

Integrating demographic and genetic studies of the Greater Glider *Petauroides volans* in fragmented forests: predicting movement patterns and rates for future testing

D. B. LINDENMAYER,¹ R. C. LACY,² H. TYNDALE-BISCOE,³ A. C. TAYLOR,⁴ K. L. VIGGERS⁵
and M. L. POPE⁶

¹Centre for Resource and Environmental Studies and Department of Geography, The Australian National University, Canberra, Australian Capital Territory, Australia 0200.

²Department of Conservation Biology, Daniel F. and Ada L. Rice Center, Brookfield Zoo, Brookfield, Illinois, 60513, USA.

³Research School of Biological Sciences, The Australian National University, Canberra, Australian Capital Territory, Australia 0200.

⁴Department of Biological Sciences, Monash University, Clayton, Victoria, Australia 3168.

⁵Division of Biochemistry and Molecular Biology, The Australian National University, Canberra, Australian Capital Territory, Australia 0200.

⁶Centre for Resource and Environmental Studies, The Australian National University, Canberra, Australian Capital Territory, Australia 0200.

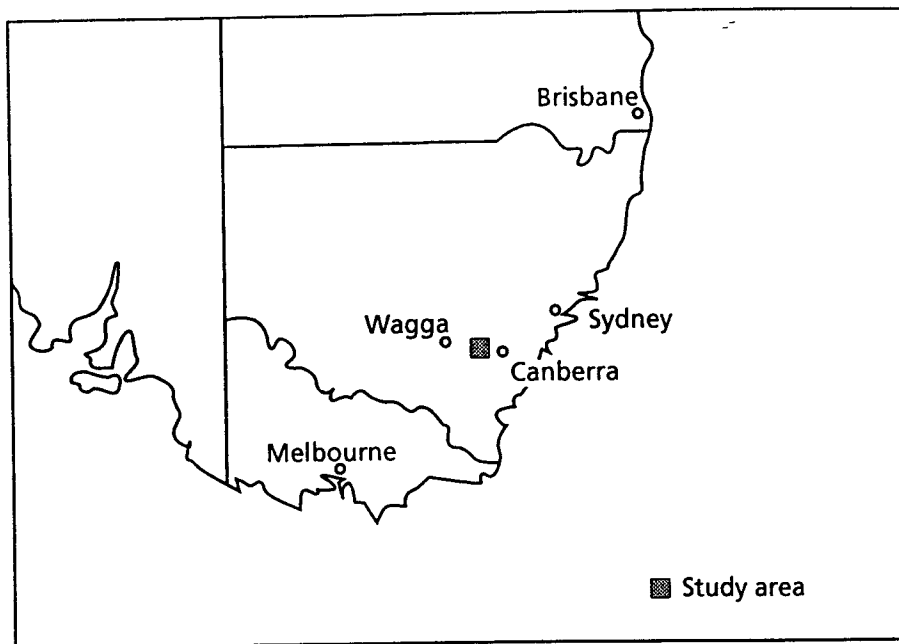
HABITAT loss and habitat fragmentation can have major effects on the distribution and abundance of species (Saunders *et al.* 1987), often in unpredictable ways (Klein 1989; Tilman *et al.* 1994; Lacy and Lindenmayer 1995; Cunningham and Moritz 1998). An understanding of responses of species, which lead to persistence or extinction in such disturbed systems, is important for the effective management of many taxa in fragmented multi-use landscapes. One way to examine population dynamics in fragmented systems is to analyse the genetic characteristics of subpopulations in remnant habitat patches (Sarre 1995), borrowing from the population genetics literature for the interpretation of key effects. For example, it is well established that a small, completely isolated population will lose genetic variation rapidly due to genetic drift (Lacy 1987). However, loss of genetic variation within, and increasing differentiation between, subpopulations will be counteracted by inter-population dispersal. Theoretical models of metapopulation structure which describe connectivity and stability can be examined using various demographic input parameters. Importantly, such models can also produce predictions for genetic structuring, making the combined use of modelling and empirical genetic data an extremely powerful tool in examining the effects of habitat fragmentation. On this basis, we have recently commenced a series of integrated

demographic and genetic studies of the Greater Glider *Petauroides volans* at Tumut in southern New South Wales. The study area near Tumut in southeastern New South Wales is characterized by an array of remnant patches of eucalypt forest (0.2–125 ha in size) that were created 15–65 years ago by the establishment of an extensive (50 000 ha) plantation of exotic softwood, Radiata Pine *Pinus radiata* and known as the Buccleuch State Forest (Routley and Routley 1975). Large areas of continuous native eucalypt forest occur at the boundaries of the plantation (Fig. 1), including those within the Brindabella and Kosciuszko National Parks, and the Bondo and Bungongo State Forests.

The proposed investigation of *P. volans* is unique because it is underpinned by studies 35 years ago by Tyndale-Biscoe and his colleagues (Smith 1969; Tyndale-Biscoe and Smith 1969a,b) in which extensive numbers of animals were collected as the original eucalypt forest at Tumut was converted to pine plantation. Moreover, some patches of native forest were exempt from clearing at this time and recent field surveys indicate that they still support populations of *P. volans* (Lindenmayer *et al.* 1999). Finally, large numbers of *P. volans* occur in the continuous eucalypt forest which exists at the boundaries of the softwood plantation in the Buccleuch State Forest (Lindenmayer *et al.* 1999).

Specimens collected in the earlier studies by Tyndale-Biscoe, as well as blood samples from extant populations of the species in the eucalypt remnants and large continuous areas of native forest, can be used in genetic analyses of fragmentation and other effects on *P. volans*. The availability of historic and current samples of *P. volans* allows us to assay genetic variation at highly polymorphic nuclear genes (microsatellite DNA) as well as mitochondrial genes. We will quantify genetic distances and gene diversity among populations, numbers of alleles per subpopulation, allele frequencies and levels of heterozygosity within populations. On this basis, our work at Tumut broadly aims to:—

- Examine patterns of genetic distance in relation to geographic distance among populations in existing continuous forest and historical populations (prior to clearing and subsequent fragmentation).
- Compare plots of genetic distance *vs* geographic distance generated from populations in continuous forest with those derived from populations in the system of eucalypt fragmentation.
- Determine if there have been changes in genetic variability at regional level (i.e., between the patch system and large continuous areas of eucalypt forest).
- Assess the distribution of genetic variability among remnant patches and infer from that the level of effective gene flow (dispersal).



Finally, we outline plans to compare actual values for a range of genetic measures against predicted estimates derived from a spatially explicit meta-population model (VORTEX [Lacy 1993a]). This represents another way to promote an understanding of the population dynamics of *P. volans* in the fragmented forest system at Tumut.

BACKGROUND — THE TUMUT STUDY AREA AND PREVIOUS STUDIES IN THE REGION

A total of 400 *P. volans* was collected during the early-mid 1960s throughout large areas of the Mason's Block and nearby eucalypt stands within the Buccleuch State Forest as the original *Eucalyptus* forest was being replaced with *P. radiata* (Tyndale-Biscoe and Smith 1969b). The exact locations where animals were taken were carefully recorded and this information remains with the specimens now lodged with various museums around Australia. We have been able to obtain access to these specimens and take a small sample of fur and skin or a tooth from 270 of them. Procedures are now underway to extract DNA from these samples.

Extensive spotlighting surveys have established that *P. volans* is absent from the Radiata Pine plantation near Tumut (Lindenmayer *et al.* 1999). However, animals occupy patches of remnant native eucalypt forest embedded within the pine matrix (Lindenmayer *et al.* 1999). For example, there are six patches of native forest, dispersed within a distance of 3 km² and located within and adjacent to the Mason's Block area. Although these patches have been surrounded by extensive stands of pine for almost 35 years, they support approximately 25 adult *P. volans*. Blood samples have been collected from these animals for DNA analyses. The time since forest fragmentation is about six generations of *P. volans*; long enough for genetic decay and divergence of initially highly variable genetic loci to reach measurable levels in such a system (Lacy 1987; Lacy and Lindenmayer 1995).

Also in the patch system, but 10 km north of Mason's Block, a detailed radio-tracking study of *P. volans* has recently been completed (Pope *et al.*,

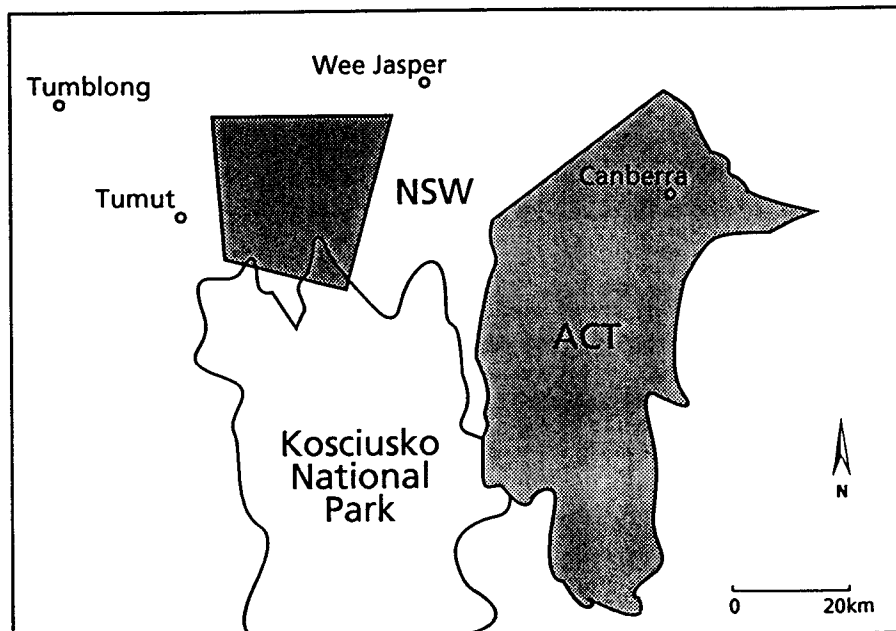


Fig. 1. The general location of the study area at Tumut, southeastern Australia.

Because of the unique nature of the material available to us, we have taken the somewhat unusual step of outlining our proposed study design and setting out some predictions about possible genetic patterns *before* they are formally tested — an approach rarely taken in the biological sciences (but see McCarthy and Lindenmayer 1998). We have done this to seek feedback and criticism from colleagues so that our work might be improved (and expanded) to better answer key

problems associated with the effects of habitat change and fragmentation not only for our target species, but wildlife populations *per se*. In this paper, we briefly describe the background to the work at Tumut and outline plans for future sampling of populations of *P. volans*. We then set out a series of key questions to be addressed as well as a number of possible animal movement scenarios against which the actual results of genetic analyses can be compared.

unpubl. data). This investigation focused on patch, nest tree and habitat use by animals occupying an ensemble of five eucalypt patches dispersed within an area of approximately 3 km². A total of 55 animals was captured in the five patches, all were blood sampled and 30 were fitted with radio collars (Pope *et al.*, unpubl. data).

Extensive field surveys in the eucalypt forest existing at the northern, eastern and southern edges of the pine plantation have shown they support large populations of *P. volans* (Lindenmayer *et al.* 1999). For the purposes of this paper, we refer to this area as the Brindabella Ranges. Populations in the Brindabella Ranges provide a natural experimental control against which to compare populations in the fragmented eucalypt patch system within the Buccleuch State Forest. Sampling of populations in the Brindabella Ranges has not yet been completed, but will be closely matched with the geographic distribution of sampling in the system of fragments located within the Buccleuch pine plantation (Fig. 2). To mimic and replicate that configuration, but in an unfragmented spatial setting, we plan to capture and take blood samples from *P. volans* at four sites within large contiguous areas of native eucalypt forest in the Brindabella Ranges. The four sites will be partitioned into two pairs. The two sites in each pair will be located 3 km apart, and the two pairs of sites will be 10 km apart (Fig. 2). A minimum of 12 *P. volans* will be sampled at each of the four sites.

KEY QUESTIONS FOR TESTING

Our aim is to better understand the demographic and genetic dynamics of *P. volans* populations in the fragmented system at Tumut. To assist in the process of examining patterns of genetic variability in *P. volans*, we outline below some key guiding questions and possible population processes (such as the level of genetically-effective inter-patch dispersal, i.e., where animals reproduce in their new location) predicted to give rise to particular genetic patterns. These general predictions provide a template against which we can compare empirical data and, in turn, assist

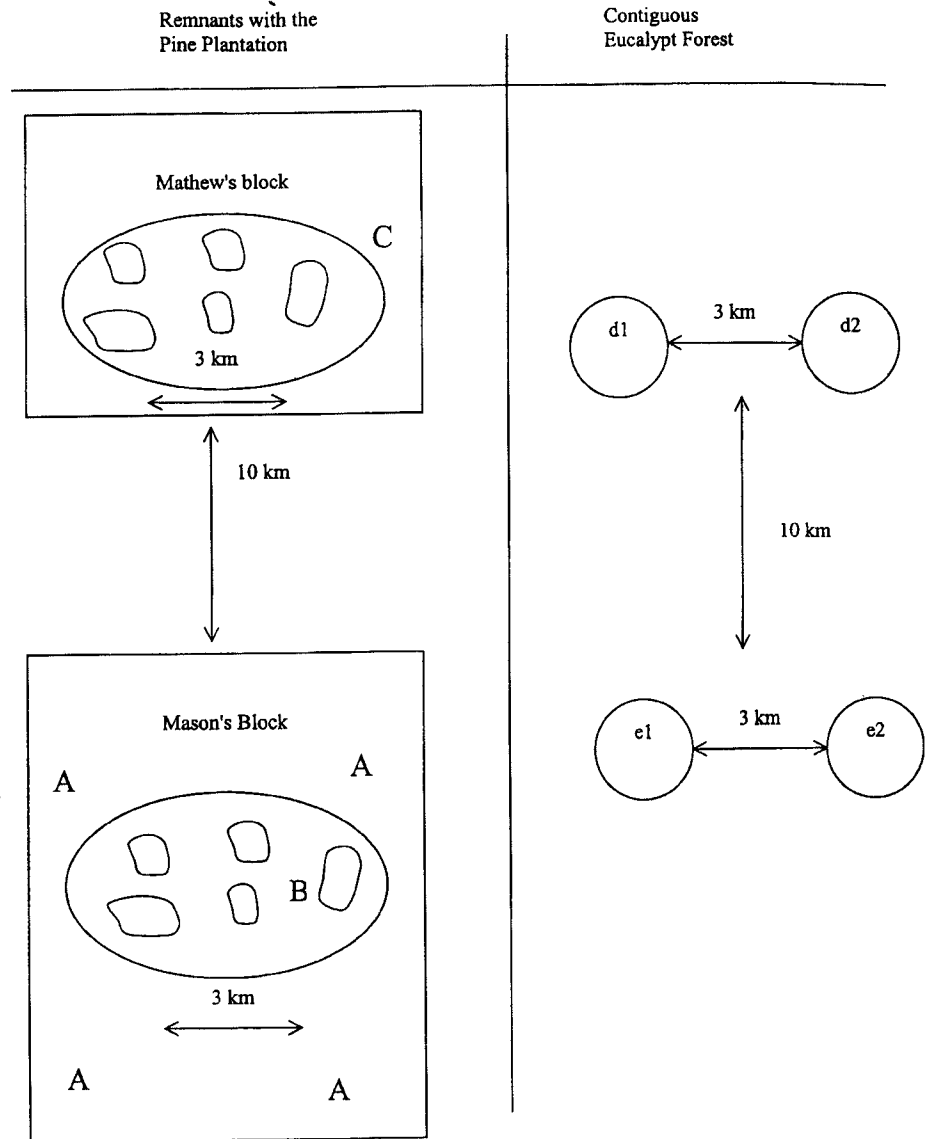


Fig. 2. Diagrammatic representation of the location of sampling or proposed sampling at Tumut within eucalypt remnants surrounded by Radiata Pine and within large contiguous areas of native forest. The Mason's Block samples correspond to those from specimens collected by Tyndale-Biscoe 35 years ago and now held in museums (sample series A — old specimens) and new samples gathered from animals still extant in the remnant patches located within Mason's Block (sample series B — new samples). Sample series C correspond to new samples gathered from Matthew's Block. Those areas proposed for sampling in continuous eucalypt forest correspond to sample series d and e — still to be obtained). See text for further discussion of the proposed sampling protocols.

us to determine what changes have taken place (if any) among populations of *P. volans* at Tumut. Our sampling design (Fig. 2), coupled with the use of highly variable genetic markers will allow us to test these questions and associated predictions.

The simple questions and generic and qualitative predictions outlined below are based on population genetic theory and broad conservation biology

principles. Table 1 summarizes the primary effects of patterns of movement on genetic variation:— (1) in intact forest and the historic populations prior to forest fragmentation, (2) within isolated patches, and, (3) among patches and between existing populations in patches. The table also summarizes expected effects on the correlation between spatial distance and genetic divergence, and between patch size and within-patch genetic

Table 1. Expected relative levels of genetic variation within populations inhabiting patches of eucalypt forest, variation among local populations, correlation between geographic distance and genetic divergence, and correlation between patch size and genetic variation for *P. volans* in remnant patches (BC), intact native forest (DE), and from historic samples (A) collected prior to patch fragmentation, under different scenarios of inter-patch dispersal and immigration from the intact forest into the patch system. Note that the codes for the types of sites (i.e., patches [BC], intact forest [DE] and historic samples [A]) correspond to those used in Figure 2. For variation within and among populations, the approximate rankings (from low to high) are indicated for the various populations.

Movement pattern	Within-population variation	Among-population variation	Size-variation correlation
High dispersal High immigration	High A = BC = DE	Low B-C = D-E = BC-DE < A-BC = A-DE	Low
High dispersal Low immigration	Moderate BC < A = DE	Low B-C = D-E < A-BC < BC-DE = A-DE	Low-Mod
Low dispersal High immigration	Mod-High A = BC = DE	Low BC-DE = D-E < B-C < A-DE < A-BC	Low-Mod
Low dispersal Low immigration	Low BC < A = DE	High D-E < A-BC < BC-DE = B-C < A-DE	High
No dispersal No immigration	v. Low BC << A = DE	v. High D-E < A-DE < BC-DE = B-C = A-BC	v. High

variation. The logic behind each of the more notable predictions is explained below. Notably, although the possible number of combinations of these key factors is large and the predicted patterns are complex, the predictions in Table 1 do provide us with the potential to discriminate among the various scenarios.

Question 1. Do populations in continuous eucalypt forest show genetic differentiation related to geographic distance?

The first step in our work will be to construct plots of genetic differentiation over different geographic distances. The first plot will be constructed from historic samples gathered from Mason's Block and nearby areas which have now been converted to pine plantation. The second plot will be generated from samples we have yet to collect but which we plan to gather from existing continuous forest that occurs at the margins of the plantation (Fig. 2). These plots will provide a calibration of the degree of spatial genetic differentiation maintained for *P. volans* in continuous forest.

Question 2. Are the populations in the fragments in the Radiata Pine plantation isolated from each other and/or from continuous eucalypt forest?

The geographic vs genetic distance plots from continuous forest will be used as comparators with a similar plot generated for subpopulations of *P. volans* in the remnant eucalypt patches surrounded by extensive

stands of Radiata Pine. This, in turn, will be an important approach to address key questions regarding the effects of habitat fragmentation on *P. volans*, particularly:— (a) Are populations in the patches genetically isolated from the continuous forest? (b) Are populations in the patches genetically isolated from one another? and, (c) Are populations in the patches genetically isolated from both continuous forest and from one another?

If the Radiata Pine matrix influences the dispersal of *P. volans*, then:—

- Genetic differentiation among patches, and/or between the patch system and continuous forest, will be greater than expected on the basis of geographic proximity.

Even if dispersal between patches is frequent, it is possible that immigration into the patch system from the continuous forest may be negligible. This is because *P. volans* dispersing from continuous forest may not move into the adjacent Radiata Pine matrix. If there is inter-patch movement, but the populations in the patches are isolated from those in continuous forest, then expected genetic outcomes are:—

- Limited overall genetic differentiation among patches (with reference to the calibration curve for expected genetic differentiation based on distance alone).
- Higher similarity between current patch and historic samples, than between patch and continuous forest

samples (again with the latter comparison weighted by geographic distance).

- No correlation or only a weak correlation between patch size and genetic variation.

If inter-patch dispersal is rare (perhaps because animals can persist for a long time in the remnants) with the only movements being immigration from the continuous forest into the patch system, the expected genetic outcomes are:—

- Higher similarity between patch and continuous forest populations than among patches.
- Higher similarity between historic and continuous forest samples than between historic and patch populations; possibly because of genetic drift in small patches.
- Genetic variation within patches will be a random subsample of that from continuous forest, depending on:— (a) distance from the source (patches closer to source areas in continuous forest may be more likely to be colonized than distant ones [Hanski 1994]), and, (b) patch size (smaller patches may be less likely to receive immigrants) although there may be confounding effects between (a) and (b).

If there has been complete isolation of *P. volans* in the patches then:—

- Patches may contain unique, or "private" alleles.
- Genetic variation within the patches will be:— (a) lower than that over a similar spatial scale in continuous

forest, (b) lower than that in the historic samples, and/or (c) positively correlated with patch size.

- Patch populations will contain a random subset of the original genetic variation (i.e., the genetic variation in the historic samples).

Question 3. What are the genetic origins of animals in the patches?

The outcomes of questions 1 and 2 should make it possible to establish the genetic origins of animals in the patches and determine whether:— (a) There has been dispersal from other patches, from continuous forest or both types of potential sources. Or, (b) The subpopulations represent “relict” populations that have survived as complete isolates since fragmentation 35 years ago. If the second scenario arises, then it may be possible to explore founder effects and other phenomena such as inbreeding (*sensu* Lacy 1993b).

COMPARISONS WITH PVA MODEL PREDICTIONS

The general qualitative trends to be predicted from different broad patterns of movement of animals in the fragmented system at Tumut are summarized in Table 1. However, the actual genetic patterns will depend on:— (a) rates and patterns of movement, (b) configuration of the habitat, (c) the spatial and temporal history of fragmentation, (d) and the demographic characteristics of the species. Given this, an additional way to examine the effects of fragmentation and landscape change on genetic stochasticity is to apply spatially-explicit modelling tools such as Population Viability Analysis (PVA) (Lacy 1993a). The widely-available, generic PVA package VORTEX (Lacy 1993a) can be parameterized with spatial information on patch locations

as well as the different types of movement rates and patterns described in the scenarios above. This makes it possible to compare model-predicted values for genetic variability with empirical data on the same measures.

PVA modelling of populations of *P. volans* in another part of the patch system at Tumut (Lindenmayer *et al.* 2000) has indicated that forecasts made by the VORTEX model can yield predictions about the numbers of occupied patches, and total number of *P. volans* remaining within the system, which match closely the observed patterns in the field. However, the model projections of demographic trends approximated reality only under some of the plausible scenarios of dispersal, immigration, and habitat quality (Lindenmayer *et al.* 2000). It is not known whether the parameters yielding successful demographic predictions are correct, rather than the results being a fortuitous consequence of a bad model and/or bad data.

The VORTEX PVA model can also make projections of changes in genetic variation within and between populations. Therefore, data on genetic patterns can be used to test further whether the models and input values, which produce accurate demographic projections, provide a good representation of the complex dynamics of the metapopulation. For example, Table 2 shows output from VORTEX in which two very different movement patterns were invoked for a metapopulation of *P. volans* in the patch system at Tumut. These were:— (1) low rates of dispersal and immigration in an “Island Model,” where dispersing animals were assumed to be equally likely to migrate to each other habitat patch, and (2) high rates of dispersal and immigration in a “Size/Distance Model,” where the

probability of a dispersing animal migrating to any other patch was proportional to the size of the recipient patch and proportional to the inverse of the square of distance between the patches. These two movement models predict similar demographic outcomes (numbers of animals per patch and numbers of patches occupied), but contrasting levels of genetic variability. Comparison of genetic patterns revealed from analysis of microsatellites to PVA model results, such as those in Table 2, will allow determination of which metapopulation model (if any) accurately describes the dynamics of populations of *P. volans* in the fragmented habitat at Tumut. In addition to the measures of gene diversity (expected heterozygosity) displayed in Table 2, VORTEX provides estimates of relative retention of rare alleles and can, with modest modification, produce a matrix of genetic distances among populations for comparison with observed genetic patterns. Uncertainty caused by the randomness of Mendelian genetics and also stochastic demographic processes (e.g., predation by Powerful Owls *Ninox strenua* (Kavanagh 1988) and dispersal is reflected in standard deviations of genetic estimates reported by VORTEX.

The sequence for the investigation of population dynamics outlined above can also be reversed. Empirical data on genetic patterns (shared alleles and similarity of alleles frequencies) can be used to estimate rates of dispersal (Wright 1951; Nei 1973; Slatkin 1987, 1995). These estimates can then be applied to PVA models to project demographic trends, and the demographic patterns compared to field data. However, the analytical methods for estimating dispersal from genetic data make a number of assumptions about

Table 2. Genetic projections from PVA runs using the generic program VORTEX (Lacy 1993b) for two models of inter-patch movement by the Greater Glider in a system of 39 patches of eucalypt forest. Demographic results from these models are presented in Lindenmayer *et al.* (2000).

Movement pattern	Within-patch variation (H)	Among-patch variation (Fst)	Size-variation correlation
Island Model			
Low dispersal	0.57	0.40	0.75
Low immigration			
Size/Distance model			
High dispersal	0.67	0.32	0.45
High immigration			

equilibrium conditions, absence of demographic fluctuations, and/or simplicity of population structure which may not be met in most natural metapopulations (Bossart and Prowell 1998), especially those in the process of undergoing rapid demographic and genetic collapse following recent fragmentation.

Integration of genetic data with measures of demographic rates and habitat characteristics by use of PVA models can provide an understanding of metapopulation dynamics that is much more detailed, specific, and useful for conservation planning than the generalized models utilized to date. Comparisons of PVA model predictions to observed genetic patterns are not only an important way to improve knowledge on fragmentation effects on wildlife populations, but also perhaps, just as importantly, they represent a valuable approach to testing the accuracy of forecasts from PVA models. This is important given the widespread use of such packages in wildlife conservation management, but the currently limited assessment of the accuracy of the predictions made using such tools — a deficiency that has been a major criticism of PVA (Caughley 1994).

FEEDBACK

This paper briefly outlines some ideas relating to patterns of movement in the patch system and nearby continuous forest at Tumut and the resulting patterns of genetic variability among populations of *P. volans*. At the core of our work is the examination of how population structure influences patterns of genetic variation. An additional key point is the effectiveness of genetic methods to discriminate between different population structures. We are acutely aware that we may have overlooked some key questions or that additional extra sampling may allow further important problems to be explored. Hence, we look forward to comments and criticisms from colleagues with an interest in advancing the resolution of problems associated with fragmentation effects on wildlife populations.

ACKNOWLEDGEMENTS

The Tumut fragmentation experiment is supported by The Land

and Water Resources Research and Development Corporation, New South Wales Department of Land and Water Conservation, NSW National Parks and Wildlife Service, State Forests of NSW, Environment Australia, Rural Industries Research and Development Corporation, CSR, Visy Board and Chicago Zoological Society, Brookfield, IL, USA. Mr Craig Tribolet, Mr Chris McGregor and Mr. Ryan Incoll have made valuable contributions to field efforts in capturing *P. volans*. The work on *P. volans* was facilitated by a special one-off grant from The Land and Water Resources Research and Development Corporation and the support of Dr Phil Price with this aspect of the study is most gratefully acknowledged.

The work at Tumut has benefited from many collaborative partnerships including those with Professor Ross Cunningham and Ms Christine Donnelly from the Statistical Consulting Unit of the Graduate School at The Australian National University, Professor Henry Nix and Ms June McMahon, Centre for Resource and Environmental Studies, The Australian National University, Professor Hugh Possingham, Dr Mike McCarthy, and Mr Ian Ball from the Department of Environmental Science at The University of Adelaide, Professor Craig Moritz and Dr David Paetkau from Department of Zoology, The University of Queensland, and Dr Rod Peakall and Ms. Heidi Hewittson, Division of Botany and Zoology, The Australian National University. DBL is most grateful for the exciting collaborative linkages that have been established as part of the work at Tumut.

The Australian Museum, The South Australian Museum, Museum Victoria, and The National Wildlife Collection (CSIRO Wildlife and Ecology, Canberra) kindly provided access to specimens and allowed us to take samples for DNA analysis. It is important to emphasize the value of these collections because the type of work we describe in this paper would not be possible without such institutions.

DBL would like to thank Professor H. Recher for encouraging the completion of this paper.

REFERENCES

- Bossart, J. L. and Prowell, D. P., 1998. Genetic estimates of population structure and gene flow: limitations, lessons, and new directions. *TREE* **13**: 202–06.
- Caughley, G., 1994. Directions in conservation biology. *J. Animal Ecol.* **63**: 215–44.
- Cunningham, M. and Moritz, C., 1998. Genetic effects of forest fragmentation on a rainforest restricted lizard (Scincidae, *Gnypetoscincus queenslandiae*). *Biol. Conserv.* **83**: 19–30.
- Hanski, I., 1994. Patch occupancy dynamics in fragmented landscapes. *Trends in Evolution and Ecol.* **9**: 131–34.
- Kavanagh, R. P., 1988. The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans*. *Aust. J. Ecol.* **13**: 445–50.
- Klein, B. C., 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* **70**: 1715–725.
- Lacy, R. C., 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population sub-division. *Conserv. Biol.* **1**: 143–58.
- Lacy, R. C., 1993a. VORTEX — a model for use in population viability analysis. *Wildl. Res.* **20**: 45–65.
- Lacy, R. C., 1993b. Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biol. and Med.* **36**: 480–96.
- Lacy, R. C. and Lindenmayer, D. B., 1995. Using Population Viability Analysis (PVA) to explore the impacts of population sub-division on the Mountain Brushtail Possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in south-eastern Australia. II. Changes in genetic variability in sub-divided populations. *Biol. Conserv.* **73**: 131–42.
- Lindenmayer, D. B., Cunningham, R. B., Pope, M. and Donnelly, C. F., 1999. The Tumut fragmentation experiment in south-eastern Australia: the effects of landscape context and fragmentation on arboreal marsupials *Ecol. Appl.* (in press).
- Lindenmayer, D. B., Lacy, R. C. and Pope, M. L., 2000. Testing a Population Viability Analysis model. *Ecol. Appl.* (in press).
- McCarthy, M. A. and Lindenmayer, D. B., 1998. Population density and movement data to predict the mating systems of arboreal marsupials. *Ecol. Mod.* **109**: 193–202.
- Nei, M., 1973. Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci.* **70**: 3321–323.

- Routley, R. and Routley, V., 1975. The fight for the forests: the takeover of Australian forests for pines, woodchips and intensive forestry. Research School of Social Sciences, The Australian National University, Canberra.
- Sarre, S., 1995. Mitochondrial DNA variation among populations of *Oedura reticulata* (Gekkonidae) in remnant vegetation: implications for metapopulation structure and population decline. *Mol. Ecol.* **4**: 395-405.
- Saunders, D. A., Arnold, G. W., Burbridge, A. A. and Hopkins, A. J. (eds), 1987. Nature Conservation: The Role of Remnants of Native Vegetation. Surrey Beatty & Sons, Chipping Norton, New South Wales.
- Slatkin, M., 1987. Gene flow and the geographic structure of natural populations. *Science* **236**: 787-92.
- Slatkin, M., 1995. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* **139**: 457-62.
- Smith, R. F., 1969. Studies of the marsupial glider, *Schoinobates volans*. I. Reproduction. *Aust. J. Zool.* **17**: 625-36.
- Tilman, D., May, R. M., Lehman C. L. and Nowak, M. A., 1994. Habitat destruction and the extinction debt. *Nature* **371**: 65-66.
- Tyndale-Biscoe, C. H. and Smith, R. F., 1969a. Studies of the marsupial glider, *Schoinobates volans* (Kerr). Population structure and regulatory mechanisms. II. *J. Anim. Ecol.* **38**: 637-50.
- Tyndale-Biscoe, C. H. and Smith, R. F., 1969b. Studies of the marsupial glider, *Schoinobates volans* (Kerr). III. Response to habitat destruction. *J. Anim. Ecol.* **38**: 651-59.
- Wright, S., 1951. The genetical structure of populations. *Annual Eugenics* **15**: 323-54.

Erratum to Volume 4 Number 4

Genbank numbers for the DNA sequences studied were omitted from Table 1 in the 1998 paper by Labrinidis *et al.* (**4**: 289-95, *Pacific Conservation Biology*). The Genbank numbers are: S.gl-B1, AF059263; S.g9-M, AF059264; S.g10-M, AF059265; S.g11-M, AF059266; S.it, AF059267; S.mur, AF059268; S.gil, AF059269; S.dol, AF059270; S.cra, AF059271; and, P.gil, AF059272.