Running Head: Fragmentation of a reptile community

Title: Extinction and outbreaks accompany fragmentation of a reptile community

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Abstract

Land clearing depletes and fragments habitat, resulting in the loss of biodiversity. Corridors of native vegetation can ameliorate the impacts of land clearing by reducing isolation of remnant vegetation. However the effectiveness of linear remnants as corridors or connecting habitat is influenced by remnant size and condition. In central New South Wales, Australia, 84-95% of native vegetation has been cleared, with remnants occurring as isolated reserves and interconnecting strips beside roads and paddocks. Do the linear remnants provide connectivity throughout the landscape for reptile populations? In three 100 km^2 agricultural locations I classified all remnants into one of ten "landscape-elements" based on shape, management and vegetation. I used generalized linear models and permutation tests to examine differences in reptile abundance among landscape-elements. Only two blind snakes were captured in paddocks, suggesting the matrix between remnants is virtually devoid of reptiles. Remnant shape had a strong affect, with fewer species in linear remnants than square reserves. Five species were significantly less abundant in linear remnants, and two of those species were absent. Three species had significantly lower abundance in grazed linear remnants and one species had lower numbers on roadsides. In contrast, five species were more abundant on roadsides, with one skink tripling in number. Limited evidence suggested that food specialization, body size and range size was not correlated with species declines. However, allozyme-electrophoresis results indicated that two declining species had stronger isolation-by-distance effects than two widespread species, implying the decliners had weaker dispersal powers or smaller effective population sizes. Comparisons with the reptile fauna from an uncleared landscape suggested that two species may be locally extinct and that three other species had inflated population sizes in the farming locations. In addition to substantially altering the reptile community, the cumulative impact of remnant management was to increase fragmentation beyond that expected from the distribution of remnant vegetation alone. At two locations, 22% of remnant vegetation was suitable for the dragon *Amphibolurus nobbi*, and the suitable remnants were subdivided into an additional 2 - 4 fragments. Extensive landscape restoration is now needed to help arrest reptile declines from highly cleared agricultural landscapes.

Key words: legless lizard, dragon, blind snake, habitat fragmentation, corridor, landscape ecology, genetic variation, allozyme electrophoresis, dispersal, conservation, livestock grazing, roads

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INTRODUCTION

Land clearing leading to habitat loss and fragmentation has long been recognized as a primary cause of biodiversity decline (Ehrlich and Ehrlich 1970, Soule 1983). Although metapopulation theory provides a mechanism by which species could survive fragmentation, where recolonization of habitat patches counters the effects of local extinctions (Hanski 1998), this has rarely been observed in anthropogenically modified landscapes (Harrison and Bruna 1999, but see Paillat and Butet 1996). In human-fragmented landscapes, population extinctions usually exceed colonization, and species gradually decline (e.g., Soule et al. 1992, Miller and Cale 2000). For example, Bolger et al. (1997) found that the number of native rodent species in urban fragments was not related to patch isolation, implying that recolonization was rare and local extinction was the dominant process. Bolger et al. (1997) concluded that rodent species were declining from the landscape, and recommended creating corridors to facilitate recolonization, and counter local extinctions.

Corridors are often recommended as the solution to species declines in fragmented landscapes (e.g., Dunstan and Fox 1996, Bolger et al. 1997) and there is increasing evidence that corridors can have positive conservation outcomes (Beier and Noss 1998, Debinski and

Holt 2000). However, predicting the efficacy of a particular corridor is difficult because permeability varies among different landscape-elements (Wiens 1997). For example, Lindenmayer and Nix (1993) found that habitat and landscape measures, and the biology of individual species needed to be considered to understand the effectiveness of corridors for arboreal marsupials. In another example, Boudjemadi et al. (1999) also found that corridor effectiveness was dependent on habitat quality for *Lacerta vivipara*, the common lizard.

Lizards and other reptiles appear to fare poorly in fragmented landscapes. It is likely that many reptile species are now experiencing severe range contractions in parallel with observed bird declines from farming landscapes (Chamberlain et al. 2000, Ford et al. 2001). Mounting evidence points towards the widespread decline of reptile species from agricultural areas (Sarre 1998, Smith et al. 1996, Brown and Bennett 1995, Covacevich et al. 1998, Dorrough and Ash 1999, Diaz et al. 2000, MacNally and Brown 2001). The condition of remnant vegetation may have an overriding impact on reptile abundance, especially loss of shrub diversity associated with livestock grazing (Hadden and Westbrooke 1996, Brown 2001, Woinarski and Ash 2002). Sarre (1996) noted that previous surveys of reptiles in the Western Australian wheat-belt had found five gecko species only in nature reserves, and not in smaller fragments. Sarre (1995) argued that a sixth gecko species *Oedura reticulata* has become extinct in 28% of woodland remnants, and predicted further extinctions based on the small size of populations and the species' poor dispersal ability.

Recognizing characteristics that predispose species to decline after fragmentation has been an important preoccupation in the fragmentation literature (Terborgh 1974, Bolger et al. 1991, Tilman et al. 1994). Dispersal ability is often recognized as a key characteristic, where weakly dispersing species are more vulnerable to decline (e.g., Hokit et al. 1999). Long-term dispersal trends can be examined using genetic methods by testing for an 'isolation by distance' effect (Wright 1943). Species with a greater rate of increase of genetic divergence with distance are presumed to have lower rates of gene flow in the absence of confounding effects of selection or historic allopatric divergence (Wright 1943, Slatkin 1993).

Genetic methods have also proven useful in the study of habitat loss and fragmentation (e.g., Mech and Hallett 2001). Fragmentation and isolation of populations results in smaller population size, which increases the rate of loss of genetic variation and divergence among populations (Lacy 1987). Under these circumstances, fragmented populations may face an increased risk of extinction due to inbreeding depression or the accumulation of deleterious mutations (Frankham 1995, Lande 1998, Higgins and Lynch 2001).

In this study I examine the distribution of reptile species in an extensively cleared agricultural landscape in New South Wales, Australia. Thirty five percent of New South Wales is classified as cleared, and most of the cleared area occurs in a single zone running north-south through the center of the state (SOE 1997). Within this zone, landscapes have been cleared down to 5-16% of their original vegetation cover (Sivertsen 1995, Sivertsen and Metcalf 1995). The most common pattern of clearing has left isolated reserves of up to a few square kilometers with interconnecting linear strips, including road and stream reserves, and traveling stock routes (Nowland 1997). The extensive network of linear remnants may serve as corridors or as habitat, and thereby reduce fragmentation. However, the linear remnants are also subject to a range of management regimes, which may affect their potential to function as connecting habitat. Therefore my broad question is: how connected, or fragmented are these agricultural landscapes for reptiles? More specifically, I ask three questions:

(1) Is the distribution of reptiles affected by habitat clearing, remnant shape, vegetation type, livestock grazing or the presence of a road?

(2) Does genetic evidence suggest populations in the agricultural locations are small and isolated, or that limited dispersal plays a role in species declines?

(3) By comparison with an uncleared location, what have been the location-wide effects of land clearing on the reptile community?

To address these questions I have used a large-scale sampling design, including three separate agricultural locations, and classified all remnants within locations according to vegetation and management history. This approach enables the application of generalized linear models and resampling methods to statistically test for effects associated with remnants of different size or condition.

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METHODS

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Study Area

I chose South-central New South Wales, Australia (Fig. 1) for study because the environment has been extensively cleared, but is adjacent to large tracts of uncleared vegetation to the north and west. This provided the opportunity to incorporate an uncleared landscape into the study.

Mallee vegetation in the study area is dominated by multi-stemmed eucalypts less than 10m high, including *Eucalyptus socialis* and *E. dumosa*. The only other common tree species is *Callitris glaucophylla*, and the community usually has a shrubby understorey (Sivertsen and Metcalfe 1995). Box woodlands with a grassy or shrubby understorey also occur in the study areas (Sivertsen and Metcalfe 1995) and are dominated by single stemmed *E. populnea* that are usually more than 10m tall. Spinifex (*Triodia scariosa*) is a clumping grass with long, stiff and very sharply pointed leaves. It is a conspicuous component of many mallee communities, and provides important habitat for reptile species (Cogger 1984). Spinifex is most abundant on sandy soils, and as the clay content increases with subtle changes in topography, the amount of spinifex decreases (Cohn 1995).

Europeans first invaded the area in 1810, but extensive land clearing did not begin until the 1940s (Bauer and Goldney 1999). Another burst of clearing in the 1970s (Bauer and Goldney 1999) denuded the landscape of about 90% of native vegetation cover. Clearing left only isolated fragments of native vegetation and an extensive network of linear remnants along roadsides, and as windbreaks around large paddocks. Typical paddocks are one to three square kilometers in area. The study landscapes are essentially flat, with elevation ranging from 160m (Pulletop, Nombinnie), to 200m (Gubbata), although there are low mountain ranges in the area that reach 400m elevation. The maximum relief within any of the study locations is less than 20m.

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Study Design and Sampling

Four locations were studied, including three agricultural locations (Pulletop, Taleeban, Gubbata) and one uncleared location (Nombinnie, Fig. 1). Each location covered an area of approximately 100 km^2. Within each of the three agricultural locations, there were 10 sample sites representing 10 “landscape-elements” (Table 1). Sites were classified according to six “main-attributes” based on remnant shape, vegetation type and management (Table 1). Four of the main-attributes (reserve, strip, grazed strip, road) were stratified by the presence or absence of spinifex (*Triodia scariosa*). Spinifex can have a strong influence on lizard faunas (Cogger 1984), and spinifex presence is correlated with sandy soil. Spinifex presence or absence is therefore indicative of potentially important environmental variation for reptiles. However, there was no spinifex in woodland or paddocks, so spinifex stratification was not possible in those elements, resulting in a total of ten landscape-elements in the three agricultural landscapes (Table 1). Sites were selected to provide good geographic coverage of each location within the limitation of where particular landscape-elements occurred. The Grazed + spinifex site at Pulletop (abbreviated site name 6P, where 6 = landscape-element and P = Pulletop) was placed in a grazed block of remnant mallee 500m wide because there were no grazed linear strips with spinifex at that location.

The fourth location included six sites in continuous, uncleared mallee (Nombinnie, Fig. 1). Three of the sites had spinifex in the understorey (N1, N3, N5); the other three did not have spinifex (N2, N4, N6). Sites were selected to ensure the spatial scale was comparable to the scale of sampling in the three agricultural locations, that the understorey composition was consistent throughout the site and to avoid recently burned sites (Caughley 1985). None of the mallee sites in the agricultural landscape had been recently burned (>25 years).

Each of the 36 sites was sampled using sixteen 22-liter pit fall traps spaced at 25 m intervals, each with 10 m of 0.3 m high drift fence. A damp cloth, block of wood and small piece of PVC pipe provided shelter for captured animals. For plots with known densities of reptiles, Schlesinger (1999) showed that understorey plant density did not affect the capture rate of reptiles. Schlesinger's (1999) study was conducted in a central Australian Mulga (*Acacia anura*) environment, and included six of the lizard species captured in this study. Two skink species that were abundant enough for individual tests (including *Ctenotus schomburgkii* from this study) showed no difference in capture rates after the experimental removal of understorey (Schlesinger 1999). I therefore assume that trap efficiency does not vary with habitat, and any differences between sites represent differences in reptile abundance.

Traps in the three agricultural locations were opened for five nights/days in each of four months during spring and summer (October 1999-January 2000). The continuous mallee sites at Nombinnie were opened for five consecutive nights in November and December 1999 and early February 2000. In analyses comparing continuous mallee and agricultural locations, October data were excluded so that sampling effort was comparable between the two areas. Traps were checked daily. Captured animals were marked by clipping two or three toes and by removing up to 20% of their tail for genetic analysis, then were released 10-15m from the trap in which they were captured. Data analyzed was the total number of each species captured during the study period, and excluded the small number of recaptured animals. Taxonomic nomenclature follows Cogger (1996).

To quantify vegetation structure, nine vegetation parameters were estimated. In 5 x 10m quadrats adjacent to each pitfall trap the number of logs >5cm diameter (number of logs) were counted and estimates made of the percentage cover of low shrubs (shrubs with branches and leaves in contact with the ground and usually <0.5m tall), tall shrubs (shrubs that contact the ground at the central stem only, and were usually 0.5-3m in height), spinifex, other grasses, canopy, thin leaf litter (scattered leaves over soil), thick leaf litter (deep mulch around the base of trees) and bare ground. Results from the 16 quadrats were pooled to produce values representative of the entire site. Remnant vegetation width for sites in linear remnants was measured, as was the distance of each site from the nature reserve using the most direct, vegetated route. For sites bisected by a road, width was the sum of vegetation width on either side of the road. This measure provided an adequate description of the narrow width of roadside vegetation.

The continuous mallee sites at Nombinnie and the agricultural locations were matched for soils (Quaternary flat to gently undulating plains of red and brown clayey sand loam and lateritic soil, Department of Mines 1967, 1968), vegetation type and as far as possible, fire history. Nevertheless, comparisons of fauna with uncleared areas in a landscape-scale study are inevitably problematic because climate often varies clinally, making it impossible to eliminate potential sources of confounding variation. Three meteorological stations provide some indication of the likely climatic variation across the study locations: Lake Cargelligo

(30km NNW Gubbata, 30km SSW Nombinnie), Yenda (30km SSE Pulletop, 40km SW Taleeban), Mt Hope (20 km WNW of Nombinnie). Climatic measures at Lake Cargelligo, Yenda and Mt Hope (respectively) include mean annual rainfall (426, 410, 387), mean daily maximum temperature (annual: 25.1, 23.5, 24.1, January: 34.1, 32.3, 33.2), mean number of clear days (135, 95, 127), mean number of cloudy days (68, 82, 39). I would therefore expect climatic variation across the three agricultural locations to be similar in magnitude to differences between Gubbata and Nombinnie, so there is not a strong climatic cline separating all agricultural locations from the continuous location.

Comparison of Nombinnie and agricultural locations may also be confounded by historic biogeographic factors. For example, the boundary between two closely related dragon species (*Pogona barbata* and *P. vitticeps*) occurs in the area between Nombinnie and Gubbata (Badham 1976). In total, natural range limits probably account for seven species occurring only at Nombinnie and two species occurring only in the agricultural locations in my data set (from distribution maps (Cogger 1996), and absence of museum records). Numerically, the Nombinnie-only species account for 17% of animals captured in the continuous mallee. In view of the biogeographic history of the area, I only compare species that are known to occur, or which recently occurred, in both the Nombinnie and agricultural locations. However, I assume that if a species is present in both locations, it is likely to have similar abundance and distribution unless it has been affected in some way by land clearing. My assumption is nevertheless bound to the caveat that species in the two areas may differ genetically due to their biogeographic history and they may experience different interspecific interactions. Biogeographic history and species interactions could therefore influence some of the observed differences between continuous and cleared landscapes. Despite this weakness, the Nombinnie location represents the closest remaining uncleared area for comparison with the agricultural landscapes, so provides the best possible idea of what reptile communities might have been like before extensive land-clearing.

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Analyses

Species were initially subdivided into five broad groups based on their distribution in the agricultural locations. The groups were: Widespread, not biased towards reserves and present at more than half of the sites, Reserve-biased, significant bias towards nature reserves (Fisher's exact test (Zar 1984) of presence/absence in reserves compared with linear strips), Patchy, not biased towards reserves and present at 3-13 sites, Rare, present at one site only in the agricultural landscape, Continuous mallee, captured only at the Nombinnie sites in continuous mallee.

Generalized linear models were used to test for an effect of each landscape-element on reptile abundance. Species used in these analyses included only those for which 30 or more individuals had been captured in the agricultural locations. This cut-off follows the rule of thumb used by Didham et al. (1998): for species used in a GLM, the number of individuals captured should at least equal the number of sites used in the study. Six species satisfied this criterion: *Lerista punctatovittata*, *L. muelleri*, *Morethia boulengeri*, *Amphibolurus nobbi*, *Ramphotyphlops bituberculatus*, *Menetia greyii*. Each analysis assumed a Poisson distribution of count data, and included a natural logarithm link function (McCullagh and Nelder 1989, Nicholls 1989). Location was fitted to each model first to take into account location-wide variation. Then four factors (distinguishing the effects of five main-attributes) were fitted, including: shape (reserves vs. linear remnants), grazing (grazed sites vs. ungrazed remnants), roadside (roads vs. remnants without roads), and vegetation type (woodland vs. mallee). For statistical testing, each factor was fitted after location and the three other factors had been included in the model. This approach of rotating factors for testing, so that the significance of each factor was determined only after all other factors were in the model, was required because the unbalanced design could not be accommodated in a single analysis. The residual (error term) was the interaction between location and a factor designating the five main-attributes. Degrees of freedom were therefore 2 for location, 1 for each of the four factors, and 8 for the residual.

Where the residual mean deviance was less than one, the dispersion parameter was held at one, which is the expected value for a Poisson model (McCullagh and Nelder 1989). However, the residual mean deviance was used as the dispersion parameter in analyses where there was evidence of over-dispersion. The lower stratum of the analysis included the spinifex factor (presence or absence of spinifex), and the interactions with three of the four factors comparing main-attributes (vegetation type was not included because woodland does not have both levels of factor spinifex). Again each interaction term was rotated so that each was tested only after all other second-order interactions had been included in the model. As with the upper stratum, the mean deviance/residual mean deviance was used to test for significance in analyses where the residual mean deviance was greater than 1, to allow for over-dispersion.

Paddocks were not included in the above GLM because they could not be sensibly classified by shape (paddocks are not reserves or strips). Therefore a separate Poisson GLM with logarithm link function was applied, with location fitted first, followed by a factor delimiting paddocks from all remnant sites.

For species that did not satisfy the criterion for analysis using GLM and occurred on three or more sites, a permutation method was used to test for differences across all main-attributes (i.e.: reserve, strip, grazed strip, roadside, woodland, paddock, but not for spinifex effects). Three sites was used as a cut-off score because there were three replicates of each landscape-element, and I regarded occurrence on all three of a particular landscape-element as an important pattern to identify. The numbers of animals at each of the 30 agricultural sites were randomly shuffled within location using the permute option of the Bootstrap procedure in GENSTAT (version 5, release 4.2, Genstat 2001). A Poisson generalized linear model with log link function (most likely to be suited to count data) was fitted, including location then a factor delimiting the six main-attributes (Main). The test statistic for each bootstrapped replicate was the additional deviance explained when Main was added to the model. The probability that the actual change in deviance could arise by chance was calculated as the number of bootstrapped results that exceeded the actual deviance divided by 5000, the number of bootstrap replicates. Results where $P < 0.1$ are reported. Confidence intervals for mean abundance for each main attribute were calculated by randomly resampling the data within main-attribute, with replacement (5000 replicates, random option of the Bootstrap procedure, GENSTAT version 5, release 4.2).

The same GLM method as used for reptiles was used in analyses of most vegetation structure variables, number of reptiles and number of species. However, in these analyses I assumed a normal distribution, and applied an identity link function (Nicholls 1989), because this approach gave a more even distribution of residuals when plotted against fitted values, compared with the Poisson model. The number of fallen logs was analyzed using a Poisson model and natural logarithm link function. Some of the vegetation variables were transformed using natural logarithms to improve the model fit (see results). Reserves and site 6P were excluded from the analysis of remnant width, so that the analysis gave a comparison of the width of linear remnants.

Preliminary step-wise linear regression analyses comparing site variables (vegetation measures etc) directly with reptile species abundance suggested that significant correlations were also correlated with landscape-elements. There are many correlated differences between landscape-elements, but the step-wise regressions could not reflect that complexity because all factors were not measured and because some measured factors were correlated. Step-wise regression tends to oversimplify relationships between wildlife and their environment due to multicollinearity among variables (MacNally 1996). Therefore, I used the site variables as a way of describing some of the differences between landscape-elements, by applying the GLM described above. This approach allows the recognition of any correlational relationships among site variables, and significant differences among landscape-elements can be related indirectly to significant patterns of lizard abundance.

At a location scale, species that are unable to use all landscape-elements will have a reduced area of occupancy, and possibly increased fragmentation. To illustrate this potential, I estimated the percentage of total remnant area that could be occupied, and the increase in fragmentation beyond that due to land clearing alone. The remnant area that could be occupied was based on the presence or absence of each species in each landscape element at each location. Increase in fragmentation was measured as the number of new habitat isolates created in the landscape when landscape-elements that were unoccupied were removed from remnant vegetation maps. Remnant areas and number of fragments were estimated from polygons drawn onto scanned and aligned images of aerial photographs using GIS software. Estimates were made for two species that showed consistent responses to landscape-elements in all three locations. These were the only cases where extrapolation to un-sampled areas based on the landscape-element classification could be justified. They also represent approximate extremes of possible responses. In calculating the number of fragments I have assumed that roads do not subdivide habitat. Roads throughout the three locations were less than 20m wide and were unsealed. While there is evidence that narrow dirt roads can be a barrier to dispersal of small mammals (reviewed by Andrews 1990), impacts on reptiles have not been examined. Because most reptiles are baskers, they may readily move a few meters into open spaces provided by roads, and road-kill evidence suggests that many species do so

(Forman and Alexander 1998, Ashley and Robinson 1996, Bennett 1991). For such species, roads may not be a strong dispersal barrier. Nevertheless, my estimates of the number of fragments should be regarded as conservative.

I expected that my analyses would have low power, because the survey design included only three replicates of each landscape-element and there was substantial spatial variation to account for. I collected a smaller reptile data set from seven of the ten landscape-elements at each agricultural location (excluding roadside +-sp. and woodland elements) in January and February 1999. Location (3 levels), Main-attribute (3 levels), Spinifex (2 levels) and the Main-attribute.Spinifex interaction were fitted in an analysis of variance to obtain variance components for input into the world-wide-web based power program "Java applets for power and sample size" (Russell Lenth, Division of Mathematical Sciences, Department of Statistics & Actuarial Science, University of Iowa, 29 March 2001, *personal communication*). Lenth's methods of power analysis were used because it was possible to include the Location blocking structure in the calculations. The method was applied to the six most common species in the data set. For main-attribute comparisons (i.e.: reserve vs. ungrazed strip vs. grazed strip), the size of the contrast between the maximum and minimum mean needed to be an average of 1.8 times the overall mean abundance of each species to obtain a power of 0.80, with an alpha of 0.05. Given this expectation of low power, results are reported where $P < 0.1$ to reduce the risk of type II errors. Using the preliminary data set, when alpha was relaxed to 0.1, the average contrast for power of 0.80 dropped to 1.5 times the overall mean.

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Distribution in Continuous Mallee

The abundance of species in the isolated reserves in the agricultural landscape was directly compared with the samples from continuous mallee at Nombinnie. Analyses were limited to species that occurred in both areas, and for which there were 12 or more captures (because 12 sites are included in the analyses, Didham et al. 1998). The October sample from the reserves was omitted from the data set to make the sampling effort at each location comparable. The Poisson generalized linear model with natural log link function included reserve-type (agricultural reserve vs. continuous mallee), spinifex (+/- spinifex) and their interaction. Over-dispersion was compensated for as in previous analyses. Fisher's exact tests were also used to compare presence/absence in continuous mallee with all agricultural sites, to help recognize species that may have declined relative to their distribution in uncleared habitat. Paddocks were excluded from the analyses so that remnant vegetation and uncleared mallee could be compared without the influence of paddocks.

3rd order head

Genetic Variation and Dispersal

Allozyme electrophoresis was used to assess population genetic structure because it has proven effective in other studies (e.g., Driscoll 1998 a, b), is relatively cheap and can be completed quickly (Hartl et al. 1994). The species selected for study included two widespread species and two species with restricted distributions in the agricultural landscape. Sample sizes for continuous mallee are indicated in results, although additional animals from previous sampling were available from the agricultural landscapes (Table 2). Electrophoretic protocols followed Richardson et al. (1986). Thirteen variable enzyme systems and fifteen loci were used including (in parentheses: number of alleles detected using cellulose acetate electrophoresis for *Amphibolurus nobbi*, *Ctenotus allotropis*, *Lerista muelleri* and *L. punctatovittata* respectively) Aspartate aminotransferase, E.C number 2.6.1.1, abbreviation AAT-1, (0, 0, 2, 3), AAT-2, (0, 0, 2, 0), Aconitase, 4.2.1.3, ACON, (0, 2, 0, 0), Alpha Esterase, 3.1.1.1, αEST-1, (3, 0, 3, 4), αEST-2, (0, 3, 3, 0), alpha-Glycerolphosphate dehydrogenase, 1.1.1.8, αGPD, (4, 2, 0, 0), Isocitrate dehydrogenase, 1.1.1.42, IDH, (0, 0, 0, 2), Malic enzyme, 1.1.1.40, ME, (0, 3, 0, 2), Mannose phosphate isomerase, 5.3.1.8, MPI, (2, 0, 0, 0), Peptidase B (leucine glycine glycine), 3.4.11, PEPB, (4, 0, 0, 2), Peptidase C (valine leucine), 3.4.11, PEPC, (3, 2, 3, 5), Peptidase D (phenylalanyl-proline), 3.4.11, PEPD, (5, 2, 4, 0), 6 Phosphogluconate dehydrogenase, 1.1.1.44, 6PGD, (0, 2, 0, 0), Glucosephosphate isomerase, 5.3.1.9, PGI, (3, 0, 2, 0), Phosphoglucomutase, 2.7.5.1, PGM, (3, 0, 0, 0).

Permutation tests (Good 1994) were used to test for loss of genetic variation in the agricultural locations compared with the continuous mallee. Gene diversity (Nei 1987) was used as the measure of genetic variation within populations. The test involved pooling all of the individuals from the two populations to be compared, and randomly resampling the same number of individuals as in one of the populations, without replacement. Individuals that were not resampled were used as the second 'population'. The difference in gene diversity was then calculated for the two randomly generated populations. I wrote a visual-basic computer program to repeat the resampling procedure 1000 times and so to build a distribution against which the actual difference in gene diversity could be compared. Actual values that were lower than the 2.5th percentile, or greater than the 97.5th percentile were considered significant. I compared populations in each of the three reserves (pooled + and – spinifex sites) with data from continuous mallee. Individuals from continuous mallee sites that were close together were pooled to increase sample size: *L. punctatovittata* (N3, N5), *L. muelleri* (N1, N2), *A. nobbi* (N3, N4, N5), *C. allotropis* (N6 only).

To examine the relative dispersal ability of declining and widespread reptile species, I tested for evidence of isolation by distance using GENEPOP (Raymond and Rousset 1995). GENEPOP allows the application a mantel permutation procedure to detect significant trends towards increasing genetic divergence with increasing distance. A Spearman Rank correlation coefficient is used as the test statistic. Populations with sample sizes of less than five were excluded from analyses to avoid undue bias in F_{st} that could arise with very small sample sizes. With a sample size of five, there is a 90% chance of sampling alleles that occur with a frequency of 0.2 (Sjogren and Wyoni, 1993), so all relatively common alleles are likely to be represented in a sample of five individuals. *Ctenotus allotropis* captured at 4G (n = 2) and 6G (n = 4) were pooled because those sites were close together, and the number of sites was very small for this species. Because of the small number of sites at which *C. allotropis* was captured, one Nombinnie site with a sample of 3 animals was also included. Data within each reserve for each species (sites 1 and 2 at each location) were pooled because these samples likely represent the same genetic population, and data from Nombinnie was pooled as described above. Preliminary analyses of genetics results indicated there were not small-scale genetic differences between populations, so pooling data from separate populations does not obscure any important relationships. Rousset (1997) recommended using transformed values of F_{st} and distance, however doing so made no difference to the conclusions that could be drawn from the results. The more straightforward relationship represented by the untransformed data is therefore used. Rousset (1997) also suggested that data sets should be truncated at lower distances, because the relationship between F_{st} and distance is unlikely to be linear. However, in the absence of additional information about dispersal ability of reptile species, it was unclear where to cut off the data set. All distance data have therefore been included.

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RESULTS

2nd order head

Reptile Associations with Landscape-elements

Five reptile species had a distribution biased towards reserves, five were widespread and nine were classified as patchy (Table 3). Seven species were only represented by one individual in the agricultural landscape, including the elapid snakes *Vermicella annulata* (5T), *Pseudonaja nuchalis* (8P), *Pseudonaja textilis* (8G), *Demansia psammophis* (9P, N1), the gecko *Gehyra variegata* (10T), and the pygopodids *Lialis burtonis* (2T) and *Aprasia inaurita* (2G).

Among the entire data set, only two blind snakes *Ramphotyphlops bituberculatus* were captured in paddocks (Table 3). Of the six species for which a paddock effect was specifically tested for, three showed a significant effect (*Lerista punctatovittata* (Deviance ratio, presented as mean deviance/residual mean deviance or mean deviance/1 (d.r.) = 40.9/5.4, P = 0.011), *L. muelleri* (d.r. = 23.6/2.5, P = 0.005), *Morethia boulengeri* (d.r. = 25.1/3.5, P = 0.013). The three species with significant effects were absent from the three paddock sites and one to four other sites (Table 3). The three species without a significant paddock effect (*Amphibolurus nobbi* (d.r. 6.7/3.0, P = 0.143), *Ramphotyphlops bituberculatus* (d.r. = 1.3/2.0, P = 0.419), *Menetia greyii* (d.r. = 9.1/3.6, P = 0.127)) were absent from paddocks and many remnant sites (Table 3).

Compared with linear remnants, reserves had significantly more reptile species (variance ratio 8.55, Fig. 2A) and more *Lerista muelleri* (d.r. = 5.68/1, Fig. 2B). *Amphibolurus nobbi* occurred in all reserve sites, but was never captured in linear remnants without spinifex (d.r. = 9.56/1, Fig. 2C). Permutation tests indicated that three additional species were significantly more abundant in reserves (*Ctenotus allotropis*, *C. schomburgkii*, *Simoselaps australis*, Table 4), although the 95% confidence interval for *C. allotropis* in reserves and grazed strips overlapped because this species occurred in a grazed strip at one location (Table 3). The snake *Suta nigriceps* was absent from reserves but occurred throughout all linear strips (P = 0.02, Table 4).

There were significantly fewer *Lerista punctatovittata* on grazed sites (d.r. = 6.12/1.39, Fig. 2D), and no *Lerista muelleri* on grazed sites without spinifex (d.r. = 10.18/2.03, Fig. 2E). *Amphibolurus nobbi* was absent from grazed sites, even though this species was able to survive in linear strips in the presence of spinifex (d.r. = 9.70/1, Fig. 2F). Permutation tests did not identify any additional grazing effects (Table 4).

The abundance of *L. punctatovittata* tripled on roadsides (d.r. = 27.55/1.39, Fig. 2G). *Morethia boulengeri* had a strong roadside by spinifex interaction, with lower numbers on roadsides with spinifex, but higher abundance on roadsides without spinifex (d.r. = 19.19/1, Fig. 2H). *Menetia greyii* showed a similar interaction to *M. boulengeri* (d.r. = 10.08/2.46, Fig. 2I). This pattern was also observed for *L. punctatovittata*, although was not significant (road + sp. Mean 9.3 (95% CI: 4.6-18.9), road – sp. 21.4 (13.7-33.5)). These patterns contributed to the significantly higher number of reptiles on roadsides without spinifex (Variance ratio 8.76, Fig. 2J). There was also slightly higher species richness on roadsides without spinifex compared to roadsides with spinifex (Variance ratio 5.12, Fig. 2K). One additional species (*Ramphotyphlops australis*) was only found on roadsides (P = 0.032, Table 4), and roadsides were the most common place to capture *Suta nigriceps* (Tables 3, 4).

In contrast to these roadophiles, *Amphibolurus nobbi* was absent from roadsides (9.70/1, Fig. 2L), as were three of the species examined using permutations (Table 4). However in the latter cases, the road effect was indistinguishable from the shape effect because these species were generally absent from linear remnants.

Vegetation type strongly influenced *Lerista muelleri*, with approximately double the number of animals captured in woodland (mean = 7 (95% CI: 4.5-10.8)) compared with mallee (3.5 (2.8-4.5), d.r. = 6.20/1, P = 0.013). *Ramphotyphlops bituberculatus* was more abundant in mallee (Woodland = 0.7 (0.1-4.5), Mallee = 1.5 (0.9-2.5), d.r. = 5.90/1.84, P = 0.089).

No significant effects were detected for seven species using permutation analyses including *Cryptoblepharus carnabyi, Ctenotus robustus, Diplodactylus intermedius, D. vittatus, Pogona barbata, Rhynchoedura ornata,* and *Varanus gouldii.*

Substantial reductions in area of occupancy, and increased fragmentation resulted when species were excluded from particular landscape-elements. Based on distribution maps of landscape-elements at each location, *A. nobbi* could only use 22% of remnant vegetation at Pulletop and Gubbata, and 68% at Taleeban. The reserve at Taleeban accounted for 58% of remnant area. The widespread species *L. muelleri* was predicted to occur in only 57% of remnants at Pulletop because the landscape-element from which it was absent (grazed without spinifex) was particularly common. *Lerista muelleri* remained in most remnants at Gubbata (95% of area predicted to be occupied), and Taleeban (94%).

The number of discrete remnants at Gubbata, Pulletop and Taleeban was 1, 13 and 3 respectively. The area occupied by each species was often substantially more fragmented than the arrangement of remnants suggested. The number of new fragments recognized when predicted unsuitable habitat was removed from each remnant vegetation map at Gubbata, Pulletop and Taleeban (respectively) was 1, 6 and 0 for *L. muelleri*, and 4, 2 and 1 for *A. nobbi*.

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Vegetation Association with Landscape-elements

The only difference in vegetation structure in the Shape analysis (comparing square reserves with linear remnants) was for the % low shrubs, with the suggestion that reserve sites without spinifex have a higher % low shrubs than other remnants (Variance ratio (v.r.) = 4.77, Fig. 3A). Grazed sites had less shrub cover than ungrazed sites (Figs 3B,C. v.r. = 4.36, 47.81 respectively) and if there was no spinifex, there were no low shrubs at all (Fig. 3B).

Although roadside sites were originally defined by the narrow width of remnants alongside a wide road (Fig. 3D, v.r. = 18.08), roadsides also differed from non-road sites by having more grass cover (Fig. 3E, v.r. = 5.46). Both tall and low shrub cover interacted with spinifex in the roadside comparisons, where roadsides with spinifex also had higher shrub cover (Figs.

3F,G. v.r. = 6.10, 9.47 respectively). Spinifex sites were characterized by having a higher % cover of spinifex, as expected (Fig. 3H, v.r. = 97.1), but they also had lower cover of other grasses (Fig. 3I, v.r. = 6.79), and more bare ground than sites without spinifex (Fig. 3J, v.r. = 6.65). Woodland sites had more tall shrubs (Fig. 3K, v.r. = 9.06), fewer low shrubs (Fig. 3L, v.r. = 6.34), less canopy cover (Fig. 3M, v.r. = 23.87) and fewer logs (Fig. 3N, d.r. = 48.03/11.56) than mallee remnants. There were no significant effects for thick leaf litter, thin leaf litter or distance from nature reserve.

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Distribution in Continuous Mallee

Two widespread species (*Morethia boulengeri*, *Ramphotyphlops bituberculatus*) and one reasonably common "patchy" species (*Menetia greyii*) were not captured in the continuous mallee (Table 3), even though the area is within their known range, and there are published records of these species from Nombinnie/Round Hill Nature Reserves (Caughley 1985, Cogger, 1984). Fisher's exact tests comparing presence/absence in continuous versus agricultural landscapes indicated these patterns had a low probability of occurring by chance (*R. bituberculatus* P = 0.027, *M. boulengeri* P < 0.001, *M. greyii* P = 0.065). In addition, the widespread *Lerista muelleri* was significantly less abundant in continuous mallee (mean at Nombinnie 0.5 (95% CI: 0.1-2.8) vs. 6.3 (3.9-10.2), d.r. = 35.4/2.2, P = 0.004) and *L. muelleri* was significantly more widely distributed in the agricultural landscape (Fisher's exact test, P = 0.02). The only other reasonably common species that was absent from continuous mallee, *Pogona barbata*, reaches its natural range limits to the south of Nombinnie (Badham 1976).

Using GLM, the abundance of five species did not differ significantly between the reserves in agricultural landscapes and continuous mallee, including *Lerista punctatovittata*, *Diplodactylus vittatus, D. intermedius, Ctenotus schomburgkii*, and *C. allotropis*. The latter two species are either confined to, or significantly biased towards nature reserves in the agricultural locations. *Lerista punctatovittata* also displayed a spinifex effect that was not detected in other analyses (mean + sp. 5.2 (95% CI: 3.5-7.6) vs. mean – sp. 2.0 (1.1-3.7), d.r. = 8.7/1.2, P = 0.03).

Only *Amphibolurus nobbi* showed a trend towards higher abundance in the continuous mallee (7.2 (95% CI: 5.2-10.0) vs. 4.2 (2.7-6.4), d.r. = 4.8/1.2, P = 0.08). In addition, *A. nobbi* and *C. schomburgkii* were significantly more widespread in continuous mallee (Fisher's exact test, P = 0.005, 0.02 respectively). *Ctenotus schomburgkii* was not captured at any of the Taleeban sites, but there is a museum record from the Taleeban reserve in 1981.

Eleven species were only captured in the continuous mallee (Table 5). Seven of those species probably meet their range limits (Cogger 1996) between Nombinnie and the agricultural landscapes of this study, and so may never have occurred in the area now extensively cleared. However, there are museum records for two of the species from the agricultural landscape in or near to my study areas. These include one record of *Ctenophorus pictus* from Taleeban reserve in 1981, and five records of *Pygopus nigriceps* from towns throughout the study area, four between 1926 and 1936, and one from 1987. The wider distribution of *C. pictus* and *P. nigriceps* at Nombinnie compared with the agricultural landscape is unlikely to have arisen by chance (Fisher's exact test, P = 0.004, 0.028 respectively). Two species were captured in farming locations in a preliminary study, but not the main study (*Pygopus lepidopodus* 2T, 3T, *Delma butleri* 6P).

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Genetic Variation and Dispersal

The reserve-bias species *Amphibolurus nobbi* had significantly less genetic variation at Gubbata compared with Nombinnie (P = 0.009, change in gene diversity = +0.079), but similar levels of variation were detected at Pulletop and Taleeban compared with continuous mallee. No difference in genetic variation was detected for population comparisons in the second reserve-bias species (*C. allotropis*), or the two widespread species *L. muelleri* and *L. punctatovittata*.

The two reserve-bias species (*C. allotropis* and *A. nobbi*) had substantially stronger isolation by distance effects (steeper slopes) than the two widespread species (*L. punctatovittata*, *L. muelleri*, Fig. 4), although the result for *C. allotropis* had a relatively high probability of occurring by chance (P = 0.09). Data for only four *L. muelleri* were available from continuous mallee, and so there were no comparisons in the highest distance categories for that species. However, a separate analysis that included the four *L. muelleri* from Nombinnie as a single population, gave results consistent with those shown: a near-flat, negative relationship (Slope = -0.0006, P = 0.02).

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DISCUSSION

Land clearing and remnant management have brought about massive changes in the mallee reptile fauna. Reptiles have been all but eliminated from 90% of the landscape through clearing, with only two individual reptiles captured in paddocks. Most reptile species are confined to remnant vegetation and do not use the matrix. Because some species did not occur in any linear strips at all, there were relatively few species available to statistically test for effects of paddocks, grazing and roadsides. Nevertheless, in addition to the near universal absence of reptiles from paddocks, there was convincing evidence of impacts of grazing, roadsides and remnant shape on reptile species.

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Grazing

In previous studies, interpretation of grazing impacts on reptiles has often been confounded by area and isolation effects, where the most severely grazed sites were also the smallest or most isolated sites (e.g.: Smith et al. 1996, Sarre 1996, Hadden and Westbrooke 1996, Miller and Cale 2000). This study now confirms the suspicions raised in previous and recent studies (Brown 2001) by demonstrating a strong negative impact of grazing on three lizard species in sites of similar size and isolation. *Lerista punctatovittata* had reduced abundance on grazed sites, grazing in the absence of spinifex eliminated *L. muelleri*, and *A. nobbi* did not occur on any grazed sites, although it could survive in linear remnants with spinifex.

The interaction between grazing and spinifex observed in *L. muelleri* was also evident in three of the four other widespread species. *Lerista punctatovittata*, *M. boulengeri* and *R. bituberculatus* either had lower abundance, or did not occur as frequently in grazed sites without spinifex compared to grazed sites with spinifex (Table 3). I speculate that spinifex is probably responsible for ameliorating the impacts of grazing (rather than some other correlated factor) because spinifex likely provides shelter, retains areas of untrampled soil, and possibly acts as habitat for prey species. Spinifex is unpalatable to sheep. Therefore, if remnant vegetation must be grazed, allowing unpalatable plant species to remain in remnants may reduce the impacts on reptiles.

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Roadsides

The most impressive pattern observed on roadsides was the extremely high numbers of *Lerista punctatovittata*, and the higher abundance of four other species. The increased abundance was primarily observed on roadsides without spinifex, a pattern that is difficult to explain. Conceivably nutrient input as run-off and as dust could increase productivity on roadsides. Increased nutrient loads can increase the percentage cover of native plants and weeds beside roads (Cale and Hobbs 1991, Lamont et al. 1994), which is consistent with the observed increased cover of grasses and shrubs on roadside sites (Fig. 3E-G). Nutrient pulses can be of more benefit to plants on sandy soil compared with clay soils (Mettler et al. 2001), which could explain higher shrub growth on roadside sites with spinifex, which also have sandier soil. Higher shrub growth would lead to increased shading, which may be detrimental to reptiles. Extreme levels of shade may prevent reptiles from reaching a suitable temperature for foraging (Riveravelez and Lewis 1994). In addition, eggs incubated at low temperatures can produce animals with reduced chances of survival (Elphick and Shine 1998). Therefore, I speculate that increased nutrient loads on roadsides may lead to increased reptile abundance, through more nutritious or more abundant food resources (Haddad et al. 2000). However, the benefit of increased resources may not be realised on sites with spinifex due to the detrimental effect of increased shading by shrubs.

In addition to increases in the abundance of widespread or patchy species, one species was significantly absent from roadsides (*A. nobbi*). Conceivably, *A. nobbi* cannot survive because the remnants are too narrow, or because it is not able to benefit through the same mechanisms as the species with increased abundance. Although some animals may be killed on roads (Bennett 1991), it is unlikely that road deaths are a primary cause of *A. nobbi*'s absence from roadsides. The small, unsealed country roads used in this study support a very small amount of traffic. In addition, evidence for road-kill effects at a population level is generally lacking (Forman and Alexander 1998), although rare, large species may be at risk (Bennett 1991). While habitat simplification through loss of understorey plants seems to be a major threat to reptiles (Brown 2001, Cogger 1989), the loss of *A. nobbi* from the shrubby roadside vegetation of this study demonstrates that reptiles can decline even with an extensive shrub layer.

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Reserves vs. linear remnants

The comparison of square reserves with linear remnants suggested that reduction of habitat area into thin strips has a strong impact on the reptile fauna, with four species absent or nearly so from strips, and the abundance of one widespread species significantly reduced. These effects were observed even though there was little evidence of additional changes to the vegetation structure. "Shape" effects may therefore be caused by the change in remnant shape, effectively the reduced area, rather than habitat quality. Hadden and Westbrooke (1996) and Kitchener et al. (1980) suggested that habitat quality was the most important limiting factor for reptiles, not remnant area, because reptiles have small home ranges that often overlap. While my results confirm the importance of habitat quality, they also suggest that remnant size may be important in limiting reptile distribution when remnants are very narrow (10-100m).

One snake species, *Suta nigriceps*, was more commonly captured in linear strips than reserves. This pattern implies that there are larger populations of *S. nigriceps* in the strips, or that *S. nigriceps* uses linear strips for movement, and is therefore more frequently captured. Among all strip sites, *S. nigriceps* was most consistently captured on roadsides without spinifex (Table 3), which were the sites with highest reptile abundance. I speculate that the observed capture rates of *S. nigriceps* may be a combination of more dispersal though linear corridors of any condition, and the accumulation of individuals in areas of high prey density (*S. nigriceps* eats skinks, *pers. obs.*).

A word of caution is warranted regarding species without significant effects. The absence of a significant association between landscape-elements and seven reptile species does not imply that those species are not declining in the agricultural landscape. Six of the seven species had patchy distributions and so may be experiencing local extinctions, but in a way unrelated to the landscape-element classifications. Alternatively, some of these species may have been poorly sampled using pitfall traps (e.g. arboreal geckos).

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Location Scale Patterns

At the location scale, the combined effects of landscape-elements suggested that reptile distributions are substantially fragmented. The distributions of one widespread (*L. muelleri*) and one reserve-bias species (*A. nobbi*) were fragmented beyond what would have been expected based on the distribution of remnant vegetation. Despite apparent connectivity throughout the agricultural landscapes, management of remnant vegetation has fragmented reptile populations, reduced the amount of habitat available, and contributed to their decline.

Although it is not possible to tease out the relative importance of fragmentation compared with habitat loss using the current data set, it is likely that both processes have an important role in species declines. Simulation models demonstrate that habitat loss alone has a strong influence on risk of extinction, but at low levels of habitat cover (10%, Fahrig 1997), or when species do not disperse into the matrix (Fahrig 2002), fragmentation can have a very strong independent effect. In the extensively cleared mallee landscapes, where most reptiles do not venture into the matrix, increased fragmentation and habitat loss are likely to have strong negative effects on remnant-dependent species.

Symptomatic of fragmentation and small population size, there was some evidence of loss of genetic variation in *A. nobbi* in the fragmented landscape. In general however, there was little evidence of depleted genetic variation in populations of reserve-bias or widespread species. To date, most remnant populations of the four species examined may have retained the genetic diversity of their former more continuous populations. However, only an extreme event is likely to be detected using allozyme heterozygosity measures over a short time span (Allendorf 1986). Therefore, with the exception of *A. nobbi* at Gubbata, the retention of genetic variation implies that populations have not experienced extreme and prolonged bottlenecks in population size in the 20-30 years since clearing was completed (Nei et al. 1975). Nevertheless, apparent loss of variation in one *A. nobbi* population supports the distributional evidence that populations in agricultural reserves may be small and geographically isolated.

For linear remnants to act as effective corridors and prevent populations from becoming isolated at the location scale, they must be appropriately managed. The results reported here suggest that corridor management needs to consider the width of linear remnants, understorey plant species, type of disturbance and potential interactions between these parameters. The combination of factors incorporated into a corridor will determine which subset of the reptile biota can use it. For example, ungrazed linear remnants with a spinifex understorey enable the dragon *Amphibolurus nobbi* to survive, but not two other reserve-bias species. Linear remnants beside roads provided an unusually good environment for some species, but were unsuitable for five reptile species, three of which were unable to use linear remnants in any condition. I draw three conclusions from these patterns. Firstly, linear remnants in any condition are better than none, because they at least enable the "widespread" category to exist. Secondly, the existing network of linear remnants do not provide connectivity for a large proportion of the reptile fauna, and so habitat reconstruction is needed to prevent populations from being permanently isolated (a point I return to below). My third point arises from the observation that roadsides had unusually high densities of some species. Management targeting those species would create narrow roadside remnants by preference. This raises the likelihood that the objective of optimal corridor design may need to be supplanted by multiple corridor designs to service the range of requirements of different species. Instead of single corridors permeating the landscape, two or more parallel corridors subject to different management regimes may be needed to effectively reconnect the biota in agricultural landscapes.

In addition to fragmentation, there may have been dramatic changes in community composition across the entire agricultural area. *Ctenophorus pictus* and *Pygopus nigriceps* appear to have become extinct throughout the agricultural study sites. *Ctenophorus pictus* may have been restricted to begin with, however museum records indicate that *P. nigriceps* was widespread. Brown and Bennett (1995) reported that *P. nigriceps* had also disappeared from agricultural landscapes to the south of my study area, suggesting that this large (>50cm long), aggressive legless lizard is especially vulnerable to land clearing. In addition to habitat change and reduced area, introduced predators, especially cats, may have contributed to the decline of *P. nigriceps*. Catling (1988) reported that 4.2% and 8% of fox and cat stomachs respectively contained *P. nigriceps*, at a site near my study areas in continuous mallee. In the arid zone of South Australia, Read and Bowen (2001) estimated that foxes and cats annually consume 260 and 700 reptiles/km^2 respectively. Given that *C. pictus* and *P. nigriceps* occur at Nombinnie in the presence of cats and foxes, their decline to local extinction may be attributed to the interaction between land-clearing impacts and introduced predators. In addition to the two local extinctions, a third species (*Ctenotus schomburgkii*) may have become extinct at one of three locations, and the abundance of *A. nobbi* may have declined in the reserves. This evidence suggests that both species may be vulnerable to extinction in the agricultural landscape. Previously, authors have suggested that small reserves will suffice to conserve small-bodied reptiles (Kitchener et al. 1980, Cogger 1989).

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Types of species that decline

Why have certain species declined, and others apparently increased in the fragmented mallee landscape? Given the plethora of possible causes of decline and increase associated with each landscape-element, it would be surprising if a simple explanatory model could be applied. This problem is confounded by a lack of detailed biological knowledge for most species. Nevertheless, there are some simple theories that bear consideration.

Tilman et al. (1994) and Loehle and Li (1996) predicted that under particular fragmentation and biological conditions, the strongest competitors (and most abundant) in uncleared landscapes should decline first as habitat destruction progresses because strong competitors are often the poorest dispersers. A contrasting, and more traditional theory holds that species with low initial densities may be more extinction-prone after fragmentation due to their small population size (Terborgh 1974, Loehle and Li 1996, Bolger et al. 1997). However, every possible combination of abundance and decline in uncleared and cleared landscapes was observed. Both widespread, abundant species (*A. nobbi, C. allotropis, C. schomburgkii*) and relatively rare species (*P. nigriceps* and *C. pictus*) in continuous mallee declined in the agricultural landscape. Rare (*L. muelleri*), and absent (*M. boulengeri, R. bituberculatus*) species in continuous mallee were among the most common species in the cleared landscape, while the most common species in the agricultural landscape, *L. punctatovittata*, was also widespread and abundant in uncleared mallee. These patterns conflict with model predictions and imply that more complex interactions must be involved in promoting or reducing species abundance after fragmentation. Alternatively, species abundance in continuous mallee may not represent species abundance prior to fragmentation of the agricultural landscapes.

Cosson et al. (1999) recognized four common traits in the species that came to dominate islands that formed in a new dam. The traits included high abundance in undisturbed forest, large body size, large geographic range, and generalist feeding and/or habitat tendencies (Cosson et al. 1999). Harrison and Bruna (1999) and Foufopoulas and Ives (1999) also suggested that fragments or islands tend to gain generalists, and lose specialists. However, none of Cosson et al.'s (1999) factors distinguish between the dominant and declining species of this study (Single factor ANOVA, all $P > 0.1$, Tables 3, 6). Although declining species may prove to be specialized if they were studied in detail, there are currently no grounds for ascribing specialization as a cause of reptile declines from mallee remnants.

The only consistent difference between declining and widespread species was from genetic evidence, where both declining species that were examined had higher rates of population divergence with increasing distance than two widespread species. This may indicate that declining species have a lower capacity for dispersal (Slatkin 1993). Dispersal limitation has often been cited as one of the key factors driving species' responses to fragmentation (Kadmon 1995, Walters et al., 1999, Lawes et al. 2000), with poorly dispersing species having an increased risk of extinction, (Laurance 1990), occupying less of the landscape (Hokit et al. 1999), and having reduced local genetic diversity (Wauters et al. 1994). Although my results are consistent with dispersal limitation being an indicator or causal factor of reptile declines, the small sample size (four species), and small data set for one species (*C. allotropis*) means there is a risk of coincidental fit. In addition, alternative interpretations of the divergence patterns are possible. Most importantly, the two declining species may generally have smaller effective population sizes than the widespread species, which would increase the rate of genetic divergence among populations of the decliners (Wright 1931). Smaller population size may also place species at a higher risk of local extinction (Lande 1998), which is consistent with the observed patterns in this study.

Although divergence was greater among populations of the two declining species, *C. allotropis* and *A. nobbi* also had relatively low F_{st} values, implying that gene flow was important in maintaining genetic similarity (Porter 1990) at the spatial scale of this study. Assuming that stabilizing selection does not act on the loci examined, which could maintain low F_{st} despite low gene flow (Neigel 1997), the data suggest that both species have historically been able to disperse at least the distances across study locations, on the order of 10km, with some migration between locations (perhaps over generations), which were approximately 30km apart. Moderately high historic levels of migration are in contrast with the distribution evidence that suggested local populations might now be isolated. A likely explanation for these contrasting results is that there has not been enough time for isolated populations to diverge in the 20-30 years since land clearing was completed.

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Conclusions and Prospects

Although some reptile species appear to be more successful in the agricultural landscape than they might have been prior to clearing, their localized success should be viewed in the broader landscape context. All but one species have declined from up to 90% of their former range due to land clearing. Furthermore, linear strips, even those in good condition, do not provide connectivity for many reptile species, either because they are too narrow (all less than 100m), or because the habitat within them is altered, for example, by grazing. The inability of many reptile species to use linear remnants has led to increased population fragmentation and substantially reduced the amount of habitat available.

Populations that are small and isolated face a very high risk of extinction, and no chance of replacement (Lande 1998, Hanski 1998, Soule et al. 1992, Stacey and Taper 1992). On theoretical grounds, and supported by evidence that two reptile species have already become locally extinct, it seems likely that additional species face extinction without major intervention because their populations are reduced to small and isolated vegetation remnants. Intervention, particularly habitat restoration (Saunders et al. 1993), and properly planned translocations (Burke 1991, Dodd and Seigel 1991, Krauss et al. 2002) are justified ethically (Hampicke 1994), and may provide a suite of material benefits including biodiversity credits (Salvin 2000), carbon credits (National Greenhouse Office 1999), reduced land degradation (Marshall and Jones 1997) and a range of ecosystem services (Balvanera et al. 2001) such as pollination, seed dispersal and the control of herbivorous insects (Traveset and Saez 1997, Nogales et al. 1998, Dial and Roughgarden 1995)). The urgency of habitat restoration is becoming increasingly apparent (Sinclair et al. 1995). Despite uncertainty of technique and doubts that near natural communities can be re-established (Saunders et al. 1993), experimental approaches that develop broad-scale restoration methods need to be applied with the same systematic rigor with which the vegetation was taken away in the first place.

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Table 1. Ten sample sites were replicated at three agricultural locations, Pulletop, Taleeban and Gubbata. + sp. = landscape-element with *Triodia scariosa* (spinifex) in the understorey. - sp. = landscape-element without spinifex. An additional six sites (3 with spinifex, 3 without) were located in uncleared mallee at Nombinnie (see text).

	Landscape-element		
	Main-Attribute	Spinifex	Description
1	Reserve	- sp.	Block of ungrazed remnant mallee, from 1.5-8 km^2.
2	Reserve	+ sp.	Block of ungrazed remnant mallee with spinifex in the understorey
3	Strip	- sp.	Ungrazed linear mallee remnant 30-100m wide
4	Strip	+ sp.	Ungrazed linear mallee remnant 30-100m wide with spinifex in the understorey
5	Grazed Strip	- sp.	Grazed linear mallee remnant
6	Grazed Strip	+ sp.	Grazed linear mallee remnant with spinifex in the understorey
7	Paddock	- sp.	Open paddock currently grazed by sheep and previously cropped, >400m from mallee remnants
8	Road	- sp.	Narrow linear mallee remnant beside a constructed gravel road (width 10-15m on both sides of road)
9	Road	+ sp.	Narrow (10-15m) linear mallee remnant beside a constructed gravel road with spinifex in the understorey
10	Woodland	- sp.	Woodland remnant beside a constructed gravel road (with or without a strip of adjacent grazed woodland)

Table 2. Sample sizes and sites used for allozyme electrophoresis in the agricultural landscapes. Site numbers refer to landscape-elements (see Table 1), letter codes refer to locations (Gubbata = G, Pulletop = P, Taleeban = T). - = not sampled at this site.

	1,2G	1,2P	1, 2T	3G	3P	3T	4G	4P	4T	6G	6P	6T	8G	8P	8T
L. muelleri	36	17	18	-	-	11	12	3	6	8	7	8	5	-	-
L. punctatovittata	30	19	15	35	7	6	9	10	12	10	-	11	27	29	12
A. nobbi	17	9	15	-	-	-	-	-	6	-	-	-	-	-	-
C. allotropis	14	-	12	-	-	-	2	-	-	4	-	-	-	-	-

Table 3. Number of animals captured at each site*. Locations: G = Gubbata, P = Pulletop, T = Taleeban, N = Nombinnie (continuous mallee). Family indicated in parentheses after species names: A = Agamidae (dragons), S = Scincidae (skinks), T = Typhlopidae (blind snakes), E = Elapidae (venomous snakes), V = Varanidae (monitors), G = Gekkonidae (geckos). *Ramphotyphlops* genus abbreviated to R.

	Reserve			Reserve +sp			Strip			Strip + sp			Grazed Strip			Grazed Strip+sp			Paddock			Road			Road +sp			Wood-land			Nomb-innie +sp			Nomb-innie -sp		
	G	P	T	G	P	T	G	P	T	G	P	T	G	P	T	G	P	T	G	P	T	G	P	T	G	P	T	G	P	T	N1	N3	N5	N2	N4	N6
WIDESPREAD																																				
Lerista punctatovittata (S)	3	1	3	6	8	4	17	4	2	3	6	4	6	0	1	4	3	4	0	0	0	25	29	13	5	8	15	9	8	3	5	5	3	1	0	4
Morethia boulengeri (S)	5	7	3	6	5	1	3	4	1	7	6	0	1	1	1	2	3	4	0	0	0	13	7	8	1	1	0	24	1	4	0	0	0	0	0	0
Lerista muelleri (S)	11	9	2	4	3	9	2	1	5	7	1	4	0	0	0	4	5	5	0	0	0	5	4	4	3	0	3	8	5	8	2	0	0	1	0	0
R. bituberculatus (T)	3	0	0	2	0	0	2	0	3	0	0	1	0	0	3	1	1	2	1	1	0	5	0	3	0	2	8	0	0	2	0	0	0	0	0	0
Pogona barbata (A)	1	2	1	0	2	3	0	1	0	0	0	2	1	0	1	1	0	0	0	0	0	5	0	1	0	0	0	0	1	1	0	0	0	0	0	0
RESERVE BIASED																																				
Morethia obscura (S)	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Ctenotus allotropis (S)	4	0	5	2	0	2	1	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	0	15
Simoselaps australis (E)	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0

Amphibolurus nobbi (A)	7 2 5	3 5 3	0 0 0	3 3 1	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	5 10 8	3 10 7
Ctenotus schomburgkii (S)	1 1 0	1 7 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 6 3	2 1 0
PATCHY												
Ctenotus robustus (S)	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 2 1	0 0 0	0 0 0	0 1 0	0 1 0	0 0 0	0 0 0
Diplodactylus vittatus (G)	2 1 0	0 2 0	1 0 0	1 0 0	0 0 0	1 1 0	0 0 0	0 0 0	0 0 0	1 0 0	0 1 2	1 3 2
Cryptoblepharus carnabyi (S)	0 0 0	0 0 0	0 0 0	0 0 0	0 0 7	0 0 0	0 0 0	2 0 2	0 0 2	1 0 1	0 0 0	0 0 0
Rhynchoedura ornata (G)	0 0 0	0 2 0	0 0 0	0 1 0	0 0 0	0 10 0	0 0 0	0 0 1	0 0 0	4 0 0	0 3 1	4 0 0
Menetia greyii (S)	0 0 2	2 0 0	0 0 3	1 3 3	0 0 0	0 1 5	0 0 0	0 5 3	0 0 1	14 0 0	0 0 0	0 0 0
Varanus gouldii (V)	0 3 0	0 0 0	0 0 1	0 1 0	1 0 1	0 1 1	0 0 0	0 0 0	0 1 0	0 0 2	1 1 0	3 0 0
Suta nigriceps (E)	0 0 0	0 0 0	2 0 0	1 0 0	1 0 0	2 0 1	0 0 0	2 1 1	1 0 0	2 1 0	0 1 1	1 0 0
Diplodactylus intermedius (G)	2 1 1	2 3 0	5 0 0	3 0 0	2 0 0	4 0 1	0 0 0	0 0 2	0 0 0	0 0 1	2 0 0	1 0 2
R. australis (T)	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 0 0	0 2 1	0 0 1	0 0 0	0 0 0	0 0 0

*Data include October-January trapping for locations Gubbata, Pulletop and Taleeban, and November – February trapping for Nombinnie. Species with only one record in the agricultural landscape are listed in the text and species captured only at Nombinnie appear in Table 5.

Table 4. Using a permutation test, five species showed non-random distributions across Landscape-elements. The mean abundance (and 95% confidence intervals) indicate that three species were significantly more abundant in reserves, one species was most abundant in linear strips, and another only occurred on roadsides.

Species	P	Reserve	Strip	Grazed Strip	Roadside	Woodland	Paddock
Ctenotus allotropis	0.012	2.16 (0.67 - 3.67)	0.33 (0 - 0.67)	0.5 (0 - 1.5)	0.00	0.00	0.00
Simoselaps australis	0.065	0.67 (0.17 - 1.33)	0.00	0.00	0.00	0.00	0.00
Ctenotus schomburgkii	0.008	1.67 (0.33 - 3.83)	0.00	0.00	0.00	0.00	0.00
Ramphotyphlops australis	0.032	0.00	0.00	0.00	0.67 (0.17 - 1.33)	0.00	0.00
Suta nigriceps	0.022	0.00	0.49 (0 - 1.17)	0.66 (0.17 - 1.33)	0.83 (0.33 - 1.33)	1 (0 - 2)	0.00

Table 5. Reptile species that were captured in continuous mallee but not in the agricultural landscape in the current data set. *Delma butleri* and *P. lepidopodus* were captured in the farming landscape in preliminary sampling, and there are museum records of *C. pictus* and *P. nigriceps* from the farming areas used in this study. The remaining seven species may reach their range limits between Nombinnie and Gubbata.

Family	**Species**	N1	N3	N5	N2	N4	N6
Agamidae	*Ctenophorus pictus*	0	0	1	1	2	0
Agamidae	*Ctenophorus fordi*	0	2	9	1	5	1
Agamidae	*Pogona vitticeps*	0	1	1	0	0	0
Gekkonidae	*Lucasium damaeum*	0	0	1	0	0	0
Pygopodidae	*Pygopus lepidopodus*	1	1	1	0	0	0
Pygopodidae	*Pygopus nigriceps*	0	2	1	0	0	0
Pygopodidae	*Delma australis*	1	0	0	1	0	0
Pygopodidae	*Delma butleri*	0	1	1	0	0	0
Scincidae	*Ctenotus atlas*	0	1	3	0	1	0
Scincidae	*Egernia inornata*	0	1	0	0	0	0
Scincidae	*Eremiascincus richardsonii*	0	0	0	0	0	1

Table 6. Three characteristics of species which remain widespread in the agricultural landscape, and species which may be extinct or have declined (reserve-bias)*. Food: g = generalist, s = specialist. Range is given as a category of the percentage of mainland Australia over which they can be found (after Cogger 1996[#1680]): 1: 0-10%, 2: 10-25%, 3: 25-50%, 4: 50-75%, 5: 75-100%. u = no data available.

	Food	Range	Size (mm)
Widespread			
Lerista punctatovittata	u	2	100
Morethia boulengeri	g	3	45
Lerista muelleri	g	4	45
Ramphotyphlops bituberculatus	s	3	300
Reserve-bias and extinct			
Morethia obscura	g	3	45
Ctenotus allotropis	g	1	55
Simoselaps australis	s	2	300
Amphibolurus nobbi	u	2	75
Ctenotus schomburgkii	g	4	45
Pygopus nigriceps	u	5	180
Ctenophorus pictus	g	3	70

*Single factor ANOVA indicated none of the characteristics differed significantly between the two reptile groups ($P > 0.1$). Data sources: Read 1998, Greer 1997, Cogger 1996, James 1991, Shine 1991, Swan 1990, Greer 1989, Chapman and Dell 1980, Smith 1976.

Fig. 1. Locations and sites indicated on maps of remnant vegetation (main location map after Sivertsen and Metcalf 1995). Main location map: speckled = uncleared mallee with woodland patches. Numbers on individual location maps indicate sites sampled for each landscape-element (see Table 1 for code). Dotted line on Nombinnie map indicates narrow, unmade vehicular track. Key latitude and longitude, Gubbata site 1: 33 38' 07", 146 33' 12", Taleeban site 1: 33 55' 33", 146 28' 23", Pulletop site 1: 33 57' 57", 146 04' 46". Grid north is directed from the bottom to the top of the page.

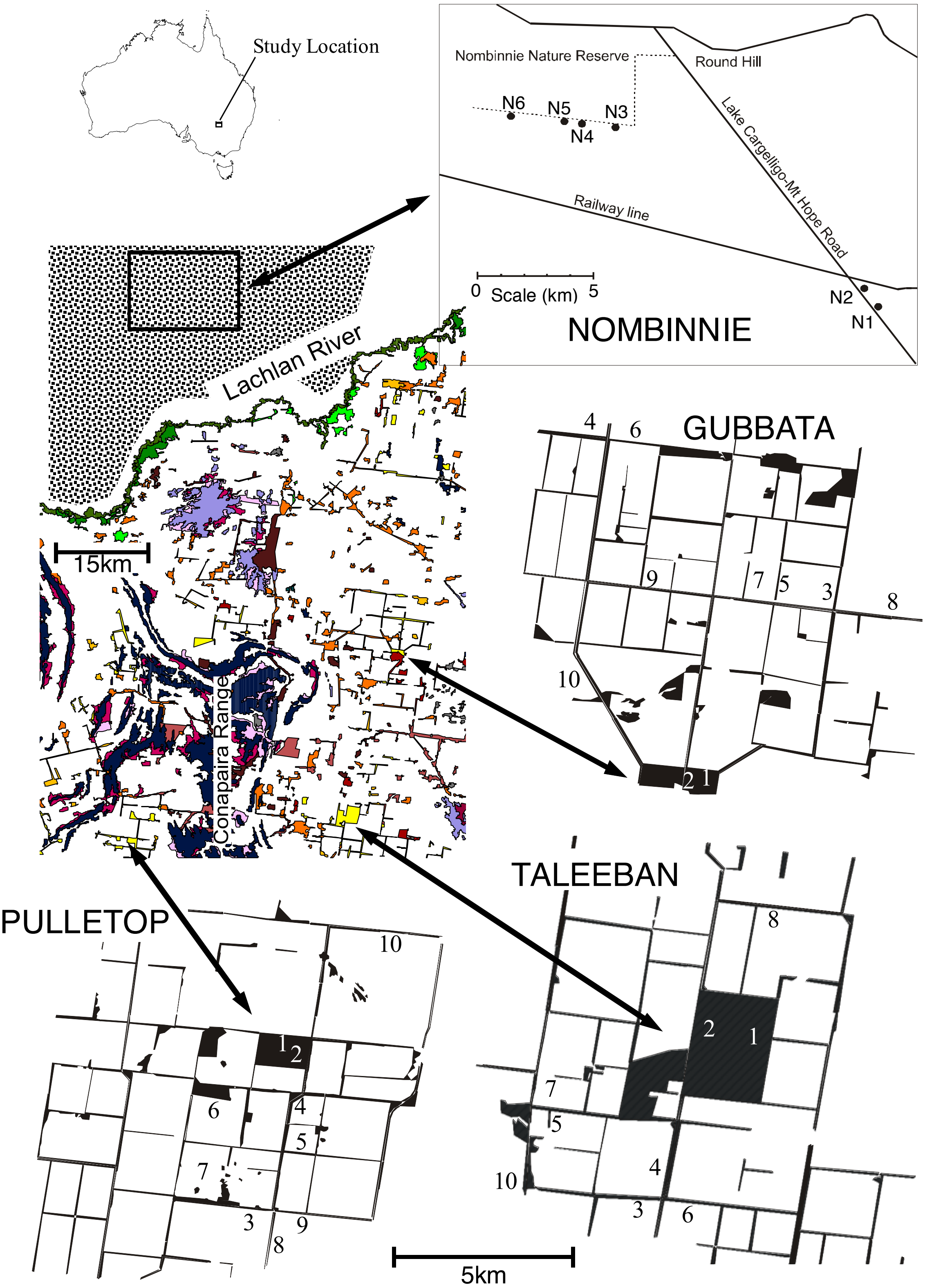
Fig. 2. Using generalized linear models, there were three significant shape effects (square reserve vs. linear strip, A-C), three significant grazing effects (ungrazed vs. grazed sites, D-F), and six significant roadsides effects (sites beside unsealed roads vs. sites that were not, G-L). Error bars indicate 95% confidence limits. Where there was a significant interaction with spinifex, sites with spinifex (+SP) are indicated by squares connected by a thick line, sites without spinifex (-SP) with diamonds connected by a thin line.

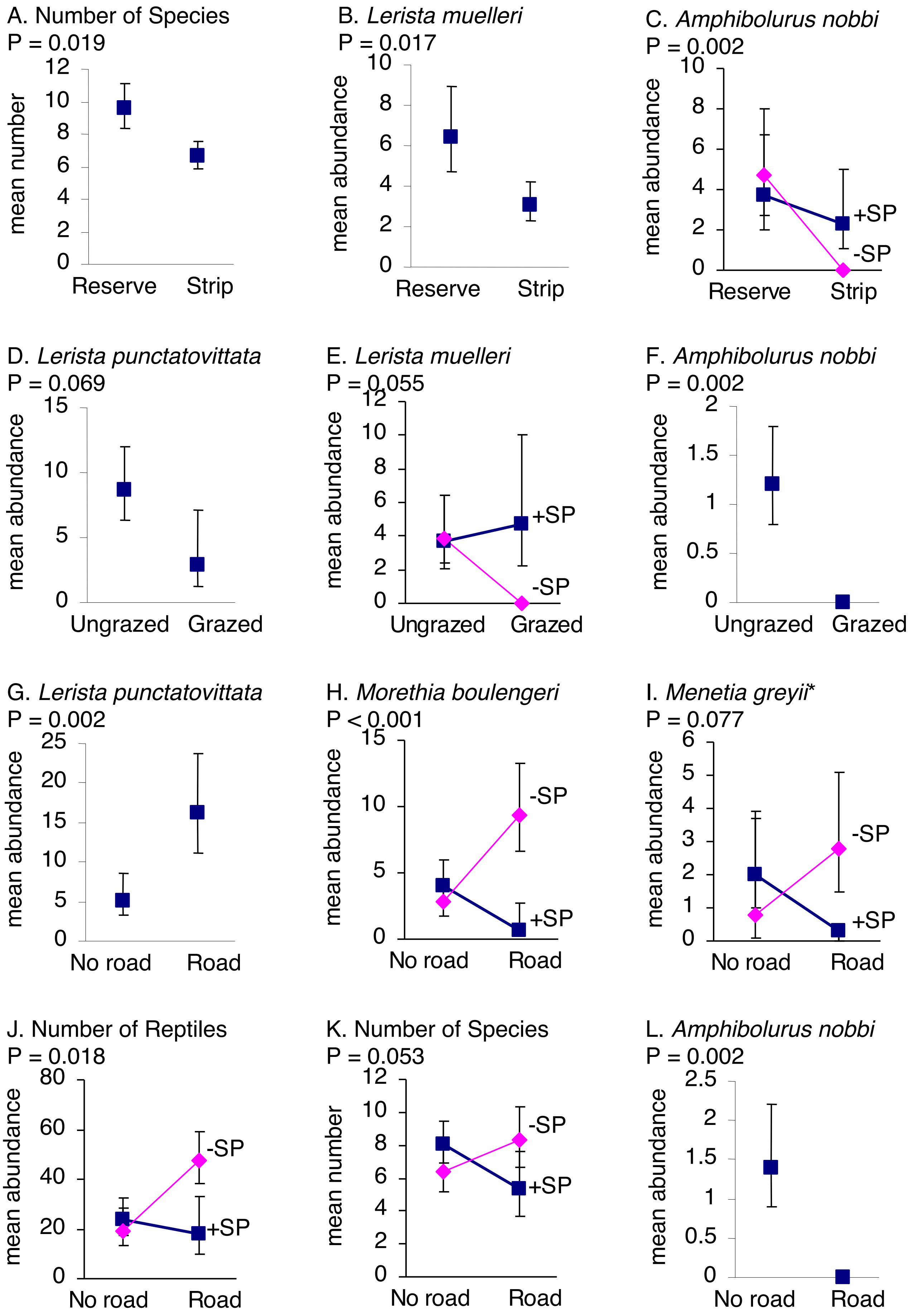
Footnote for Fig. 2: * Confidence limits for *M. greyii* (I) on roadsides with spinifex were over inflated (0-76) due to a poor fit of the model, judged by examination of residuals plotted against fitted values. Nevertheless the patterns reported here reflect those in the data if the high CI is ignored (cf. Table 3).

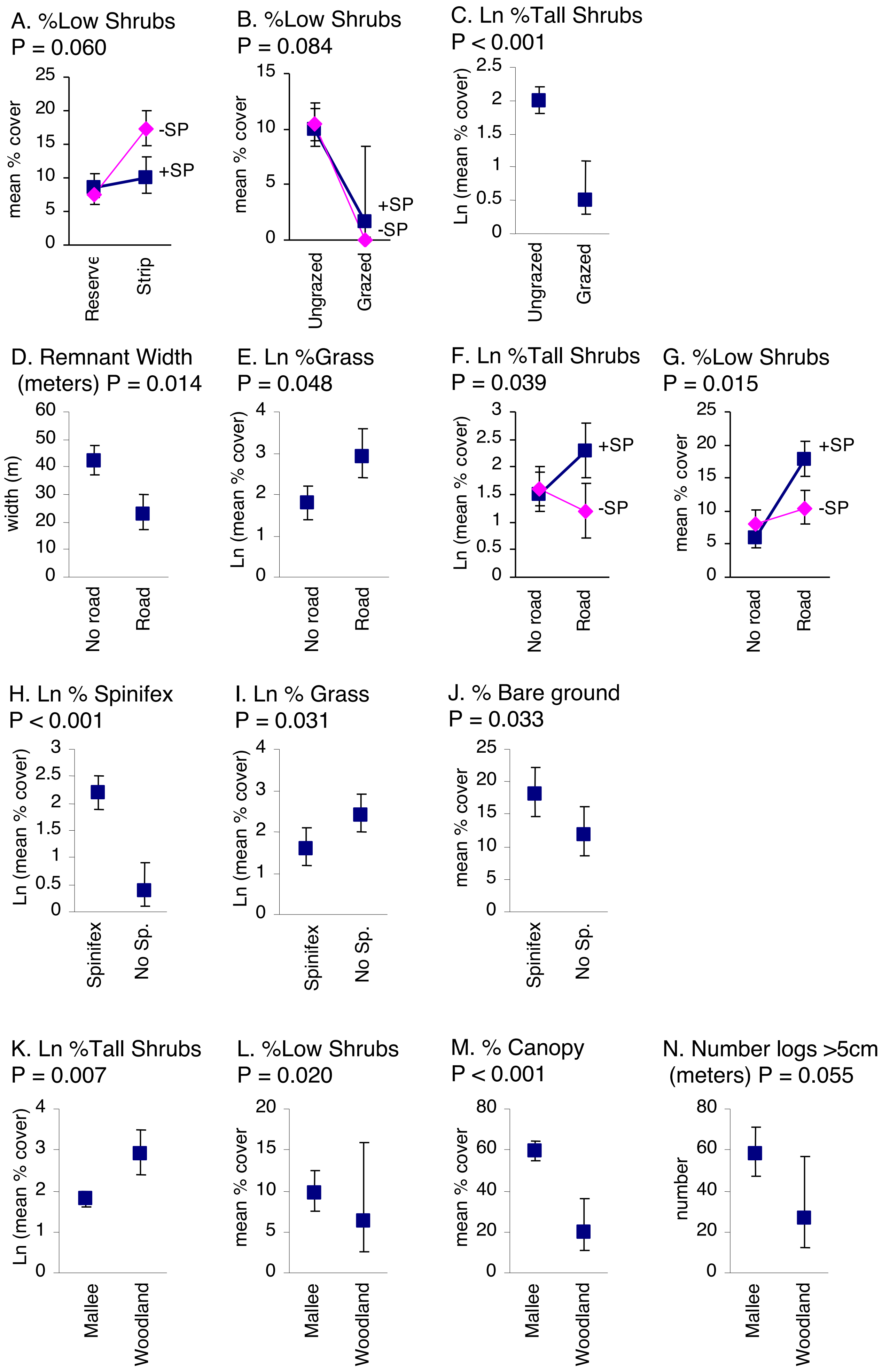
Fig. 3. The application of generalized linear models identified 14 significant relationships between landscape-elements and 11 parameters describing the site, including nine vegetation parameters, remnant width and distance from the reserve at

each location. Significant effects were observed for factors Shape (square reserve vs. strip, A), Grazing (B, C), Roadsides (comparing remnants beside roads to those without a road, D-G), Spinifex (sites with spinifex in the understorey vs. sites without, H-J), and vegetation type (comparing mallee with woodland, K-N). Error bars and other graph details as in Fig. 2.

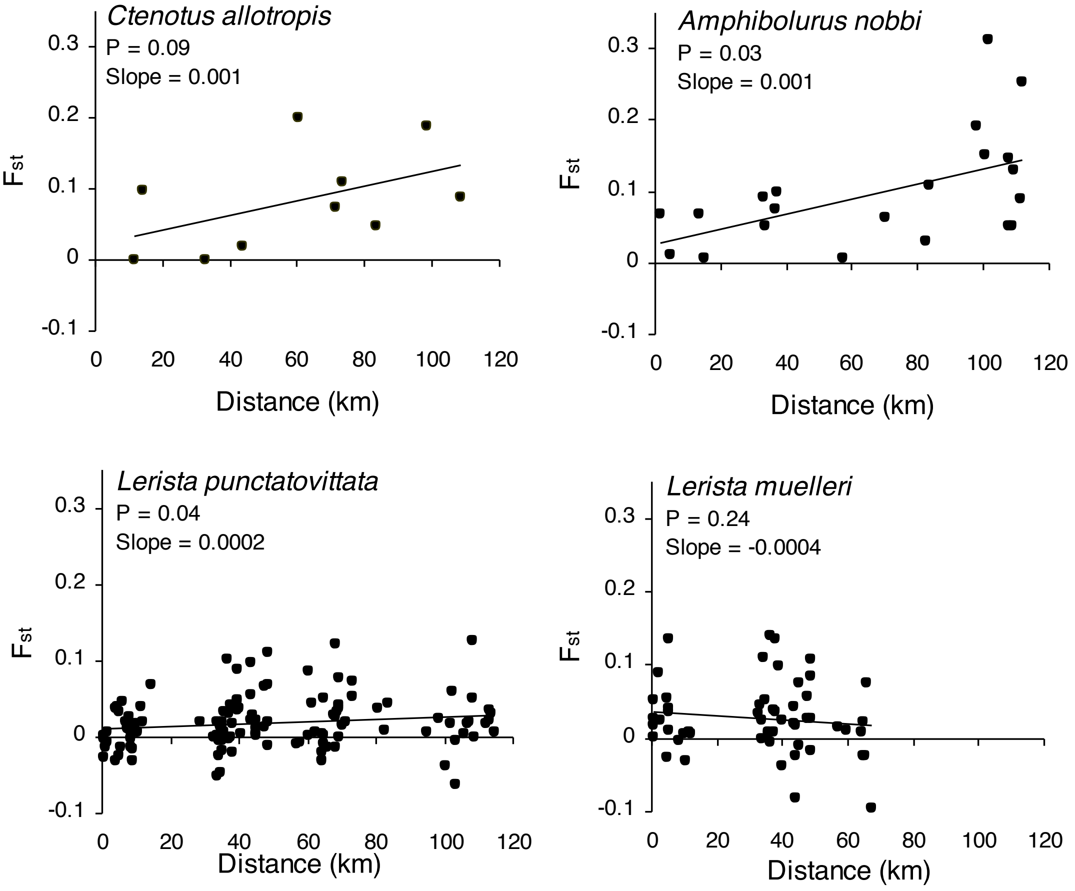
Fig. 4. Relationship between genetic divergence (F_{st}) and distance between sample sites for two reserve-bias species (*C. allotropis*, *A. nobbi*), and two widespread species (*L. punctatovittata*, *L. muelleri*). P values from mantel permutation tests.


Study Location
Nombinnie Nature Reserve
Round Hill
N6
N5
N3
N4
Lake Cargelligo-Mt Hope Road
Railway line
0
Scale (km)
5
N2
N1
NOMBINNIE
Lachlan River
15km
Conapaira Range
GUBBATA
4
6
9
7
5
3
8
10
2
1
TALEEBAN
8
2
1
7
5
4
10
3
6
PULLETOP
10
1
2
6
4
5
7
3
9
8
5km


A. Number of Species
P = 0.019
mean number
0
2
4
6
8
10
12
Reserve
Strip
B. *Lerista muelleri*
P = 0.017
mean abundance
0
2
4
6
8
10
Reserve
Strip
C. *Amphibolurus nobbi*
P = 0.002
mean abundance
0
2
4
6
8
10
+SP
-SP
Reserve
Strip
D. *Lerista punctatovittata*
P = 0.069
mean abundance
0
5
10
15
Ungrazed
Grazed
E. *Lerista muelleri*
P = 0.055
mean abundance
0
2
4
6
8
10
12
+SP
-SP
Ungrazed
Grazed
F. *Amphibolurus nobbi*
P = 0.002
mean abundance
0
0.5
1
1.5
2
Ungrazed
Grazed
G. *Lerista punctatovittata*
P = 0.002
mean abundance
0
5
10
15
20
25
No road
Road
H. *Morethia boulengeri*
P < 0.001
mean abundance
0
5
10
15
-SP
+SP
No road
Road
I. *Menetia greyii**
P = 0.077
mean abundance
0
1
2
3
4
5
6
-SP
+SP
No road
Road
J. Number of Reptiles
P = 0.018
mean abundance
0
20
40
60
80
-SP
+SP
No road
Road
K. Number of Species
P = 0.053
mean number
0
2
4
6
8
10
12
-SP
+SP
No road
Road
L. *Amphibolurus nobbi*
P = 0.002
mean abundance
0
0.5
1
1.5
2
2.5
No road
Road



A. %Low Shrubs
P = 0.060
mean % cover
0
5
10
15
20
25
-SP
+SP
Reserve
Strip
B. %Low Shrubs
P = 0.084
mean % cover
0
5
10
15
+SP
-SP
Ungrazed
Grazed
C. Ln %Tall Shrubs
P < 0.001
Ln (mean % cover)
0
0.5
1
1.5
2
2.5
Ungrazed
Grazed
D. Remnant Width
(meters) P = 0.014
width (m)
0
10
20
30
40
50
60
No road
Road
E. Ln %Grass
P = 0.048
Ln (mean % cover)
0
1
2
3
4
No road
Road
F. Ln %Tall Shrubs
P = 0.039
Ln (mean % cover)
0
0.5
1
1.5
2
2.5
3
+SP
-SP
No road
Road
G. %Low Shrubs
P = 0.015
mean % cover
0
5
10
15
20
25
+SP
-SP
No road
Road
H. Ln % Spinifex
P < 0.001
Ln (mean % cover)
0
0.5
1
1.5
2
2.5
3
Spinifex
No Sp.
I. Ln % Grass
P = 0.031
Ln (mean % cover)
0
1
2
3
4
Spinifex
No Sp.
J. % Bare ground
P = 0.033
mean % cover
0
5
10
15
20
25
Spinifex
No Sp.
K. Ln %Tall Shrubs
P = 0.007
Ln (mean % cover)
0
1
2
3
4
Mallee
Woodland
L. %Low Shrubs
P = 0.020
mean % cover
0
5
10
15
20
Mallee
Woodland
M. % Canopy
P < 0.001
mean % cover
0
20
40
60
80
Mallee
Woodland
N. Number logs >5cm
(meters) P = 0.055
number
0
20
40
60
80
Mallee
Woodland


Ctenotus allotropis
P = 0.09
Slope = 0.001
Amphibolurus nobbi
P = 0.03
Slope = 0.001
Lerista punctatovittata
P = 0.04
Slope = 0.0002
Lerista muelleri
P = 0.24
Slope = -0.0004
F_{st}
0.3
0.2
0.1
0
-0.1
0
20
40
60
80
100
120
Distance (km)