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Andrew J. Tyre

University of Nebraska at Lincoln, atyre2@unl.edu

Gregory D. Kerr

Flinders University of South Australia

Brigitte Tenhumberg

University of Nebraska - Lincoln, btenhumberg2@unl.edu

C. Michael Bull

Flinders University of South Australia, michael.bull@flinders.edu.au

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Identifying mechanistic models of spatial behavior using pattern-based modeling: An example from lizard home ranges

Andrew Tyre,¹ Gregory D. Kerr,² Brigitte Tenhumberg,³ and C. Michael Bull²

1. School of Natural Resources, University of Nebraska–Lincoln, 416 Hardin Hall, Lincoln, NE 68583-0974, USA

2. School of Biological Sciences, Flinders University of South Australia, GPO 2100 Adelaide, SA 5001, Australia

3. School of Biological Sciences, University of Nebraska–Lincoln, Lincoln NE 68583, USA

Corresponding author – A. Tyre, tel 402 472-4054, fax 402 472-2946, email atyre2@unl.edu

Abstract

Landscape and population level patterns form through the aggregation of responses of individual organisms to heterogeneity. Spatial organization 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. However, traditional experimental methods are not always practical or possible. Pattern-based modeling 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 behavioral component. The random use model, the fixed total range model, incorporated all refuge sites within a circle of radius h . The behavioral model, the variable total range model, probabilistically incorporated refuge sites based on nearest neighbor 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 modeling showed substantial promise as a means for identifying behavioral mechanisms underlying observed patterns.

Keywords: pattern based modeling, home range analysis, space use

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 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 modeling” (Grimm et al., 1996, 2005; Wiegand et al., 2003).

Spatial organization 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 modeling 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 modeling 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 modeling has been used to identify demographic and movement parameters in invading species from genetic data (Estoup et al., 2004).

Pattern-based modeling 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 modeling allows insights into which of a large number of alternative parameter values most closely resembles the real biological situation. In addition, the patterns generated from a series of structurally different models can be included in the comparison, providing a decision cri-

terion 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 modeling 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 modeling to compare simulated lizard behaviors with observed consequences of lizard behavior. 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 behavior and ecology of a species can be incorporated into models to provide deeper insights and greater predictive power.

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 home ranges and refuges over much of the spring season

when they are most active (Bull, 1988; Bull et al., 1998). Males overlapped extensively with other males in their total home ranges, but overlapped little or not at all with other males in their core areas (Kerr, 2005). These core areas are closely associated with refuge sites. In this paper we restricted our focus to observations of male–male overlap. We derived the spatial organization of male lizards in a number of simulations based on various rules of refuge site use, and then compared those simulated results with the empirically observed pattern. The basis for this study was that the set of model conditions that generated patterns closest to reality, might give important insights into the biological processes in the population. In our simulations we considered two classes of models. In the first, a lizard occupied a home range with a number of overnight refuge sites, and selected those refuges at random each night. In the second, spatial constraints and interactions with other conspecific males influenced refuge site use.

2.1. The patterns

The empirical data used in this analysis were derived from a study of movement patterns of radio-tagged sleepy lizards in a 1.5 km² area of homogeneous chenopod shrubland composed predominantly of the blue-bush (*Maireana sedifolia*) at the Bunday Bore study site north of Mt. Mary, SA (33°55'S, 139°21'E) (Kerr et al., 2003, 2004b; Kerr and Bull, 2004a, 2004b). In each of four years (2000–2003) each of 30–50 lizards was located on usually four days a week throughout the four-month period of maximum lizard activity (September–December). All permanent resident lizards within the study area were included in the analysis, and each lizard was located at least 20 times, but usually over 60 times in a year. Each lizard total home range included many potential refuge sites, and individual lizards were observed using between 1 and 56 (median = 16) overnight refuges within this home range over a season. Ranges were determined using hierarchical incremental cluster polygons (ICP) (Kenward, 2001). The mean range area, estimated from the ICP core area containing 90% of observations, was 14426 m² (95% CI [12 850, 16 001], $n = 88$) in climatically normal years. In a year of exceptionally low rainfall (2002) activity was diminished (Kerr et al., 2004a; Kerr and Bull, 2006b), and ranges were smaller (Kerr and Bull, 2006a).

Kerr and Bull (2006a) used hierarchical cluster analysis in Ranges6 (Kenward et al., 2003), to identify multi-nucleate core areas (Kenward, 2001; Kenward et al., 2001) within lizard ranges. This analysis sequentially adds locations that are closest to locations already included, leading to clusters of locations in areas most commonly used within the home range. A single large cluster of locations generally formed when 90–100% of all location fixes of a lizard were included in the analysis. As the proportion of available fixes used was reduced the range fragmented into a series of smaller clusters (Figure 1), which were interpreted as core areas (*sensu* Samuel et al., 1985) within the home range.

2.2. Pattern analysis

In this paper we derived home ranges from simulated lizard locations using hierarchical cluster analysis implemented

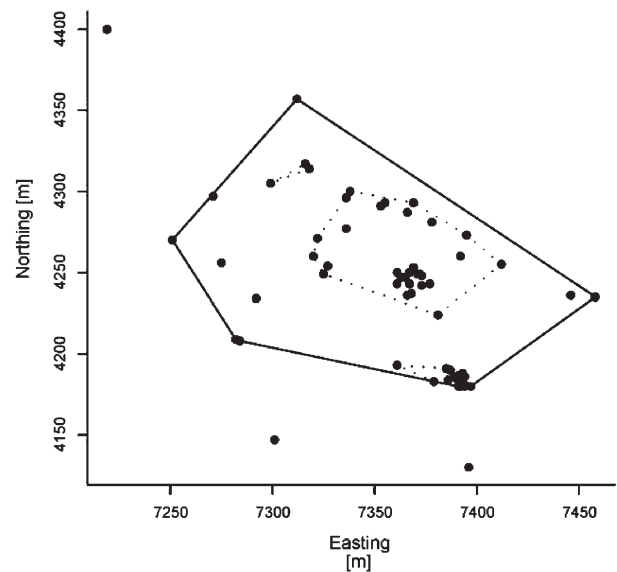


Figure 1. 95% (solid lines) and 80% (dotted lines) range polygons calculated using hierarchical cluster analysis for a single female lizard with overnight refuge fixes in all years included. The 95% polygon covers 16,488 m².

in the statistical software R (Version 1.8.0; Ihaka and Gentleman, 1996). Our analysis differed slightly from that in the Ranges6 software, most notably in the absence of a boundary strip (the lizard fixes were 95% accurate to < 2 m in this case). In a few cases the exact order in which clusters were merged, as more location fixes were included differed between the two programs. However, visual comparisons of home range polygons showed high congruence between the two implementations. For consistency, all analyses in this paper were carried out using the R software (available from 1st author) for both empirical and simulated data.

Kerr and Bull (2006a) reported an empirical pattern in which both the number of neighboring lizards with overlapping home ranges, and the area of home range overlap decreased hyperbolically as the percentage of available fixes used decreased (i.e. as the home range area was more closely restricted to the core of activity; Figure 2). We quantified this pattern by fitting generalized linear models (GLM) of the form

$$\log(y) = a + b \log(x) \quad (1)$$

where x is the proportion of fixes used to generate the home range, and y is either the total area of overlap or the number of lizards with home ranges that overlap that of a focal lizard. We estimated parameters for this model using the GLM function in R. We used a Poisson error distribution for the number of overlapping home ranges, and a quasi-likelihood distribution with variance proportional to the mean, for the area of overlap. In both cases we used a log link function. The parameter a can be interpreted as the logarithm of overlap in either numbers of overlapping home ranges, or total area of overlap when 100% of fixes are used. The parameter b describes the decrease in log overlap as the proportion of fixes included is reduced from 100% to ~ 37% ($\log(0.37) = -1$).

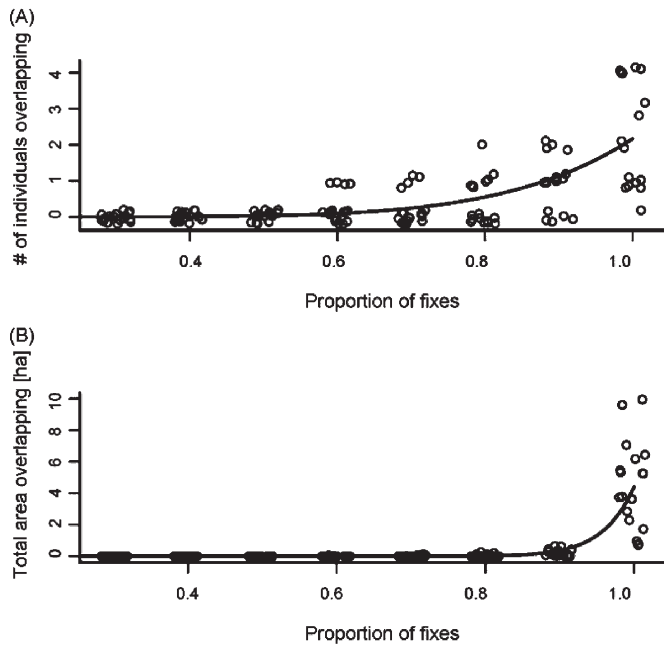


Figure 2. Examples of empirical patterns of male-male overlap in 2000: (A) # of individual lizards overlapping with a focal lizard as a function of the proportion of GPS fixes included for male-male interactions; individual points are “jittered” to prevent overlap. The curve is the predicted mean from the GLM; the estimated intercept (SE) was 0.77 (0.14) and the slope (SE) was 6.13 (0.86). (B) Total area overlapping (m^2) between a focal lizard and all other lizards as a function of the proportion of fixes included for male-male interactions. The estimated intercept (SE) was 10.7 (0.17) and the slope (SE) was 23.6 (5.10).

Note that this analysis is distinctly different from the common practice of plotting estimated range area against the absolute number of fixes that have been obtained as a method of identifying a minimum sufficient number of fixes (e.g. Gautestad and Mysterud, 1993, 1995). In our case the total number of fixes of lizard position is set to 100%, and then we search for the tightest cluster or clusters of locations around smaller percentages of those fixes to identify core areas.

2.3. Simulation models

We derived parameters for the model using data from the studied sleepy lizard population in the Mt. Mary region, where individual home ranges are approximately 200 m across. Tyre (1999) calculated Jolly-Seber estimates of lizard density from random capture data described in Bull (1995), ranging from 15 to 420 lizards/ km^2 . The median lizard density was 100 lizards/ km^2 . The model operates in two phases. During the initial “setup” phase, each lizard identifies its “total range set”, the set of refuges it will use during the year. In the second “activity” phase, lizards move among the refuges in their total range set and the virtual ecologist records their locations. The time scale of the activity phase was 210 days, 1st September to 31st March, over a normal lizard activity season. Movement of lizards was modeled each day. For the rest of the year, late autumn and winter, the lizards were assumed to be completely inactive.

The simulated landscape consisted of the lizards and their nocturnal refuge sites. There were N randomly distributed refuges in a $1 \text{ km} \times 1 \text{ km}$, used by L lizards. The range of each lizard was initiated with a randomly chosen refuge. Each lizard uses a subset of the N available refuges; we referred to this subset of refuge sites that a lizard might use as the “total range set” of refuges. In alternative models we used two algorithms to allocate refuge sites to total range sets during the setup phase, the fixed total range and variable total range. We describe these in detail below.

In all models, at the beginning of each model day, all lizards were in the overnight refuges in which they had spent the previous night. In the next step of the daily cycle each lizard moved around its range before choosing a new refuge for the next night; only the nighttime refuges are tracked in the model. Lizards moved from one overnight refuge to another overnight refuge chosen randomly with equal probability from among those in their total range set. Note that this meant they could spend consecutive nights in the same refuge, and that more than one lizard could occupy a refuge overnight. We assumed that individual lizards could move over their entire range during the day, and that there was no systematic bias either toward or away from particular kinds of refuges, or from their previously occupied refuge. To match the pattern of collection of empirical data, we assumed a virtual ecologist sampled the location of lizards once each six days, or 35 times, over the activity season. Recommended minimum sample size required in order for ICP range size to stabilize is 30 fixes or greater (Kenward, 2001). All lizards whose total ranges were initiated more than 100 m from the boundary of the simulated $1 \text{ km} \times 1 \text{ km}$ study area were sampled. This ensured that sampled home ranges were not influenced by the edge of the simulated landscape. The actual location of each simulated overnight refuge site was sampled with normally distributed independent error in both x and y coordinates with a standard deviation of 1 m. This corresponded to the average error in empirical GPS fix locations estimated at the study site for the GPS unit used.

We varied the parameters in the fixed and variable total range models, described below, by forming a Latin hypercube (Blower and Dowlatabadi, 1994; Tenhumberg et al., 2004). Briefly, this approach assumes that uncertainty in a parameter follows a specific probability distribution. Each distribution is divided into K equi-probable segments. A set of parameters for a single run of the model is created by sampling from these distributions without replacement resulting in K unique parameter combinations. We set $K = 100$ for this initial test of the model, well over the empirical rule of $K > 4M/3$, where M is the number of parameters for Latin hypercube sensitivity analysis (Mckay et al., 1979). For example, for the fixed total range model we generated a series of 100 alternative values for range radius, number of lizards occupying the study area, and the number of refuges in the study area (Table 1); the Latin hypercube procedure then effectively shuffles these sets of parameter values. This ensures that regardless of how many parameters are in each model, the multidimensional parameter space is thoroughly sampled. In general, we assumed parameter uncertainty followed uniform distributions across a broad range of reasonable parameters (Table 1). We assumed all parameters varied independently.

Table 1. Ranges of parameter estimates used to generate the simulated patterns for the fixed and variable range models

Variable	Minimum	Maximum	Integer
Fixed range model			
Lizards	25	200	✓
Numrefuges	2500	7500	✓
H	50	200	×
Variable range model			
Lizards	25	100	✓
Numrefuges	5000	15000	✓
r	1	10	×
s	35	200	×
Λ	0.005	0.1	×
H	0	10	×

Variables with a check in the integer column were always rounded to nearest integer values.

2.3.1. Fixed total range model

In the fixed total range (FTR) model all refuges within a fixed distance h of the initial refuge site were included in the total range set during the setup phase. This is the simplest scenario that can be implemented and assumes no effect of refuge quality, refuge location, or interaction with conspecifics.

2.3.2. Variable total range models

The variable total range (VTR) model included an algorithm determining the size of the total range set. This algorithm was applied iteratively during the setup phase, adding one refuge to the range of each lizard in the population before proceeding to add the next refuge for each lizard. Each lizard had a probability of stopping the increase in total range size given by

$$p(\text{stopping}) = 1 - e^{-(t/r)^s} \quad (2)$$

on iteration t . Note that t here is the iteration during the setup phase, not the day within the activity phase. The parameter s was inversely proportional to the variance in the number of refuge sites included in a home range, while r was the average number of refuges in a range set. If a new refuge was to be added, which refuge was selected depended on both the distance of the refuge from the existing total range set, and the number of other conspecifics using each refuge. Both mechanisms are described in detail below.

2.3.3. Varying effects of refuge location

In the FTR model, home ranges were constructed to include all refuge sites within a fixed radius h of an initial, randomly selected refuge site. The VTR model assumed that lizards were more likely to choose refuge sites that are close to each other. Each lizard had a randomly selected first refuge site, but new refuge sites were added to the total range with a probability determined by the distance to the nearest other refuge site already in the home range

$$p(i) = e^{-\lambda d_{ij}} \quad (3)$$

where i is the current refuge considered for inclusion, j is the index of the refuge nearest to i already in the home range, and d_{ij} is the distance between refuges i and j . λ is a positive constant describing the relative effect of distance. Thus, the probability that a refuge was included decreased with the distance to all refuges in the current total range set.

The random model corresponded to $p(i) = 1$ for $d_{i0} < h$, where $j = 0$ is the first refuge in the home range set. At each step, a refuge was randomly selected from the landscape and accepted with probability $p(i)$. If that refuge was rejected (probability $1 - p(i)$) another refuge was selected at random. This continued until a refuge was selected, or 1000 attempts were made. The algorithm selected the refuge with the smallest nearest neighbor distance if no refuge had been selected after 1000 attempts.

2.3.4. Varying the effect of conspecific use of refuges

Use of refuges by conspecifics also influenced the selection of refuge sites in the VTR model. We incorporated this effect by modifying (3) to include a negative effect of the number of other conspecific males that had already selected that refuge within their total range set:

$$p(i) = e^{-\lambda d_{ij} - \eta n_i} \quad (4)$$

where η is a positive constant indicating the relative influence of conspecific use on refuge selection. The ratio η/λ was the increase in nearest neighbor distance that is equivalent to the effect of an additional competitor including that refuge.

2.4. Pattern comparisons

The empirical observations of the total ranges of male lizards showed decreasing number of home ranges that overlapped with a focal lizard, as the proportion of available fixes was reduced (Figure 2). From these observations, we derived parameters defining intercept (a) and slope (b) of the curves describing that relationship. We derived equivalent parameters from the spatial patterns that were sampled from each of the 100 FTR model simulations, and each of the 100 VTR model simulations.

We then plotted slope against intercept for each of the 200 models and for the one empirical data point (Figure 3). The empirical data point was represented with an approximate 95% confidence ellipse. In Figure 3, and subsequent analyses, we discuss the data that were derived from considering the area of other male total ranges that overlay the focal male lizard's total range. Similar patterns were found when we considered the number of overlapping ranges, but those were highly correlated with the area of overlap, so we use only one pattern. Piou et al. (2007) used a similar pattern based on a regression of population size versus time, but focused on the predicted response as the point of comparison, rather than the regression parameters.

We compared simulated and empirical observations by calculating discrepancies. The unscaled discrepancy D for a given pattern and parameter combination was simply the Euclidean distance between the observed intercept (a) and

slope (b), and the simulated intercept and slope

$$D = \sqrt{(a - \tilde{a})^2 + (b - \tilde{b})^2} \quad (5)$$

These unscaled discrepancies did not account for the fact that our target pattern (the empirical observation) was not precisely observed. The parameters a and b were also estimates, and the uncertainty in these estimates was described with a variance-covariance matrix \mathbf{V} . We chose to scale the discrepancies by the magnitude of a 95% confidence ellipse around our target pattern

$$\mathbf{\Pi} = \left(\frac{\mathbf{P}}{\sqrt{2f}} \right) \mathbf{L}^{-1} \quad (6)$$

where \mathbf{P} is a matrix of the observed and simulated patterns, f is the 95th quantile from an F distribution with the appropriate degrees of freedom (2, 142; the size of covariance matrix, and the number of datapoints in the pattern: 1), and \mathbf{L}^{-1} is the inverse of the Cholesky decomposition of the variance-covariance matrix \mathbf{V} obtained from the GLM fit of (1). This transformation of the coordinate system converted the 95% confidence ellipse into a unit circle. $\mathbf{\Pi}$ was then a matrix of the scaled patterns; the scaled discrepancies Δ were the Euclidean distances between the scaled observed pattern and each scaled simulated pattern. If the scaled discrepancy for a parameter combination was less than one, it fell inside the 95% confidence ellipse around the observed pattern. If the scaled discrepancy was larger than one it fell outside the confidence ellipse. We could combine the discrepancies using the geometric mean, because the discrepancies were scaled such that one was the dividing line for "close". The geometric mean placed greater weight on small

discrepancies. Thus, in this analysis lower scaled discrepancy values signified parameter values that produced range patterns closer to the empirically observed pattern. Although we only have one two-dimensional pattern (intercept and slope), the approach is naturally extensible to both multiple patterns and multidimensional patterns (e.g. Steele et al., 2006).

3. Results

The target empirical patterns (intercept a , and slope b) showed strong decreases in both area of overlap and the number of individuals overlapping with decreasing proportion of fixes included (Figure 2). The discrepancies calculated for the number of individuals overlapping and total overlapping area were highly correlated ($r = 0.87$), indicating that the information contained in the two patterns was not independent. Therefore we used only the pattern of total overlapping area for the remainder of our results. This had smaller discrepancies for both FTR and VTR models.

Figure 3 illustrates the performance of the simulations in reproducing the empirical data point. Points inside the ellipse, close to a vertical line through the empirical point, were simulations that replicated the intercept. Similarly, points inside the ellipse close to a horizontal line through the empirical point replicated the slope well. Most parameter combinations of the FTR model were poor at replicating the target patterns (Figure 3), but they were best at replicating the area of overlap at 100% of GPS fixes (the intercept). The drop-off in overlap (slope) as the percent of fixes was reduced was never as steep in the FTR models as that observed in the real data. In addition, there was little variation in the slope among the different parameter combinations. This reflects the random placement of total ranges in these models yielding a relatively constant reduction. The VTR models were considerably better at replicating the target pattern, with many points inside the confidence ellipse scattered across a range of both slope and intercept (Figure 3).

In the next step, we plotted the effect of varying specific parameter values on the discrepancies with the empirical data point. A systematic pattern of discrepancies along a parameter range would indicate that this parameter was important in reproducing the pattern of total range overlap. On the contrary, if there was no relationship between discrepancy and the parameter, the pattern would reveal little information about the parameter. For the FTR models, we plotted the discrepancy versus number of lizards, number of refuges, total range radius and lizards per refuge (Figure 4). The discrepancies relative to the empirical pattern were generally large and erratic indicating that the pattern of total range overlap provided little information about the actual number of lizards and refuges on the landscape. Intermediate values of total range radius provided the best overlap (smallest discrepancies), and the discrepancies increased with the ratio of lizards to numbers of refuge sites.

For VTR models, the discrepancy plots (Figure 5) indicated that the patterns of total range overlap contained in-

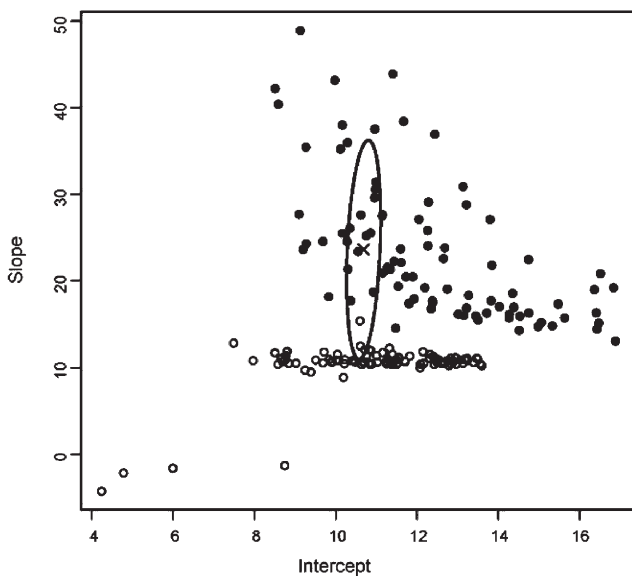


Figure 3. Direct plot of the empirical pattern for area of overlap with simulated patterns. Open circles: FTR model; filled circles: VTR. The empirical pattern was marked with a cross; ellipse indicates an approximate 95% confidence ellipse on the empirical pattern.

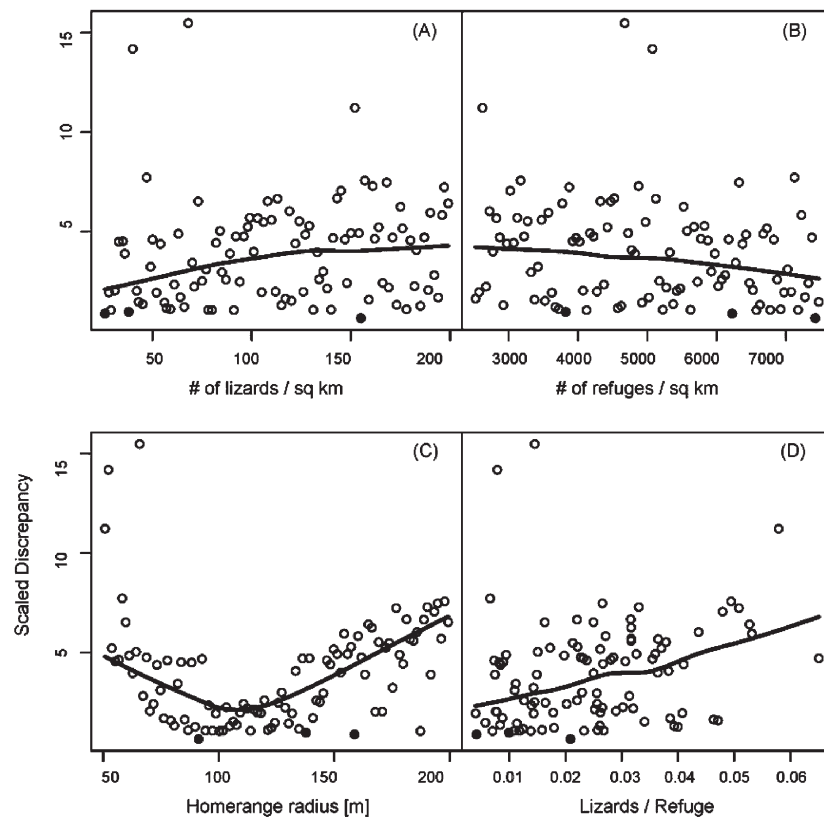


Figure 4. Scaled discrepancies between empirical and simulated total area of overlap for the FTR model. Solid lines are locally weighted regression smooths to indicate the trend; filled circles indicate points with scaled discrepancies < 1 .

formation about some components of the alternate models. The information in the pattern about the ratio of lizards to refuges (Figure 5A) was higher compared to either of the parameters alone (individual parameters not shown). As with the FTR models the discrepancies increased with the ratio of lizards to refuges, but the range of lizard to refuge ratios included in the VTR models was smaller. Of the parameters controlling the number of refuge sites incorporated into the total range (r and s : Figure 5B and C) only r had an effect; the discrepancy was reduced at small values of the exponent r . Nearest neighbor distance (λ , Figure 5D) had the strongest effect on the discrepancies. The discrepancies were smallest for $\lambda > 0.05$, which means refuges more than ~ 20 m ($1/\lambda$) from refuges already in the set have low probabilities of inclusion. There was relatively little scatter around the smooth line, indicating that the effect of this parameter likely overrode variation in other parameters. The pattern for conspecific effect on inclusion of new refuges, η , appeared weak, with smaller discrepancies occurring at higher values (Figure 5E). However, we saw the opposite effect when scaling η by the magnitude of the distance effect λ . Conspecific effects that were large compared to distance effects were not consistent with the observed patterns (Figure 5F).

4. Discussion

Lizards make choices about range size and location. These choices may be influenced by spatial variation in pred-

ator (Bauwens et al., 1999) and parasite density (Duffield and Bull, 1996), interspecific competition (Patterson, 1992; Grover, 1996; Howard and Hailey, 1999; Vitt et al., 2000), and habitat requirements (Cooper and Whiting, 2000). This paper examined whether the distribution of overnight refuges in the environment and the interactions with conspecifics influences range size and overlap of the Australian sleepy lizard.

In the simplest case lizard's refuge choice was random. However, the results of this work indicate that the performance of random models in reproducing the pattern of range overlap found in empirical observations of lizard movement is poor compared to models that construct ranges using nearest neighbor linkage and incorporating a weak effect of conspecific interference. We would not have been able to come to this conclusion by comparing a random model to the data in isolation. For example, Austin et al. (2004) compared grey seal movements to correlated random walk models. They found that some seals fitted the model, while others were over- or under-predicted. They were able to account for some of these departures by using a Lévy flight model for the movement length distributions. Similarly, Burns and Thomson (2005) used a Monte Carlo simulation to measure the performance of foraging honeybees. Performance in excess of the simulation was taken as evidence that the bees were using spatial memory. These comparisons would have been significantly more powerful if multiple mechanisms were simulated and compared to the observed patterns, as done by Zhang et al. (2007). These examples, and our own, reinforce recent (Stamps et al., 2005) and older calls for stud-

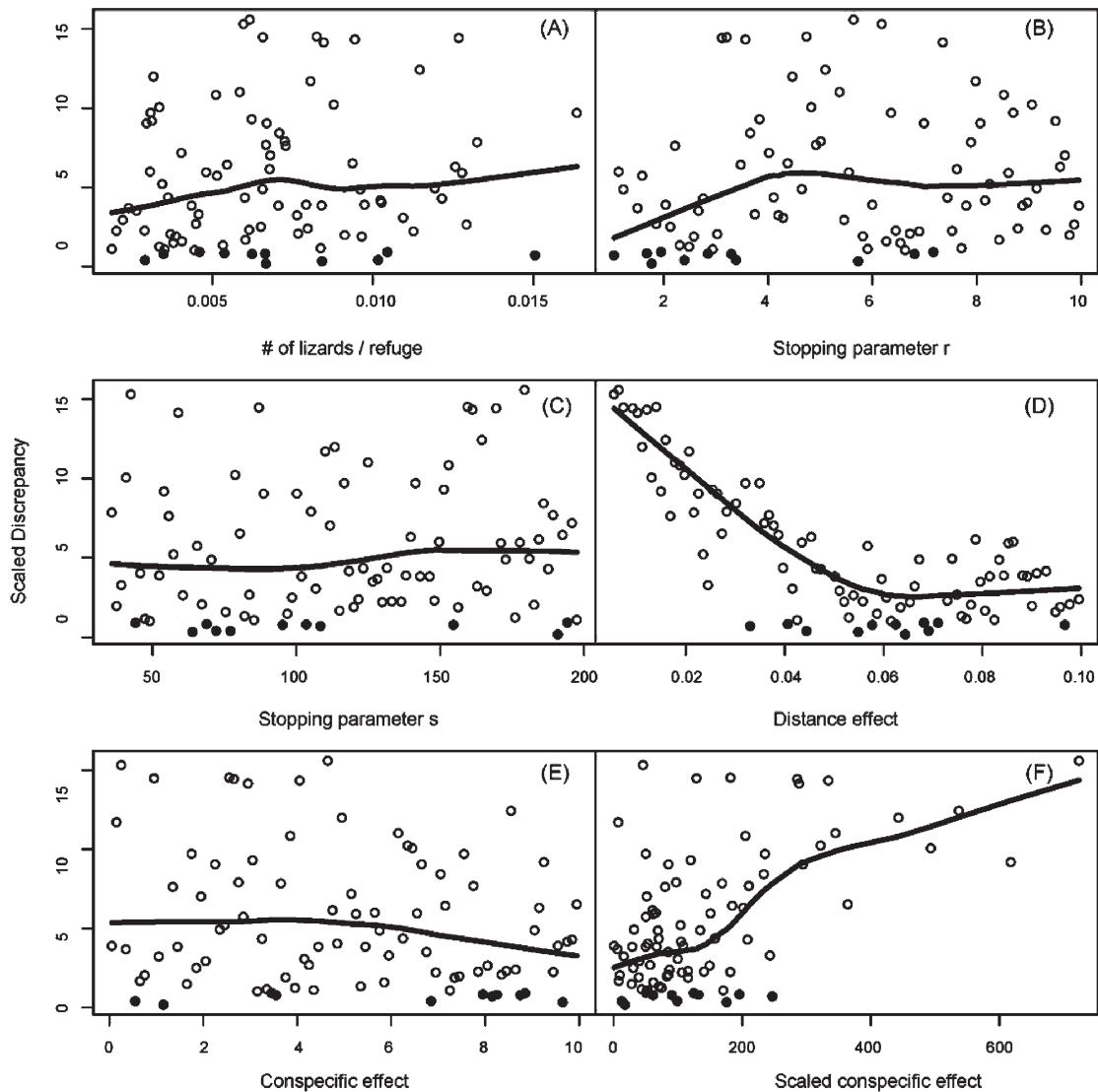


Figure 5. Scaled discrepancy between empirical total area of overlap and overlap simulated from the VTR model. Solid lines are locally weighted smooth regressions; filled circles indicate points with scaled discrepancies < 1 . Scaled conspecific effect is the ratio η/λ .

ies to use multiple model structures – multiple hypotheses in effect – in studies of behavior. Pattern-based modeling lends itself admirably to making comparisons of multiple models with data.

Simulation models have been used in different ways to analyze how organisms use space; recent work includes models of root or rhizome growth in plants (Smith et al., 2007; Wu et al., 2007), individual feeding behavior (Swain et al., 2007), the structure of animal groups (Mirabet et al., 2007), and the formation of home ranges (Wang and Grimm, 2007). Although it is common practice to carry out sensitivity analysis of parameters not constrained by direct estimates, much recent work still does not make comparisons with emergent patterns or compare multiple models. When direct comparisons are made, it is common practice to only show the best matching parameter set (e.g. Boone et al., 2006); this provides no information about how sensitive the pattern is to the unknown parameters. In contrast, pattern based modeling shows a wide range of discrepancies between the pat-

tern and the simulation across a wide range of parameter values (e.g. this paper and Piou et al., 2007).

Robertson et al. (1998) quantitatively compared range analysis methods by sub-sampling locations from two empirical trajectories of animal movements sampled at high frequency for long periods of time. They stressed the importance of finding methods for simulating realistic observations of animal movements that do not make the same assumptions as the statistical models used to analyze them. However, even their sub-sampling approach suffered from the fact that only two different trajectories were available, casting some doubt on their ability to compare how home range analyses perform across many individuals of those species. Gautestad and Myrsetrud (1993, 1995) carried out interesting analyses of simulated data demonstrating an approach for correcting for small sample sizes based on power law scaling. Their simulations used correlated random walks which may be mechanistically appealing for some species. Boone et al. (2006) used correlated random walks to examine

wood frog movements. However, partially territorial species such as the sleepy lizards will dramatically violate the assumptions of a correlated random walk which does not incorporate the boundary conditions of a territory.

Our approach circumvented these issues by calibrating mechanistic models against real observational patterns. It would then be straightforward to use the calibrated simulation to generate test data for comparing home range analyses. One potential area of concern is that using one range analysis for the calibration may predispose the model to generate data suited for that method. This is readily circumvented by calibrating the model using different methods to see if this affects the performance of the home range models. The key point is that our mechanistic simulation did not make the same assumptions (e.g. those locations are a sample from a bivariate normal distribution) as the ICP range analysis method.

A given biological pattern may provide little or no information about some parameters of a mechanistic model. However, combining multiple independent patterns can provide considerable support for choosing the "best" model. The range analyses presented in this paper revealed that the patterns produced from the VTR model were consistent with empirical patterns of conspecific interactions, the spatial distribution of refuges (nearest neighbor distance) and the ratio of lizards to refuges. This is consistent with previous work where patterns related to the dynamics of parasitic ticks using sleepy lizards as hosts were little influenced by either refuge or lizard density alone, but were strongly affected by the ratio of lizards to refuges (Tyre et al., 2006). Combining the range patterns of the host with the parasite population patterns may provide us with considerable information on all parameters.

The analysis of individual locations over time is a common approach to understanding how animals use their habitat. Recent work (Kenward et al., 2001) makes it clear that while great strides in developing methods for understanding such data have occurred, connecting the results of those analyses to biological hypotheses remains fraught with difficulty. Our work here provides an alternative for comparing multiple, biologically realistic models with observations of space use. Pattern-based modeling has considerable promise for extracting useful insights from space use data.

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