

How do we conserve the squirrel glider in Brisbane's urban matrix?

Ross L. Goldingay and David J. Sharpe

School of Environmental Science & Management, Southern Cross University, Lismore, NSW 2480

email: rgolding@scu.edu.au

ABSTRACT

Forested habitat has been extensively cleared in south-east Queensland. We used the ALEX computer program to conduct a preliminary population viability analysis (PVA) for squirrel gliders *Petaurus norfolcensis* living in a set of habitat fragments, embedded in an urban matrix in Brisbane. Our basic aim was to guide management to ensure the long-term persistence of the squirrel glider in this region. Corridors linking the fragments in our study area are poorly vegetated and many are cut by arterial roads. Five remnants that we believe define the likely limit of glider dispersal (the glider metapopulation), had an unacceptably high probability of glider extinction after 100 years. When catastrophes such as wildfire of modest frequency (1 in 20 years) were included, the probability of extinction increased. It appears that large nearby remnants must be functionally linked to the metapopulation to ensure long-term persistence. This may require some novel approaches to habitat restoration to achieve. The habitat quality of all connecting corridors must be enhanced to reduce mortality during dispersal. Edge effects such as tree die-back are also likely to reduce the available cover of habitat over time and will need to be managed. Our review of the life history of the squirrel glider has highlighted how poor our understanding is of most components that form important inputs to a PVA. The significance of this was evident by increasing annual mortality above the approximate values used. This led to a marked increase in the probability of metapopulation extinction, suggesting predictions should be viewed with caution. Further detailed field studies are needed to refine the use of PVA for the squirrel glider.

Key words: squirrel glider, *Petaurus norfolcensis*, population viability analysis, urban remnants

Introduction

Conserving populations of species throughout their geographic ranges should be a fundamental element of any conservation strategy (e.g. Goldingay 1996). Species with very wide distributions, such as the squirrel glider *Petaurus norfolcensis*, will pose a particular challenge to managers because detailed ecological data will be required across many sites. This species is distributed broadly in eastern and southern Australia, from Cape York in north Queensland (Qld), south to the central coast of New South Wales (NSW) (Quin *et al.* 1996; Eyre 2004; Kavanagh 2004; Winter *et al.* 2004). Its range extends west of the divide in the Hunter Valley region north of Sydney (Quin *et al.* 1996; Kavanagh 2004), and then south along the western plains of NSW into central northern Victoria (Menkhorst 1995). A 185-km disjunction to an outlying segment of the range in central western Victoria, is interrupted by a single site record (Menkhorst *et al.* 1988; Traill 1998). There are several isolated populations of squirrel gliders in NSW, including one on Barrenjoey Peninsula on the north side of Sydney, and one on the NSW mid-south coast (Davey 1990). Records of possible sightings on the far-south coast of NSW (see Braithwaite 1983) have never been confirmed, despite extensive field surveys in the source areas (Kavanagh 1984, 2000; Goldingay and Kavanagh 1995; Goldingay and Daly 1997). The most abundant populations of squirrel gliders appear to occur in south-east Qld (Rowston

et al. 2002; Eyre 2004), north-east NSW (Sharpe and Goldingay 1998; Sharpe 2004), and central-coastal NSW (Smith and Murray 2003; Kavanagh 2004). Severe habitat fragmentation now appears to be characteristic of much of the geographic range of this species.

The squirrel glider is listed as endangered in Victoria by the *Flora and Fauna Guarantee Act* 1988 (Menkhorst 1995). In NSW it is listed as vulnerable, and two populations are listed as endangered under the *Threatened Species Conservation Act* 1995. The squirrel glider is currently regarded as common in Qld under the *Nature Conservation Act* 1992, but this is in need of review, and is likely a reflection of a poor understanding of its distribution and abundance (see Eyre 2004). Bioclimatic modelling suggests that the core of the squirrel glider's distribution (the area with the most suitable climatic profile) occurs in south-east Qld and north-east NSW (Quin *et al.* 1996). In Qld, this coincides with areas that have been extensively cleared and fragmented (Catterall *et al.* 1997). The area managed by Brisbane City Council (approximately 12000 ha) is a case in point. In this area about 80% of all lowland vegetation has been cleared. Furthermore, 80% of remaining habitat now consists of remnants that are less than 20 ha in size (Brisbane City Council 2002). Further fragmentation of habitat is likely as additional areas are developed for housing. As a consequence, Brisbane City Council recognises the squirrel glider as a species of conservation priority

(Brisbane City Council 2002). Within this region, the squirrel glider is particularly associated with lowland dry forest and woodland dominated by several species of iron bark (e.g. *Eucalyptus melanophloia*, *E. siderophloia*), spotted or lemon-scented gum (*Corymbia citriodora*) and several species of red gums (e.g. *E. tereticornis*, *E. seeana*) (Rowston *et al.* 2002; Sharpe and Goldingay unpubl. data).

We used Population Viability Analysis (PVA) to explore the impact of habitat fragmentation on squirrel glider population viability within one part of the Brisbane City Council area. Our aims were: i) to conduct a preliminary PVA to identify management options that could enhance population viability, and ii) to use the PVA to identify gaps in our understanding of the ecology of this species that limit our ability to manage its populations more effectively.

Simulation model

Population Viability Analysis was undertaken using the ALEX computer simulation program (Possingham and Davies 1995). ALEX has been used extensively to examine viability under a range of scenarios for a number of species including the greater glider (Possingham *et al.* 1994), the bilby (Southgate and Possingham 1995), Leadbeater's possum (Lindenmayer and Possingham 1995, 1996), and the yellow-bellied glider (Goldingay and Possingham 1995). This model allows: i) a complex spatial configuration of habitat patches to be examined, ii) dispersal movement between patches to be modelled, and iii) the effect of catastrophes to be modelled.

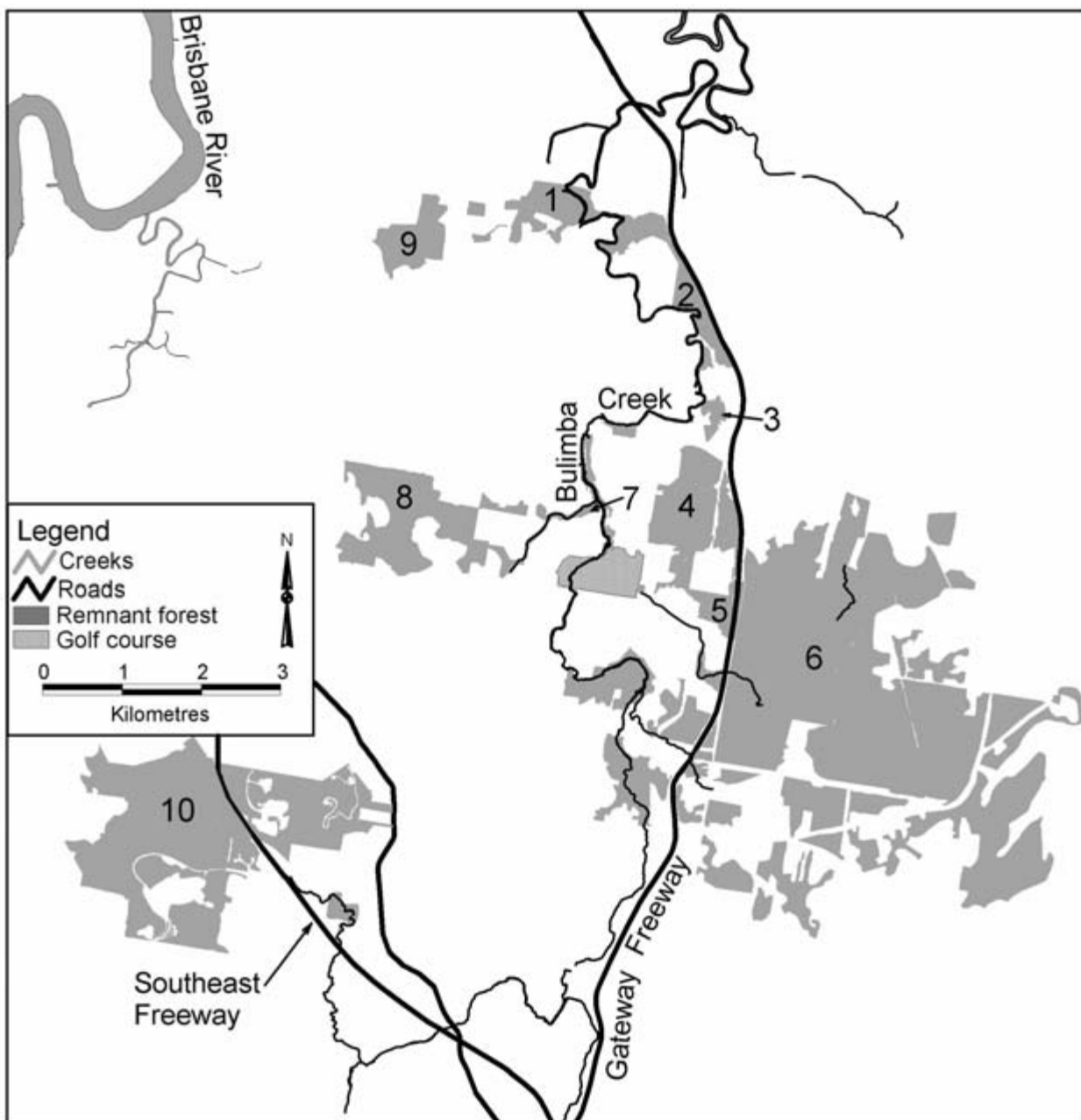


Figure 1. Map of the study area showing the locations of the forest remnants (indicated by numbers). The white area is the urban matrix. The stippled patch is a golf course. 1. Minnippi Parklands, 2. Meadowlands, 3. Wright St, 4. Belmont Hills, 5. Belmont Hills South, 6. Mt Petrie, 7. Golf Course, 8. White's Hill, 9. Seven Hills, 10. Toohy Forest.

A preliminary PVA for the squirrel glider has also been conducted by Hill (1997) for the Brisbane study area using a broader set of remnants. His study focussed on comparing the structure and relative outputs of two other simulation programs, and provides limited insight for the current study.

Brisbane study area

The study area was located <10 km east of the Brisbane Central Business District. Within this landscape is a high density of residential development and its associated infrastructure, with a scattering of remnant forest and woodland habitat, particularly along several large creek systems (Fig. 1). These previously rural lands are being displaced by residential development as the population of Brisbane expands.

One area of remnant habitat is known as Minnippi Parklands. It contains some recreational parkland but also approximately 60 ha of remnant forest habitat straddling Bulimba Creek. Several short-term studies had been conducted on squirrel gliders in the western part of the remnant, which has been the subject of a development proposal. These studies had established that there was a resident population of at least 30 squirrel gliders (Catterall *et al.* 1996; Warren & Associates 2000). A detailed trapping program in the western area during 2002 revealed that the site contained about 40 adult female gliders (Sharpe and Goldingay unpubl. data).

One important consideration for our study was to determine how many habitat patches in the surrounding landscape should be included in the modelling exercise. Habitat patches in the study area were variously isolated by housing and roads, and a major freeway cut across the area in a north-south orientation (Fig. 1). There is little information about the dispersal ability of the squirrel glider (see Quin 1995; van der Ree 2002), so it was not immediately obvious which patches to include or exclude from our system of potentially linked remnants. Squirrel gliders have been observed foraging in isolated trees and are known to cross roads (van der Ree 2002; van der Ree and Bennett 2003), so we were guided by proximity and the availability of linking vegetation that might function as a corridor. For this reason we excluded the remnant at Toohey Forest that is known to contain squirrel gliders (see Rowston *et al.* 2002) because it was located >2 km south of the nearest remnant we have considered (White's Hill), and the intervening area is dominated by houses and dissected by several major arterial roads.

The study area consisted of three, closely-linked northern remnants, two closely-linked southern remnants and three, outer remnants (Table 1). The southern remnants were separated from the northern remnants by Old Cleveland Road, a 4-lane arterial road (Fig. 2). However, due to the short distance between these remnants, we considered that occasional dispersal may be possible between sites 3 and 4 (Wright St and Belmont Hills). Site 6 is separated from sites 4 and 5 by the Gateway Freeway (Fig. 3). The presence of forest each side of the 30 m wide open freeway

Table 1. Description of the size and relative location of the habitat remnants in the study area. Distance is the distance to the remnant listed in the adjacent description.

Remnant Name	Size (ha)	Distance (m)	Description of linkages between patches
Northern Linked Remnants			
1. Minnippi Parklands	60		Focal habitat patch
2. Meadowlands	30	200	Connected to site 1 by open ground and scattered trees. Tree spacing of 50-60 m.
3. Wright St	12	300	Connected to site 2 along Bulimba Creek by a narrow corridor of trees and along a roadside. Tree spacing of 50 m, including a road crossing.
Southern Linked Remnants			
4. Belmont Hills	107	100	A 4-lane road separates from site 3. There is a tree spacing of about 30 m. (see Fig. 2)
5. Belmont Hills South	20	300	There is one broad link with site 4 with a few 20 m tree gaps. (see Fig. 3)
Outer Remnants			
6. Mt Petrie	707	80	Separated from sites 4 & 5 by the Gateway Freeway. This creates a tree gap of about 80 m. Both sides of the freeway are densely vegetated and there are no fences to impede dispersal. (see Fig. 3)
7. Golf Course	10	1000	This site connects through a golf course equally with sites 4 and 5 by a broad area of scattered trees. Tree spacing of 50 m. There is a 1500 m north connection along Bulimba Ck with site 3 and tree gaps of 20 m. A road traverses the connection with site 5.
8. White's Hill	148	100	A narrow band of trees connects with site 7. Tree gaps of 50 m. A road traverses the connection. (see Fig. 4)



Figure 2. Aerial photo showing connection across Old Cleveland Road between northern remnants and southern remnants.

should allow some dispersal among these sites, though we assume such movements would be quite rare. Site 7 is small and would function as a habitat stepping stone, so it was only considered when site 8 was considered (Fig. 4). Due to an arterial road, and the distance to site 4, we assume that dispersal among these sites would also be minimal.

Life history data input

The values chosen as life history data inputs to the model influence the estimates of viability and must be selected with care. Incorrect assumptions in PVA models can have profound implications for management (e.g. Price and Kelly 1994). For this reason parameter inputs were subjected to a sensitivity analysis to gain an understanding of how each value might influence the output. Furthermore, if a parameter is imprecisely known, and has been identified as having a strong influence on viability, then future research can be directed to obtain a more precise estimate.

Life history data that were used as inputs to ALEX (Table 2) were derived from several studies on the squirrel glider (Quin 1995; Sharpe 2004, unpublished data; Rowston 1998; van der Ree 2000, 2002). We also used studies on the sugar glider (Suckling 1984; Sadler and Ward 1999) to help guide the choice of some parameter values.

Social System and Home-range Size

Squirrel gliders live in small groups containing adults and juveniles (Menkhorst 1995; Quin 1995; Sharpe 2004; van der Ree 2002). Understanding the social system (i.e. group composition) of this species is fundamental to accurately

estimating its population density or size. ALEX requires an input of the minimum living area for females. However, this value may vary if groups contain multiple adult females or single adult females. Furthermore, home-range size can be expected to vary among locations depending on habitat quality (e.g. Goldingay 1992).

In two studies of short duration in north-east NSW, group structure varied. Quin (1995) observed members of two groups. One group, observed periodically over 19 months, never contained more than a single adult female. A second group, monitored periodically over just 4 months, contained two adult females. Sharpe (1996) used radio-tracking to facilitate observations on six groups over a 10-month period. All groups contained adult pairs. Approximately 24 months after this work, at least some groups increased in size and contained additional adult females. Observations in central Victoria on five groups during one 6-week field period suggested that some groups contained a single adult female and some had multiple adult females (van der Ree 2002).

The number of adult females in a group will have a profound influence on viability. It appears that flowering intensity has a strong influence on breeding and ultimately group structure, and that years of poor flowering may lead to a reduction in group size and therefore, a switch from polygyny (multi-female groups) to monogamy (single-female groups). Conversely, years of heavy flowering may encourage female philopatry and the adoption of a polygynous social structure (D. Sharpe pers. obs.; see also Goldingay 1992). Thus, the squirrel glider social system

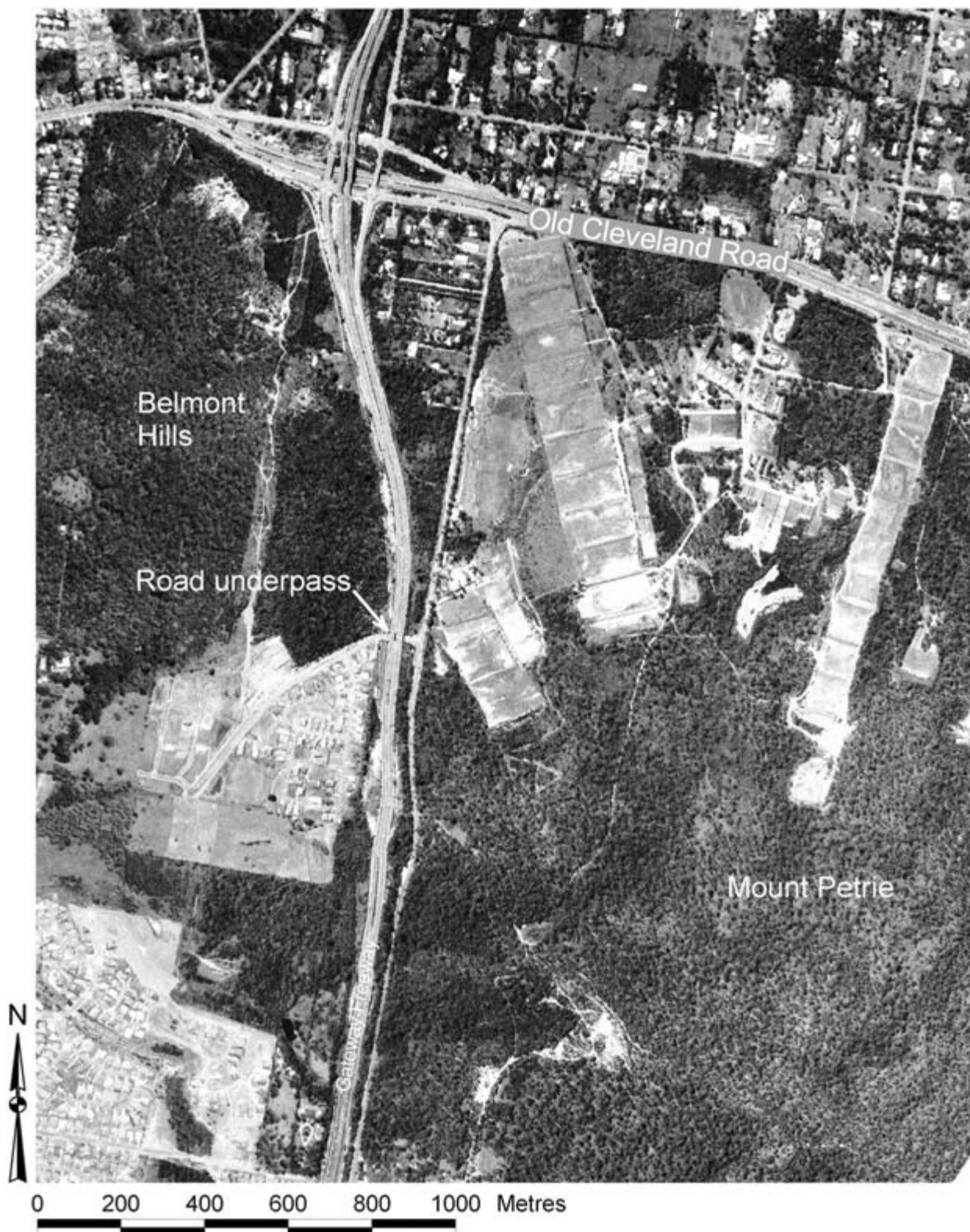


Figure 3. Aerial photo of connection between Belmont Hills and Mt Petrie.

may be a mixture of the two group types. Preliminary field work on group structure in the study area has confirmed this (Goldingay and Sharpe unpublished data).

van der Ree and Bennett (2003) described seasonal home-ranges of 2.4-3.4 ha for female squirrel gliders in central Victoria. For two females tracked in each of four seasons, the annual home-range was the same or larger than the home-range for a single season. This suggests

that home-ranges estimated over shorter time periods will underestimate the area.

Consultancy studies centred on the Minnippi study area in southeast Qld revealed that squirrel gliders range over several hundred metres and have large home-ranges (>4 ha) but studies have not been conducted for a sufficient period to provide accurate estimates (Catterall *et al.* 1996; Warren & Associates 2000; Rowston 2000a).



Figure 4. Aerial photo of connection between Belmont Hills and White's Hill.

In northern NSW, squirrel glider groups had a mean home-range area of 8.8 ha (minimum convex polygon) based on radio-telemetry data (Sharpe 1996). Home-ranges overlapped by an average of 35%. Overlap was determined by summing the proportion of common grid squares, representing capture points, relative to the total number used in that home-range (D. Sharpe unpublished data). Thus, each female in a monogamous group had exclusive use of a mean area of about 5.8 ha. Multi-female groups appeared to occupy the same home-range size as single-female groups (D. Sharpe unpublished obs.). We estimate that each female in a polygynous group would effectively have half this area (i.e. 2.9 ha). Allowing for an alternation between a monogamous and polygynous structure suggests that a home-range size of about 4.0 ha would be appropriate. Therefore, we have assumed female density averages 0.25 per ha. This value was used to set the number of females in every remnant except Minnippi where the quality of the habitat appears to be higher than elsewhere (pers. obs.). Our trapping study revealed that Minnippi contained approximately 40 adult females in 2002 (i.e. a density of 0.67 per ha).

Reproduction

Female squirrel gliders can breed early in their second year (Quin 1995; D. Sharpe unpublished data). The mean litter size varies from 1.6 to 1.9 (Quin 1995; Rowston 1998; Millis and Bradley 2001; Sharpe 2004). Annual natality rates are between 1.8 and 2.4 (Quin 1995; Rowston 1998). van der Ree (2002) reported that 11 out of 78 adult females produced a second litter in one year, but he did not know whether this was a consequence of losing the first litter. In common with the mahogany glider *Petaurus gracilis* (Jackson 2000), it is possible that a second litter is born only if the first is lost. In north-east NSW, a mean of 78% of females bred in any given year (Quin 1995) but in Victoria the value was 100% (van der Ree 2002).

The sex ratio at birth of petaurids has been reported in several studies to be 1:1 (Suckling 1984; Sadler and Ward 1999; Jackson 2000). Assuming this is also the case for the squirrel glider, litters were assigned a 5% probability of producing no females, a 90% chance of producing one female and a 5% chance of producing 2 females. This recognises a small probability of no female young or two female young being produced.

Mortality and lifespan

Data on mortality for the squirrel glider are scant. Quin (1995) presented data that suggested that juvenile mortality at his site was about 30%. van der Ree (2000) reported the mortality of 7 (64%) out of 11 radio-collared juvenile gliders in remnant habitat in one period. Six deaths were attributed to owls and one to a feral cat. It is not known how representative this is of juvenile mortality at his site or elsewhere. Suckling (1984) estimated that >50% of female sugar gliders of one cohort disappeared between their first trap record at weaning and when they had matured. Quin (1995) observed that over 40% of female sugar gliders disappeared by their age of maturity. These values include an undetermined component of dispersal. Suckling also estimated losses of 5% during pouch life and 16% during the nestling stage. We used a juvenile stage to encompass both the nestling and nestling to maturity stages. We selected an average annual mortality value of 35% for this stage.

The maximum longevity recorded for the squirrel glider is 6 years (Quin 1995; D. Sharpe unpublished data) suggesting that gliders survive as adults for at most 4-5 years. Thus, it appears that adults have a 30-40% chance of death in a given year, so a value of 35% was selected as the baseline (Table 2).

Table 2. Values of life history parameters used to model the population viability of the squirrel glider.

Parameter	Value
Breeding system	Mixed monogamous /polygynous
Female home-range size	4 ha
Age at first breeding	1-2 years
Maximum longevity	6
Sex ratio at birth	1:1
Age structure of population	
0-1 yr	newborn-juvenile
≥1 yr	adult
Maximum no. of young per year	2.4
Probability of offspring per year	
0 female	5%
1 female	90%
2 female	5%
Mortality rates of females	
newborn-juvenile	35%
adult	35%
Population threshold for dispersal	60% of carrying capacity
Probability of juvenile dispersal	50%
Mean maximum dispersal distance	1.5 km

Environmental variability

Environmental variability (EV), as simulated by ALEX, has two components. Firstly, a variable is drawn at random from a normal distribution of values with a specified mean and standard deviation between 0 and 1 (Possingham and Davies 1995). We chose 0.8 ± 0.3 because these values were found to approximate the mean and standard deviation of rainfall in a previous PVA (Goldingay and Possingham 1995). Anecdotal evidence suggests that variation in rainfall has an influence on glider population dynamics. A value is selected for each patch at the start of each year. The second component to modelling EV is that the operator designates parameter values at which all females in a population breed (best conditions) and values at which no females breed (worst conditions). At intermediate values a proportion of females breed. In the present model, best conditions were set at 0.7 and worst conditions at 0.5. Environmental variation was assumed to be the same across the whole study region.

ALEX models EV by a user determined function for the proportion of females that breed each year. We have used this component to also represent the survival of pouch young. Observations have been made on small petaurids that the proportion of females that produce pouch young each year is very high but the survival of pouch young may be determined by environmental conditions (Smith 1984; Suckling 1984; Quin 1995; Sharpe 2004). Moreover, our setting for EV may not be sufficiently variable. This requires more long-term data.

Dispersal

ALEX allows two forms of inter-patch movement, diffusion and migration (Possingham and Davies 1995). Diffusion only occurs where a corridor connects patches, the width of which determines the number of animals dispersing per year. There is no mortality associated with diffusion. In contrast, migration allows animals to move in random directions from a source patch and whether they successfully reach another patch depends on an operator-specified mortality distance. We modelled dispersal in ALEX with the migration submodel only because 7 of 8 patches surrounding the Minnippi remnant require a road crossing to move between patches and the urban matrix surrounding all remnants has a diffuse cover of trees. Therefore, dispersal must have a strong element of mortality associated with it and although several rudimentary corridors exist, gliders may disperse in many directions from a source patch.

The potential for squirrel gliders to move between remnants is also supported by the following observations. van der Ree (2002) studied squirrel gliders in Victoria in road-side woodland strips of 20-50 m width. He reported that they may forage in isolated clumps of trees up to 240 m from a habitat remnant. The maximum canopy gap leading to the isolated trees was 70 m. van der Ree (2002; pers. comm.) observed the carcasses of two squirrel gliders on the Hume Highway in Victoria adjacent to remnant habitat. A road-kill has been observed in north-east NSW (D. Sharpe pers. obs.). Squirrel gliders have been observed crossing roads along the ground in Qld (C. Corben pers. comm.) and Rowston (2000b) observed squirrel gliders in the Brisbane area in vegetated strips of approximately 50 m width. She also reported one glider crossing a road and another two crossing a powerline easement. Suckling (1984) observed sugar gliders regularly crossing 250 m of open pasture to reach a food tree, and recorded dispersal between remnants that required movement across 200 m of treeless pasture. He also observed that several gliders dispersed between remnants using a long (1.5 km) road-side strip of 20 m width. These observations suggest that squirrel gliders have a capacity to travel among isolated habitat remnants and will attempt to cross roads of moderate width.

The migration submodel has three, operator-specified components (Possingham and Davies 1995). Firstly, the percentage of the carrying capacity at which dispersal can occur must be specified; below this value it will not occur. Secondly, the probability that an individual within a cohort will disperse must be specified. This probability can be applied to any juvenile cohort as well as to the adult cohort. Thirdly, the mean maximum distance that an animal can disperse must be specified. This is the average distance an animal can disperse before it dies. Animals disperse in random directions from the source patch.

We set the model to allow a 50% probability of juveniles dispersing when the population was at least 60% of carrying capacity. We consider a high population threshold to be appropriate here due to the low suitability of the surrounding matrix for dispersal. We set the mean dispersal distance to 1.5 km. Suckling (1984) observed a maximum dispersal distance by sugar gliders in remnant habitat of 1 km by a female and 1.9 km by a male. We believe our value is conservative, because most trapping studies greatly underestimate dispersal (e.g. Price *et al.* 1994).

Catastrophes

Up to three different types of catastrophes can be modelled by ALEX. These catastrophes can represent events such as fire, logging or disease. Each catastrophe has three, operator-specified components. Firstly, whether a catastrophe is a local (i.e. patch-specific) or global (affecting all patches simultaneously) event. Secondly, whether the probability of a catastrophe occurring is dependent upon the current state of the population or the habitat. If a catastrophe is dependent, it will only occur once a specified threshold has been reached. Thirdly, the immediate effect of the catastrophe on both the population and its habitat. This requires specifying a range for the proportional reduction in the population and the habitat variable. When a catastrophe occurs the actual value chosen is drawn at random from that range of values. Thus, successive catastrophes may not lead to the same reduction in population size or habitat value.

While catastrophes will clearly influence squirrel glider populations, their properties are largely unknown. A wildfire burnt through 85% of the study area used by Quin (1995) to study the population ecology of the squirrel glider in north-eastern NSW. The fire appeared to disrupt patterns of flowering in key nectar-producing tree species and lead to increased dispersal and mortality. Sharpe (2004) observed that drought-related flower failure reduced the number of adult squirrel gliders in his study area to 55% of its mean size determined over a 4-year period.

Given the uncertainty associated with the effect of a catastrophe, we adopted a cautious approach. We ran the model to investigate the influence of the frequency of a catastrophe only. Therefore, we set the model so a catastrophe was local in effect and not dependent on the population size or habitat value of a patch. We varied the frequency of the catastrophe, using probabilities of 0.01, 0.05 and 0.10. We specified that the impact of the catastrophe could vary from 10% mortality up to 50% mortality. This allows for a relatively negligible effect up to the effect of a high intensity fire. All runs that examined catastrophes used the default settings with the five-patch study system.

Model simulations, time intervals, sensitivity analysis and scenarios

In order to assess the influence of habitat fragmentation on the probability of extinction, we considered several different configurations of the habitat patches. We then assessed the influence of catastrophes of different frequency. Sensitivity analyses were then conducted to determine which parameters had the greatest influence on extinction probability. Such an analysis can highlight which values should be chosen more conservatively to ensure that viability is not overestimated. We used a seven patch configuration that included White's Hill for the analysis of catastrophes and the sensitivity analysis.

Each scenario was simulated 500 times over a 200-year period, although only a 100 year interval is considered in terms of extinction probabilities. The longer period was needed to assess the median time to extinction for populations that persisted beyond 100 years. We

estimated the probability of extinction (i.e. the percentage of the 500 runs that the metapopulation became extinct within a given time interval) over a 100 year time frame. The population is viewed as viable in the absence of management if the mean probability of extinction is at or below 5% during this period. This is arbitrarily defined but is consistent with earlier studies (e.g. Goldingay and Possingham 1995). It is not intended that these values be treated as hard numbers but as a guide to indicate when predictions are such that active management should be considered to improve population viability.

Results

How many habitat patches are needed to minimise extinction?

Using the default input values (Table 2) it is clear that a metapopulation consisting of the three habitat patches that currently have reasonable connectivity have a high probability of extinction after about 30 years (Fig. 5). This probability increases steadily over longer periods. The significance of these three remnants is that dispersing gliders are not required to traverse roads to move among them. However, the inclusion of any further remnants requires that gliders cross open road surfaces to disperse to these outer remnants. When five remnants are included in the metapopulation, the probability of extinction increases to 11% over a 60-year period (Fig. 5). After 100 years, the probability of extinction is 20%. That is well above the 5% cut-off point for a population to be treated as viable over a 100-year period.

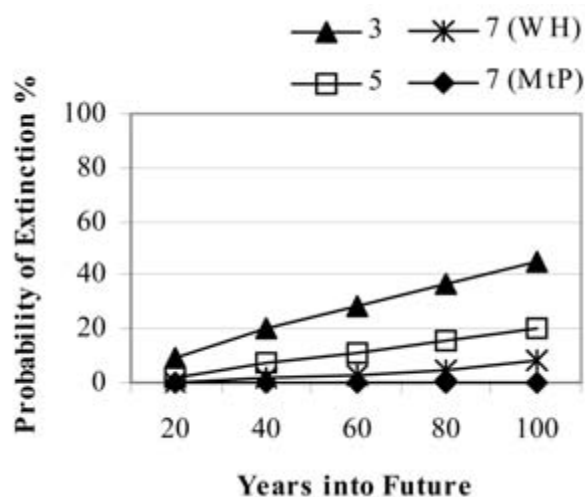


Figure 5. Probability of extinction of gliders for metapopulations of different numbers of remnants. WH = Whites Hill; MtP = Mt Petrie.

We also ran the model by adding in turn, a larger outer patch to the metapopulation. In one scenario we added the White's Hill reserve (150 ha), and the small (10 ha) satellite remnant located between White's Hill and Belmont Hills (Table 1). These inclusions in the metapopulation led to a low probability of extinction over a 100-year period. In the other scenario, the much larger Mt Petrie remnant (700 ha) was added. The predicted probability of extinction was zero over a 100-year period. At present, we do not know whether these

large outer patches are part of the metapopulation, but due to the presence of major arterial roads which cross the connections, we assume that any dispersal between these outer remnants must be quite rare.

The influence of catastrophes

When a catastrophe had a low frequency (1 in 100 years), the probability of extinction was only slightly greater than when there was no catastrophe (Fig. 6), though it was above 10% after 100 years. If the frequency was increased to 1 in 20 years, there was a significant probability of extinction after 60 years and double this after 100 years. If the frequency was increased to 1 in 10 years, then the probability of extinction was at a level of concern (above 10%) after 40 years and was very high after 100 years.

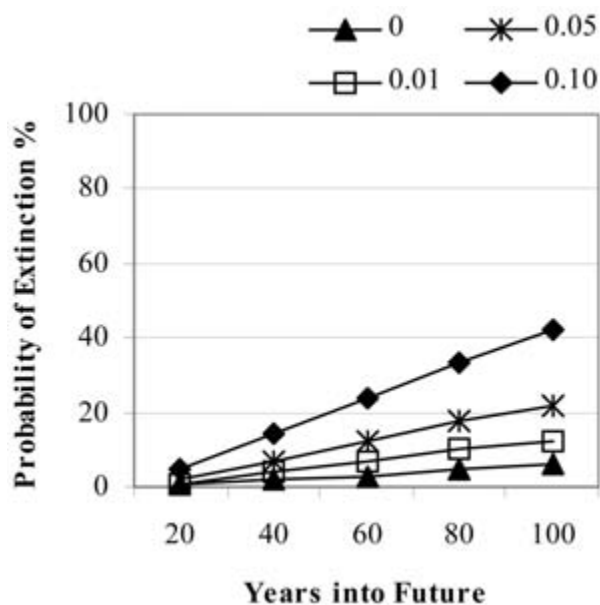


Figure 6. Probability of extinction when catastrophes are included.

Sensitivity analyses

Juvenile mortality

Varying the annual probability of juvenile mortality had a moderate influence on the probability of extinction (Fig. 7). Reducing the probability of mortality to a value of 25% led to a negligible probability of extinction over a 100-year period. However, if annual mortality was increased to 45%, then the probability of extinction was more than four times higher after 100 years. The median time to extinction for every value was >100 years.

Adult mortality

Varying the annual probability of adult mortality had a strong influence on the probability of extinction (Fig. 8). Raising the value to 40% produced an extinction probability after 40 years of approximately 10%. If mortality was increased to 45%, then the metapopulation was clearly at risk of extinction after just 20 years. However, it is only at this much higher level of mortality that the median time to extinction dropped below 100 years.

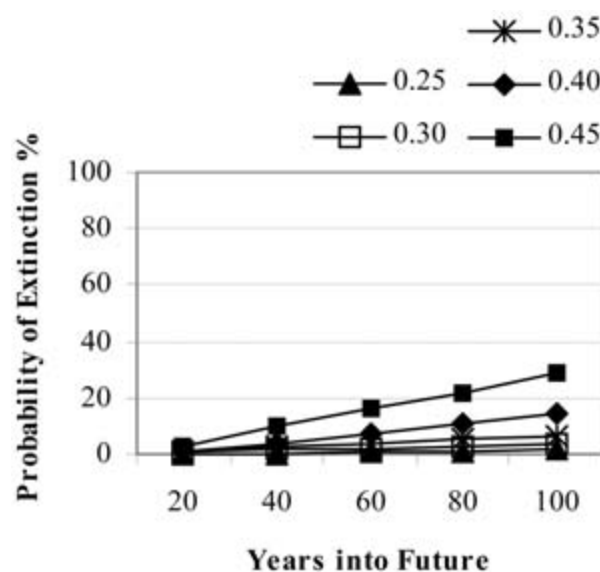


Figure 7. Probability of extinction when the annual mortality (%) of juvenile gliders is varied.

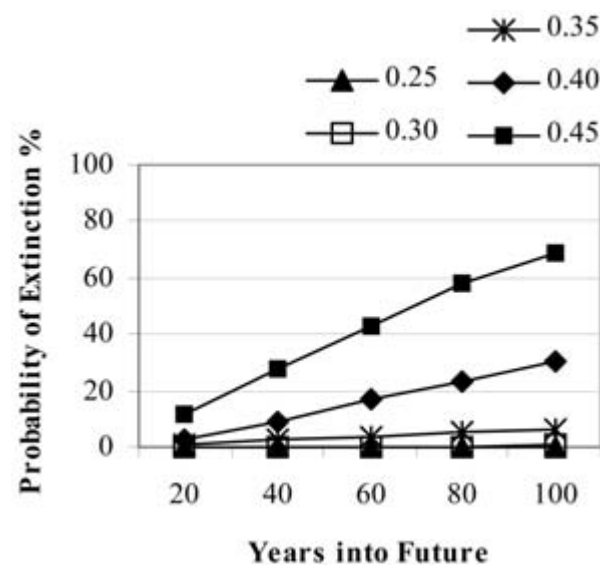


Figure 8. Probability of extinction when the annual mortality (%) of adult gliders is varied.

Dispersal attributes

We conducted sensitivity analyses on the three components of dispersal: the population threshold for dispersal, the probability that a given juvenile will disperse, and the distance they can disperse.

The population threshold for juvenile dispersal had a strong influence on the probability of extinction (Fig. 9). When the threshold value was reduced, the probability of extinction increased strongly. This suggests that there was a high cost of dispersal because most dispersers did not reach another patch, so allowing dispersal at low population densities was analogous to higher juvenile mortality.

The probability of juvenile dispersal had a lesser influence on population viability (Fig. 10). Increasing the likelihood from 30% to 70% that an animal dispersed led to a 5-fold increase in the probability of extinction.

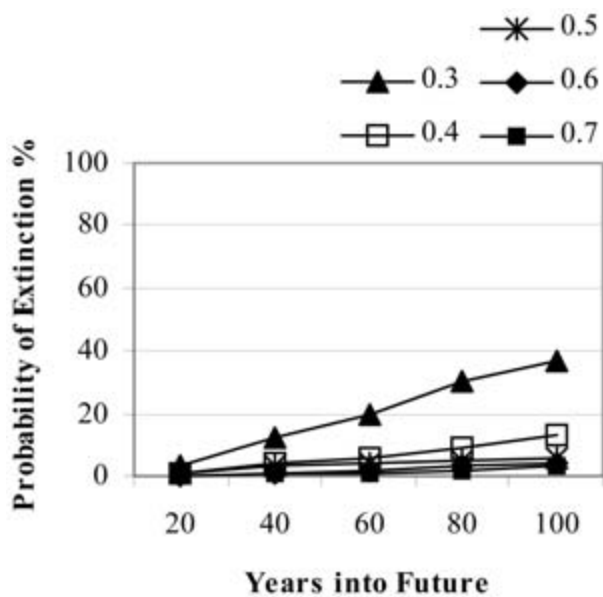


Figure 9. Probability of extinction when the minimum population threshold (% of carrying capacity) for dispersal is varied.

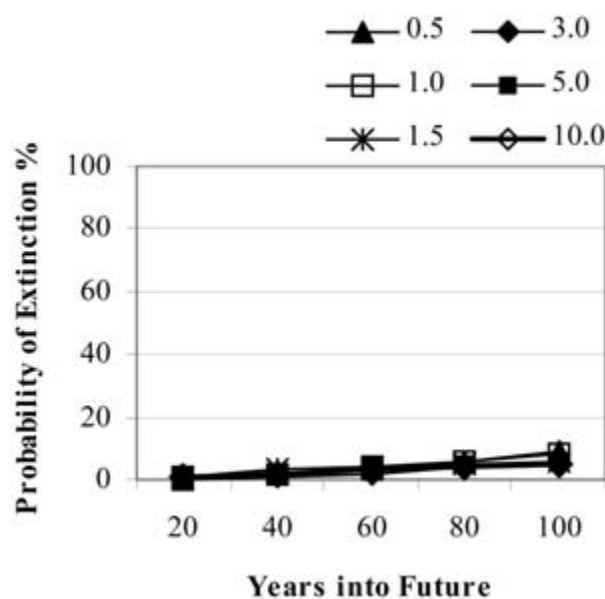


Figure 11. Probability of extinction when the mean dispersal distance is varied (0.5-10.0 km).

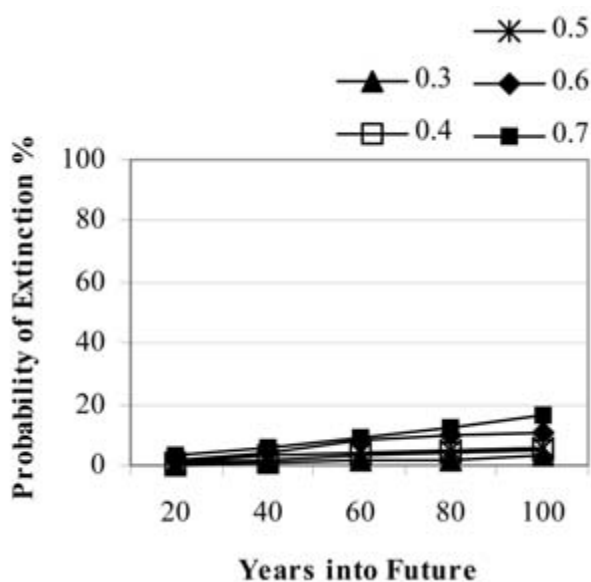


Figure 10. Probability of extinction when the probability of juvenile dispersal is varied.

The maximum mean dispersal distance was varied substantially from 0.5 to 5 km. Changes to this value had a relatively small influence on population viability over a 100 year period (Fig. 11). This is likely because several of the remnants are within about 1 km of each other. Therefore, it does not appear critical how precisely this value is estimated.

Discussion

Is there value in conducting a PVA?

There has been much recent debate about the usefulness of PVA to accurately predict extinction risk (e.g. Brook *et al.* 2002; Ellner *et al.* 2002). While Coulson *et al.* (2001) concluded that “the predictions of PVAs should

be treated with extreme caution” if the input values are poorly known, they also concluded that there is value in using PVAs to compare the consequences of alternative management strategies. We acknowledge that the quality of the information available on the life history of the squirrel glider is poor, and regard our PVA as a preliminary analysis that will be built upon as more detailed field data become available. A key intention of evaluating management options with our PVA was to compare a “do nothing” management approach (also referred to as “benign neglect” – see Soule *et al.* 1979) with active management that requires money to be spent to achieve specific conservation objectives. We believe that this is a valuable exercise, and one that can be generalised to the conservation of the squirrel glider elsewhere.

Our study differed from that of other recent PVAs on arboreal marsupials. Lindenmayer *et al.* (2000) tested the performance of models and parameters against observed patch occupancy by three species in a system of 39 remnants (none >41 ha) embedded in a matrix of pine forest. McCarthy and Lindenmayer (2000) assessed the influence of fire frequency and patchiness on the risk of extinction of Leadbeater’s possum in 27 remnants (none >16 ha) embedded in a matrix of regrowth eucalypt forest. Dispersal among remnants through the forested matrix in both these systems is likely to be unimpeded. Our study system included only 8 patches and half were >60 ha. However, the greatest departure of our study from earlier studies is the fact that the remnants are embedded in an urban matrix and the linkages among the patches are poor, often being comprised of narrow strips of trees with arterial road disjunctions (see Fig. 4). Nevertheless, we predict that dispersal among remnants is likely but it will be associated with high levels of mortality.

Influence of life history attributes on the PVA

There are two components to assessing the influence of inputs to the model on our predictions. One is a straightforward consideration of how appropriate are the values chosen as model inputs. The other is how well the model is able to represent the ecology of the target species. Possingham *et al.* (1993) stated that conducting a PVA is useful in forcing a critical review of the extent and quality of information that is available on the life history of a species. Our review of studies on the squirrel glider revealed that many life history attributes are still inadequately known, though the current level of understanding has improved substantially during the last 10 years. The values used for annual mortality are at present informed guesses. For example, the baseline value used for juvenile mortality was 35%. van der Ree (2000) reported 64% predation (mostly by large owls) on 11 radio-collared juvenile squirrel gliders. If such a value is common place in fragmented habitat, then we have greatly underestimated the probability of extinction in our PVA. The presence of domestic cats in an urban setting could also lead to high mortality values. However, we observed no owls large enough to prey on a squirrel glider nor cats in the Minnippi Parklands remnant during 18 months of intensive field work (Goldingay *et al.* unpubl. obs.). The observations of van der Ree suggest that caution is required in choosing a mortality value.

We have explored the influence of annual mortality and other elements of the PVA model on extinction probabilities by employing sensitivity analysis, particularly to highlight those elements that should be targeted in future research in order to improve confidence in model output. Annual mortality had a predictably strong influence on the probability of extinction, particularly adult female mortality. It is likely that adult mortality can be estimated more accurately than juvenile mortality because trapping studies conducted over a sufficient length of time will reveal the approximate maximum age when individuals disappear from a population. Such disappearance is likely to indicate the death of the individual, though dispersal by adult petaurids is not unknown (e.g. Smith 1984; Craig 1985). In contrast, most juvenile petaurids attempt to disperse at some stage and are likely to move beyond a trapping area (e.g. Smith 1984; Suckling 1984; Quin 1995). Thus, the probability of disappearance from the trapping record cannot be equated directly with mortality.

The issue of dispersal is very important to any PVA (e.g. Lindenmayer and Possingham 1996; Lindenmayer *et al.* 2000). The probability of extinction in our study was sensitive to variation in the population threshold at which dispersal occurred. Allowing dispersal to occur when the population is at 70% of carrying capacity had a probability of extinction that was about one-third of that when the population was at 40%. This result arises because the direction of dispersal is chosen at random by ALEX and individuals die if they fail to reach a remnant. When the threshold is set higher, many of these juveniles are able to mature into adults within the source patch. Lowering the dispersal threshold is similar to raising the level of juvenile

mortality in the model, and leads to mortality associated with dispersal being included twice. Brook (2000) refers to such occurrences as "double dipping" and suggests that it leads to model predictions being pessimistic. Earlier studies using ALEX had set this parameter at 20-30% but had not conducted sensitivity analysis of its influence (e.g. Possingham *et al.* 1994; Lindenmayer & Possingham 1995; McCarthy & Lindenmayer 2000). Field studies on petaurids are unable to shed any light on this issue, but one would expect a greater resistance to dispersal by juveniles (i.e. philopatry) when the population is well below carrying capacity. Studies in fragmented habitat should consider this issue and it may even be feasible to conduct an experimental study using the sugar glider as a model (e.g. Suckling 1984). It appears that the correct way to model dispersal is not obvious and may differ among species (Lindenmayer *et al.* 2000). Detailed population studies of squirrel gliders in different-sized remnants may provide important insights into some of the above parameters.

The social system of the squirrel glider is another life history attribute that remains poorly understood. The social system will influence how many female gliders live in a given remnant, with higher densities expected when social groups contain >1 adult female. Thus, the social system will influence the reproductive capacity of a site. Current evidence suggests that social groups contain one or two adult females, and that both may occur at one site (Quin 1995; van der Ree 2002; Sharpe unpubl. data; Goldingay *et al.* unpubl. data). Thus, any PVA of the squirrel glider should reflect a mixed social structure. How this interacts with habitat-mediated variation in population density is unknown, so further research on group structure is required.

Viability of the local metapopulation

This PVA has provided a preliminary assessment of the viability of the Brisbane squirrel glider metapopulation. We have done this with only a basic understanding of the suitability of the habitat in the remnants. A detailed trapping study in the Minnippi remnant during 2002 revealed a density of squirrel gliders of about 2 per ha (Sharpe *et al.* unpubl. data). The quality of habitat appears to be high due to the presence of a large number of tree species that provide food resources (Dobson *et al.* in press) and a high number of hollow-bearing trees (Beyer 2003). We have conducted only preliminary surveys in the other remnants, which suggest that habitat quality is much lower than at Minnippi. So we have assumed habitat quality to be equivalent across all other remnants but field work is required to demonstrate this. Furthermore, we ignored a 50 ha remnant (Seven Hills) located 800 m west of Minnippi (see Fig. 1), because it contained few hollow-bearing trees, and repeated efforts to locate squirrel gliders there had failed. It is obvious that much more information is needed on habitat suitability to refine this PVA. We have commenced trapping in additional remnants to clarify this issue.

Our interpretation of the modelling of the 5-patch metapopulation is that it has an unacceptably high probability of extinction over a 100-year period. That is, that benign neglect is likely to lead to local extinction of the squirrel glider in this part of Brisbane

within several decades. This situation is likely to be repeated in other parts of the Brisbane urban area and southeast Qld. The uncertainty associated with several life history parameters requires caution. It is likely that the estimates of annual mortality are too low, causing us to overestimate metapopulation viability. For example, the baseline value for juvenile mortality of 35% per year predicts that the probability of extinction for the metapopulation is around 6% after 100 years. However, if juvenile mortality is 45% per year, then the probability of extinction is at 10% after just 40 years. When catastrophes (e.g. fire, drought) are included in the PVA, the extinction probabilities rise considerably (see also Jackson 1999). Although their frequency is unknown, management should aim to conserve populations that are sufficiently robust to cope with such events (Coulson *et al.* 2001). It is also likely that the frequency of successful dispersal is lower than what the model allows (i.e. dispersal is dependent on corridor quality not distance as is currently modelled). Roads sever most connections between adjoining remnants in the 5-patch system so dispersal might be very hazardous.

Challenges for management

Perhaps the greatest challenge for the long-term conservation of the squirrel glider within Brisbane's urban forest remnants is the establishment of functional corridors that link the remnants in the Bulimba Creek system. Most corridors are poorly vegetated and are cut by roads (Figs 2-4). Gliders that are forced to travel along the ground and over roads to move among

forested areas must be prone to high levels of mortality (i.e. predation, road-kill). Enhancing the habitat quality of the connecting corridors by tree planting programs may improve the probability of safe dispersal. We are currently investigating the merit of using nestboxes to facilitate movement by gliders through these corridors (Beyer 2003). Other novel habitat enhancement measures may also be required.

Our finding that adding a large remnant to the patch system is required to substantially reduce the probability of extinction is not a trivial result. It could not be predicted before this modelling that the squirrel glider population across the more easily linked 5-patch system was at risk of extinction. However, linking a large remnant to the 5-patch system is required to minimise this risk. This is a considerable challenge because the largest remnant (Mt Petrie), which would have the greatest influence on metapopulation viability, is currently disconnected from the system by a 30 m wide high traffic volume freeway (Fig. 3). Successful dispersal across this freeway at present seems unlikely. However, a corridor connection could be created by revegetation to allow gliding across the gap, and perhaps by the installation of tall (30 m high) gliding poles on each side of the freeway and within the median strip. There is a broad road easement under the freeway (Fig. 12) at the southern end of Belmont Hills that links with Mt Petrie (Fig. 3). This could be modified to serve as a connecting corridor. Tree plantings on each side of this underpass, in combination with landscaping within the underpass may facilitate access by gliders.



Figure 12. Road underpass under the Gateway Freeway between Belmont Hills and Mt Petrie. The forest of Belmont Hills is visible in the background.

Although the White's Hill remnant is located over 1.5 km from the 5-patch system (Fig. 1), it may be more feasible to establish a functional connection with this remnant than with Mt Petrie. There is presently a rudimentary corridor, comprising a 50-100 m wide band of scattered trees along Bulimba Creek and another extending west across to White's Hill (Fig. 4). There are also scattered bands of trees connecting through a golf course to this remnant. Again, several roads cut through this potential corridor. A revegetation program is needed to enhance the suitability of these connections. There is a need for on-going research to help to describe and understand the usage of different elements of this highly modified landscape by squirrel gliders.

A basic assumption in this PVA exercise is that the area of the remnants will be fixed through time. This is unlikely to be true and one that has led to the underestimation of extinction risk. The remnants are likely to be subjected to severe edge effects that will require management attention. Edge effects, such as tree dieback and increased predation, will influence habitat quality and lead to incremental loss of habitat area (e.g. Bolger *et al.* 1997). For example, wind-throw and insect-induced die-back (e.g. Landsberg *et al.* 1990) may lead to the edge advancing into remnants over time. Predation by feral predators (e.g. house cats) may be higher close to edges relative to core areas within remnants, and it will be exacerbated by advancing edges. A detailed study that investigates edge effects is required to provide important insights that will guide the on-going

management of these urban habitat remnants. Current information does not allow prediction of the severity of edge effects but we note that much of the Minnippi remnant is affected by such factors. There are some opportunities for planting programs to enlarge remnants in the northern part of the study area which may assist in reducing the edge effects.

We have focussed our discussion of squirrel glider conservation in Brisbane on a single population (or metapopulation). We can view this as a model system for understanding the effects of habitat fragmentation on the squirrel glider in an urban setting. However, conservation of the squirrel glider must involve more than one population to provide additional security against local extinction. The number required is open to debate but conserving three or more isolated populations of a species within a small regional area has been advocated previously (e.g. Goldingay and Lewis 1999). The Brisbane City Council area is an appropriate basis for such a strategy. It is 12000 ha in size and has been substantially cleared (Brisbane City Council 2002), as has much of the lowland forests of southeast Qld that are preferred by the squirrel glider (Rowston *et al.* 2002). Finally, the broader conservation strategy should be to replicate this conservation effort throughout the geographic range of the squirrel glider. This will provide protection against adverse environmental conditions acting on all populations at once, and conserve genetic variability and adaptation to the local environment.

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References

- Beyer, G. 2003. *The value of nest boxes in managing hollow-using arboreal marsupials*. Honours thesis, Southern Cross University, Lismore.
- Bolger, D.T., Alberts, A.C., Sauvajot, R.M., Potenza, P., McCalvin, C., Tran, D., Mazzoni, S. and Soule, M.E. 1997. Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7: 552-63.
- Braithwaite, L.W. 1983. Studies on the arboreal marsupial fauna of eucalypt forests being harvested for woodpulp at Eden, N.S.W. I. The species and distribution of animals. *Australian Wildlife Research* 10: 219-29.
- Brisbane City Council 2002. *State of Environment Report 2001*. Brisbane City Council, Brisbane.
- Brook, B.W. 2000. Pessimistic and optimistic bias in population viability analysis. *Conservation Biology* 14: 564-6.
- Brook, B.W., Burgman, M.A., Akcakaya, H.R., O'Grady, J.J. and Frankham, R. 2002. Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. *Conservation Biology* 16: 262-3.
- Catterall, C.P., Rowston, C. and Piper, S. 1996. Ecology of a squirrel glider *Petaurus norfolcensis* population within selected Cannon Hill bushlands. Report prepared for Brisbane City Council and Hudson Conway, Brisbane.
- Catterall, C.P., Storey, R.J., and Kingston, M.B. 1997. Reality versus rhetoric: a case study monitoring regional deforestation. Pp. 367-77 in *Conservation Outside Nature Reserves*, edited by P. Hale & D. Lamb. Centre for Conservation Biology, University of Queensland, Brisbane.
- Coulson, T., Mace, G.M., Hudson, E. and Possingham, H. (2001). The use and abuse of population viability analysis. *Trends in Ecology & Evolution* 16: 219-21.
- Craig, S.A. 1985. Social organisation, reproduction and feeding behaviour of a population of yellow-bellied gliders, *Petaurus australis* (Petauridae: Marsupialia). *Australian Wildlife Research* 12: 1-18.
- Davey, S.M. 1990. Methods for surveying the abundance and distribution of arboreal marsupials in a south coast forest of New South Wales. *Australian Wildlife Research* 17: 427-445.
- Dobson, M., Goldingay, R.L. and Sharpe, D.J. (in press). Feeding behaviour of the squirrel glider in remnant habitat in Brisbane. *Australian Mammalogy*.

- Ellner, S.P., Fieberg, J., Ludwig, D. and Wilcox, C. 2002. Precision of population viability analysis. *Conservation Biology* 16: 258-61.
- Eyre, T.J. 2004. Distribution and conservation status of possums and gliders of southern Queensland. Pp. 1-25 in *The Biology of Australian Possums and Gliders*, edited by R.L. Goldingay and S.M. Jackson. Surrey Beatty & Sons, Chipping Norton, NSW.
- Goldingay, R.L. 1992. The socioecology of the yellow-bellied glider, *Petaurus australis*, in a coastal forest. *Australian Journal of Zoology* 40: 267-78.
- Goldingay, R.L. 1996. The green and golden bell frog *Litoria aurea* - from riches to ruins: conservation of a formerly common species. *Australian Zoologist* 30: 248-56.
- Goldingay, R.L. and Kavanagh, R.P. 1995. Foraging behaviour and habitat use of the feather-tail glider (*Acrobates pygmaeus*) at Waratah Creek, New South Wales. *Wildlife Research* 22: 457-70.
- Goldingay, R.L. and Daly, G. 1997. Surveys of arboreal and terrestrial mammals in the montane forests of Queanbeyan, New South Wales. *Australian Mammalogy* 20: 9-19.
- Goldingay, R. and Lewis, B. 1999. Development of a conservation strategy for the green and golden bell frog in the Illawarra Region of NSW. *Australian Zoologist* 31: 376-87.
- Goldingay, R.L. and Possingham, H.P. 1995. Area requirements for viable populations of the Australian gliding marsupial *Petaurus australis*. *Biological Conservation* 73: 161-7.
- Hill, D. 1997. *A comparative study of population viability models for squirrel gliders in Brisbane*. Honours thesis. Griffith University, Queensland.
- Jackson, S.M. 1999. Preliminary predictions of the impacts of habitat area and catastrophes on the viability of mahogany glider *Petaurus gracilis* populations. *Pacific Conservation Biology* 5: 56-62.
- Jackson, S.M. 2000. Population dynamics and life history of the mahogany glider, *Petaurus gracilis*, and the sugar glider, *Petaurus breviceps*, in north Queensland. *Wildlife Research* 27: 21-37.
- Kavanagh, R.P. 1984. Seasonal changes in habitat use by gliders and possums in south-eastern New South Wales. Pp. 527-543 in *Possums and Gliders*, edited by A.P. Smith and I.D. Hume. Australian Mammal Society, Sydney.
- Kavanagh R. P. 2000. Effects of variable-intensity logging and the influence of habitat variables on the distribution of the Greater Glider *Petauroides volans* in montane forest, southeastern New South Wales. *Pacific Conservation Biology* 6:18-30.
- Kavanagh, R.P. 2004. Distribution and conservation status of possums and gliders in New South Wales. Pp. 130-148 in *The Biology of Australian Possums and Gliders* edited by R.L. Goldingay and S.M. Jackson. Surrey Beatty & Sons, Chipping Norton, NSW.
- Landsberg, J., Morse, J. and Khanna, P. 1990. Tree dieback and insect dynamics in remnants of native woodland on farms. *Proceedings of the Ecological Society of Australia*. Proc. Ecol. Soc. Aust. 16: 149-65.
- Lindenmayer, D.B. and Possingham, H.P. 1995. Modelling the impacts of wildfire on the viability of metapopulations of the endangered Australian species of arboreal marsupial, Leadbeater's possum. *Forest Ecology & Management* 74: 197-222.
- Lindenmayer, D.B. and Possingham, H.P. 1996. Modelling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. *Landscape Ecology* 11: 79-105.
- Lindenmayer, D.B., Lacy, R.C. and Pope, M.L. 2000. Testing a simulation model for population viability analysis. *Ecological Applications* 10: 580-97.
- McCarthy, M.A. and Lindenmayer, D.B. 2000. Spatially-correlated extinction in a metapopulation model of Leadbeater's possum. *Biodiversity and Conservation* 9: 47-63.
- Menkhorst, P.W. 1995. Squirrel Glider. Pp 113-14. in *Mammals of Victoria* edited by P.W. Menkhorst. Oxford University Press, Melbourne.
- Menkhorst, P.W., Weavers, B.W. and Alexander, J.S.A. 1988. Distribution, habitat and conservation status of the squirrel glider *Petaurus norfolcensis* (Petauridae: Marsupialia) in Victoria. *Australian Wildlife Research* 15: 59-71.
- Millis, A.L. and Bradley, A.J. 2001. Reproduction in the squirrel glider, *Petaurus norfolcensis* (Petauridae), in south-east Queensland. *Australian Journal of Zoology* 49: 139-54.
- Possingham, H.P. and Davies, I. 1995. ALEX: a model for the viability analysis of spatially structured populations. *Biological Conservation* 73: 143-50.
- Possingham, H.P., Lindenmayer, D.B., and Norton, T.W. 1993. A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* 1: 39-45.
- Possingham, H.P., Lindenmayer, D.B., Norton, T.W. and Davies, I. 1994. Metapopulation viability analysis of the greater glider *Petauroides volans* in a wood production area. *Biological Conservation* 70: 265-76.
- Price, M.V. and P. Kelly. 1994. An age-structured demographic model for the endangered Stephens' kangaroo rat. *Conservation Biology* 8: 810-21.
- Price, M.V., Kelly, P.A. and Goldingay, R.L. 1994. Distances moved by Stephens' kangaroo rat (*Dipodomys stephensi*) and implications for management. *Journal of Mammalogy* 75: 929-39.
- Quin, D.G. 1995. Population ecology of the squirrel glider (*Petaurus norfolcensis*) and the sugar glider (*P. breviceps*) (Marsupialia: Petauridae) at Limeburners Creek, on the central north coast of New South Wales. *Wildlife Research* 22: 471-505.
- Quin, D.G., Smith, A.P. and Norton, T.W. 1996. Ecogeographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). *Australian Journal of Zoology* 44: 19-45.
- Rowston, C. 1998. *The squirrel glider: an autecological study in a fragmented landscape*. PhD thesis. Griffith University, Queensland.
- Rowston, C. 2000a. Squirrel glider home ranges, movement patterns and habitat usage. Bushland Management & Consulting Services. Report prepared for Brisbane City Council, Brisbane.
- Rowston, C. 2000b. Fitzgibbon squirrel glider study. Bushland Management & Consulting Services. Report prepared for Brisbane City Council, Brisbane.
- Rowston, C., Catterall, C.P. and Hurst, C. 2002. Habitat preferences of squirrel gliders, *Petaurus norfolcensis*, in the fragmented landscape of southeast Queensland. *Forest Ecology and Management* 164: 197-209.
- Sadler, L.M. and Ward, S.J. 1999. Coalitions in male sugar gliders: are they natural? *Journal of Zoology* 248: 91-96.
- Sharpe, D. 1996. *Foraging ecology of the squirrel glider*. Honours Thesis, Southern Cross University, Lismore, NSW.

- Sharpe, D.J.** 2004. Effect of flower failure on a population of squirrel gliders (*Petaurus norfolcensis*) in northeast New South Wales. Pp 339-349 in 'The Biology of Australian Possums and Gliders', edited by R. L. Goldingay and S. M. Jackson. Surrey Beatty and Sons, Chipping Norton, NSW.
- Sharpe, D.J. and Goldingay, R.L.** 1998. Feeding behaviour of the squirrel glider at Bungawalbin Nature Reserve, north-eastern New South Wales. *Wildlife Research* 25: 243-54.
- Smith, A.P.** 1984. Demographic consequences of reproduction, dispersal and social interaction in a population of Leadbeater's possum (*Gymnobelideus leadbeateri*). Pp. 359-73. In *Possums and Gliders*, edited by A.P. Smith and I.D. Hume. Australian Mammal Society: Sydney.
- Smith, A.P. and Murray, M.** 2003. Habitat preferences of the squirrel glider (*Petaurus norfolcensis*) and associated possums and gliders on the New South Wales central coast. *Wildlife Research* 30: 291-301.
- Soule, M.E., Wilcox, B.A. and Holtby, C.** 1979. Benign neglect: a model of faunal collapse in the game reserves of East Africa. *Biological Conservation* 15: 260-72.
- Southgate, R. and Possingham, H.** 1995. Modelling the reintroduction of the greater bilby *Macrotis lagotis* using the metapopulation model Analysis of the Likelihood of Extinction (ALEX). *Biological Conservation* 73: 151-60.
- Strahan, R.** 1995. *The Mammals of Australia*. Reed Books, Chatswood.
- Suckling, G.C.** 1984. Population ecology of the sugar glider, *Petaurus breviceps*, in a system of fragmented habitats. *Australian Wildlife Research* 11: 49-75.
- Trail, B.J.** 1998. Identification of squirrel gliders and sugar gliders in Victoria. *Victorian Naturalist* 115: 135-141.
- van der Ree, R.** 2000. Ecology of arboreal marsupials in a network of remnant linear habitats. PhD thesis, Deakin University, Melbourne.
- van der Ree, R.** 2002. The population ecology of the squirrel glider (*Petaurus norfolcensis*) within a network of remnant linear habitats. *Wildlife Research* 29: 329-40.
- van der Ree, R. and Bennett, A.F.** 2003. Home range of the squirrel glider *Petaurus norfolcensis* in a network of linear habitats. *Journal of Zoology (London)* 259: 327-336.
- van der Ree, R., Bennett, A.F. and Gilmore, D.C.** 2003. Gap crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. *Biological Conservation* 115: 241-249.
- Warren, J. & Associates** 2000. Minnippi Community Links Golf Course Squirrel Glider (*Petaurus norfolcensis*) Impact Assessment. Report prepared for Design Marketing & Management and BMD Group, Brisbane.
- Winter, J.W., Dillewaard, H.A., Williams, S.E. and Bolitho, E.E.** 2004. Possums and gliders of North Queensland: distribution and conservation status. Pp 26-50 in *The Biology of Australian Possums and Gliders* edited by R.L. Goldingay and S.M. Jackson. Surrey Beatty & Sons, Chipping Norton, NSW.