



Habitat loss, fragmentation and degradation effects on small mammals: Analysis with conditional inference tree statistical modelling



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ABSTRACT

Anthropogenic habitat loss, fragmentation and degradation often co-occur in a landscape and their relative influence on a native animals' health and survival can be difficult to determine. We examined the influence of these environmental variables on the estimated relative abundance of some small mammal species in a large area (~2500 km²) of southeastern Australia. Using the agile antechinus (*Antechinus agilis*) as a model, we also examined the association between these variables and three population performance indices, mass-size residuals (MSR; indexing fat reserves), the neutrophil/lymphocyte ratio (N:L; indexing physiological stress) and red blood cell counts (RBC; indexing regenerative anaemia). Study sites were in either highly disturbed and fragmented, or relatively undisturbed, continuous *Eucalyptus* forest.

We generated conditional inference tree statistical models to identify the relative importance of up to 49 ecological variables in explaining variation in small mammal abundance and performance indices. Habitat loss was important in explaining small mammal abundance, as were the abundances of the same species in neighbouring study sites. The models also suggested that the habitat area required to support a 'healthy' population was greater in the larger species examined. Autocovariates of neighbouring site same-species abundances and habitat fragmentation were the next most important influences on small mammal relative abundance, implying that metapopulations may be important for population persistence, especially in bush rats (*Rattus fuscipes*). Habitat degradation, reflected in structural and floristic features, was less important, but explained some variance in relative abundances. For agile antechinus populations, time of year, degree of forest fragmentation and extent of native tree cover were important in explaining performance indices. Results indicated that habitat reduction *per se* was a significant threatening process for small mammals. Habitat loss requires at least the same research attention as that currently devoted to anthropogenic habitat fragmentation and degradation.

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1. Introduction

Studies of vertebrate conservation are largely concerned with the effects of anthropogenic habitat loss, fragmentation and degradation on native biota. Substantial evidence indicates that anthropogenic habitat fragmentation negatively affects terrestrial vertebrate assemblages and populations (Andr en, 1994). Fewer studies have examined the effects of anthropogenic habitat degradation, and habitat loss *per se* has received the least research attention (Fazey et al., 2005), despite a general consensus that it is probably the world's leading cause of native species' decline (Fahrig, 1997; Foley et al., 2005). One underlying difficulty is that habitat loss, fragmentation and degradation often co-occur in a

landscape, and thus their independent effects can be difficult to isolate (Fischer and Lindenmayer, 2007).

Vertebrate conservation studies in anthropogenically-disturbed landscapes are typically concerned with comparing a population response variable (e.g. site occupancy or abundance) or performance indices (such as brood size or level of physiological stress) (Fletcher et al., 2007) with multiple environmental variables in order to identify possible relationships. Survivorship and reproduction are products of complex interactions of an animal's genome, behaviour, physiology and autecology. Demographic studies can be informative about whether a population is declining or at risk, but to understand why a population is declining functional studies must be undertaken and they must involve a whole-organism consideration of behaviour, physiology and genetics. This functional approach has been advocated and discussed by several authors (Homyack, 2010; Janin et al., 2011). Such performance measurements can be useful as conservation tools. For example, because

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physiological stress can, in some situations, deterministically reduce reproductive output and survivorship, elevated physiological stress must always be considered at least a potential early warning sign, even if populations appear to be stable. Stress measurements can sometimes be used to index features of autecology that might not be easy to measure, such as parasite loads (Martínez-de La Puente et al., 2011) or food availability (Herring et al., 2011). However, these performance-ecological relationships may well be species-specific (Johnstone et al., 2012b) and for them to be useful more work is needed to ascertain if there are generalisable relationships or if each endangered vertebrate species would need to be studied independently. The tendency in small mammal research has been to examine metrics of population distribution or demography, whilst not considering other features of the animal's relationship with its environment. Behavioural studies of small mammals are sometimes conducted (e.g. Banks and Dickman, 2000; Cockburn and Lazenby-Cohen, 1992; Dickman, 1986) that are informative about a species' use of environment and its relationship with other species. However, physiological ecology is perhaps less well studied in mammals than is behaviour, and certainly much less focus has been given to mammal ecophysiology than bird ecophysiology. Here, for one of the small mammal species studied, we examined (a) indices of physiological stress, which may be both indicative of, and contributing to, decline of free-living vertebrates in degraded or fragmented habitats (Johnstone et al., 2012a; Martínez-Mota et al., 2007; Suorsa et al., 2004); and (b) body condition indices, which can be informative about metabolic reserves in individual animals (Peig and Green, 2009; Schulte-Hostedde et al., 2005).

Experimental field manipulations are useful for testing potential animal-environment relationships (Mac Nally and Horrocks, 2002), but are not always feasible because of cost or ethical considerations (studying habitat loss through large-scale experimental habitat removal would be contentious, to say the least; (Diamond, 1983). Consequently, most large-scale studies use a naturally-occurring experimental design (a natural experiment *sensu* Diamond, 1986). However, there may be multiple, correlated, environmental factors that influence a population, and factors may interact, have synergistic effects or partially negate one another (Laurance and Cochrane, 2001). The variables measured or indexed may be continuous, ordinal or nominal (or a mixture of these) and data may be non-linear or non-normally distributed. Linear regression approaches must be modified using non-Gaussian distributions and/or non-linear equations in order to characterise these sorts of data (Zuur et al., 2007), whereas conditional inference tree models can represent non-linear relationships with relative ease. For example, a conditional inference tree will model a U-shaped or J-shaped curve if such a relationship exists, whereas such curves are impossible to model using standard general linear or additive models and require careful use of non-linear link functions for generalised linear or additive models. A conditional inference tree could furthermore easily represent a complex wave-like relationship with multiple peaks that would not easily be represented by a mathematical equation. Such relationships are either absolutely outside the realm of general or generalised linear/additive models or so complex as to be effectively so. A further advantage of conditional inference tree model approaches is that they are the first step towards a random forests analysis. Random forests analysis is a powerful, predictive, model-averaging approach, where random bootstrapped samples of predictor variables are used to general a 'forest' of models, and from this forest the relative importance of predictor variables can be calculated. Random forests analyses are being increasingly applied when exploring complex relationships in ecology (Cutler et al., 2007; Prasad et al., 2006) and genetics (Bureau et al., 2005). Random forests approaches tend to outperform other modelling techniques for predicting known

relationships. Lawler et al. (2006) found that a random forests approach consistently outperformed generalised linear models, generalised additive models, artificial neural networks and genetic algorithms for rule-set prediction for predicting actual species presence or absence. The authors further reported that a random forests approach allowed for better prediction of species presence or absence than just relying on the single best conditional inference tree model.

Conditional inference tree modelling is an intuitive, easily implemented and interpreted statistical method that copes well with complex data, but it is underused in ecology. It is a tool for examining the relationship between a single response variable and multiple potentially explanatory variables (Quinn and Keough, 2002; Zuur et al., 2007). Such models are popular in medical and genetic research, probably because they tend to be better at predicting known relationships from data than more commonly used methods, such as logistic regression (Nagy et al., 2010). The models produced are predictive and robust to non-linearity, non-normality, multicollinearity and multiple interactions among explanatory variables (Quinn and Keough, 2002; Zuur et al., 2007). From a conservation management perspective, conditional inference tree models are useful because they generate decision trees. By using conditional inference tree models, clear decision paths can be used to determine, for example, how much habitat in a given area would correlate with a given mean response variable, be this species richness, occupancy, abundance or performance metrics. We used conditional inference tree models to investigate the relative roles of habitat loss, fragmentation and degradation and other environmental variables in determining the relative abundance or performance indices of three native Australian small mammal species common to modified forests in south-eastern Australia.

2. Materials and methods

2.1. Defining habitat fragmentation, degradation and loss

Here we define habitat loss as the complete removal of native canopy cover. In the area studied, habitat loss was usually the result of agriculture, and in particular the creation of open fields for grazing domestic stock. The native small mammals studied are not thought to make extensive use of open fields, and there are no reports of these species being caught at high numbers in open fields. It remains possible of course that individuals may make exploratory incursions into fields or move across fields between habitat patches, but once tree-cover is removed the landscape no longer has the foraging patches or nest sites that would be required for persistence of a population.

Habitat fragmentation was defined as any separation of habitat (contiguous native tree-cover) by matrix where the separation distance was >20 m from the edge of the canopy (not tree-trunks) to the nearest canopy. A researcher walked around the perimeter of all fragments used in the study (i.e. those that were <300 ha in size) and measured canopy gaps. Potential corridors were also noted and recorded, but they were discarded from the analysis, as indices derived from number of corridors per fragment and apparent corridor quality did not help to explain variation in any of the small mammal population metrics measured.

Habitat degradation is harder to define than habitat loss or fragmentation. The reason is that in order to know precisely what constitutes degradation of habitat for a given species, all aspects of the species' ecology must be known. For the species in this study, we considered degradation to comprise windfall at forest edges, livestock grazing in forest, firewood collection, recreational trail-bike riding and invasion of a forest by non-native plants and animals.

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