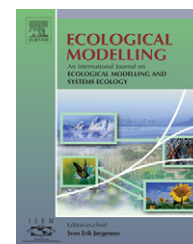


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# Identifying mechanistic models of spatial behaviour using pattern-based modelling: An example from lizard home ranges

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## ABSTRACT

Landscape and population level patterns form through the aggregation of responses of individual organisms to heterogeneity. Spatial organisation within a population can range from random overlap of individual home ranges, to completely exclusive territories, with most populations falling somewhere between these two extremes. A fundamental question in behavioural ecology concerns the factors that influence the degree of spatial overlap of home ranges, and the processes that determine how likely it is that an individual will access resources over its home range. However, traditional experimental methods are not always practical or possible. Pattern-based modelling is an alternative, non-intrusive technique for explaining observed patterns. We explored behavioral mechanisms for home range overlap in a Scincid lizard, *Tiliqua rugosa*, by constructing a spatially explicit individual based model. We tested two mechanisms, one that used refuge sites randomly and one that included a behavioural component. The random use model, the fixed total range model, incorporated all refuge sites within a circle of radius  $h$ . The behavioural model, the variable total range model, probabilistically incorporated refuge sites based on nearest neighbour distances and use by conspecifics. Comparisons between the simulated patterns and the observed patterns of range overlap provided evidence that the variable total range model was a better approximation of lizard space use than the fixed total range model. Pattern-based modelling showed substantial promise as a means for identifying behavioral mechanisms underlying observed patterns.

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## 1. Introduction

Landscape and population level patterns form through the aggregation of responses of individual organisms to heterogeneity. In general, when making broad predictions, we assume that small-scale responses can be characterized through their asymptotic properties, such as the mean and

variance. However, if there is evidence that a simple representation of the small scale process is incorrect, then we need to develop biologically more sophisticated models faithful to the small scale process to reproduce the larger scale patterns. For example, the distribution of home ranges may be controlled by spatial constraints or by small scale interactions with conspecifics. This paper examines the effect of different small

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scale biological processes on the generation of the pattern of home range overlap and refuge use of the Australian sleepy lizards, *Tiliqua rugosa* using “pattern-based modelling” (Grimm et al., 1996, 2005; Wiegand et al., 2003).

Spatial organisation within a population can range from random overlap of individual home ranges, to completely exclusive territories, with most populations falling somewhere between these two extremes. A fundamental question in behavioral ecology concerns the factors that influence the degree of spatial overlap of home ranges, and the processes that determine how likely it is that an individual will access resources over its home range. There are two traditional ways that have been used to address these questions. One method has been to compare observations made at different times or places with variable levels of one or more factors that might influence the process. Thus, when we compare among surveys, if higher population densities are associated with greater home range overlap, we might deduce that density related interactions have an important role. A second method has been to conduct experimental manipulations, for instance of population density, to investigate the importance of the manipulated factor. However, these traditional methods are not always available, or are sometimes logistically difficult to achieve, for instance among large vertebrates with small populations. When a simple experiment is the object of prediction, for example, comparing trap selection by female *Drosophila* (Stamps et al., 2005), then it is often possible to exactly calculate the likelihood of an observation under different mechanistic models and use the powerful methods developed for comparison of likelihoods (Burnham and Anderson, 1998). However, when the patterns and mechanisms are complex and/or measured at large spatial and temporal scales, such as range overlaps among troops of chimpanzees (Lehmann and Boesch, 2003), then calculating the likelihood becomes difficult or impossible.

Pattern-based modelling is an alternative, non-intrusive technique, that can explore existing hypotheses, identify models that are not realistic representations of the biological processes, and indicate directions that more detailed observation or experimentation should focus on (Grimm et al., 1996, 2005; Wiegand et al., 2003). The pattern-based modelling approach appears to work even with “weak” patterns that can be produced by many different possible mechanisms. By combining several weak patterns, strong inferences about model parameters and structure can be generated (Grimm et al., 1996, 2005). For instance, pattern-based modelling has been used to identify demographic and movement parameters in invading species from genetic data (Estoup et al., 2004).

Pattern-based modelling begins by identifying and quantifying biological patterns, essentially any non-random relationship in the data. A mechanistic model with a specific set of parameters can then simulate the same type of data, and the generated pattern can be compared with the empirically observed pattern. Multiple simulations can be generated using a range of values for each of the model parameters. The closer the fit of the model to the empirically derived pattern, the more realistic the assumptions of the model are assumed to be. Pattern-based modelling allows insights into which of a large number of alternative parameter values most closely resembles the real biological situation. In addition, the pat-

terns generated from a series of structurally different models can be included in the comparison, providing a decision criterion on the degree of model complexity that is sufficient to capture the relevant ecology. Close resemblance between reality and model outputs does not, of course, imply the model is correct, but lack of resemblance would be stronger evidence against a model. Like all model selection procedures (e.g. information theoretic methods Burnham and Anderson, 1998) pattern-based modelling cannot determine if an alternative model structure that has not been considered, would do better.

The pattern of home range overlap and refuge use of the Australian sleepy lizard (*Tiliqua rugosa*) influences the population dynamics of its ticks (Bull, 1978), and is an example where small scale processes influencing the opportunities for survival and transmission of parasites can have broader influence on the larger scale populations of both host and parasite. In South Australia, sleepy lizards are active during the day time, but will generally seek a shelter refuge for the night (Kerr et al., 2003). They also use those refuges during the day when temperatures are too cold or too hot for normal activity. For lizards in this habitat, refuges include bushes, hollow logs, large tussocks of grass, and burrows dug by rabbits or wombats (Kerr et al., 2003). The number of days before a refuge site is revisited by a lizard is critical for tick population dynamics, because ticks wait in lizard refuges to find new hosts, and their survival decreases with increased time spent waiting. Thus, the distribution of return times to refuge sites influences the transmission rates of parasites between host individuals. Recent observations have suggested that not all potential refuge sites are equally likely to be used by lizards (Kerr et al., 2003), and that there is significant internal structure in the home ranges of sleepy lizards (Kerr and Bull, 2006a). Lizards maintain core areas around high quality refuge sites that are rarely entered by conspecifics of the same sex. High quality refuges are large bushes with foliage in contact with the ground that are highly efficient in protecting lizards against high temperatures (Kerr et al., 2003).

In this paper, we combined these observations to identify a model of lizard refuge use that reproduces patterns of home range internal structure and overlap, and can be incorporated into individual based models of lizard and tick dynamics. We used pattern-based modelling to compare simulated lizard behaviours with observed consequences of lizard behaviour. Our results suggested that local constraints in refuge choices by individual lizards (identified by a minimum nearest neighbor distance) were critical in generating the pattern of home range overlap. In contrast, interactions with conspecifics appeared to weakly influence this pattern. Although we used a specific lizard social system, the broad principle we illustrate is that fine scale detail of the behaviour and ecology of a species can be incorporated into models to provide deeper insights and greater predictive power.

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## 2. Methods

This paper aimed to explore behavioral mechanisms that might generate observed spatial patterns of home range overlap. Sleepy lizards form monogamous partnerships and share

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