 gliders per ha, which is similar to greater glider density estimates in similar forests (see Pope et al. 2004, Smith et al. 2007). Excluding area covered by infrastructure (i.e., roads, quarry, water towers), we estimate that Karawatha offers approximately 750 ha of greater glider habitat and, therefore, supports a subpopulation of approximately 270 greater gliders. The Greenbank remnant appears to offer similar habitat to that in Karawatha so we have used the Karawatha density to estimate a subpopulation size of 1600 gliders. We conducted extensive spotlighting surveys across 10 transects within Kuraby bushland, concurrent with those we conducted in Karawatha (Taylor and Goldingay, unpubl. data). These surveys revealed that greater gliders were confined to an area of mature forest immediately north of the wildlife overpass. Based on this, we estimate that approximately 12 adult gliders would be present, but the habitat should be able to support 20 individuals.

The habitat in the remaining remnants is clearly of a lower quality than Karawatha, mostly due to the paucity of hollow-bearing trees. Rather than simply apply the Karawatha animal density to the area of these remnants, we have scored their quality on a four-point scale equivalent to 25%, 50%, 75%, and 100% of that in Karawatha. The Drewvale and Heathwood remnants are characterized by young forest with few tree hollows so we scored them as 25% of that of Karawatha (subpopulation estimates of 8 and 22, respectively). The Parkinson remnant also has large areas with few tree hollows interspersed with patches where large hollows are present, so we scored it as 50% of the Karawatha density (subpopulation estimate of 72).

Catastrophes

We have included wildfire as a catastrophe in some of our models. Several of the remnants in our landscape have experienced wildfire two to three times in the last 20 years. For example, Karawatha has experienced three fires during the last 20 years that have burnt out 20%–50 % of the reserve. The Parkinson remnant has experienced two fires in the last 10 years that have burnt >50% of the remnant. Based on these observations, we have used annual probabilities of 5%–10% for fire frequency. Although the response of greater gliders to wildfire is largely unknown, it is likely that a fire that reaches the forest canopy will have an immediate effect on this species because it is a strict folivore, and foliage

Table 1. Parameters and values used in the PVA for the basic model.

Category	Parameter	Value (SD)
Scenario settings		
	No. of iterations	500
	No. of years	100
	Extinction definition	1 sex remains
Species description	Inbreeding depression	none
	Environmental concordance in survival and reproduction	1
Reproduction system	Mating system	polygyny
	Age at first breeding for F	2 yr
	Age at first breeding for M	2 yr
	Maximum reproductive age	15
	Max. no. progeny per year	1
	% M at birth	50
Reproduction rates	% adult females breeding (EV)	100 (10)
	% adult females with litter size of 1	70
Mate monopolization	% males in breeding pool	100
Mortality rates (%)	Females – age 0 to 1 (SD)	20 (3)
	Females – age 1 to 2 (SD)	25 (3)
	Females – age >2 (SD)	25 (3)
	Males – age 0 to 1 (SD)	20 (3)
	Males – age 1 to 2 (SD)	25 (3)
	Males – age >2 (SD)	25 (3)
Dispersal	Age range	1–2 yr
	Dispersing sex	both
	% survival of dispersers	70
	Annual dispersal prob. among populations	0.5%
Initial population size	Stable age distribution	
Carrying capacity	Defined by initial population size	(5)

will be in short supply for 1–2 weeks following a fire. We have modeled this as potentially causing a 30%–50% reduction in survival of animals and a 50% reduction in breeding. We treat these as worst-case scenarios.

Model simulation scenarios

We initially contrasted two low rates of dispersal (0.1% and 0.5% annual probability) with no dispersal between Karawatha and Kuraby as a way of assessing the benefit of a low level of dispersal that might occur via the crossing structures over Compton Road. A scenario of no dispersal was plausible because we believe the road creates a tree gap beyond the gliding ability of the greater glider, and fencing with metal flashing along the roadside makes it physically impossible for this species to cross the road along the ground. Although we have no evidence that this species will use crossing structures, we believe it is plausible that these structures will enable a low level of dispersal between the two remnants.

The distance between the remnants is short (~50 m) and the variety of crossing structures allows several modes of movement; the three canopy bridges may enable animals to cross by climbing, the wooden poles may enable gliding, and the vegetated land bridge may enable movement along the ground or through a shrub layer. Because we did not want to overstate this, we have used low values for rates of dispersal (0.1%, 0.5%). In modeling, the dynamics of a greater glider metapopulation embedded in an exotic pine matrix, the lowest dispersal value used by Lindenmayer et al. (2000) was 10%. It is unknown whether the narrow crossing points in our study area would restrict dispersal due to behavioral interactions with resident individuals living near the crossing structures. However, no animals were ever spotlighted within 300 m of the structures on the south side of the road. Furthermore, Goosem et al. (2005) reported multiple individuals of lemuroid ringtail possums and Herbert River ringtail possums (*Pseudochirulus herbertensis*) using a single rope canopy bridge in northeast Australia.

The combined Karawatha–Kuraby metapopulation was then subjected to a number of different catastrophe (wildfire) scenarios. Our final scenario considered the influence of adding more forest remnants to the expanded metapopulation, assuming a relatively small amount of dispersal (0.5% per year). This scenario included the effect of catastrophes on metapopulation viability because these are an inherent element of this landscape.

Each scenario was simulated 500 times over a 100-year period. The probability of extinction was estimated as the proportion of simulations in which a population became extinct (Lindenmayer and Lacy 1995). We regarded demographic stability to equate with a 5% or lower mean probability of extinction (*P(E)*) in 100 years, which is consistent with other PVA studies (see Soulé 1987, Goldingay and Possingham 1995, Brito and Grelle 2004).

RESULTS

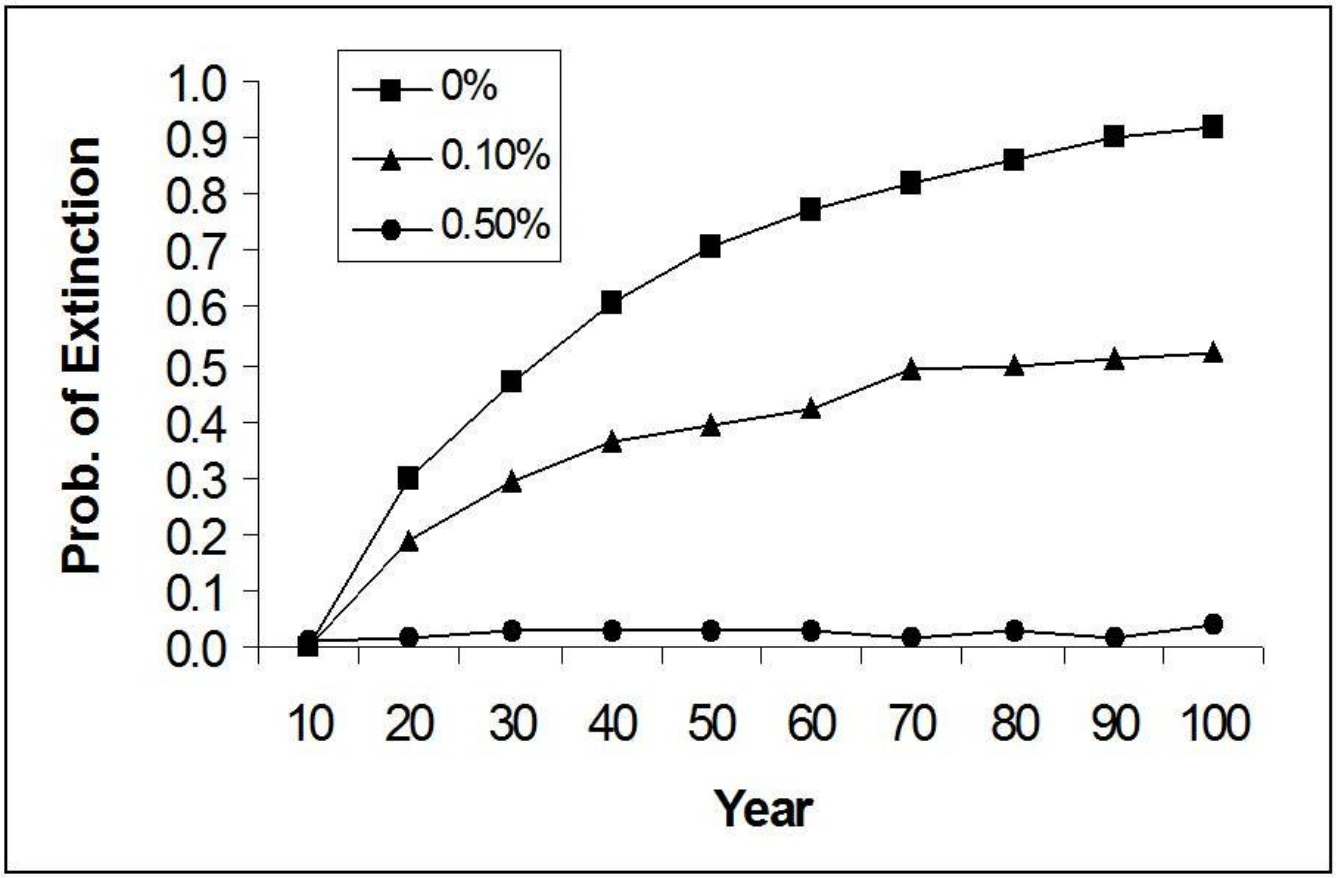
Influence of the Land Bridge in Connecting Two Forest Remnants

In this scenario, we have focused on the probability of extinction in the Kuraby remnant if dispersal has been facilitated by the land bridge. We contrast the outcome for no dispersal with two low rates of annual dispersal (0.1%, 0.5%). Our modeling shows that if no dispersal occurs across Compton Road, the Kuraby subpopulation has a very high probability of extinction (Fig. 4), reaching 0.92 after 100 years. However, with a dispersal rate of just 0.5%, the subpopulation is repeatedly rescued from extinction and should be able to persist over a 100-year period (Fig. 4).

Influence of Catastrophes

Our catastrophe scenario considered the potential reduction in fecundity and survivorship caused by wildfire and its effect on population viability. Catastrophe scenario two (annual probability of fire is 10%; if fire occurs 0.5 of females breed; 0.5 of animals survive) resulted in a very high likelihood of extinction (0.82) after 100 years. However, if fires occur at a lower frequency (catastrophe 3) or survivorship after fire is higher (catastrophe 1), then the probability of extinction after 100 years is much lower (Fig. 5).

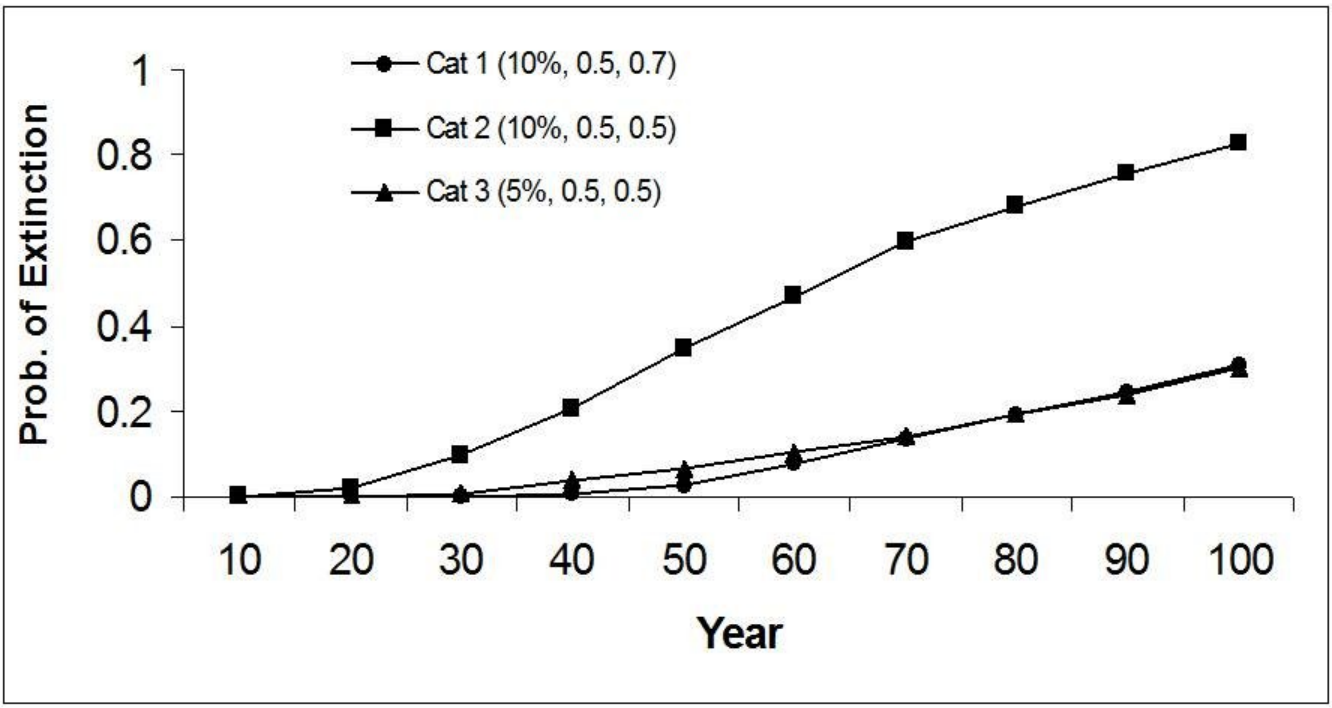
Fig. 4. Probability of extinction within Kuraby Bushland with different values for probability of dispersal from the larger Karawatha Forest remnant (based on 500 iterations). Dispersal has been set at 0, 0.1%, and 0.5% per year. Initial population size in Kuraby was 12, but with carrying capacity set at 20.



Influence of Adding Forest Remnants to the Metapopulation

We conducted modeling to understand the influence of an expanded metapopulation with more forest remnants. In this case, we started with the three southern remnants that straddle the Logan Motorway. We have assumed that a small amount of dispersal could occur (rate of 0.5% per year). If no catastrophes are included, then there is a low probability (0.02) of extinction after 100 years (Fig. 6). However, including catastrophe scenario 1 (10% fire frequency; 50% breeding females; 70% survivorship) has a dramatic influence on the probability of extinction, which is 0.32 after just 10 years and rises to 0.92 after 100 years (Fig. 6). That is, if roads isolate these remnants and wildfires have a severe effect on breeding and survival, the greater glider is assured of extinction in these remnants. Expanding this metapopulation to include Karawatha and Kuraby reduces the probability of extinction after 100 years to 0.32. However, if we model catastrophe scenario 2 (10% fire frequency; 50% breeding females; 50% survivorship), then the probability of extinction rises to 0.82. These probabilities can be reduced to 0.04 by connecting the five-remnant metapopulation to the much larger subpopulation in Greenbank ("Plus Greenbank").

Fig. 5. Probability of extinction of the greater glider within the Karawatha and Kuraby metapopulation under different catastrophe scenarios. Catastrophes have three attributes: a frequency (annual probability of 5%–10%), and an influence on the proportion of females breeding (0.5), and proportion of individuals surviving (0.5–0.7). We modeled three types of catastrophes (cat. 1–3), which comprise different values of these attributes.



DISCUSSION

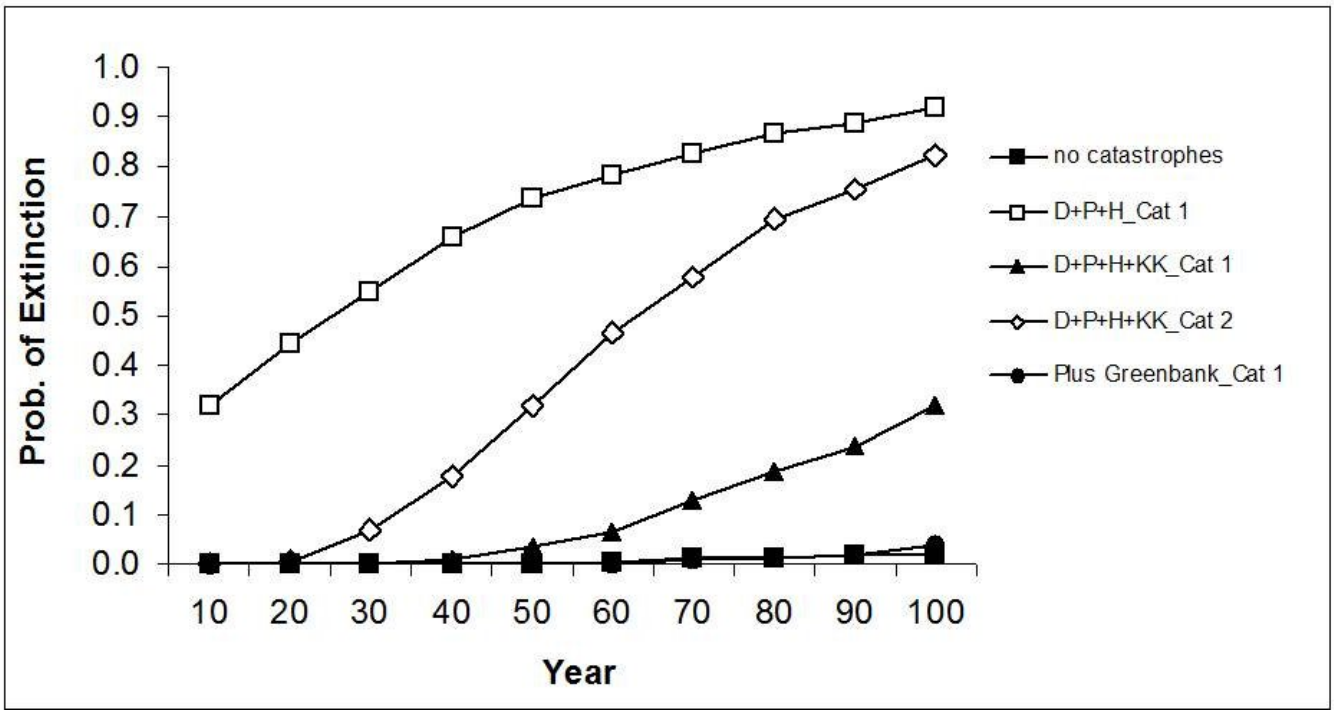
Habitat Fragmentation in Urban Landscapes

Urban landscapes are characterized by a complex mosaic of land uses that gives rise to a combination of developed land and remnant vegetation (Andersson 2006). The extent to which remnant habitat will retain its biodiversity will depend on its area, habitat quality, distance and connectivity to other habitats, and the resistance of the matrix to dispersal (e.g., Soulé et al. 1988, McCarthy and Lindenmayer 1999, Verbeylen et al. 2003). An obvious key to managing biodiversity in remnant habitat in urban landscapes is ensuring its functional connectivity (see Taylor et al. 1993, Tischendorf and Fahrig, 2000, Fitzgibbon et al. 2007). The approach taken to achieve this will vary among taxa and may also vary among landscapes.

Our study landscape provides a typical example of poorly planned urbanization that results in large-scale habitat fragmentation with few or no dispersal corridors retained to connect remaining habitat patches (see Garden et al. 2006). This now requires that expensive retrofitting of habitat connections be undertaken to minimize the potential barrier effect of roads. An example of this is the set of road-crossing structures that have been installed across Compton Road. A variety of vertebrate wildlife has been shown to use some of these structures (Bond and Jones 2008) and our modeling shows the benefit that can accrue to the subpopulation of greater gliders in the smaller of the linked remnants, providing there is no behavioral aversion to the crossing structures.

Although it might seem sensible in our landscape for conservation biologists to simply focus on the single largest forest remnant present, there is no

Fig. 6. Probability of extinction for the greater glider metapopulation with (cat. 1 or 2) and without (no catastrophes) the inclusion of catastrophes (refer Fig. 4) for different combinations of remnants or for all remnants (Plus Greenbank). Drewvale (D), Parkinson (P), Heathwood (H), Karawatha–Kuraby (KK).



guarantee that this area will be retained in its present form over the next 100 years. The Greenbank remnant is a military training area and is likely to come under urban development pressure in future years as the local population grows. This scenario has occurred in Sydney, Australia's largest city, where a large remnant (1500 ha) of original vegetation in the western suburbs that had been owned and managed by the Australian Defence Industries was sold to a development company for conversion to urban expansion (Cook and Ruming 2008). Thus, retaining a set of remnants and maintaining connectivity among them is vital to overall conservation in our study landscape. Small remnants can contribute to urban conservation but will lose elements of biodiversity if allowed to become fully isolated from other remnants (e.g., Soulé et al. 1988).

Model Constraints

In our modeling, we have assumed that the density of animals derived from one of the remnants can be the basis of the subpopulation estimates for other remnants in our landscape. Recent spotlighting surveys in the Parkinson and Heathwood remnants has failed to detect any greater gliders (G. Brierley, pers. comm.; B. Taylor and R. Goldingay, unpubl. data). A single greater glider was detected during 23 h of spotlighting surveys in 2005 (Place Environmental Consultants, unpubl. report). It may be the case that the presence of the motorways during the last 20 years has reduced the capacity for greater glider dispersal and led to their decline in these remnants. This should be verified by further field surveys.

Another potential shortcoming of our study is that we have assumed that the area of habitat in the remnants will be constant over time. This is unlikely to be true due to a variety of endogenous (e.g., loss

of hollow-bearing trees) and exogenous (e.g., edge effects) factors affecting remnant quality over time (see Soulé et al. 1988, Goldingay and Sharpe 2004). Furthermore, urbanization in this landscape is continuing so contraction in the area of many of the remnants can be expected. These factors and the output of our model suggest that the persistence of greater gliders in this landscape is strongly contingent on achieving functional connectivity among the remnants.

Greater Glider Dispersal and Response to Fire

A fundamental element of the life history of the greater glider where data are poor concerns its dispersal behavior (see Lindenmayer et al. 1999, 2000). Minimizing the risk of extinction for our metapopulation in various scenarios was dependent on successful dispersal among subpopulations. Observations have been reported of greater gliders dispersing distances of 1–7 km (Fleay 1947, Tyndale-Biscoe and Smith 1969a, Pope et al. 2004, Taylor et al. 2007). The distances between adjoining remnants in our landscape are not great (50–100 m), so the key issue is whether gliders can successfully disperse across motorways and other major arterial roads, or use road-crossing structures to do so. We hypothesize that successful dispersal would be negligible and the probability of road mortality with motorway-crossing attempts would be high without facilitated crossing. Research on this topic is obviously needed with genetic techniques the most likely to provide insight (e.g., Riley et al. 2006, Taylor et al. 2007).

A key element to our PVA was the inclusion of catastrophes in the model. Fire is a common element of landscapes within Australia (Whelan 1995, Bradstock et al. 2002, Lindenmayer et al. 2008), so it is appropriate to treat fire as a catastrophe in a PVA model for the greater glider (Possingham et al. 1994), unless there is compelling evidence that fire suppression is effective (Lindenmayer et al. 2001). In our study landscape, wildfires have occurred within several of the forest remnants at least once in the last 20 years (BCC, unpubl. data; T. Fensham, pers. comm.). Due to the rapid urbanization of the landscape within this period, earlier fire records are unlikely to be relevant. We predict that fire frequency will increase as the local human population increases, and in response to climate change. The critical issue for our model is the response of greater gliders to wildfire. Currently there are few data on this to guide inputs to a PVA, but Possingham et al. (1994) assumed that 50%–100% of greater gliders would be killed immediately in mountain ash (*Eucalyptus regnans*) forest where wildfires are very hot. We have modeled scenarios that allow for 30%–50% of a subpopulation to be killed by fire.

The forests in our landscape are not dominated by very large old-growth trees but they do contain a modest availability of hollow-bearing trees (B. Taylor and R. Goldingay, unpubl. data). Thus, greater gliders may be vulnerable to death during the passage of fire. Furthermore, the loss of the greater glider's eucalypt foliage food resource for at least a week following fire may lead to some mortality. We expect that the nutritional stress caused by this for surviving individuals would result in a decline in reproduction in the following year. Lindenmayer et al. (2008) present data on the greater glider in relation to a wildfire, but few insights are apparent due to enormous variation among survey transects and a substantial decline in mean abundance on burnt and unburnt sites over a 3-year period following the wildfire. Our assumptions can be viewed as worst-case scenarios until data become available. Their importance in the predictions we make indicates that research must be conducted to address these data gaps. Wildfires have become an unavoidable element of this landscape and this increases the need for inter-patch movement by greater gliders.

Gliding Capability

Disruption to habitat connectivity for a gliding mammal will largely depend on tree height and inter-tree distance. These attributes, in combination with the gliding ability of the species, will determine whether a specific tree gap can be crossed without incurring increased predation pressure. This is a subject for which there are few quantitative data (see Jackson 1999). Gliding ability will vary depending on the area of the gliding membrane and other morphological attributes, and this largely manifests itself as the angle from the horizontal of the glide (Jackson 1999). Wakefield (1970) questioned several early accounts of the gliding ability of the greater glider and stated that the glide angle for this species was approximately 40° based on extensive field observations. R. Kavanagh (pers. comm.) measured a maximum glide of 75 m from a tree canopy 45 m high, which gives a glide angle of 31°.

At Compton Road, each side of the road has a 2.5 m high fence with metal flashing that would need to be cleared by a gliding mammal. The fences are 45 m apart and the closest existing trees are approximately 5–10 m back from the fence. Using the lower glide angle, and that animals would need to land 2.5 m above the ground to clear the fence, the tallest roadside tree would only allow a horizontal glide distance of 38 m, which would be insufficient to clear the fence. Distances between opposite roadside trees along the motorways in our study area are even greater, and highlight the difficulty that greater gliders will have in crossing these roads. Gliding distance is a topic that requires specific research because having a better understanding of gliding performance will allow more detailed analysis of tree gaps caused by roads and evaluation of some management responses (see below).

Motorways and Urban Conservation

Conserving forest-dependent wildlife within urbanized landscapes poses an enormous challenge. This is exacerbated where motorways and other major arterial roads create potential barriers to the dispersal of such wildlife. Species that are dependent on tree cover for food and shelter will be particularly vulnerable to road impacts. This has been shown by the high level of road mortality on a population of koalas living in forest remnants approximately 5–20 km from our study landscape (Dique et al. 2003). The greater glider is another such species that will be vulnerable because it requires tree cover to move, and is slow and clumsy when attempting to move across the ground (Fleay 1947). The distance between trees on each side of a road is critical to determining its movement through the landscape, as is whether vehicle traffic creates a behavioral aversion to roads for this species. The motorways in our study area have created gaps in forest cover of 50–100 m. Roadside trees reach a maximum height of approximately 30 m, which would enable a glide of 50 m (see above). This suggests that there would be only a few locations where animals might make a glide crossing. Instead, animals would be required to travel along the ground to cross a road. Therefore, these motorways almost certainly create some level of barrier to dispersal by greater gliders and place the viability of the metapopulation at high risk or extinction.

The land bridge on Compton Road between two of our remnants provides one model of how forest remnants can be reconnected. This has eight wooden poles (6–7 m high) across it to facilitate crossings by gliding mammals and three canopy rope bridges for arboreal mammals in general. The land bridge now has a thick cover of 4 m high shrubs that may also facilitate crossings by arboreal mammals. We have evidence of use of the wooden poles by another gliding mammal, the squirrel glider (*Petaurus norfolcensis*) (B. Taylor and R. Goldingay, unpubl. data). However, we currently have no information about whether greater gliders use any of the crossing structures, but fences with metal flashing and the width of the road prevent crossing except via these structures. Further research needs to be conducted to determine whether or not greater gliders use these structures. Until it is demonstrated, it can only be regarded as an hypothesis that greater gliders will use road-crossing structures.

Ball and Goldingay (2008) have shown that wooden poles can be used to reconnect habitat for the squirrel glider where a gap in habitat exceeds its gliding capability. Installing poles on a land bridge as at Compton Road is a very costly approach to providing habitat connectivity for a gliding mammal where roads occur, although this land bridge was installed to cater to a broad range of wildlife. Another option for gliding mammals is simply to install wooden poles on each side of a road as well as in the median strip where one is present. The motorways in our study area have a median strip of 7–8 m width, which provides ample space for poles and an associated safety barrier for vehicles. The installation of wooden poles 20 m in height should enable a glide of approximately 33 m and potentially allow the movement of greater gliders across the motorways in our study area.

Other potential approaches to reconnecting habitat should also be tried. At one location along the Gateway Motorway, a bridge with a 160-m span crosses over a creek. This is sufficiently high (4 m) that a series of connected wooden poles could be installed under the road bridge to allow arboreal mammals to climb across under the bridge. Rope bridges are another option and have been used by rainforest possums (Goosem et al. 2005) and primates (Kirathe and Parry 2003) to cross roads. Employing several options may be the best strategy to ensure the crossing of large roads such as the motorways in our study area. Given that the effectiveness of all of these road-crossing structures

is currently unknown for gliding mammals, their deployment must be coupled with research. Providing an effective road-crossing solution will be fundamental to the urban conservation of arboreal species such as the greater glider.

Management Recommendations

There are several management recommendations that arise from this study. Firstly, the output of our model shows that the dual effects of wildfire and road-mediated dispersal barriers threaten the persistence of the greater glider in this landscape. Therefore, we urge that management should be focused on lessening the likely barrier effect of the roads by providing crossing structures to link all remnants. Our model results suggest that even low levels of dispersal may be effective to maintain persistence. It is predicted that higher levels of dispersal will result if crossing structures are installed at multiple locations, so we suggest that structures not be limited to a single location between adjoining remnants. Secondly, it is currently unknown whether any of the crossing structures are effective to enable greater gliders to traverse a road barrier. We have evidence that the smaller squirrel glider will use the gliding poles, which provides promise for other gliding species. However, data are required to demonstrate definitively which measures will be effective for the greater glider so management can proceed with some certainty. Given that gliding poles are relatively inexpensive (Ball and Goldingay 2008), trials could initially commence with such structures. Lastly, the most difficult crossing points for gliders in our study landscape will be either side of the Drewvale remnant where motorways need to be traversed by dispersing animals. Thus, we suggest that a priority for reconnection with crossing structures should be the Greenbank to Parkinson remnants while research is conducted around Drewvale.

CONCLUSION

Until recently, arboreal mammals had been largely overlooked by road authorities attempting to mitigate road impacts. Most studies of crossing structures have involved road underpasses (e.g., Taylor and Goldingay 2003, Dodd et al. 2004, Ng et al. 2004, Clevenger and Waltho 2005). In Australia, several different options for arboreal mammals have been undergoing trials, including rope bridges (Goosem 2004, Goosem et al. 2005), wooden poles for gliding (Goldingay et al. 2006, Ball and Goldingay 2008), and land bridges (Bond and Jones 2008). In southern Brazil, a wooden bridge structure over a road was provided for primates and was used (Valladares-Padua et al. 1995). In the USA, poles for gliding mammals are currently being tried (C. Kelly, pers. comm.). Thus, there is growing recognition that specific crossing structures are needed to meet the needs of arboreal mammals, but extensive testing and monitoring is required before such structures should be deployed more broadly. Our use of PVA modeling has assisted in this regard by testing certain management scenarios and identifying future research needs. Indeed, our study landscape in Brisbane is one in which further testing of such structures should be conducted because several species of arboreal mammal are still widespread and urbanization is rapidly severing habitat connections.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/vol14/iss2/art13/responses/

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