

Small mammals, habitat patches and PVA models: a field test of model predictive ability

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Received 3 October 2000; received in revised form 25 April 2001; accepted 15 May 2001

Abstract

The results are described of comparisons between actual values for patch occupancy for two species of Australian small mammals (Bush Rat *Rattus fuscipes* and Agile Antechinus *Antechinus agilis*) determined from field sampling and predictions of patch occupancy made using VORTEX, a generic simulation model for Population Viability Analysis (PVA). The work focussed on a fragmented forest in south-eastern Australia comprised of a network of 39 patches of native eucalypt forest surrounded by extensive stands of exotic softwood Radiata Pine (*Pinus radiata*) plantation. A range of modelling scenarios were completed in which four broad factors were varied: (1) inter-patch variation in habitat quality; (2) the pattern of inter-patch dispersal; (3) the rate of inter-patch dispersal; and (4) the population sink effects of the Radiata Pine matrix that surrounded the eucalypt patches. Model predictions were made for the total number of animals, the distribution of animal density among patches, the total number of occupied patches, and the probability of patch occupancy. Predictions were then compared with observed values for these same measures based on extensive field surveys of small mammals in the patch system. For most models for the Bush Rat, the predicted relative density of animals per patch correlated well with the values estimated from field surveys. Predictions of patch occupancy were not significantly different from the actual value for the number of occupied patches in half the models tested. The better models explained 10–16% of the log-likelihood of the probability of patch occupancy. While some of the models gave reasonable forecasts of the number of occupied patches, even in these cases, they had only moderate ability to predict which patches were occupied. Field surveys revealed there was no relationship between patch area and population density for the Agile Antechinus—an outcome correctly predicted by only a few models. Five of the 18 scenarios completed for the Agile Antechinus gave predicted numbers of occupied patches not significantly different from the observed number. In each of these five cases, large standard deviations around the mean predicted value meant uncertainty generated by the simulation model limited the predictive power of the PVA. Some of the models gave reasonable predictions for the number of occupied patches, but those models were unable to predict which ones were actually occupied. The results of our study suggest that key processes influencing which specific patches would be occupied were not modelled appropriately. High levels of variability and fecundity drive the population dynamics of the Bush Rat and Agile Antechinus, making the patch system unpredictable and difficult to model accurately. Despite the fact that both the Bush Rat and the Agile Antechinus are two of the most studied mammals in Australia, there are attributes of their biology that are presently poorly understood (which were not included in the VORTEX model), but which could strongly influence patch occupancy. For example, local landscape features may be important determinants of inter-patch movement and habitat utilisation in the patch system. Further empirical studies are needed to explore this aspect of small mammal biology. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Fragmentation; VORTEX; *Rattus*; *Antechinus*

1. Introduction

Habitat loss and the fragmentation of the reduced remaining areas of habitat are regarded by many work-

ers as key factors influencing the distribution and abundance of many species around the world (Andrén, 1994; Bennett, 1998). Many complex and often interacting factors can underpin the response of species to landscape change ranging from: (1) reduced population sizes and, in turn, increased risks of extinction from environmental variation and catastrophic events

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(Lande, 1993); (2) reduced genetic variation and increased inbreeding (Lacy, 1993a; Saccheri et al., 1998); (3) changed dynamics of individuals within population, such as skewed sex ratios (McCarthy et al., 1994), single-sex patches (Temple and Cary, 1988), and Allee effects (Lacy, 2000a); (4) changed dynamics of interactions between populations (e.g. increased nest predation or nest parasitism at the edges of habitat fragments (Paton, 1994); and (5) changed ecological processes (e.g. pollination or decomposition) that are essential to maintain viable populations of organisms (Klein, 1989). These processes interact (Gilpin and Soulé, 1986), making it difficult to test their effects, particularly at the landscape scale. Because of these complexities, many workers have employed simulation-modelling approaches such as Population Viability Analysis (PVA) to explore landscape change and habitat fragmentation effects on population dynamics and species persistence (e.g. Akçakaya and Atwood, 1997; Letcher et al., 1998). Boyce (1992) defines PVA as a process that:

...entails evaluation of data and models for a population to anticipate the likelihood that a population will persist for some arbitrarily chosen time into the future.

The application of PVA can have a number of uses. Some of the most important are simply their heuristic value in synthesizing what is known and not known about a species (Burgman et al., 1993) and, in turn, identifying key areas for further work (Lindenmayer et al., 1995). Another use of PVA is to help assess the relative effectiveness of conservation strategies by comparing forecasts of extinction risk in response with different management actions (Possingham et al., 2001). Even such relative comparisons are underpinned to some extent by the accuracy of forecasts from PVA. While there are many hundreds of examples of the use of the approach in the conservation biology literature, the models have rarely been tested (but see Brook et al., 1997, 2000; Mills et al., 1997; Lindenmayer et al., 2000). In this study, we examine the accuracy of predictions made using the widely available and generic PVA model VORTEX (Lacy, 1993b, 2000b). We use the model to make forecasts of patch occupancy, animal abundance in patches, and overall population size for two species of small mammals in a fragmented landscape at Tumut in south-eastern Australia—the Bush Rat (*Rattus fuscipes*) and Agile Antechinus (*Antechinus agilis*). We compare such predictions to data generated from detailed field sampling, in order to determine whether the model accurately predicts on a local scale the key outputs of PVA—probabilities of local extinction, relative rates of decline, and population sizes. In addition, we compare the results of this study of two species of small mam-

mals with the outcomes of an earlier investigation in which the predictive ability of VORTEX was assessed for three species of arboreal marsupials in the patch system at Tumut (Lindenmayer et al., 2000).

2. Methods

2.1. The study area

The study was conducted in the Tumut region of south-eastern Australia, which is characterised by large areas of exotic softwood Radiata Pine (*Pinus radiata*) plantation which cover approximately 45 000 ha. The plantation was established from the mid-1930s onward by clearing the original native *Eucalyptus* forest. The majority of patches were created between 1976 and 1985 (see Appendix A). Remnant patches of native forest still remain in the area and they are now surrounded by extensive stands of Radiata Pine (Fig. 1). For this study we focussed on a 5000 ha subsection of the Radiata Pine plantation and the 39 patches of remnant native forest contained within it. The dimensions of the study area are approximately 11 km (east–west) and 4 km (north–south).

We completed extensive field reconnaissance of the study area. This, coupled with aerial photography, GIS analysis, and accurate historical clearing records kept by State Forests of New South Wales, enabled us to determine the precise size, spatial location and inter-patch distances for all the eucalypt remnants, as well as the year each one was fragmented (Lindenmayer et al., 1999a). The remnant patches varied in size from 0.4 ha to 40.5 ha, and were dominated by different tree species—Ribbon Gum (*Eucalyptus viminalis*), Narrow-leaved Peppermint (*E. radiata*), Swamp Gum (*E. camphora*) and Red Stringybark (*E. macrorhynca*; see Appendix A). The 39 patches covered 450 ha, which is <10% of the study area. The eastern boundary of the study area is abutted by an extensive area of continuous native eucalypt forest that includes the Brindabella National Park, Kosciuszko National Park and Bondo State Forest. Further details on the study area are provided by Lindenmayer et al. (1999a).

2.2. The study species

Two species of small mammals were targeted for investigation—the Bush Rat (*Rattus fuscipes*) and the Agile Antechinus (*A. agilis*). Unlike most PVA studies that focus on rare, endangered or threatened species, the Bush Rat and the Agile Antechinus are common and widespread in south-eastern Australia. However, both are susceptible to disturbance and habitat fragmentation (Dunstan and Fox, 1996; Lindenmayer et al., 1999b). This, together with the fact that the biology and ecology of both species are well known, suggests they should be good candidates for PVA testing. A brief

outline is presented later of key aspects of the biology of both taxa that relate to input variables used to parameterise VORTEX. Life history data for both the Bush Rat and Agile Antechinus are summarised in Table 1.

2.3. Summary of the ecology of the Agile Antechinus

A taxonomic study by Dickman et al. (1998) revealed the species formerly known as the Brown Antechinus (*Antechinus stuartii*) is a species-complex comprised of a suite of taxa with different geographic distributions, morphological features, and patterns of genetic variability. Based on the descriptions provided by Dickman et al. (1998), it appears that the most common species of Antechinus at Tumut is the Agile Antechinus (*A. agilis*), although further work is required to confirm this. For the purposes of this study, we refer to the species targeted for investigation and model testing at Tumut as the “Agile Antechinus”. The information outlined later and used to parameterise VORTEX is summarised from field studies completed in south-eastern Australia, particularly those by Dickman (1980) that were undertaken in an area relatively close to ours and where the species is most likely to be the Agile Antechinus.

The Agile Antechinus is a scansorial dasyurid marsupial that feeds on invertebrates including spiders, beetles, and cockroaches (Hall, 1980). Generations of males are discrete because all of them die following an intensive period of mating (Lee and Cockburn, 1985). Many females die after weaning their young and about 20% survive to breed in two successive years. Population densities vary substantially between studies but values of 1–2 animals per ha were recorded in an investigation completed in an area close to ours (Dickman, 1980). The sex ratio is 1:1 until the male die-off. At Tumut, mating occurs in August and all females are pregnant during September (Lindenmayer et al., unpublished data). Litters of 6–10 young are weaned after 3–4 months (Lee and Cockburn, 1985). Agile Antechinus at Tumut typically have six pouch young (Lindenmayer et al., unpublished data).

Dispersal in the Agile Antechinus is male-biased with all males leaving the natal territory after weaning (Cockburn et al., 1985). Animals move across several home ranges before becoming established (Cockburn, 1992), and afterwards they may move considerable distances between communal nests (Cockburn and Lazenby-Cohen, 1992). The success of female dispersers

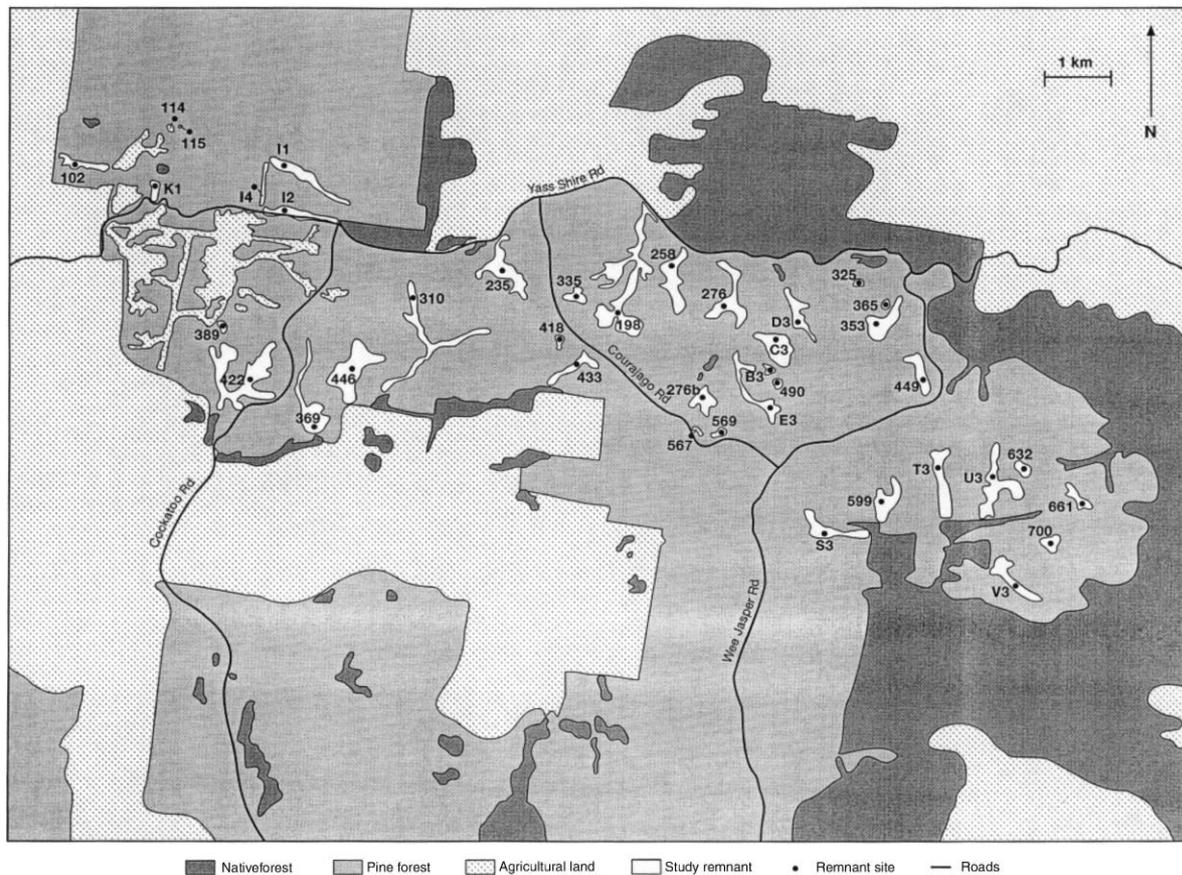


Fig. 1. The spatial location of patches of remnant native eucalypt forest in the Tumut study area.

into new territories is dependent on the effects of seasonal factors (like drought) on the preceding year's population. Successful dispersal is highest in wet, post-drought years with immigrants comprising 30–60% of the population.

2.4. Summary of the ecology of the Bush Rat

The Bush Rat is a terrestrial murid rodent with an omnivorous diet of fungi, seeds, fruit, plant tissue and arthropods (Warneke, 1971). The information outlined later is summarised from different field-based studies in south-eastern Australia. Population densities of the Bush Rat can exceed 10 animals per hectare. Sex ratios among adults do not differ significantly from parity (Press, 1987). Home ranges of breeding males overlap extensively (Lunney, 1983). Home range sizes vary from 0.1 to 0.4 ha and are typically about 200 m in diameter (Watts and Aslin, 1981).

More than one litter may be produced in "good" (wet) years. Litter sizes can vary from 1 to 8 (Warneke, 1971), but the average is about five (Taylor and Horner, 1973). Young are independent 1–2 months after birth and most do not breed until the following spring (Watts and Aslin, 1981). There is heavy mortality among adults after breeding, and the longevity of most animals is typically less than 15 months. Only a few animals (<5%) survive to breed a second year (Robinson, 1987).

Juveniles remain in the natal territory for 2–3 months before dispersing (Robinson, 1987). No information is available on the distances moved by dispersing individuals. However, animals may move up to 0.5–2 km as

part of normal nightly movements (Lunney, 1983; Press, 1987), and dispersal distances could be longer than this.

Most studies of the relationships between environmental factors and the dynamics of populations of the Bush Rat relate to responses to fire and logging (e.g. Fox and McKay, 1981; Lunney et al., 1987). The Bush Rat appears to be dependent on access to water (Watts and Aslin, 1981) and, while this is likely to make populations vulnerable to the effects of drought, there are no studies specifically addressing the response to this environmental factor.

2.5. Field surveys for small mammals

Surveys of small mammals in the 39 eucalypt remnants were completed between January and February 1997 using aluminium box or "Elliott" traps, baited with a mixture of peanut butter, honey and rolled oats. Sites were surveyed by establishing a flagged transect from the edge of a patch into its centre. Transect selection focussed on obtaining estimates for the average density of animals per patch and at no stage was trapping targeted to maximise the number of captures (see Lindenmayer et al., 1999b). The length of the transect was scaled according to patch size; 200 m long patches up to 2 ha in size; 400 m for patches 2–3 ha in size and a maximum of 600 m in length for patches 3 ha or larger. The approximate area trapped in the minimum length transects (for the smallest sites) was 200×50 m (= 1 ha). The total number of animals captured on each transect was divided by the area trapped (1, 2, or 3 ha) to give a density estimate per ha to give values for comparison with model predictions (see later).

Table 1

Values for life history attributes input parameters to VORTEX for simulating populations of small mammals in remnant patches of eucalypt forest at Tumut, south-eastern Australia^a

Parameter	Bush Rat Mean (Range)	Agile Antechinus Mean (Range)
Breeding age	1	1
Mating system	Polygyny	Polygyny
Mean litter size	6.4 (2.0–10.0)	4.7 (2.0–6.0)
Environmental variation (EV) in litter size (as a S.D.)	3.0	1.0
% mortality in first year	59.0 (70.0–50.0)	56.5 (70.0–50.0)
EV in first year mortality	13.0	6.0
% Mortality in year 2 (subsequent to first breeding season)		
Males	100.0	100.0
Females	97.3 (100.0–95.0)	86.6 (90.0–85.0)
EV in 2nd year female mortality	2.0	5.0
Density (No. per ha)	8.24 (0.0–15.0)	1.35 (0.0–2.00)
Probability of drought catastrophe	0.143	0.143
Multiplicative impact of catastrophes on:		
Reproduction	0.27 (0.0–0.50)	0.47 (0.20–0.60)
Survival	0.41 (0.0–0.75)	0.62 (0.35–0.75)
Mean deterministic growth rate (lambda)	1.344	1.006

^a Mean values listed for demographic rates are those that were used for models in which there was no variation in habitat quality. The range of values for each parameter shows the values assigned to models with habitat quality variation, with the first value being assigned to patches with a quality score of zero, the second being assigned to patches with a quality score of ten and intermediate quality patches being assigned rates linearly proportional to their habitat quality scores.

Traps were set at 50-m intervals along the flagged line of each transect and left in place for 5 successive days. The traps were checked each day and all captured animals were marked, sexed, weighed and then released (see Lindenmayer et al., 1999b). A piece of ear tissue was collected from each trapped animal and this marking ensured individuals were not double-counted.

An additional set of trapping surveys was undertaken in the Radiata Pine matrix that surrounded the eucalypt patches. The protocol for trap spacing was identical to that employed for the patches of remnant native forest exceeding 3 ha in area (i.e. a 600 m long transects trapped at 50-m intervals). One 5-day trapping event was completed for each eucalypt patch as well as the sites located in the Radiata Pine matrix.

The detailed results of trapping, with statistical analyses of the relationships between the characteristics of sites and the presence and abundance of animals, are presented in Lindenmayer et al. (1999b).

2.6. The PVA Model (VORTEX)

The PVA program VORTEX (Version 7.4) used in this study has been employed in numerous studies of a wide array of taxa (e.g. Lacy, 1993b; Lindenmayer and Lacy, 1995a, Miller and Lacy, 1999). A detailed description of the model is presented in Lacy (1993b, 2000b) and Miller and Lacy (1999). Modifications of the program since earlier versions and important for this investigation included: (1) Dispersal among populations can be restricted to one sex and/or a limited age cohort. This was important for the small mammal taxa in this study because of male-biased dispersal among sub-adults. (2) Emigration from a population can be restricted to occur only when the number of animals in the population exceeds a specified proportion of the carrying capacity. (3) Dispersal mortality can be specified as a probability of death for any migrating animal, which is in addition to age-sex specific mortality. (4) The source population in the intact habitat adjacent to the study area was modelled as part of the system, but was not included in the tallies of performance of the metapopulation (i.e. measures of extinction and population size).

In addition to the life history parameters summarized in Table 1, a range of other input parameters are required to run VORTEX, and these are described briefly later. The process of habitat loss and habitat fragmentation in the study area has been gradual, as compartments of Radiata Pine systematically replaced the original native eucalypt forest. To model such changes in landscape composition, one male and one female dispersed into each patch that was currently below 50% of its carrying capacity until the year the compartment of Radiata Pine forest was established surrounding that patch (see Appendix). Supplementation of

populations maintained numbers at half or more of the carrying capacity, and prevented populations from becoming inbred, prior to isolation. Populations were simulated from 1972 to 1997 when extensive field surveys were completed.

Although VORTEX can model many types of catastrophes (see Lacy, 1993b), only the effects of droughts were included. Droughts and rainfall events are known to influence the dynamics of populations of small mammals (e.g. Gullan and Robinson, 1980). Drought was modelled as a random event occurring with a probability of 1/7, or a drought on average every 7 years. The frequency of dry years was based on inspections of rainfall records gathered over the past 35 years at the Bondo Forest Office, approximately 10 km south of the study area. Populations of small mammals were reduced by between 30 and 70% in drought years depending on the severity of the dry period and the quality of the patch within which animals occurred (see later). Other factors such as fires that can dramatically influence small mammal populations in Australian forest ecosystems (e.g. Lunney et al. 1987) were not modelled. This is because the forest management agency at Tumut (State Forests of New South Wales) takes active steps to suppress fires to protect the plantation estate.

VORTEX is structured so that environmental variation in demographic rates can be correlated between patches (thereby affecting sets of populations simultaneously) or it can impact on patch populations independently. The Tumut study area is characterised by heterogeneity across the landscape in terrain attributes and topographic relief (e.g. gullies versus midslopes and ridges). In addition, fine scale climate surface modelling using the computer-based program BIOCLIM (Nix and Switzer, 1991) revealed landscape heterogeneity in climatic conditions such as annual mean temperature and annual mean precipitation (Lindenmayer and Nix, unpublished data). The distribution patterns of tree species such as Swamp Gum and Ribbon Gum reflect, in part, the influence of key climate and terrain factors. Thus, in drought years, some patches such as those on south-facing slopes with deeply dissected gullies may be mesic refugia within which populations of small mammals have higher rates of survival and fecundity than other patches (e.g. exposed ones on northerly and westerly aspects with high values for incoming radiation). Given inter-patch differences in climatic and terrain conditions, a correlation coefficient of 0.75 was used to model between-remnant differences in environmental variation. The same value was used in simulations of the Bush Rat and the Agile Antechinus because both taxa are uncommon in the Radiata Pine matrix surrounding the eucalypt patches, and the limited available data on movement suggests that the dispersal distances for both species are similar.

VORTEX has the capacity to model interacting genetic and demographic effects on population dynamics (Lacy, 1993b). Inbreeding depression was modelled with an initial two lethal equivalents per animal—a value halfway between the value typical for mammals (3.14—see Ralls et al., 1988) and that which has been measured in a captive population of the related Australian Plague Rat (*Rattus villosissimus*) (Lacy and Horner, 1997)—a species which maintains a more fecund and rapid reproductive strategy than the Bush Rat.

2.7. Scenarios used in modelling

Many permutations of different factors can be modelled using PVA, making it important to focus on a subset of key parameters for testing. We modelled four broad factors to generate predictions for comparison with our field data on the Bush Rat and the Agile Antechinus: (1) spatial variation in habitat quality of patches; (2) the patterns of dispersal between habitat patches; (3) the rate of dispersal between habitat patches; and (4) the potential for the Radiata Pine matrix surrounding habitat patches to have “sink” effects on small mammal populations. Not all combinations of these four factors were tested. Eighteen scenarios were completed. Table 2 shows a nested hierarchy of scenarios that tested the four factors listed earlier. Further details of factors tested are outlined later.

2.7.1. Variation in habitat quality of remnant patches

Studies elsewhere in Australia have highlighted the importance of floristic composition and vegetation structure as key predictors of habitat quality for small

mammals (e.g. Lindenmayer et al., 1994, Catling and Burt, 1995). Thus, spatial variation in these attributes can have a marked influence on the abundance of these animals. Spatial variation in habitat quality also will alter the spatial distribution of animals among patches within a metapopulation, and therefore may influence metapopulation dynamics and population persistence (Thomas, 1994).

To assess the effects of spatial variation in habitat quality, for some scenarios we assigned a uniform value for habitat quality across all eucalypt remnants. Carrying capacity was determined simply by patch area (Appendix) and home range size. In other scenarios, the carrying capacity of each eucalypt patch for each species was adjusted according to a habitat quality value that was based on a subjective ranking score. The Radiata Pine matrix was assumed to have no value as habitat for the Bush Rat and the Agile Antechinus. The assumption was based on extensive small mammal surveys in Radiata Pine plantation forests at Tumut that have shown that small mammals are extremely rare in these areas (Lindenmayer et al., 1999b).

Field studies at Tumut have involved extensive surveys of topographic variation, vegetation structure, plant cover, and plant species composition within each remnant (see Lindenmayer et al., 1999a, 1999b). These types of patch attributes have been shown to influence the presence and abundance of both the Bush Rat and the Agile Antechinus in other studies in south-eastern Australia (see earlier). A ranking score for habitat quality (to a maximum value of 10) was based on the known extent of wet gully vegetation, ground and understorey plant cover and the distribution and abundance of large logs, rock piles and trees with hollows

Table 2
The 18 PVA simulation models tested for the Bush Rat and Agile Antechinus^a

K proportionality	Dispersal pattern	Dispersal rate	Sink effect	Model code
Area	No dispersal	–	–	A0xx
	K/D^2 dispersal	Low	None	ADL0
		High	None	ADH0
	Island dispersal	Low	None	AIL0
High		None	AIH0	
Area × Quality	No dispersal	–	–	Q0xx
	K/D^2 dispersal	Low	High (2)	QDL2
			Low (1)	QDL1
			None	QDL0
		High	High (2)	QDH2
			Low (1)	QDH1
			None	QDH0
	Island dispersal	Low	High (2)	QIL2
			Low (1)	QIL1
			None	QIL0
		High	High (2)	QIH2
			Low (1)	QIH1
None			QIH0	

^a Not all combinations of carrying capacity (K), dispersal pattern, dispersal rate, and sink effects of the Radiata Pine matrix were tested. See text for an explanation of each model component.

which provide shelter and nesting sites for small mammals. Different values were derived for each species in each patch (see Appendix) because of inter-patch heterogeneity and inter-specific differences in habitat requirements (Lindenmayer et al., 1994). The carrying capacity (K) of each patch was then modified by multiplying the maximum K by 0.1 times the habitat ranking score. The carrying capacities in the models that did not include variation in habitat quality were the values obtained by setting habitat quality in all patches to the area-weighted mean for the species (5.49 for the Bush Rat and 6.75 for the Agile Antechinus). Thus, the total carrying capacity of the metapopulation was the same in all models (4344 for the Bush Rat and 586 for the Agile Antechinus).

Inter-patch habitat quality differences not only influenced carrying capacity, but they also affected reproductive output, survival, and mortality (both during drought and non-drought years). Thus, habitat quality was a potentially important determinant of patch-level sub-population dynamics. The stimulus for modelling such effects was that refugia often characterise many heterogeneous landscapes (Morton, 1990). Populations in refugia may maintain high growth rates and reproductive output (e.g. they are population sources) relative to elsewhere in the landscape (places often termed population “sinks”; Pulliam et al., 1992). VORTEX was parameterised so that populations within high habitat quality patches such as those with permanent water, extensive vegetation cover in the ground layer, and numerous nesting and shelter sites: (1) produced larger litters; (2) experienced lower levels of juvenile and adult mortality; and (3) had greater levels of adult survivorship particularly during droughts. Demographic rates were set to be linear functions of habitat quality. For example, in the Bush Rat, juvenile mortality in non-drought years ranged from 70% for patches with a habitat quality score of 0–50% where the habitat score was 10. For the Agile Antechinus, the reduction in populations during a drought was 65% for patches with a habitat quality score of 0, and 25% where the score was 10. In the case of litter sizes for the Agile Antechinus, mean values increased linearly from two in the lowest quality patches to six in highest quality ones. In models without variation in habitat quality, the demographic rates were set to those that would be assigned to patches with the mean habitat quality (see Table 1).

2.7.2. *Patterns of dispersal*

Animal dispersal is poorly understood and very difficult to measure (Gaines and Bertness, 1993). For almost all species of vertebrates, there are only limited data (if any) on the way they disperse through the landscape (Wolfenbarger, 1946; Stenseth and Lidicker, 1992). A range of dispersal models can be invoked in VORTEX (see Lacy, 2000b; Lindenmayer et al., 2000), but three

simple movement patterns were explored in this study. These were: (1) complete isolation, with no movement between patches or into the study area from surrounding potential source areas in large adjacent blocks of continuous eucalypt forest; (2) the island model of inter-patch dispersal in which animals were assumed to be equally likely to migrate to each other habitat patch; and (3) the K/D^2 model in which the probability of migrating to a patch was proportional to the carrying capacity (K) of the recipient patch and the inverse of the distance (D) squared.

For the second and third of these movement patterns, VORTEX was parameterized so that the probability of an animal dispersing was proportional to the current density (N/K) of animals in the patch. The maximum probability (when $N \geq K$) that a given animal dispersed from its resident patch in any particular year was set to 33% for females and 67% for males for the Bush Rat, and to 25% for females and 50% for males for the Agile Antechinus. This reflected the male-biased dispersal patterns observed in both species. For all scenarios, we assumed that all patches were at half carrying capacity at the start of the simulations. A total of 500 simulations were then completed for each scenario, as recommended by Harris et al. (1987). This provided probabilities of extinction and population sizes with standard errors typically $\leq 2\%$ of the predicted values.

2.7.3. *Variation in the rate of inter-patch dispersal*

The rate of migration of animals between subpopulations can have a major effect on population persistence (Forney and Gilpin, 1989), population size (Lindenmayer and Lacy, 1995a), genetic variability (Lacy and Lindenmayer 1995; Mills and Allendorf, 1996) and thus patch occupancy in a metapopulation system (Lindenmayer and Lacy, 1995b; Hill et al., 1996). The island and distance-restricted dispersal patterns were modelled first at low rates of movement between patches. Simulations were then repeated using high rates of inter-patch movement.

Large continuous areas of native eucalyptus forest occur at the boundary of Radiata Pine plantation containing the eucalypt patches in our study area. These extensive areas of eucalypt forests were a potential source of immigrants to the patch system. The population in the continuous forest was modelled with a carrying capacity equal to that of the combined metapopulation within the patch system. The source population was supplemented with sufficient numbers of animals each year of the simulation to maintain it near its carrying capacity. The rate of immigration into the patch system from the continuous source population was half that of the rate of between-patch migration. Because the metapopulation in the patch system was often at about half its carrying capacity, this resulted in about the same number of immigrants into the system as there were dispersers among patches each year.

2.7.4. “Sink” effects of the pine matrix surrounding remnant patches

The suitability of the landscape matrix and the ability of animals to move through it may influence population persistence in patchy and fragmented landscapes (Sisk et al., 1997). Thus, population sizes in the remnants may be, in part, determined by the suitability of the surrounding landscape or matrix (Blake, 1983). For a number of the modelling scenarios, the Radiata Pine forest surrounding the remnant patches was assumed to be unsuitable habitat for use by small mammals, but it did not influence mortality patterns during inter-patch movements (i.e. dispersal mortality was the same as estimated for intact forest). In the “Sink” scenarios, mortality rates above those in Table 1 were imposed on animals dispersing through the Radiata Pine matrix and thus between habitat patches. Hence, the matrix acted as a “sink” (*sensu* Holt and Gaines, 1993) in these simulations. Additional dispersal mortality among small mammals in the Radiata Pine matrix may be important for several reasons. There is an extensive logging road network in the study area and each remnant is surrounded by a major gravel track. Furthermore, very large numbers of semi-permanent bush tracks are created along every third row of planted trees throughout the Radiata Pine matrix by heavy machinery as part of timber harvesting operations. Even small roads may be barriers to the movement of small mammals (Barnett et al., 1978). In addition, introduced predators such as the Red Fox (*Vulpes vulpes*) and Feral Cat (*Felis catus*) that prey on small mammals are common at Tumut. The road network at Tumut may facilitate the movement of exotic predators (May and Norton, 1996).

Survival during dispersal was set to 50% in the “Sink 1” scenario and 25% in a more severe “Sink 2” scenario. The sink scenarios were tested only with models that included variation in habitat quality (see Table 2).

2.8. VORTEX output used for comparison with field data

A wide array of measures associated with metapopulation and subpopulation demography and genetic variability are generated by VORTEX (Lacy, 1993b). We focussed on a small subset of these measures for comparison with field data. These were: (1) the probability of occupancy of each patch (\pm S.D.); (2) the overall number of occupied patches (\pm S.D.); (3) the predicted density of animals per patch (per ha) (\pm S.D.); and (4) the total population size summed across all patches (\pm S.D.). The standard deviations provided measures of variation among iterations in the simulated population dynamics. Comparisons were made between field data and model predictions for the year 1997.

2.9. Methods for comparing between model predictions and field data

We used three kinds of criteria to contrast predictions from simulation modelling with field data for the Bush Rat and the Agile Antechinus and thus assess the predictive ability of the models. These were: (1) the relationship between patch area and actual patch occupancy versus the relationship between patch area and predicted patch occupancy; (2) the actual number of occupied patches versus the predicted number of occupied patches; and (3) the ability of the model to correctly predict which patches were occupied and which were vacant. Although not one of these criteria alone would provide a strong test of the adequacy of the PVA models by itself, the examination of these several aspects of model adequacy can help reveal which models appear to describe the metapopulation system well, and in what ways model predictions deviate from field observations.

PVA is often used to make predictions about population size, and risks of decline below biological or management thresholds. We do not have data on the absolute numbers of animals within each patch, but we can compare model predictions with relative densities of animals across patches and to the probabilities that patches are occupied at all. The relationship between population density and patch size was quantified with Pearson correlations. We compared these correlations in the field data to the same correlations in the model results, in order to determine whether the population dynamics in the models were mirroring the relationships to patch size observed in the field. We also examined correlations between model predictions and observed animal density for each patch, as a means of assessing which models predict better the observed probabilities of decline vs. growth.

A defining characteristic of PVA is the generation of estimates of population extinction. We examined two aspects of the prediction of patch occupancy, or its converse, local extirpation: (1) the ability of the model to predict the overall number of occupied patches; and (2) the ability of the model to predict which patches are more likely to be occupied. Logistic regression analysis (Hosmer and Lemeshow, 1989) was used to assess the ability of the models to predict both of these aspects of patch occupancy. For each model examined, the actual values (0 vs. 1) for patch occupancy were regressed against the logit of the predicted probability of a given patch being occupied. Two diagnostics of the regression models were examined. These were: (1) the deviation of the fitted line from the mid-point of a 45° line, which would be a perfect fit between predicted and actual values for mean patch occupancy; and (2) Rho-squared, which is the proportion of the log-likelihood of the null (no predictor) model accounted for by the model being

tested. The deviation from the midpoint of the 45° line was assessed by testing whether the number of occupied patches deviated significantly from 50% when the probability of occupancy generated by the PVA model was 50%. This test examines whether the observed values tend to fall systematically above or below the predicted values, indicating an under- or over-prediction of the mean probability of local extirpation. The Rho-squared values are analogous to R^2 -values of linear regression, but Rho-squared tends to be lower than R^2 for a comparable goodness of fit (Steinberg and Colla, 2000). For the simple, one-predictor, logistic regressions used here, Rho-squared values are directly proportional to deviance and to the likelihood-ratio statistic—two other commonly applied measures of the adequacy of logistic regressions used to explain variation among data points. Significance of the regressions was tested by comparing the likelihood-ratio statistics with the chi-square distribution with one degree of freedom.

The logistic regression analyses assume that occupancy of each patch is an independent observation. This assumption is probably violated in any metapopulation with dispersal or correlated environments, so regression tests may yield P -values that are too small (McCarthy et al., 2000). In addition, in systems that are highly stochastic, even a model that perfectly describes the processes controlling population dynamics may have relatively little predictive power. Indeed, there was substantial variation in simulated patch occupancy among replicate iterations of each model. Therefore, a lack of fit of the observed data to the overall model prediction could have been caused by the inherent unpredictability of the biological system, rather than the model poorly representing the processes that governed patch occupancy. To test this possibility, we compared the distribution of the fits of individual runs with the mean predicted probabilities of occupancy to determine whether the fit of the actual data to the mean predicted pattern was outside of the range of the individual simulations.

3. Results

3.1. Field surveys

Trapping surveys showed that the Bush Rat and the Agile Antechinus occurred in 20 and 26 eucalypt remnants, respectively. For the Agile Antechinus and for the Bush Rat, the number of animals captured per patch varied from zero to 24. The number of animals captured in each site is given in Appendix A. These data reveal considerable variation between patches and some unexpected outcomes. For example, some large patches had low densities of animals (e.g. patch Nos. 422, 258, and 198), whereas some small patches supported relatively

high densities of animals (e.g. patch No. 661 for the Agile Antechinus; see Appendix A).

Trapping surveys showed that the Bush Rat and the Agile Antechinus were uncommon in the Radiata Pine matrix surrounding the eucalypt patches—there were a total of eight detections of the Bush Rat and the Agile Antechinus. This supported the view that the system of eucalypt fragments could be acting as a metapopulation and that the matrix “sink” models would be appropriate for testing.

3.2. Comparisons between field data and model predictions for the Bush Rat

The results of modelling for the Bush Rat are summarised in Table 3. The correlation between the area of eucalypt remnants and field data for population density in each patch was 0.28. This indicated a tendency for animal density to be higher in larger patches, although this relationship was weak and marginally non-significant ($P=0.08$). The equivalent correlations for the simulation models were always stronger than identified in the observed data. Forecast population densities generated by almost all of the scenarios were significantly positively correlated with patch area (Table 3). The exceptions were in scenarios with the island model of dispersal and uniform habitat quality across all the remnants (Models AIH0 and AIL0). In these two cases, there were significant negative correlations, with population densities higher in the small eucalypt remnants. For most of the models, the predicted relative density of animals per patch correlated well with the estimated values from field surveys [$r(\text{Dens})$ in Table 3]. Thus, the models performed well in forecasting high and low densities of animals in a given patch, as resulting from local decline or growth of numbers. The exceptions were the two island models (AIH0 and AIL0) in which there was no correction for inter-patch differences in habitat quality. Here, the correlation values were negative (see Table 3) indicating that these models predicted the opposite patterns of animal density than occurred in the field data.

The Bush Rat was trapped in 20 of the 39 patches. The predicted number of occupied patches varied widely between models—from approximately 12 to 38. Predictions of patch occupancy in nine of the 18 models were not significantly different from the actual value for the number of occupied patches. However, forecasts in several of these cases were somewhat different from field data (e.g. the distance-restricted models with uniform habitat quality), but a lack of a significant difference between the predicted and actual numbers of occupied patches occurred because of the very high standard deviations associated with mean predicted values (Table 3). The models that performed best were the distance-restricted dispersal models with a severe sink

effect of the matrix surrounding the eucalypt remnants, and between-patch variations in habitat quality (Models QDH2 and QDL2 in Table 3). However, there were a number of other models that gave very similar results.

Table 3 contains the results of logistic regression modelling comparing actual patch occupancy with the predicted probability of occupancy of each patch. The Rho-squared values showed that the models that had significant logistic regressions explained 8–16% of log-likelihood of local extirpation. Models that yielded predictions for average patch occupancy that were not significantly divergent from the observed data were also those that explained statistically significant proportions of the observed variation in which patches were occupied. Fig. 2 shows the logistic regression relationship for each of the models tested. When the logistic regression lines fall below the 45° line, the predicted rates of occupancy are higher than observed in the field. The opposite occurs for values above the 45° line. The island and distance-restricted models typically predicted higher rates of patch occupancy by the Bush Rat than observed in the field (Fig. 2). A close fit was obtained for the

simplest model, in which there was no dispersal and uniform habitat quality across patches.

The P -values in the last column of Table 3 indicate whether the lack of fit of each model to the observed pattern can be accounted for by the stochasticity of the system, as reflected by high levels of variability between iterations of the simulations for a given scenario. In many of the models with uniform habitat quality across patches, there was high variability in predicted patch occupancy between iterations. An example of this (for Model A0xx) is shown in Fig. 3a. Here, the differences between field data and model predictions could be explained by the extensive variability between runs. For many other scenarios for the Bush Rat, the individual simulations clustered more tightly around the mean values calculated across all 500 runs. Consequently, in Model ADL0 (Fig. 3b) and in all scenarios in which habitat quality was varied for patch characteristics, the differences between actual patch occupancy and predicted patch occupancy could not be attributed to stochastic nature of the system [$P(r_i < r_o) < 0.05$]. This suggested that key processes influencing which patches

Table 3
Results from PVA simulation models for Bush Rats in 39 patches of Eucalyptus^a

Model	Total population size: <i>N</i> (S.D.)	Area-Density correlation: <i>r</i> (A,D)	Model-Field correlation in density: <i>r</i> (Dens)	Patch occupancy: # Occ (S.D.)	Fit to 50% predicted occupancy: <i>P</i> (0.5)	Variation in occupancy explained: Rho ²	Fit relative to simulation uncertainty <i>P</i> ($r_i < r_o$)
Observed	740	0.28		20			
A0xx	1661 (1417)	0.72	0.36	17.4 (9.5)	<i>0.55</i>	0.117	0.224
AIH0	2729 (1632)	-0.89	-0.40	38.2 (3.5)	0.00	0.037	0.058
AIL0	2769 (1645)	-0.87	-0.40	37.4 (5.5)	0.00	0.038	0.080
ADH0	2818 (1489)	0.35	0.20	33.9 (7.1)	0.03	0.160	0.054
ADL0	2589 (1601)	0.41	0.21	32.0 (8.8)	0.09	0.147	0.042
Q0xx	2142 (700)	0.51	0.35	11.8 (1.8)	<i>0.58</i>	0.057	0.000
QIH0	2785 (945)	0.54	0.38	33.0 (2.5)	<i>0.37</i>	0.026	0.002
QIL0	2717 (946)	0.54	0.38	32.7 (2.8)	<i>0.37</i>	0.028	0.002
QDH0	2805 (835)	0.60	0.43	24.1 (3.2)	<i>0.46</i>	0.083	0.000
QDL0	2720 (880)	0.60	0.41	23.3 (3.5)	<i>0.47</i>	0.088	0.000
QIH1	2696 (995)	0.53	0.38	32.8 (2.7)	<i>0.36</i>	0.030	0.000
QIL1	2718 (918)	0.53	0.38	32.4 (3.4)	<i>0.36</i>	0.033	0.000
QDH1	2676 (923)	0.59	0.42	23.7 (3.4)	<i>0.47</i>	0.086	0.000
QDL1	2627 (901)	0.59	0.41	22.7 (3.6)	<i>0.47</i>	0.093	0.000
QIH2	2615 (993)	0.53	0.38	32.3 (3.8)	<i>0.37</i>	0.030	0.002
QIL2	2547 (917)	0.51	0.36	31.6 (4.5)	<i>0.37</i>	0.035	0.004
QDH2	2600 (877)	0.58	0.41	22.7 (3.4)	<i>0.47</i>	0.095	0.000
QDL2	2570 (881)	0.58	0.40	21.9 (3.6)	<i>0.48</i>	0.095	0.000

^a The first row of results are the data observed in field surveys of the study area for: estimated total number in the system (number trapped/proportion of patch trapped); the correlation [r (A,D)] between patch area and animal density (number trapped/area trapped); and the number of patches (# Occ) in which Bush Rats were found. Model codes for the subsequent simulations are given in Table 2. Results for each simulation model include the mean number (N) in the patch system, with the S.D. of N across iterations of the simulation; the correlation [r (A,D)] between patch area and mean predicted density; the correlation [r (Dens)] between the mean density of Bush Rats in each simulated patch and the observed density in each patch; the mean (and S.D. across iterations) of the number of patches occupied; the proportion of patches occupied [P (0.5)] when the PVA model predicted 50% occupancy; the proportion of the log-likelihood of patch occupancy explained by the logistic regression model (Rho²); and the proportion of individual iterations that had a lower correlation of patch occupancy with the mean model result than did the observed patch occupancies [$P(r_i < r_o)$]. Numbers in bold indicate significant ($P < 0.05$) correlations [r (A,D) and r (Dens) columns] or regressions (Rho² column). Numbers in italics indicate that the simulation model result did not differ significantly ($P > 0.05$) from the observed field data with respect to number of patches occupied (# Occ), or that the proportion of patches occupied when the model predicts 50% occupancy [P (0.5)] did not differ significantly from 0.50.

would be occupied were not modelled appropriately in these scenarios.

In summary, our analyses showed that while some of the models gave reasonable forecasts of the number of occupied patches, they were usually unable to forecast accurately which patches were occupied.

3.3. Comparisons between field data and model predictions for the Agile Antechinus

Table 4 shows there was no relationship in the field data between patch area and population density for the Agile Antechinus ($r = -0.04$, n.s.). Hence, there was no tendency for animals to occur at higher or lower densities in large or small patches. Only the models with adjustments for habitat quality and island patterns of dispersal correctly predicted this lack of a relationship between patch area and population density in the observed data. The other models yielded significant correlations for this relationship but the nature of this relationship varied markedly between models. It was

negative for the island dispersal models with carrying capacity determined only by size, indicating that the highest densities of animals were predicted to occur in the smaller patches. The other significant correlations were positive, with the highest densities of animals predicted to occur in the largest patches. As in the case of the Bush Rat, the best correlations between the actual patch area-population density relationship and the model predictions [$r(\text{Dens})$] were for scenarios in which there was spatial variation between patches in habitat quality.

The Agile Antechinus was trapped in 26 of the 39 eucalypt remnants. Of the 18 scenarios, five gave predicted numbers of occupied patches that were not significantly different from the observed number. However, in several of these cases, the predicted number was not close to the observed number, but large standard deviations around the mean prediction value meant the confidence intervals included the actual number of occupied patches (Table 4). The distance-restricted models always under-predicted the number of

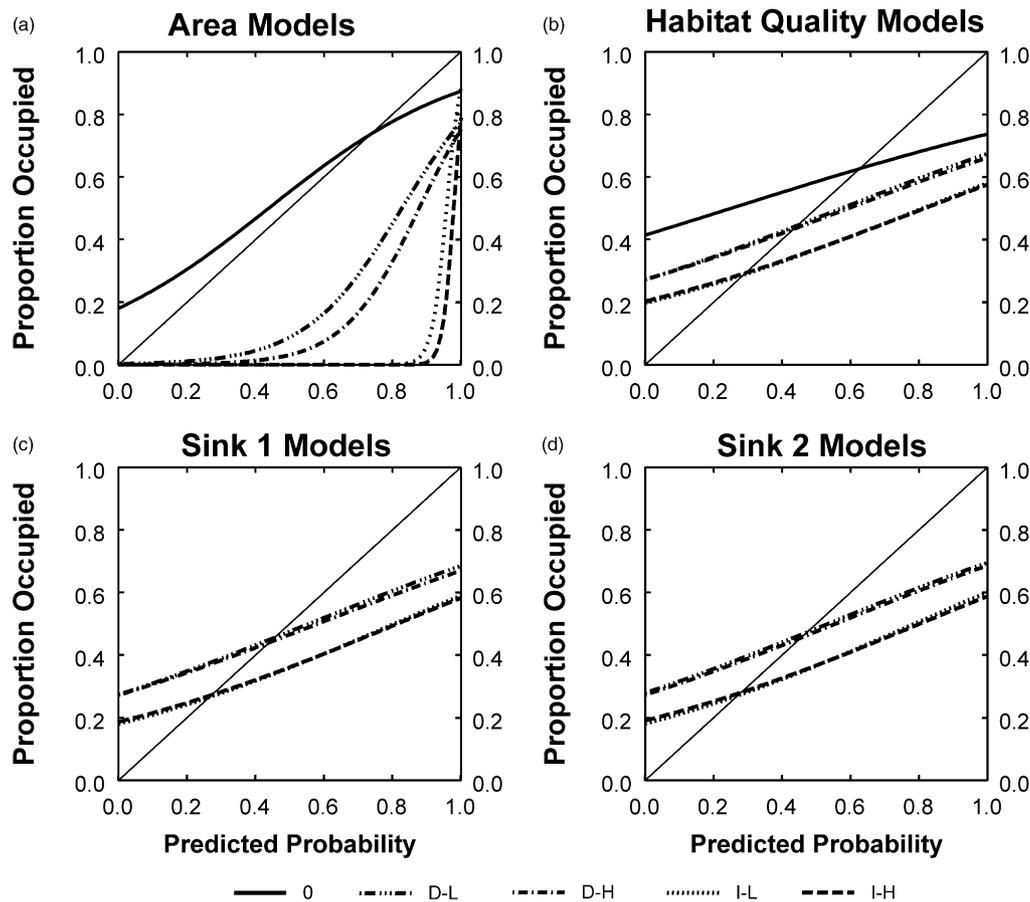


Fig. 2. Logistic regression lines fitted to the relationships between patch occupancy (as the 0/1 response variable) and the probability of occupancy predicted from each model (on the X-axis) for metapopulation models of *Rattus fuscipes*. (a) Models in which patch capacity is determined by area. (b) Models in which habitat quality is varied. (c) Models with variable habitat quality, and 25% mortality of dispersing animals. (d) Models with variable habitat quality, and 50% mortality of dispersing animals. Within each type of habitat model, dispersal models are (1) No dispersal (solid lines); (2) distance-restricted dispersal at low rates (D-L); (3) distance-restricted dispersal at high rates (D-H); (4) island model of dispersal at low rates (I-L); and (5) island model of dispersal at high rates (I-H).

occupied patches, whereas the island models forecast that most of the patches were occupied.

Logistic regression analysis showed that none of the models correctly forecast which patches were likely to be occupied. The Rho-squared values in Table 4 showed that the models explained little of the variation in the data on patch occupancy, and none of the regressions were significant. The limited predictive ability of the models is further highlighted in Fig. 4, which shows the relatively poor fit of the logistic regression relationship derived from each of the models.

Table 4 contains P -values for the Agile Antechinus that indicate whether the lack of fit of a given model could be due solely to stochasticity of the system, as reflected in high levels of variability between iterations of the simulations for a given model. In the case of the island models, there was a substantial range in variation in predicted patterns of patch occupancy between iterations

(see Fig. 3d). The P -values showed that the relationships between the model prediction and the observed values fell well within the range of the individual simulations. There was much less variability between iterations in the distance-restricted models; the correlations of the observed patch occupancies with the predicted values were outside all, or nearly all, of the correlations for individual iterations of the simulations. The models that predicted best how many patches were occupied by the Agile Antechinus were often poor at predicting which patches were occupied. Thus, one or more processes influencing the distribution of the Agile Antechinus may not have been modelled appropriately.

In summary, some of the distance-restricted models gave reasonable predictions for the number of occupied patches, but not for which patches were actually occupied. The island models over-predicted the number of occupied patches and had limited overall predictive ability.

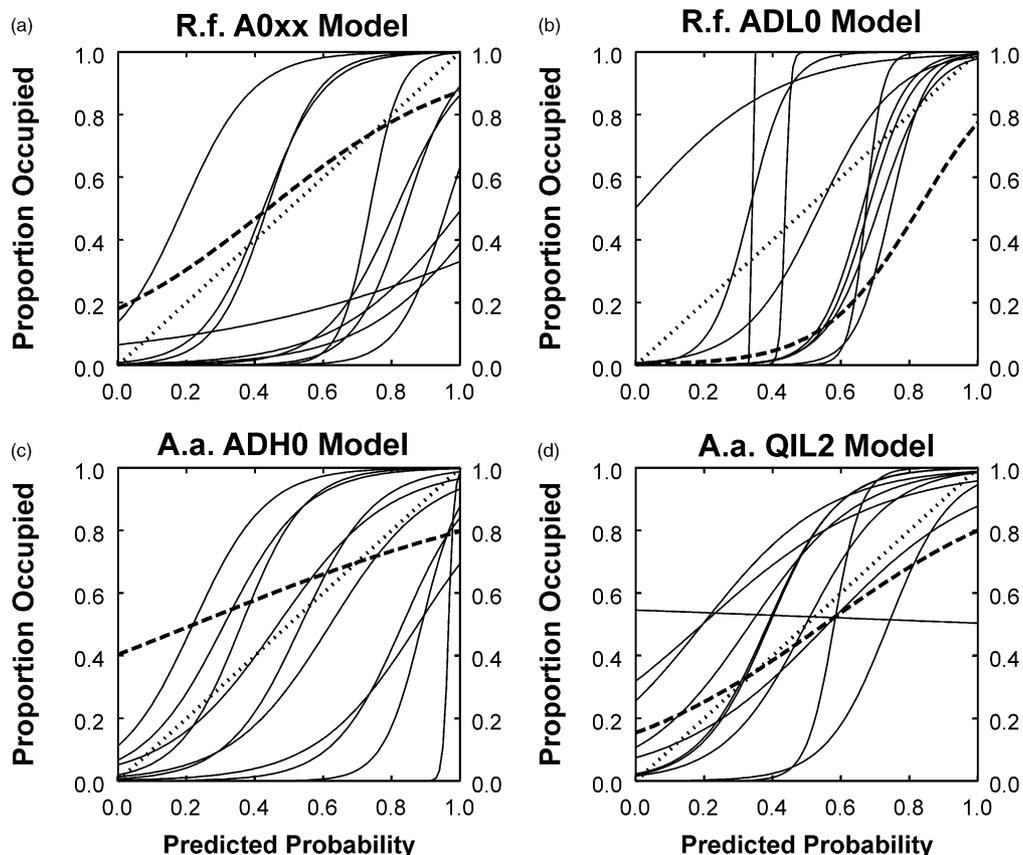


Fig. 3. Examples of fit of observed patch occupancies to model predictions compared to fits of 10 simulations of the model: (a) A highly variable case in which the model (A0xx for the Bush Rat) showed a good fit to the number of patches occupied [$P(0.5)=0.55$], and was within the stochastic uncertainty of the individual simulations [$P(r_i < r_o)=0.224$]; (b) A case in which the model (ADL0 for Bush Rats) showed a poor fit to the number of patches occupied [$P(0.5)=0.09$], and was not within the stochastic uncertainty of the individual simulations [$P(r_i < r_o)=0.042$]; (c) A case in which the model (ADH0 for Agile Antechinus) showed a good fit to the number of patches occupied [$P(0.5)=0.62$], but was not within the stochastic uncertainty of the individual simulations [$P(r_i < r_o)=0.000$]; (d) A case in which the model (QIL2 for Agile Antechinus) showed a good fit to the number of patches occupied [$P(0.5)=0.46$], and was within the stochastic uncertainty of the individual simulations [$P(r_i < r_o)=0.168$]. The heavy dashed line shows the logistic regression line for the observed patch occupancies vs. the predicted probabilities of occupancy from the model. Thinner lines show the logistic regression lines for patch occupancies for 10 sample simulations vs. the model predictions. The thin dotted line on the diagonal shows the relationship expected for a perfectly predictive model.

Table 4
Results from PVA simulation models for the Agile Antechinus in 39 patches of eucalypt forest^a

Model	Total population size: <i>N</i> (S.D.)	Area-Density correlation: <i>r</i> (A,D)	Model-Field correlation in density: <i>r</i> (Dens)	Patch occupancy: # Occ (S.D.)	Fit to 50% predicted occupancy: <i>P</i> (0.5)	Variation in occupancy explained: ρ^2	Fit relative to simulation uncertainty $P(r_i < r_o)$
Observed	679	-0.04		26			
A0xx	79 (91)	0.91	-0.01	5.0 (4.3)	0.53	0.009	0.004
AIH0	376 (171)	-0.81	-0.10	37.4 (3.2)	0.00	0.074	0.224
AIL0	296 (182)	-0.78	-0.11	35.2 (5.7)	0.19	0.014	0.202
ADH0	329 (127)	0.40	0.25	25.2 (5.2)	0.62	0.062	0.000
ADL0	263 (132)	0.48	0.17	20.8 (6.2)	0.66	0.037	0.000
Q0xx	221 (111)	0.69	0.30	8.3 (3.6)	0.70	0.003	0.010
QIH0	461 (152)	-0.11	0.48	36.9 (1.9)	0.14	0.055	0.154
QIL0	421 (166)	-0.07	0.47	35.8 (3.6)	0.20	0.053	0.174
QDH0	384 (123)	0.68	0.33	20.7 (2.6)	0.66	0.017	0.000
QDL0	368 (129)	0.71	0.34	19.6 (2.8)	0.67	0.017	0.000
QIH1	387 (164)	-0.24	0.47	36.1 (2.9)	0.17	0.062	0.116
QIL1	368 (170)	-0.07	0.45	34.2 (4.7)	0.28	0.047	0.184
QDH1	340 (127)	0.67	0.34	19.5 (2.7)	0.67	0.015	0.000
QDL1	326 (132)	0.70	0.33	18.3 (3.2)	0.67	0.013	0.000
QIH2	309 (164)	-0.31	0.43	36.1 (2.9)	0.27	0.050	0.190
QIL2	284 (154)	-0.04	0.41	30.6 (6.5)	0.46	0.032	0.168
QDH2	294 (129)	0.65	0.34	18.0 (3.0)	0.68	0.012	0.000
QDL2	279 (132)	0.68	0.33	16.7 (3.5)	0.68	0.012	0.000

^a Columns and indications of statistical significance are as in Table 3.

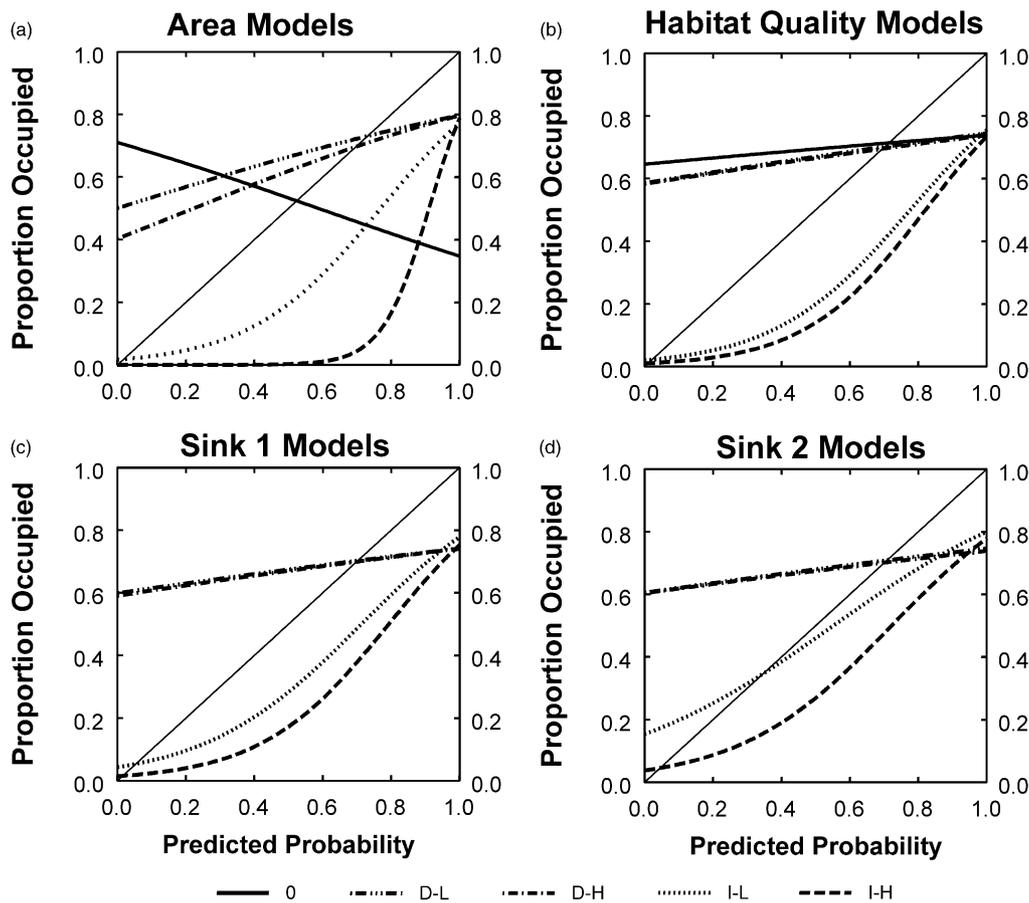


Fig. 4. Logistic regression lines fitted to the relationships between patch occupancy (as the 0/1 response variable) and the probability of occupancy predicted from each model (on the X-axis) for metapopulation models of the Agile Antechinus. (a) Models in which patch capacity is determined by area. (b) Models in which habitat quality is varied. (c) Models with variable habitat quality, and 25% mortality of dispersing animals. (d) Models with variable habitat quality, and 50% mortality of dispersing animals. Within each type of habitat model, dispersal models are (1) No dispersal (solid lines); (2) distance-restricted dispersal at low rates (D-L); (3) distance-restricted dispersal at high rates (D-H); (4) island model of dispersal at low rates (I-L); and (5) island model of dispersal at high rates (I-H).

4. Discussion

4.1. General findings

Many of our simulation models had limited ability to predict fine-scale population dynamics. While some models gave reasonable predictions of the number of occupied patches, few correctly forecast which patches were actually occupied. This was especially true for the simulations of the Agile Antechinus where there were no significant regressions between actual and predicted patch occupancy (Table 4). Lack of fit of field data to model predictions could have resulted from inaccurate estimates of some model parameters. For example, following published reports, we assumed that starting densities of animals would be much higher for the Bush Rat than for the Agile Antechinus. Consequently, predicted population sizes were much greater for the Bush Rat. However, total field counts of the two species were very similar (Appendix), and counts of Agile Antechinus sometimes considerably exceeded the assumed typical densities. If Agile Antechinus are present at much higher densities than assumed, this could lead to underestimation of various measures of population viability. However, the models with the best fits for relative densities and patterns of patch occupancy generally over-predicted, rather than under-predicted, the number of patches occupied by the Agile Antechinus.

4.2. Model limitations and the life history attributes and movement patterns of small mammals

The limited ability of the models to predict patterns of patch occupancy appeared to be due to the high inherent variation in population dynamics, as indicated by the variation between iterations for each model. In some scenarios such as those with island-dispersal for the Agile Antechinus, the variability between runs of a given scenario was often much greater than the differences between different scenarios (see Table 4). Large differences between runs of the same model suggested that high levels of variability in population dynamics result from high fecundity, high environmental variability in demographic rates, and metapopulation processes (local extinction and recolonisation of very small local populations). This inherent variability makes the system unpredictable and difficult to model accurately. Consequently, it is also difficult to validate model performance against observed data. However, substantial between-run variability could not explain the lack of fit for some of the models such as those for the Bush Rat that included inter-patch differences in habitat quality (Table 3, Fig. 3b). In these cases, the individual simulations clustered tightly around the mean values calculated across all 500 runs and the differences between actual patch occupancy and predicted patch occupancy

could not be attributed to the stochastic nature of the system. This indicates that particular aspects of the patch system and/or the biology of both target species were not modelled well by VORTEX. For example, a number of the very small patches at Tumut were occupied by the Agile Antechinus (Appendix)—an outcome that was rarely correctly forecast by the simulation models. Thus, there appear to be aspects of the dispersal biology of small mammals that strongly influence patch occupancy, but which presently remain poorly understood. In the case of the Bush Rat, the results of preliminary ecological studies suggests it disperses along watercourses (Lindenmayer and Peakall, 2000), although further investigations are required to determine if this is true. Thus, the ecological distances between patches may not be the direct or euclidean distances between patches. Linkages such as riparian vegetation that can increase connectivity between patches (and reduce the geographic distance between them) can be included in VORTEX simulations only if all pairwise probabilities of dispersal between patches can be specified. A differently configured set of models to the ones employed in this study would be required to simulate these types of movement patterns. However, before further modelling work is instigated, the results reported in this paper suggest that more fieldwork is required to establish the patterns (rather than the rates) of dispersal among populations of small mammals. This conclusion is based on a comparison of the predictions of some of the different models which show that measures of patch occupancy and population size were more sensitive to differences in dispersal patterns such the island versus the distance-restricted models, than they are to the rate of inter-patch dispersal (Tables 3 and 4). For example, the number of successfully dispersing animals is eight times greater in the simulations with a high rate of dispersal and no sink effects than those with a low rate of dispersal and strong sink effects. Yet, predictions from the two models were similar (Table 3). Given the need for new information on dispersal patterns in the patch system at Tumut, we have recently commenced a set of empirical and genetics studies to address this knowledge gap.

Another limitation of VORTEX we identified during this study was that there is presently no capacity in the model to deal with spatial correlation in environmental conditions between patches. For example, patches close together would be expected to experience climate regimes that are more similar than in more isolated sets of patches. This could be critical in the case of small mammals, which appear to respond strongly to environmental conditions such as droughts and wet years, making features like mesic refugia among adjacent patches important for population dynamics.

Some attributes of the life history of the Bush Rat and the Agile Antechinus may add to the difficulty in

modelling them. For the Bush Rat, relatively small mesic areas within eucalypt patches could provide suitable refugia for residual populations during droughts. Field experience from several years of trapping at Tumut has shown that animals can be difficult to trap during such times. In addition, such small mesic refugia could be easily overlooked (and not trapped) leading to an incorrect conclusion that a patch is unoccupied when in fact it supports a small population of animals. Population recovery following drought may occur via breeding of animals remaining in a patch rather than immigration from neighbouring areas. The results of a new integrated demographic and genetic study that is presently underway may allow us to determine if this is true. A second factor related to high levels of fecundity is that if dispersal does occur, then a small number of successful dispersal events could rapidly reverse localised extinction in a particular eucalypt patch. Therefore, patterns of patch occupancy may change comparatively often and quickly. Such high rates of turnover would make it extremely difficult to forecast which patches are unoccupied at a given time. Finally, some life history attributes of small mammals could not be readily modelled using the existing structure of VORTEX. In the case of the Agile Antechinus, it appears there is multiple paternity of the one litter (F. Kraajveld-Smit, personal communication) that could affect the patterns of genetic variability in the patch system.

At the start of this study, we anticipated that the Bush Rat and the Agile Antechinus would be excellent species to model because they have been well studied and their life history attributes are well known. However, as outlined earlier, factors such as high fecundity, short life spans, and high environmental variability can lead to large fluctuations in population size and marked changes in population trajectory within a short time. This can make it difficult to make accurate predictions of measures like population size and, in turn, patch occupancy at a fine spatial scale for a specific point in time. For example, the time when field sampling is completed can significantly influence estimates of animal abundance—values could be markedly different during droughts versus good years (Walton and Richardson, 1989). Hence, the year selected for comparisons between model predictions and field data could have a strong impact on perceived levels of congruence. As a result, it can be difficult to determine whether a PVA model is a good representation of the processes driving population dynamics, unless (and until) large numbers of populations are monitored for a number of years.

4.3. Modelling single populations versus fragmented populations

Studies by other authors (e.g. Brook et al., 1997, 2000) have found good predictive ability for PVA models for a

range of species. This contrasts with the findings of this study in which the predictive ability for measures such as the occupancy of particular patches was limited for the majority of models. We believe that the differences in results are due, in part, to the fact that Brook et al. (2000) focussed on the dynamics of single populations, whereas our work targeted a more complex system comprised of multiple patches of varying size, spatial location, isolation, and habitat quality. Accurate predictions of population dynamics will be difficult in such complex systems because of the additional (and often inter-acting) processes that influence multi-patch systems. These include rescue effects (Brown and Kodric-Brown, 1977), extinction–recolonisation dynamics (Hanski, 1999), spatial correlation in distribution patterns (Koenig, 1998), and environmental correlation between habitat patches (Stacey and Taper, 1992).

The type of species modelled is another important factor that may have contributed to the differences in the predictive ability of models. Our study focussed on small mammal species that have highly variable population dynamics with numbers that fluctuate substantially between years—making it potentially difficult to accurately predict measures like relative density within patches. In contrast, Brook et al. (2000) focussed their modelling on single populations of taxa characterised by more stable types of population dynamics that may be more accurately forecast. This conclusion is reinforced by the findings of an earlier study using VORTEX which found better congruence between model predictions and field data (Lindenmayer et al., 2000). That study examined three species of arboreal marsupials that are longer lived, less fecund, and have more stable population dynamics than the two species of small mammals modelled in this investigation.

4.4. Caveats and future tests of patterns of genetic variability

Models for the Agile Antechinus showed limited ability to predict individual patch occupancy and the total number of occupied patches. Closer congruence was found for a number of the models for the Bush Rat. However, we are acutely aware that close congruence between field data and model predictions does not mean that the model has accurately represented the true dynamics of the system. The match between field data and predictions could be fortuitous and occurring for the wrong reasons. A further test of the models would be to examine the processes that underpin the dynamics of the system and which produce the most accurate patterns of patch occupancy. One way to further test model predictions, including dispersal patterns and variation in demographic rates, would be to examine patterns

of genetic variability among small populations in the patches. The different dispersal models and rates of inter-patch migration used in VORTEX give rise to different patterns of genetic variability in patchy populations of the Bush Rat and Agile Antechinus (data not shown). Thus, while the models have been run to extract demographic data for comparison with field data, genetic predictions from the best fitting of these scenarios will be used for comparison with laboratory tests of tissue samples collected from small mammals at Tumut. It is possible that the results of genetic analysis and tests of the accuracy of genetic predictions made by VORTEX could suggest different types of movement and population processes than resulted in this study. For example, recently developed molecular genetics methods presently being applied in studies of small mammals at Tumut will help determine which patches are sources of dispersers to colonise other patches (Lindenmayer and Peakall, 2000).

4.5. The heuristic value of PVA in patch modelling

Although the models applied in this study were found to have limited predictive ability, it does not mean that PVA simulation modelling of such systems is not useful. As indicated in the definition at the beginning of this paper, the PVA process includes the evaluation of data and models for populations (see Burgman et al., 1993). The assembly of data and subsequent detailed modelling undertaken in this investigation have been highly instructive and indicated which factors had a substantial impact on population dynamics and which others did not. Moreover, the application of PVA has helped identify key knowledge gaps that need to be addressed

to better understand the response of small mammals to landscape modification.

Acknowledgements

Many people have made major contributions to studies at Tumut. Associate-Professor Ross Cunningham was responsible for the statistical and experimental design of field work conducted in the region. Ms. Christine Donnelly, Professor Henry Nix, Professor Hugh Possingham, Dr. Rod Peakall, Dr. Mike McCarthy, and Dr. David Patkeau have made important intellectual contributions to the Tumut fragmentation studies. Mr. Matthew Pope, Mr. Craig Tribolet, Mr. Ryan Incoll and Mr. Lee Halasz assisted with field surveys. The work at Tumut is funded by The Winnifred Violet Scott Trust, The Land and Water Resources and Research Development Corporation, The Rural Industries Research and Development Corporation, NSW Department of Land and Water Conservation, State Forests of NSW, NSW National Parks and Wildlife Service, VISY Industries, CSR Ltd, and a private donation from Mr. Jim Atkinson and Ms. Di Stockbridge. DBL would like to thank Professor Andrew Cockburn for detailed discussions on the biology and ecology of small mammals and Dr. David Patkeau and Dr. Rod Peakall for collaborative studies on the genetics of small mammal populations at Tumut. Mr. Chris McGregor assisted with the collation of published material on small mammals. Comments by Associate-Professor Mark Burgman, Associate-Professor Tim New and an anonymous referee greatly improved earlier versions of the manuscript.

Appendix A

The size and dominant forest type of remnant patches of eucalypt forest in the study region at Tumut. Extensive field reconnaissance was used to identify the dominant tree species in each remnant. Habitat scores are calculated as a function of vegetation cover and gully vegetation within each patch based on extensive field-based vegetation surveys and on-ground reconnaissance (see text). The values in the seventh and eighth columns are numbers of animals trapped in each patch.

Patch Number	Dominant tree species	Patch size (ha)	Year of Isolation	Assigned Habitat Score		Counts of animals	
				Bush Rat	Antechinus	Bush Rat	Antechinus
102	<i>E. radiata</i>	6.6	1985	6	3	0	0
114	<i>E. macrorhynca</i>	0.6	1985	0	1	0	0
115	<i>E. macrorhynca</i>	0.7	1985	0	1	0	0
198	<i>E. camphora</i>	40.5	1978	7	8	0	0
235	<i>E. camphora</i>	15.2	1977	4	5	0	1
258	<i>E. camphora</i>	15.1	1978	2	5	0	0

(continued on next page)

Appendix (continued)

Patch Number	Dominant tree species	Patch size (ha)	Year of Isolation	Assigned Habitat Score		Counts of animals	
				Bush Rat	Antechinus	Bush Rat	Antechinus
272	<i>E. radiata</i>	1.0	1979	1	4	0	1
276a	<i>E. camphora</i>	20.7	1979	5	7	0	4
276b	<i>E. camphora</i>	20.5	1982	7	8	0	0
310	<i>E. viminalis</i>	18.8	1977	6	3	24	3
335	<i>E. radiata</i>	2.4	1978	1	6	1	0
353	<i>E. viminalis</i>	12.7	1980	2	8	10	4
365	<i>E. radiata</i>	1.7	1980	1	2	0	1
369	<i>E. radiata</i>	18.9	1982	0	7	2	1
389	<i>E. radiata</i>	0.4	1983	0	2	0	0
418	<i>E. camphora</i>	1.6	1976	3	3	0	2
422	<i>E. macrorhynca</i>	38.0	1983	8	8	1	0
433	<i>E. camphora</i>	22.1	1976	7	4	2	0
446	<i>E. radiata</i>	30.1	1977	3	9	13	11
449	<i>E. viminalis</i>	9.0	1980	3	8	3	18
490	<i>E. radiata</i>	1.6	1982	0	6	0	4
567	<i>E. radiata</i>	0.7	1982	0	3	0	2
569	<i>E. radiata</i>	2.3	1982	0	5	0	1
599	<i>E. viminalis</i>	16.2	1983	8	8	3	18
632	<i>E. radiata</i>	4.9	1984	1	9	5	5
661	<i>E. radiata</i>	4.4	1985	0	9	3	24
700	<i>E. radiata</i>	5.6	1985	0	7	1	0
B3	<i>E. radiata</i>	0.8	1979	1	2	1	3
C3	<i>E. radiata</i>	20.1	1979	9	9	0	5
D3	<i>E. viminalis</i>	8.7	1979	5	9	4	13
E3	<i>E. viminalis</i>	13.5	1982	8	8	15	13
I1	<i>E. camphora</i>	9.1	1986	2	4	0	0
I2	<i>E. viminalis</i>	5.0	1983	0	5	0	1
I4	<i>E. radiata</i>	2.0	1985	1	3	0	1
K1	<i>E. radiata</i>	4.1	1985	0	5	3	0
S3	<i>E. camphora</i>	10.6	1973	10	2	9	2
T3	<i>E. viminalis</i>	18.7	1983	8	7	22	16
U3	<i>E. radiata</i>	20.5	1984	9	7	10	3
V3	<i>E. viminalis</i>	9.0	1985	8	5	5	7

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