Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape

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Abstract

In fragmented landscapes, a species' dispersal ability and response to habitat condition are key determinants of persistence. To understand the relative importance of dispersal and condition for survival of *Nephrurus stellatus* (Gekkonidae) in southern Australia, we surveyed 92 woodland remnants three times. This gecko favours early post-fire succession conditions so may be at risk of extinction in the long-unburnt agricultural landscape. Using N-mixture models, we compared the influence of four measures of isolation, patch area and two habitat variables on the abundance and occurrence of *N. stellatus*, while taking into account detection probability. Patch occupancy was high, despite the long-term absence of fire from most remnants. Distance to the nearest occupied site was the most informative measure of patch isolation, exhibiting a negative relationship with occupancy. Distance to a nearby conservation park had little influence, suggesting that mainland-island metapopulation dynamics are not important. Abundance and occurrence were positively related to %-cover of spinifex (*Triodia*), indicating that niche-related factors may also contribute to spatial dynamics. Patterns of patch occupancy imply that *N. stellatus* has a sequence of spatial dynamics across an isolation gradient, with patchy populations and source-sink dynamics when patches are within 300 m, metapopulations at intermediate isolation, and declining populations when patches are separated by > 1-2 km. Considering the conservation needs of the community, habitat condition and connectivity may need to be improved before fire can be reintroduced to the landscape. We speculate that fire may interact with habitat degradation and isolation, increasing the risk of local extinctions.

Keywords Cattle grazing, dispersal, fragmentation, invasive weeds, land clearing, metacommunity, neutral theory, patch-matrix model, reptile, species-sorting

Introduction

Understanding the spatial dynamics of populations is critical for developing effective management responses to habitat loss and fragmentation (Huxel and Hastings 1999), and is fundamental to appraising the importance of competing metacommunity and metapopulation theories (Harrison 1991; Leibold et al. 2004). However, there is substantial debate over the relative importance of dispersal limitation and the influence of habitat condition. Dispersal limitation is a key driver of neutral processes such as neutral metacommunity theory and classic metapopulations (Hanski 1998; Hubbell and Lake 2003; Levins 1969). Habitat effects drive deterministic processes as described by species-sorting metacommunity theory and deterministic metapopulation theory (Cottenie 2005; Driscoll 2007; Thomas 1994). The uncertainty surrounding the relative importance of these phenomena contributes to the ongoing debate about the best approach to landscape management and restoration (Hanski 2010; Hodgson et al. 2009). Empirical research is needed to help resolve these uncertainties.

Information about spatial dynamics of species usually comes from long-term, genetic, demographic and dispersal studies, all of which are difficult or costly to implement. For species that are readily surveyed, one tractable and powerful approach is to use the information available in the current pattern of occurrence because these represent the outcome of many generations of population processes (Etienne et al. 2004). If isolation, patch size or condition of patches influence the distribution of populations, this information can be recovered from a snap-shot survey and used to infer the likely spatial dynamics (Hanski et al. 1996). Recent statistical advances enable ecologists to take the probability of detecting a species into account using records from multiple surveys at each site (MacKenzie et al. 2006; Royle 2004). The factors influencing occupancy can therefore be modelled without the hazard of confounding by false absences (Risk et al. 2011).

In this study we examine the likely spatial dynamics of the starred knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape from South Australia. Different gecko species have contrasting spatial dynamics in fragmented landscapes (Hoehn et al. 2007), and a range of dynamics is plausible for *N. stellatus*. *Nephrurus stellatus* is an early successional species, with a peak in abundance approximately five to ten years after fire (Driscoll and Henderson 2008; Driscoll et al. In press; Smith et al. 2012). Fire has been extensively suppressed throughout the agricultural landscape, therefore *N. stellatus* and other early successional species may face a substantial risk of deterministic extinction associated with post-fire succession (Driscoll and Henderson 2008). Some reptiles in our study landscape have declined with increasing distance from large nature reserves, implying that mainland-island metapopulation dynamics (Harrison 1991; Pulliam 1988) may help to sustain populations of some species in remnant vegetation (Schutz and Driscoll 2008; Williams et al. In press). Finally, genetic analyses (A. Smith unpublished data) suggest *N. stellatus* has high dispersal in continuous mallee areas. If they also have high dispersal in the fragmented landscape, patchy populations are likely where a single demographic population occupies many separate habitat patches (Harrison 1991).

To obtain a rapid insight into the possible spatial dynamics of *N. stellatus* in fragmented agricultural landscapes, we asked; to what extent is abundance and occupancy influenced by habitat quality, patch size or patch isolation, after taking into account detection probability? We used three measures of isolation; one to test for a mainland effect, and two assessing the effects of nearby populations (the amount of habitat surrounding a remnant and the distance a patch is from an occupied patch). Using distance from an occupied patch is rarely possible in fragmentation studies, but often provides the best predictions of patch occupancy (Prugh 2009; Prugh et al. 2008).

Answering our research question will contribute to resolving ongoing debate about the relative importance of habitat quality and dispersal limitation. Habitat loss and fragmentation are among the leading causes of biodiversity decline (Millennium Ecosystem Assessment 2005), and is set to have an even larger impact as it interacts with climate change (Driscoll et al. 2011). Developing a body of empirical evidence is essential for understanding which components in a landscape are most important and therefore which can be best targeted to reduce the risk of biodiversity loss.

Methods

Mallee woodlands consist of low (up to 6 m in our study area) multi-stemmed *Eucalyptus* species, predominantly *E. costata* and *E. socialis*, with some native pine *Callitris verrucosa*. The understory is typically dominated by the shrub *Melaleuca uncinata*, with a range of other small shrubs and forbs. The prickly clumping grass spinifex (*Triodia irritans*) is also a dominant feature of the understory at many sites. *Triodia* species are an important habitat element for many reptiles (Driscoll 2004; Pianka 1969). Fires can recur in mallee after 10-15 years, but mallee may remain unburnt for more than a century (Clarke et al. 2010; Haslem et al. 2011). The fauna shows a range of responses to time since fire, spanning a continuum from early to late successional species (Driscoll and Henderson 2008; Kelly et al. 2010; Menkhorst and Bennett 1990). Loss of long unburnt mallee can be particularly detrimental for birds that depend on complex habitat structure and nesting hollows (Brown et al. 2009).

Mallee woodlands have been extensively cleared for agriculture, with most clearing occurring before 1939. Outside of the nature reserve in our study area, 13% of the mallee vegetation remains, predominantly as linear remnants on sand dunes and beside roads (Fig. 1). The dunes are not cleared because crops have low yields on deep sand. The land between the remnant vegetation is ploughed, fertilised, sprayed for weeds and insect pests and sown to cereal crops, most often wheat in two years out of three. On many properties, sheep are later introduced between the harvests to graze the wheat stubble or are grazed on exotic pasture grasses for one year.

The small remnants are adjacent to a large nature reserve (Pinkawillinie Conservation Park, Fig. 1). Large proportions of the reserve in our study area were burnt six years prior to our surveys (burnt in December 2005). *Nephrurus stellatus* was frequently captured during sampling within this 2005 fire area (Driscoll and Henderson 2008; Driscoll et al. In press; Smith et al. 2012), and thus the reserve has the potential to act as a "mainland" source of colonists for the nearby small remnants.

#Figure 1 approximately here#

Nephrurus stellatus is a nocturnal, actively foraging generalist insectivore with an average snout-vent length of 65mm in males and 71 mm in females in our study area (J. Lazzari, unpublished data),. *Nephrurus stellatus* digs burrows in sandy soil where they shelter during the day and on cold nights. Eggs are laid in early summer (November-December) and juveniles emerge in January. They have a well established response to fire, with very low abundance in mallee that has not been burnt for two or three decades. Abundance increases within two years of fire and peaks after 5-10 years (Driscoll and Henderson 2008; Driscoll et al. In press; Smith et al. 2012). Gene flow research in continuous mallee at a scale comparable to our study landscape suggests that *N. stellatus* is a strong disperser (A. L. Smith, unpublished data). We selected *N. stellatus* for study because it is an early successional species and therefore is at risk of decline in the long-unburnt remnants, and because it can be readily surveyed by spotlighting at night, allowing a large number of sites to be surveyed with the resources that we had available.

Survey design

In January and February 2011 (summer), we surveyed 92 sites three times in a landscape of approximately 64 km^2 (Fig. 1). Sites were surveyed at night with two people walking at a constant pace and searching for eye-shine of geckos that was reflected in the beam of headlamps. Survey routes spanned 300-500 m depending on the size of the site. In the first survey period 40 sites were surveyed for 15 min. Subsequently, surveys were standardized at 10 min. Due to constraints on field survey time, a small number of surveys (22 out of 276) were less than 10 minutes, curtailed after the first *N. stellatus* was located. These differences in survey times were accommodated in the analysis (see below). During each survey, we recorded cloud-cover, rainfall and wind as possible detection covariates. Cloud was recorded as clear, overcast or raining. Wind was categorized as calm, light or strong. As an index of temperature, we used the average of the minimum and maximum daily temperature recorded at a nearby meteorological station (Kimba township). We also recorded environmental variables at each site: soil type (loose sand vs sandy clay), and percentage cover of spinifex, leaf litter, bare ground, weeds, tree canopy and ground disturbed by livestock. Percentage cover was estimated using two 5 × 5 m quadrats, one on the dune top and one on the dune slope spaced 25m apart. Schutz and Driscoll

(2008) did not capture any *N. stellatus* in matrix sites in our study region, and Driscoll (2004) only captured two blind snakes in paddocks in a different mallee region. We therefore did not survey the cropped areas because occupancy was expected to be near zero.

Using digital polygons of remnant vegetation in ArcMap version 9.2, we measured the following spatial variables: area, distance to nature reserve, distance to nearest occupied site, proportion of native vegetation within 100 m and proportion of native vegetation within 1000 m. Roadside remnants can extend for several kilometres, making it difficult to obtain a meaningful area estimate. We arbitrarily chose a 1 km strip centred on the survey area as the estimate of area for roadside sites.

Analysis

We used N-mixture models to identify variables influencing detection probability, abundance, and occurrence (Royle 2004). We therefore used two data sets, one using all sites to investigate patterns of presence/absence, and a second using only occupied sites to investigate abundance patterns. Occurrence was modelled using zero-inflated binomial models (MacKenzie et al. 2006). Abundance at each site was modelled as a random effect, assuming a Poisson distribution (Kery et al. 2005; Royle 2004). It is possible to assume a negative binomial distribution, but these can lead to unrealistic predictions so we use only the Poisson models (Kery et al. 2005). The N-mixture model assumes that populations are closed between the repeated surveys. Mark-recapture studies suggest that abundance in *N. stellatus* can vary substantially between monthly trapping sessions, but this varies with year and location (Smith et al. 2012). If this kind of population change occurred in our data set, we expected that Julian date should be a strong predictor of detection probability. However, preliminary analyses revealed no relationship with date, and so the assumption of population closure may reasonably represent the data.

Our model selection procedure began by selecting the best detection model. Preliminary analysis revealed that detection probability was similar on clear and raining nights, so we compared clear/raining with overcast. We also simplified the wind category into two levels: no/light wind and strong wind. We fitted all combinations of main effects for temperature, wind, cloud cover and duration of survey, plus models with all combinations of two-way interactions including main effects of the variables used in interactions. This resulted in 78 models plus the null model, which we ranked according to Akaike's Information Criterion for small samples (AICc: Burnham and Anderson 2002). We used the best detection models (those with a probability of minimizing information loss > 5%) as the null models for site level model selection. The probability that a model minimizes information loss is exp (AICc(min) - AICc(model))/2 (Burnham and Anderson 2002).

Our site-level model selection procedure involved fitting all possible combinations of main effects of seven site-level variables, including 126 combinations: area, nearest occupied site, distance to nature reserve, proportion of native vegetation within 100m (veg100), proportion of native vegetation within 1000m (veg1000), % cover spinifex and soil type. In the presence/absence analysis, there were two best detection models and so 252 models were compared, while in the abundance analysis there was one best detection model and therefore 126 models were ranked according to AICc. We selected the best models as those which minimized information loss with a probability > 5% (Burnham and Anderson 2002). For these best models, we then added all combinations of two-level interactions of the detection covariates in the best models (including main effects) in additional models then ranked the interaction models along with the original 126 (or 252) models. This approach was taken to reduce the number of interaction models that needed to be compared. We used model averaging to estimate parameter values and confidence intervals across models that minimized information loss with a probability > 5%. Models were fitted using the unmarked R library (Fiske et al. 2011), with R 2.12.0 (R Development Core Team 2010).

To determine the scale of spatial autocorrelation for abundance and occupancy, we calculated Moran's I with the correlog function of the pgirmess R library (Giraudoux 2011). We used Sturges' method for selecting the number of bins (Sturges 1926). To illustrate spatial clumping patterns we used Akima's interpolation method with the function interp from the akima R library (Akima et al. 2009) and the linear option.

To understand factors influencing spinifex cover, we fitted nine variables (area, veg100, veg1000, soil type, % cover of litter, bare-ground, weeds, canopy, and disturbed ground) to percentage cover of spinifex. All combinations of main effects were included in a Generalized Linear Model where we assumed a normal distribution of errors and an identity link function. In all models, an approximately linear relationship between residual and fitted values suggested that assuming a normal error distribution was reasonable. Models were ranked by AICc and parameters were estimated by averaging over models that had a probability of minimizing information loss > 5%. Analyses were performed with R library glmulti 1.01 (Calcagno and de Mazancourt 2010).

Results

Nephrurus stellatus occurred at 75 of the 92 survey sites. There were two best detection models in the presence/absence analysis, and these included temperature + cloud cover or temperature + survey duration (Table 1). However, only temperature + cloud cover was included among the best occurrence models (Table 1). The probability of detecting *N. stellatus* increased with air temperature, and was higher if it was overcast rather than clear or raining (Fig. 2A). Taking detection probability into account, three variables appeared in the two best models of occurrence (Table 1, Supplementary Table 1A). The probability that a site was occupied increased with the percentage cover of spinifex (Fig. 2B), declined substantially with increasing distance to the nearest occupied site (Fig 2C), and very slightly increased with increasing distance from the nature reserve (Fig. 2D). The influence of distance to the nearest occupied site (Fig 2C) indicates very high probability of occurrence for sites within approximately 300 m of occupied sites, steeply declining occupancy between 300 and 700 m, and very low chances of occupancy for sites at larger distances from occupied sites. Other environmental and spatial variables were not important in the models including soil type, remnant area, proportion of native vegetation within 100 m and the proportion of native vegetation within 1000 m. In the abundance models (Table 1, Supplementary Table 1B), the probability of detecting individuals was described by a single best model that included temperature + cloud cover (Fig. 2E). When detectability was accounted for, abundance increased with percentage cover of spinifex (Fig. 2F).

#Table 1, Figure 2 approximately here#

Occurrence and abundance were both positively spatially auto-correlated, with significant Moran's I values to 1.74 km (Table 2). The combined influence of spinifex and spatial effects is evident in the interpolation of percent cover of spinifex (Fig. 3). A close association of zero counts of *N. stellatus* with low spinifex cover is apparent. Spatial effects can be seen in the SE of the figure where *N. stellatus* was absent from a site with moderate spinifex cover, but the site was surrounded by sites without spinifex and where *N. stellatus* was absent or in low abundance. The opposite pattern is evident in the north central part of the plot, where *N. stellatus* occurred on a site with low spinifex cover, but was surrounded by occupied sites.

#Table 2, Figure 3 approximately here#

Our analysis of spatial and site level factors that influenced spinifex identified 26 models with a probability of minimizing information loss > 5%, with all nine variables represented in at least one model (Supplementary Table 2A). Model averaging indicated that only three of these had effect sizes that were likely to exceed zero (95% CI did not span zero: Supplementary Table 2B), including soil type (sand estimate = 8.33 ± 5.3), and the percent cover of weeds (-0.27 ± 0.08) and canopy (-0.21 ± 0.11).

Discussion

A combination of deterministic and dispersal-limited processes most likely explains the pattern of patch occupancy in *Nephrurus stellatus*. This combination means it is possible that patchy populations, mainland-island, deterministic and possibly classic metapopulations (Hanski 1998; Harrison 1991; Thomas 1994) all could operate within the same landscape simultaneously, as first emphasised by Hill et al (1996) for butterflies. In *N. stellatus*, patchy populations seem likely at small spatial scales in fragmented landscapes. The relationship between probability of occupancy and distance to the nearest occupied site suggests there may be very high dispersal up to 300 m (Fig. 2C). Such high dispersal means that single demographic populations may exist across groups of remnants if the remnants are close enough, consistent with the patchy populations concept (Harrison 1991). This high dispersal may also drive small-scale source-sink dynamics (Pulliam 1988), where *N. stellatus* occur in sites with low spinifex cover due to frequent immigration.

At distances beyond 300 m, the influence of nearby occupied sites diminishes, although the spatial autocorrelation implies that there may be a dispersal effect to 1.74 km. Within this range of patch spacing, metapopulation dynamics are possible, with some evidence that such dynamics could be deterministically driven by changes in spinifex cover, a point we return to below. Stochastic extinctions cannot be ruled out and therefore classic metapopulation dynamics are possible. In contrast, in mallee patches that are isolated by more than approximately 1 km (Fig. 2C) or 2 km (Table 2), dispersal likely plays no substantial role in patch occupancy. Local extinctions, either deterministic or stochastic, could therefore result in non-equilibrium populations as *N. stellatus* declines from the landscape.

Our findings emphasise that the type of spatial dynamics depends on the spatial scale of dispersal relative to the scale of habitat patchiness (Ovaskainen and Hanski 2004). This can result in a sequence of spatial dynamics across an isolation gradient. For example, Florida scrub lizards *Sceloporus woodi* show the same continuum as we suggest applies to *N. stellatus*, but at a smaller spatial scale (Hokit et al. 2010; Hokit et al. 1999). *Sceloporus woodi* have patchy populations and source-sink dynamics at a scale of tens of meters, metapopulations at intermediate scales and declining non-equilibrium populations when patches are separated by more than 750 m (Hokit et al. 2010; Hokit et al. 1999). Patchy populations among nearby sites grading into metapopulations in more widely spaced sites have also been reported for other animal taxa (Harrison and Taylor 1997; Sutcliffe et al. 1997; Werner et al. 2009). In contrast, open glades required by collared lizards *Crotaphytus collaris* are typically further apart than the distance that most collared lizards can disperse (Templeton et al. 2011). Collared lizards therefore do not have an opportunity to develop patchy populations, even though their dispersal distances may be similar to or longer than dispersal by *N. stellatus*.

Our inferences about dispersal assume that there is not some other cause of increased extinction with increasing isolation. Higher predation or competition is possible in more isolated patches, although increasing and decreasing responses have been reported previously. For example, with increasing isolation, there have been declines of water-fowl predation by mammals (Zoellick et al. 2004) and declines of dominant invertebrate species including predators (Davies et al. 2000; Driscoll et al. 2010). In contrast, predators of reptiles increased with proximity to housing developments (and presumably increasing habitat isolation) (Audsley et al. 2006). Further, Dunstan and Fox (2006) reported higher rat abundance in more isolated rainforest remnants. Introduced rats are predators of reptiles (Hoare et al. 2007b; Towns et al. 2007). Nevertheless, reports of increased predation with increased isolation are rare, and thus dispersal limitation seems a more likely explanation. However, the predation hypothesis cannot be dismissed and warrants further examination.

Some landscape features which we expected might be important had little or no influence on abundance or occupancy. There was no evidence that the large nature reserve acted as a mainland source for colonising remnant islands of mallee. Landscapes with a mainland-island structure can, but do not always have species that exhibit mainland-island metapopulation dynamics (Banks et al. 2005; Driscoll 2008). Our study suggests the lack of mainland effect can arise when dispersal is limited relative to the distance between mainland and island patches. The weak negative relationship with distance from the nature reserve likely arose from the high proportion of sites without spinifex that happen to also be near to the nature reserve (Fig. 3).

Patch area did not have a strong effect on patch occupancy, which is surprising given the important role of patch size in island biogeography and metapopulation theory (Hanski 1998; MacArthur and Wilson 1967), and in many empirical fragmentation studies that report area effects (e.g. Driscoll 2004; Hokit et al. 1999; Templeton et al. 2011). This may be related to poor estimation of patch size (Moilanen 2002); canopy cover may not correspond well with suitable habitat given the evidence that a spinifex understory is important. High dispersal (within 300m) could also mask area effects (Debinski and Holt 2000). Reviews acknowledge that many species are influenced by patch size, but emphasise that such effects are either weak (Prugh et al. 2008) or often absent (Debinski and Holt 2000). The lack of an area effect on *N. stellatus* in this study emphasises that patch area (measured as native vegetation extent) may not correspond with population size and therefore does not correspond with extinction risk.

In addition to spatial influences on *N. stellatus*, habitat quality influenced abundance and occupancy. Changes in spinifex cover have the potential to drive deterministic metapopulation dynamics (Thomas et al. 2001), for patches in the metapopulation 'goldilocks' zone (some dispersal, but not too much dispersal). For *N. stellatus*, we suggest this zone could be when patches are spaced between 300 m and one or two kilometres. In continuous mallee in nature reserves, we have not previously found a relationship between spinifex and *N. stellatus* (Driscoll et al. In press). The association of *N. stellatus* with spinifex in our study landscape may arise in response to livestock grazing impacts (Driscoll 2004), a pressure which is absent from the nature reserves. The precise mechanism requires investigation but could relate directly to avoided trampling, or to indirect effects associated with the thermal environment, food resources or predation avoidance (Daly et al. 2008). Shade is likely to be lower (Brown 2001), the invertebrate community different (Driscoll and Weir 2005) and predation pressure higher (Castellano and Valone 2006) in the agricultural remnants compared with the nature reserves (although for an alternative predation response to increased grazing see Hoare et al. 2007a).

With spinifex providing an important habitat element in the fragmented landscape, factors that might drive its loss are of conservation interest. Spinifex was negatively correlated with weed cover but positively correlated with loss of canopy cover. Spinifex can out-compete woody plants on sand dunes, so reduced canopy cover may be driven by spinifex expansion, and not vice versa (Nano and Clarke 2010). Invasive agricultural weeds such as *Brassica tournefortii*, the salt-accumulating *Mesembryanthemum crystallinum*, and the fire-promoting grass *Pennisetum setaceum* may compete with spinifex, particularly in the modified agricultural environment that is subject to fertilizer and insecticide spray drift. Spinifex may also be reduced by cattle grazing, and fire followed by heavy grazing (Driscoll et al. In press; Letnic 2004).

Without population turnover data we do not know at what rate the inferred spatial dynamics might occur. Given the association of *N. stellatus* with soil type, and the low cover of spinifex on clay soils, we expect that some remnant patches of mallee may never offer suitable habitat; there is likely to be a static component to patch occupancy. Population turnover that is linked to spinifex loss and recovery may take place over six or more years (Caughley 1985). Long term occupancy data and dispersal studies are needed to provide direct evidence.

Management

Given the long term exclusion of fire from most of the remnants, we feared that early successional species may be rare throughout the landscape (Driscoll et al. In press; Teasdale et al. in review) but this was not the case for *N. stellatus*. Although speculative, disturbance by livestock and edge effects including wind erosion could maintain conditions that are similar to the post fire landscape. A possible analogous case was reported by Blevins and With (2011), where collared lizards (*C. collaris*) occurred more often in burnt sites, or, if fire was absent, in sites grazed by bison. Changes to the environment that advantage this early successional species may also disadvantage late successional species (e.g. *Ctenotus schomburgkii*,Caughley 1985; Williams et al. In press). Burning small remnants would further disadvantage late successional species but would not have the expected benefits for some early successional species. That is, normal cycles of fire may have perverse outcomes when they interact with disturbance.

While introducing fire may not benefit *N. stellatus* and could disadvantage other species, fire exclusion may not be appropriate either. Our knowledge of faunal succession in intact landscapes implies that fire exclusion is unlikely to be an ecologically sustainable management approach (Driscoll and Henderson 2008). Further, Williams et al (In press) reported that another early successional species (*Ctenophorus fordi*) was absent from linear remnants in our study region, suggesting that not all early successional species benefit from the disturbed environment in the way that *N. stellatus* does. Restoration in these landscapes is therefore likely to require more than the reintroduction of fire (Perry et al. 2009). Restoration is likely to require improvements to vegetation condition and connectivity, and it is likely that these two approaches will need to be implemented before fire can be reintroduced without the risk of perverse outcomes.

Key components of restoring vegetation condition will be to minimize weed invasion and spinifex loss, actions that would benefit *N. stellatus*, and many other species that use spinifex (Driscoll et al. In press; Kelly et al. 2010). For enhancing landscape connectivity, management should keep all remnant native vegetation and re-establish native vegetation in cleared areas. While stepping stones at < 300 m spacing would benefit *N. stellatus*, many other species need direct habitat connections (Driscoll 2004; Driscoll and Weir 2005). Achieving revegetation in these landscapes at a large scale is becoming possible with the development of whole of paddock approaches to restoration (McDonald and Williams 2009) and with new legislation in Australia that will fund large scale revegetation from carbon tax revenue.

Conclusion

Our research adds a valuable new example of dispersal and habitat limitation in a poorly studied taxon (reptiles, McGarigal and Cushman 2002) and using a measure of isolation that is rarely reported in the fragmentation literature (the distance to the nearest occupied patch, Prugh 2009; Prugh et al. 2008). Taking into account detectability, we found that the gecko *Nephrurus stellatus* does not exhibit evidence of mainland-island metapopulation dynamics, despite the proximity of a large nature reserve to remnant woodland patches, probably due to limited dispersal. Patterns of occupancy in *N. stellatus* suggest that a spectrum of spatial dynamics occur, depending on patch isolation, including small-scale source-sink dynamics, patchy populations, declining non-equilibrium populations, deterministic metapopulations and possibly classic metapopulations (Harrison 1991; Thomas 1994). This range of inferred dynamics spans a spatial scale of patch isolation from patchy populations at approximately 300 m to declining populations in patches isolated by one or two kilometres. Other examples from the literature suggest that it may be common for dispersal limited species to exhibit a sequence of spatial dynamics across an isolation gradient (Harrison and Taylor 1997; Hokit et al. 2010; Hokit et al. 1999; Sutcliffe et al. 1997; Templeton et al. 2011; Werner et al. 2009).

Landscape restoration to improve the condition and increase the amount and proximity of native vegetation would benefit *N. stellatus* and many other species in the extensively cleared agricultural landscape (and in most intensive-use landscapes globally, Hobbs and Harris 2001; Saunders et al. 1993). It is possible that such restoration needs to take place first, before fire can be reintroduced to these landscapes. Without restoration, fire may interact with disturbance to disadvantage many species and advantage few (Keeley 2006). Integrating a range of approaches to restoration will often be important for achieving conservation outcomes in landscapes where multiple ecosystem processes have been altered (Noss et al. 2006).

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Table 1. The best presence/absence (p/a) and abundance models for detection only, then detection and occurrence or abundance. Neg Log-Like = negative log likelihood, nPars = number of parameters, n = number of sites, Rsq = R squared, AICc = Akaiki Information Criterion for small samples, ΔAICc = change in AICc.

Model type	Best detection model	Best occurrence/abundance model	Neg Log-Like	nPars	n	Rsq	AICc	ΔAICc
p/a, detection only	~temp+ cloud	~ 1	168.7	4	92	0.26	365.2	0.0
p/a, detection only	~temp + duration	~1	169.3	4	92	0.25	366.5	1.3
p/a, detect + occurrence	~temp+ cloud	~ nearest_occupied + spinifex	157.0	6	92	0.23	352.9	0.00
p/a, detect + occurrence	~temp+ cloud	~ nearest_occupied + Dist_to_NR + spinifex	154.9	7	92	0.27	354.5	1.58
abund., detection only	~temp+ cloud	~ 1	334.9	4	75	0.80	726.2	0.00
abund., detect + abundance	~temp+ cloud	~spinifex	328.5	5	75	0.16	724.9	0.00
abund., detect + abundance	~temp+ cloud	~ 1	334.9	4	75	0.00	726.2	1.30

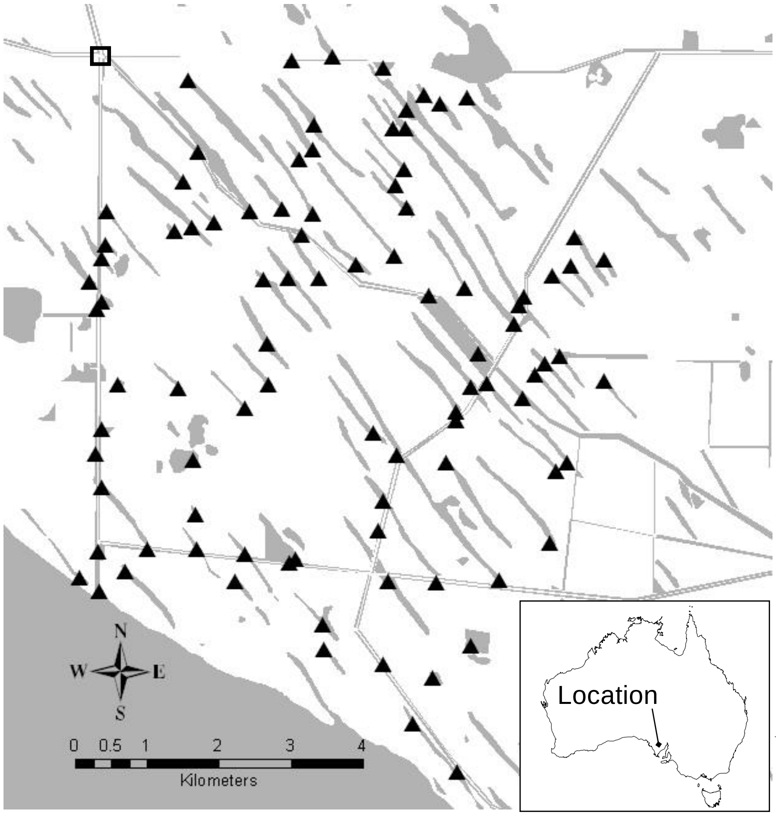
Table 2 Moran's I, P value and number of pair-wise distances (n) based on presence/absence data and abundance data (with zeros excluded)

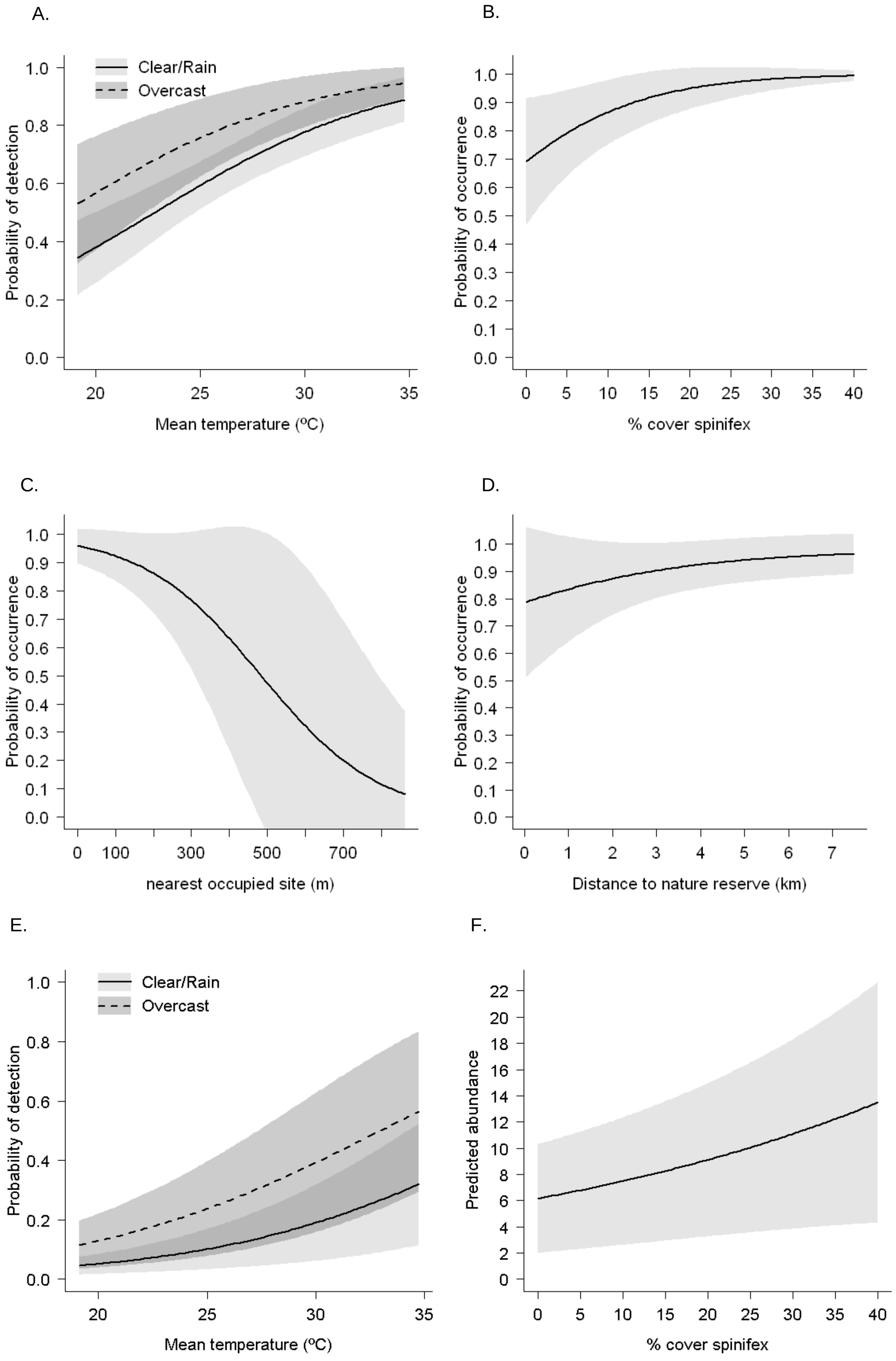
Distance	Presence/Absence			Abundance		
class (km)	Moran's I	P	n	Moran's I	P	n
0.42	0.30	0.001	242	0.14	0.086	184
1.08	0.17	0.003	506	0.08	0.115	348
1.74	0.10	0.018	770	0.10	0.041	544
2.40	-0.07	0.877	836	0.07	0.085	586
3.06	-0.05	0.787	980	-0.03	0.614	696
3.72	0.00	0.364	1002	-0.04	0.722	736
4.38	-0.05	0.831	976	-0.11	0.959	632
5.04	-0.04	0.724	930	-0.16	0.997	616
5.69	-0.05	0.738	748	-0.07	0.780	456
6.35	-0.12	0.943	582	-0.05	0.655	316
7.01	-0.04	0.617	394	-0.16	0.916	192
7.67	-0.23	0.979	272	0.04	0.225	156
8.33	-0.18	0.870	114	-0.19	0.855	70
8.99	-0.11	0.500	20	0.04	0.203	18

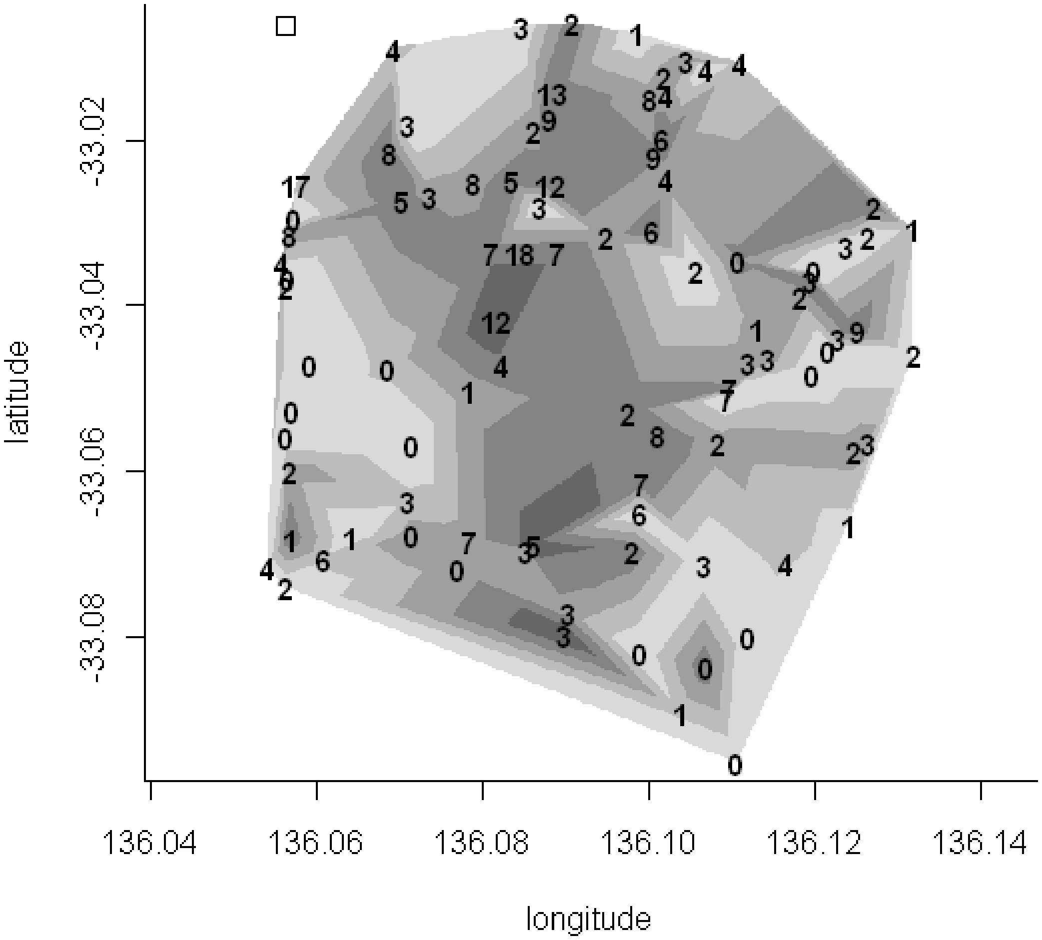
Figure 1. Location and spatial arrangement of sample sites (triangles) and remnant vegetation (grey) that remain in a wheat and sheep farming matrix (white) on the Eyre Peninsula, South Australia. The large block of remnant vegetation in the SW is a part of Pinkawillinie Conservation Park. The hollow square in the NW is a geographic reference point: latitude -33.006193, longitude 136.056295.

Figure 2. Weather-related factors influencing detection probability using occurrence (A) or abundance (E) data, and the environmental and spatial variables influencing occurrence (B-D) or abundance (F) of *Nephrurus stellatus*. Records of cloudiness were divided into two categories; (1) overcast, (2) clear or raining.

Figure 3. The abundance of *Nephrurus stellatus* (indicated by the numbers) overlying a spatial interpolation of the percent cover of spinifex. Grey scale grades from light (spinifex absent) to dark (spinifex cover 40%). The hollow square in the NW is the same geographic reference point as in Fig. 1.


N
W
E
S
0
0.5
1
2
3
4
Kilometers
Location


A.
Clear/Rain
Overcast
Probability of detection
0.0
0.2
0.4
0.6
0.8
1.0
20
25
30
35
Mean temperature (ºC)
B.
Probability of occurrence
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
5
10
15
20
25
30
35
40
% cover spinifex
C.
Probability of occurrence
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
100
300
500
700
nearest occupied site (m)
D.
Probability of occurrence
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
1
2
3
4
5
6
7
Distance to nature reserve (km)
E.
Clear/Rain
Overcast
Probability of detection
0.0
0.2
0.4
0.6
0.8
1.0
20
25
30
35
Mean temperature (ºC)
F.
Predicted abundance
0
2
4
6
8
10
12
14
16
18
20
22
0
5
10
15
20
25
30
35
40
% cover spinifex


latitude
-33.02
-33.04
-33.06
-33.08
136.04
136.06
136.08
136.10
136.12
136.14
longitude

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