

INFERRING PROCESS FROM PATTERN: CAN TERRITORY OCCUPANCY PROVIDE INFORMATION ABOUT LIFE HISTORY PARAMETERS?

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Abstract. A significant problem in wildlife management is identifying “good” habitat for species within the short time frames demanded by policy makers. Statistical models of the response of species presence/absence to predictor variables are one solution, widely known as habitat modeling. We use a “virtual ecologist” to test logistic regression as a means of developing habitat models within a spatially explicit, individual-based simulation that allows habitat quality to influence either fecundity or survival with a continuous scale. The basic question is how good are logistic regression models of habitat quality at identifying habitat where birth rates are high and death rates low (i.e., “source” habitat)? We find that, even when all the important variables are perfectly measured, and there is no error in surveying the species of interest, demographic stochasticity and the limiting effect of localized dispersal generally prevent an explanation of much more than half of the variation in territory occupancy as a function of habitat quality. This is true regardless of whether fecundity or survival is influenced by habitat quality. In addition, habitat models only detect a significant effect of habitat on territory occupancy when habitat quality is spatially autocorrelated. We find that habitat models based on logistic regression really measure the ability of the species to reach and colonize areas, not birth or death rates.

Key words: demographic stochasticity; dispersal; habitat quality–occupancy relationships; habitat vs. individual-based model; life history parameters; logistic regression; observed pattern; *Petauroides volans*; source vs. sink habitat; territory occupancy; virtual ecologist.

INTRODUCTION

A fundamental problem faced by wildlife managers is which habitats to conserve (Morrison et al. 1992, Block and Brennan 1993). This problem often arises when choices must be made about which habitats to include in a reserve system (Pressey et al. 1996). Clearly, the answer involves identifying the characteristics of “good” habitat for a species. At the simplest level, good habitat is simply habitat that allows birth rates to exceed death rates (source habitat), as opposed to habitat where death rates exceed birth rates (sink habitat; Pulliam 1988). Therefore, rational decision making about population management requires information about how birth and death rates vary with changes in habitat characteristics such as vegetation structure and topography (Possingham et al. 1993). Furthermore, many populations occur on fragmented or spatially heterogeneous landscapes. In such situations, information about the ability of a species to disperse between different-quality habitat patches is crucial to understanding the responses of populations to managed or sto-

chastic changes (Fahrig and Merriam 1994, Sutcliffe et al. 1997, Wiegand et al. 1998).

Howe et al. (1991) clearly demonstrated the need to accurately identify birth and death rates for patches in source/sink metapopulations. The presence of sinks could increase global population sizes in some circumstances. However, they could also obscure a deterministic decline to extinction, remaining occupied even though the entire metapopulation was doomed.

Obtaining quantitative information about key population processes such as birth, death, and dispersal rates is costly in both time and money (Stacey and Taper 1992). Paradis and Croset (1995) estimated survival rates for only two different kinds of habitat for Mediterranean Pine Voles (*Microtus duodecimcostatus*), requiring substantial trapping effort over three years. Measuring dispersal by juveniles away from natal habitat is also particularly difficult (Kareiva 1990). For example, Nelson (1993) needed 14 yr of weekly airborne radio tracking to measure natal dispersal distances in only 86 juvenile white-tailed deer (*Odocoileus virginianus*) from a single population. Relating these dispersal distances to characteristics of the source population or home ranges would require a dramatic increase in the amount of sampling effort required.

Decisions about habitat reservation or management are generally made on short time scales—much shorter than needed to gather robust demographic and dispersal

Manuscript received 10 April 2000; revised 6 November 2000; accepted 29 November 2000.

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data. An extreme case in point is the negotiation of Regional Forest Agreements in Australia over the past five years (Commonwealth of Australia 1992). In the North East Forests region of New South Wales alone, it was necessary to obtain information about habitat requirements for 2211 species of plants (National Park and Wildlife Service 1994b) and 405 species of vertebrates (National Park and Wildlife Service 1994a). Often the only information available is the intuition of what constitutes good habitat by an ecologist who has spent years studying the species in the wild, or inferences from similar species. However, failing to act because of a lack of accurate information is also a management action with associated costs (Parma et al. 1998).

The combination of few resources and a pressing need for information leads to increased reliance on observations of the presence or absence of a species in different kinds of habitat (habitat occupancy). When sites with certain characteristics are more likely to be occupied, or have higher population abundances, it is commonly assumed that these sites are better quality habitat (Davey 1989). This approach uses the probability of occupancy as a surrogate for habitat quality. Presence/absence data can be collected in single surveys without observing population processes. The key issue in interpreting the results of survey data is whether extrapolating to population dynamics parameters from observations of habitat occupancy is valid.

There are two stochastic processes at work when an ecologist collects a sequence of observations of habitat occupancy: population dynamics and observation. The population may be increasing or declining in an area, and these changes may merely be chance. Observation is a stochastic process; even if the species is present at a site, it may not be detected (Lindenmayer et al. 1999). This is especially important if the population is present in low numbers, if each site is surveyed briefly in order to increase the number of sites sampled, or if there are problems in field survey methodology.

With these issues in mind, we address two questions in this paper. First, to what extent does demographic stochasticity and dispersal interfere with the accurate detection of habitat quality–occupancy relationships, when all other possible sources of error are eliminated? Second, what does a positive relationship between habitat quality and occupancy tell us about the fundamental population processes of birth, death, and dispersal?

We address these questions by creating a “virtual ecologist” who samples inside a spatially explicit individual-based simulation. Our simulated species is *Petauroides volans* (greater glider), an arboreal marsupial. Greater gliders have been the focus of several population modeling exercises, including models where habitat quality data was used to parameterize the model (Possingham et al. 1994). Our primary interest is not in this species, but in answering the two questions and introducing the methods. The simulated landscape

is artificially generated with a fractal algorithm. The virtual ecologist samples the simulated landscape and then uses statistical modeling to estimate the driving forces behind habitat quality. Before we detail the simulation and results, we briefly review the practice of habitat modeling. To avoid confusion, we will always refer to the statistical habitat model as the “model,” and the process simulation model as the “simulation.”

HABITAT MODELING

Many statistical methods exist for estimating the probability of occurrence from a set of observed characteristics. Logistic regression, a type of Generalized Linear Model (GLM) that estimates the log-odds of occupancy as a linear function of some habitat variables, is widely used (Austin et al. 1990, Lindenmayer et al. 1990, Buckland and Elston 1993, Pearce et al. 1994, Mysterud and Ims 1998, Dorrough and Ash 1999, Parris and McCarthy 2000). Recent advances such as autologistic regressions have also incorporated spatial dependency (Augustin et al. 1996), a key feature of population distributions. Other approaches for identifying good habitat include linear optimization (Biggins et al. 1993), other types of generalized linear models (Pedlar et al. 1997), generalized additive models (Austin and Meyers 1996), univariate descriptive statistics and correlations (Collins and Lichvar 1986, Hayward et al. 1993, Merendino and Ankney 1994, Donald et al. 1996), canonical correspondence analysis (Fiedler and Reilly 1994, Anderson and Gribble 1998), indices based on expert opinion (Houston et al. 1986), and regression combined with multivariate discriminant functions or principal-components analysis (Braithwaite et al. 1983, Prescott and Collister 1993, Rotenberry and Wiens 1998, Southwell et al. 1999). This list is not exhaustive. The point is that many methods are being used to identify habitat from either static or repeated surveys of occupancy or animal abundance.

Combining static survey data with measurements of habitat occupancy can be done at a range of spatial scales, from day-to-day microhabitat selection within a home range (e.g., Mysterud and Ims 1998, Rotenberry and Wiens 1998, Cox et al. 2000), to measurements of home range occupancy (e.g., Lindenmayer et al. 1990), up to abundance at population scales (e.g., Braithwaite et al. 1983, Buckland et al. 1996). A few studies have also examined habitat–abundance correlations at a range of scales (Wiens et al. 1987, Pedlar et al. 1997). If the goal of habitat modeling is to provide information about spatial variation in population processes like survival or reproduction, then the most logical scale is one that identifies individual patterns of habitat selection, while integrating over time scales appropriate to survival and reproduction. For this reason, we concentrate on sampling at the scale of a single home range with an annual time step. We also limit ourselves to using logistic regressions, as these are increasingly employed in habitat modeling, and have the simplest data re-

quirements for the response variable (presence/absence; Austin et al. 1994). Furthermore, single home ranges will be either occupied or not for solitary, territorial species such as the greater glider.

The assumption that an increased probability of occupancy or abundance indicates high habitat quality or positive population growth is plausible (although see Temple and Cary [1988]). However, a variety of processes could obscure the relationship, decreasing the power of these statistical tests to detect habitat occupancy patterns and, consequently, habitat quality. Metapopulation models (e.g., Levin 1974) show that even good habitat is sometimes unoccupied when colonization and extinction processes are at equilibrium. This general conclusion is widely supported by population subdivision models (see review in Kareiva [1990]). More sophisticated metapopulation models (e.g., Day and Possingham 1995) and empirical results (Fritz 1979, Kindvall and Ahlen 1992) show that the proximity of good habitat patches to each other also influences the likelihood that a patch is occupied. In other words, bad habitat close to good habitat could be more often occupied than good habitat far from any other good patch. When demographic stochasticity and limited dispersal ability are considered, the amount of variation interfering with the detection of a relationship between habitat characteristics and occupancy is enormous. Finally, Van Horne (1983) highlighted several examples in which correlations failed to adequately identify high quality habitat defined on the basis of population processes. The conclusion was that density or occupancy is particularly likely to fail as a predictor of habitat quality when population densities are high. This is because increased competition for high-quality habitat leads to increased numbers in lower quality habitat.

There are at least four ways to obtain a quantitative measure of how good a presence/absence habitat model is: error rate, specificity, sensitivity, and the area under a receiver operating characteristic (ROC) curve (Elith 2000). The first three require an arbitrary choice of a probability threshold above which the site is predicted to be occupied. For example, if the threshold is 0.5, sites with a predicted probability of occupancy larger than 0.5 are positive predictions of occupancy. The error rate is simply the proportion of errors made by the model; how many sites are predicted to be occupied that were not, and vice versa. A low error rate is better. Specificity and sensitivity are the two sides of the error rate coin. A model is more "specific" if most sites that are actually unoccupied are predicted to be unoccupied. A high specificity means that the model is doing a good job of predicting where the animal does not occur. Conversely, a model is more "sensitive" if most sites that are actually occupied are predicted to be occupied. A high sensitivity means that the model is doing a good job of predicting where the animal does occur.

The ROC curve is a measure borrowed from the

TABLE 1. Baseline parameters and ranges of the greater glider in the sensitivity analysis.

Parameter	Symbol	Minimum (or fixed value)	Maximum
Newborn survival	S_0	0.55	...
Juvenile survival	S_1	0.82	0.9
Adult survival	S_2	0.82	0.9
Adult fecundity	F	0.4	0.5
Dispersal mortality	d	0.005	0.02
Fractal dimension	H	2.1	2.9
Habitat selectivity	α	0	19

Note: Life history parameters for the greater glider are from Possingham et al. (1994).

medical literature, and is a plot of the sensitivity vs. 1-specificity at all possible threshold probabilities for a positive prediction; Hanley and McNeil 1982, Elith 2000). The area under an ROC curve ranges from zero to one, with values close to unity indicating better predictive power; an area of 0.5 indicates that the model is not predicting better than a random choice. Elith (2000) considered that models with a ROC curve area of >0.75 were useful for management purposes. The area under the curve has a convenient interpretation as the probability that a randomly chosen pair of occupied and unoccupied sites is correctly ranked by a marker. In our case, the marker is the predicted probability of occupancy from the logistic regression. We will use the area under the ROC curve as a measure of predictive quality in this paper, because it avoids the arbitrary choice of a prediction threshold.

THE SPECIES AND ITS ECOSYSTEM

Tall eucalypt forests in southeastern Australia are inhabited by several arboreal marsupial species. Many of these are of conservation concern, because their habitats are threatened by timber harvesting. We selected the greater glider (GG, *Petauroides volans*) because we have access to life history data, habitat requirements, and parameter estimates from other studies (Table 1). Greater gliders are entirely folivorous, consuming predominantly eucalypt leaves (Hume et al. 1984), and prefer tall open forest. Greater gliders have patchy distributions in otherwise continuous forest (Lindenmayer et al. 1990), indicative of habitat quality variation and/or demographic stochasticity. Females are solitary occupants of their territory for most of the year (Lindenmayer 1997). Greater gliders mature after one year as juveniles.

THE PROCESS SIMULATION

To use our virtual ecologist to test the ability of habitat models to find good habitat, we must create a reasonable underlying process simulation of the species concerned. The simulation was individual based, tracking the location and life history state of all females in the population at one-year intervals. We ignored males in this implementation for simplicity and because they

do not contribute individually to population growth in this species. That is, females are the limiting sex. The basic spatial unit was a female home range. All runs of the simulation were performed on a 128×128 grid of home ranges, using a six-cell hexagonal neighborhood. There were four important components of the simulation: (1) the landscape of spatially varying habitat quality, (2) the population of individuals, (3) the connection between habitat quality and vital rates (survival and fecundity) of individuals, and (4) the dispersal rules used by individuals to move around on the landscape. The parameters of the model are summarised in Table 1.

Landscape construction

Each home range on the landscape had an associated habitat quality. We used a midpoint displacement algorithm (Saupe 1988) to create surfaces with a specific fractal dimension, H . We used a range of values for H uniformly distributed within 2.1–2.9 (see *Scenarios and sensitivity analysis*). There was more fragmentation at higher fractal dimensions, with large patches of high-quality home ranges splitting into a larger number of smaller patches, and increased interspersions of poor-quality habitat with high-quality habitat (Fig. 1). An example of a high-dimension habitat variable is the number of hollow bearing trees (Lindenmayer et al. 1990). Landscape processes lead to trees occurring in clusters. Slope or soil type are examples of habitat variables with a lower fractal dimension. We linearly rescaled the output of the fractal algorithm to give habitat quality within the range 0–100.

Births and deaths

Each individual has an annual probability of giving birth to a single female offspring and (independent of birth) dying due to predation, aging, or another catastrophe. The heterogeneous landscape influenced individuals through either their probability of surviving from one age class to the next, or their probability of giving birth to a daughter. Both of these vital rates are probabilities, and are bounded between zero and one. The logistic, or log-odds, transformation scales a probability onto the real number line (bounded by $\pm\infty$). We assumed that habitat quality has a linear effect on the log-odds of survival or reproduction. This was obviously only one of an infinite range of possible connections between habitat quality and individual life history parameters. There was no empirical data to support a more complex effect, and the consequences of simpler connections (i.e., binary source/sink quality) have been explored elsewhere (e.g., Keitt and Johnson 1995, With et al. 1997). Furthermore, more complex relationships could be reduced to a combination of variables with a linear effect (Meents et al. 1983, Austin et al. 1990). We also assume animals can detect small differences in this habitat quality variable. The consequences of coarse habitat quality detection will not be explored

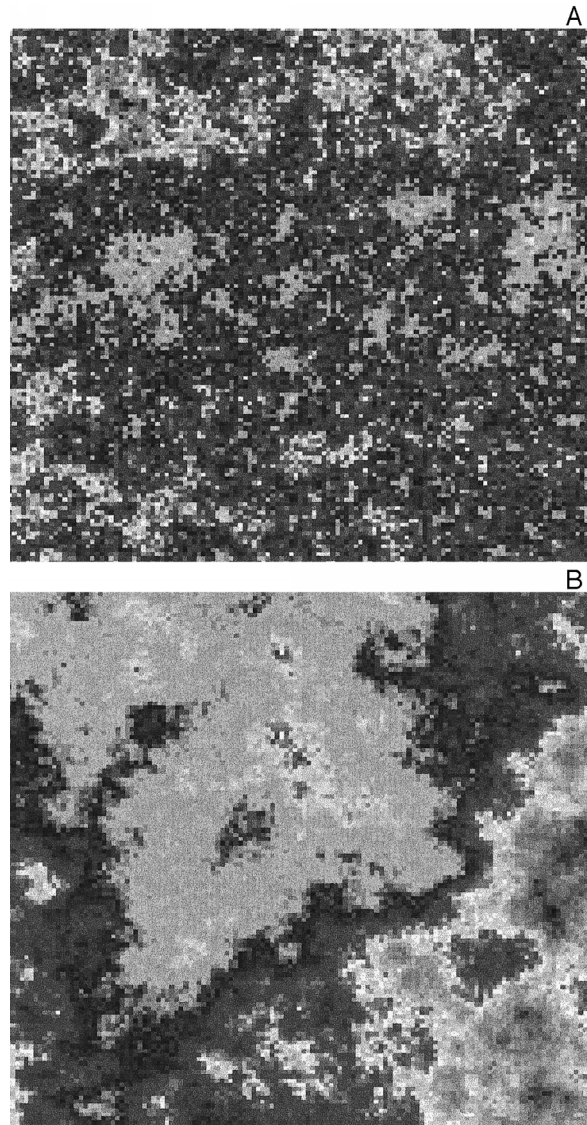


FIG. 1. Examples of fractal landscapes. Each cell is a territory: (A) $H = 2.9$; (B) $H = 2.5$.

here. We must also ensure that artificial habitat landscapes do not introduce differences in average quality simply from variation in spatial patterns.

The annual probability of an age i female in home range x giving birth to a daughter was $p_{x,i}$. This probability was modified by the local habitat quality in home range x , Q_x according to the equation

$$\ln\left(\frac{2p_{x,i}}{1 - 2p_{x,i}}\right) = b\left(\frac{Q_x}{\bar{Q}} - 1\right) + \ln\left(\frac{2p_i}{1 - 2p_i}\right) \quad (1)$$

where b was the effect of habitat quality on fecundity, \bar{Q} was the 90th-percentile habitat quality, and p_i was the annual fecundity of age class i in a territory of quality \bar{Q} . The two in the denominator and numerator of the log-odds transformation is a correction for ignoring males. We assumed the sex ratio is 1:1. There-

fore, when the probability of reproduction in a year was one, the maximum probability of having a female offspring is 0.5. The exact distribution of habitat quality values differed between replicate landscapes. The 90th percentile habitat quality \bar{Q} (mean value 72 when $H = 2.9$; mean value 70 when $H = 2.5$) corrects for differences in the distribution of habitat quality values between different random landscapes. It ensures that only 10% of home ranges have fecundity (or survival) rates greater than p_i regardless of the exact details of the landscape. When $b > 0$, individuals have increased fecundity when $Q_x > \bar{Q}$, and decreased fecundity when $Q_x < \bar{Q}$. We use a similar transformation for the effect of habitat quality on survival:

$$\ln\left(\frac{s_{x,i}}{1 - s_{x,i}}\right) = a\left(\frac{Q_x}{\bar{Q}} - 1\right) + \ln\left(\frac{s_i}{1 - s_i}\right) \quad (2)$$

where $s_{x,i}$ is the probability of surviving to the end of age class i in territory x , and a is the effect of habitat quality on survival. We choose the values of a , b and \bar{Q} to ensure that approximately half of the landscape was occupied at equilibrium, based on preliminary runs. Runs where habitat quality changes survival are "survival scenarios" ($a = 0.6$, $b = 0$), and runs where habitat quality changes fecundity are "fecundity scenarios" ($a = 0$, $b = 11$). A smaller amount of variation in survival leads to the same population level response, because the sensitivity (sensu Caswell 1989) of the population growth rate to the survival parameters, particularly adult survival, is much higher than the sensitivity to fecundity, for this species.

The intrinsic rate of population growth from a projection matrix quantifies the effect of habitat quality on population-level parameters (Fig. 2). In the results, territories with intrinsic population growth rates less than one are "sink habitats" (Stenseth and Lidicker Jr. 1992), and territories with intrinsic population growth rates of greater than one are "source habitats." Individuals in a sink habitat do not produce enough offspring to replace themselves.

Dispersal

There is some empirical evidence that dispersing or translocated arboreal marsupials suffer additional mortality over and above that due to aging (Tyndale-Biscoe and Smith 1969, Pietsch 1995). Therefore, we incorporate a per step probability of dying, so the probability of surviving dispersal (S_d) is given by the following:

$$S_d = (1 - d)^n \quad (3)$$

where d is per step probability of mortality (uniformly distributed within 0.005–0.02), and n is the number of steps taken before settling. Note that n is different for every individual and also depends on the local density of individuals, because in crowded conditions unoccupied territories are rare (McCarthy 1997). In combination with the fact there can be only one individual per territory, this is the only point at which density

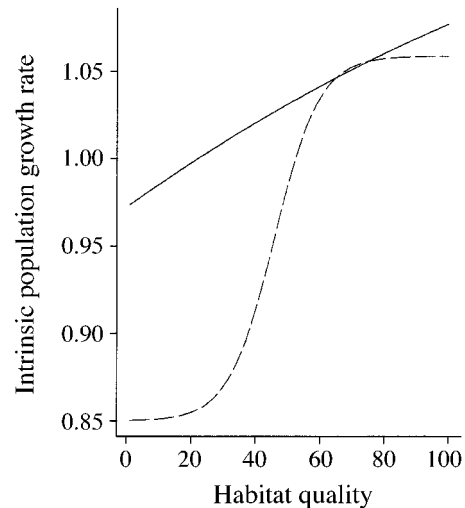


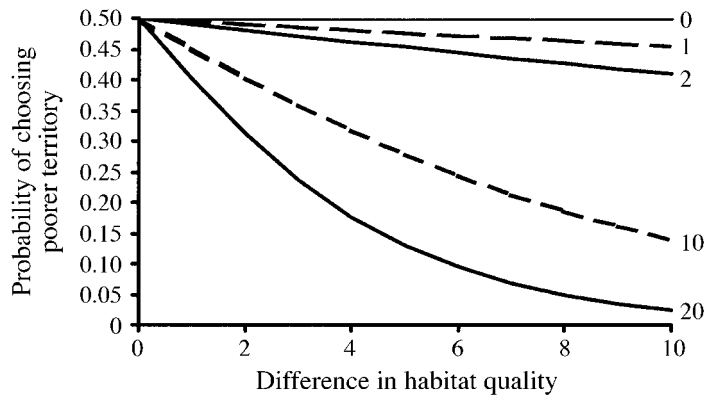
FIG. 2. Effect of habitat quality on intrinsic population growth rates, assuming a landscape with $\bar{Q}_{90} = 75$ and that habitat quality influences fecundity (dashed line) or survival (solid line). The annual probability of birth at quality zero is approximately zero when fecundity is influenced by habitat quality. Note that quality ranges from 0 to 100; growth rates are relative to a value of 1, which indicates not net population change.

dependence enters the simulation. This range of dispersal mortalities corresponds to an average individual being minimally able to search 50–200 home ranges before succumbing to dispersal mortality, ignoring neighboring territories that are sampled but not visited. We now describe the specific movement algorithms.

Little is known about how individuals choose where to disperse in a heterogeneous landscape (Wolfenbarger 1946, Gustafson and Gardner 1996, Zollner and Lima 1999). We assumed that individuals move towards territories with higher habitat quality, using the following rule. Let the six directions have qualities q_1, \dots, q_6 . Let P_n be the proportion of quality in direction n : $P_n = q_n / \text{sum}(q_1, \dots, q_6)$. Now, raise each P_n to the power of α and renormalize back to unity to determine the probability of moving in direction n . Now if $\alpha = 0$, all directions are equally likely regardless of their relative qualities. If $\alpha = 1$, each direction is chosen in direct proportion to its habitat quality. If $\alpha > 1$, good quality directions are weighted even more (Fig. 3). For high α values, this strategy leads dispersers to remain in high-quality habitat during dispersal. Field studies indicate that some species stay within favorable habitat during dispersal (e.g., Wolfenbarger 1946, Holekamp 1984, Merriam and Lanoue 1990, Kindvall and Ahlen 1992, Nelson 1993, Haas 1995). We call this rule the "biased random walker."

The biased random walker is quite distinct from a "correlated random walk" (e.g., Kareiva and Shigesada 1983, Zollner and Lima 1999) or "self-avoiding random walk" (Gustafson and Gardner 1996), where the direction chosen is correlated with the previous

FIG. 3. The probability of moving to a territory of quality 50 as a function of the quality of another adjacent territory for different values of α . If the number of adjacent territories is larger, the differences between the best and worst cells would be smaller than this, unless all cells but one have the higher quality. See Table 1 for range of α .



direction, but has nothing to do with variation in the underlying landscape. Dispersal models responsive to landscape heterogeneity have been used for brown bears (Wiegand et al. 1998) and birds (Brooker et al. 1999).

Individuals stopped moving when they encountered a vacant territory, regardless of the habitat quality. Early simulations experimented with more sophisticated stopping rules that incorporated some measure of habitat quality. However, these extensive tests revealed no strong differences in the relationship between habitat quality and occupancy for simple or complex stopping rules, unless dispersal mortalities were unrealistically low ($d < 0.001$ per step) or landscapes were completely random. For brevity, only results for the relatively simple stopping rule we have discussed are presented. Dispersing individuals settle only in unoccupied territories under the assumption that older individuals (i.e., dispersers from previous years) were able to repel inexperienced territorial invaders without significant cost to themselves. If two or more juveniles stopped in the same unoccupied territory, the resulting dispute is settled randomly, with neither individual having an advantage (50% win/loss). The loser continued dispersing from the disputed location. These assumptions about dispersal have been used for other species, e.g., water voles (Rushton et al. 2000), and are not particularly specific to greater gliders.

THE VIRTUAL ECOLOGIST

Our concept of the "virtual ecologist" is a tool for testing both the power of statistical analyses, and for relating the output of the analysis to underlying population processes. The relationship between habitat characteristics and population processes is completely known in the simulation. Therefore, by using a virtual ecologist to sample the simulation output in a manner similar to a real ecologist, and utilizing standard statistical methods, the output of the statistical tests can be related to the original demographic processes that lead to spatially varying occupancy patterns in a heterogeneous landscape. We call the virtual ecologist VERA—Virtual Ecologist Random Assessor.

In statistics, it is common practice to test new statistics by generating data from the statistical model itself, and then refitting the model. The virtual ecologist is subtly different from this, because the model generating the data has very little to do with the form of the statistical model used. The processes and random distributions are completely different. The virtual-ecologist approach extends traditional statistical testing methods to include the way in which data is actually generated by ecologists, as opposed to statistical models. This concept is being used increasingly often in the ecological literature (e.g., McGuinness 2000).

VERA chooses sites to be sampled using a method we call "extensive random," because preliminary runs indicated that this sampling scheme led to better regression models than either simple-random or regular sampling schemes. Extensive-random sites are chosen by categorizing all territories into 10 groups based on the habitat variable, 0–9, 10–19, . . . , 90–100, and then choosing $n/10$ territories randomly from each category. If there are $< n/10$ sites in a category, then all sites are chosen, and the remainder are randomly chosen from other categories, one per category starting with the lowest category. VERA's extensive-sampling method is a form of stratification that ensures the full range of habitat quality values are represented in the sample, and it can be performed only with knowledge of the distribution of habitat variables prior to conducting a statistical analysis.

VERA samples 100 sites in the last year of a simulation run. This compares favorably with actual empirical studies of this nature, and is well above sample sizes of 35–70 recommended in the literature for this type of study (Morrison et al. 1992). VERA samples the simulation after juvenile dispersal takes place, but before annual mortality. VERA's samples coincide exactly with the home range grid, a happenstance impossible in reality. Furthermore, VERA makes no errors in detection; if the species is present it is recorded. The only contributions to unexplained deviance in the statistical models are the limited number of observations and demographic stochasticity.

VERA performed all statistical analyses in S-PLUS

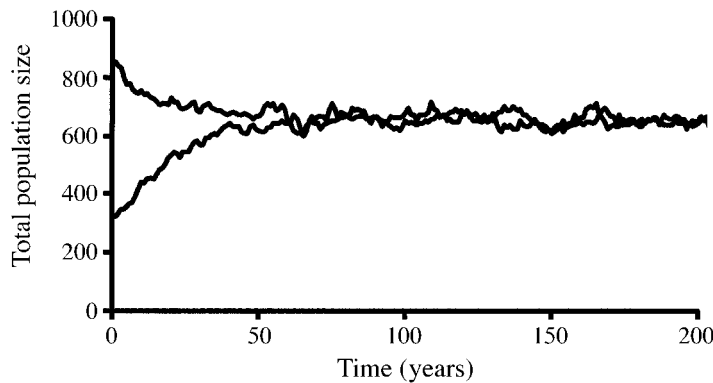


FIG. 4. Population dynamics for greater gliders; $b = 10.0$, $\bar{Q} = 90$. The total population size converges to quasiequilibrium within 50 yr from most initial population sizes. The maximum possible population size for this run was 1089 (i.e., 33^2).

4.0 for Windows. The logistic regression model predicts the probability that a site is occupied using standard generalized linear modeling techniques (McCullagh and Nelder 1989). The receiver operating characteristic (ROC) curve area was calculated using SPLUS functions available from the Mayo Clinic.⁵

SCENARIOS AND SENSITIVITY ANALYSIS

There are two life history scenarios (F = habitat quality affects fecundity, and S = habitat quality affects survival). We ran 200 replicate simulations of 200 yr for each. A different random landscape was generated for every replicate simulation. Within each scenario, we varied several parameters randomly for each replicate (Table 1), drawing numbers from uniform random distributions. We used partial rank correlation coefficients (PRCC; Blower and Dowlatabadi 1994, Rushton et al. 2000) to look for monotonic effects of variation in each input parameter on two output parameters: true population size, and the receiver operating characteristic (ROC) curve area. True population size was also included as an input parameter in the sensitivity analysis for ROC curve area, because variation in population size in the year sampled is large, even for identical parameters, and this variation has an influence on ROC curve area. We also examined scatter plots of all input parameters against population size and ROC curve area for discontinuities and nonmonotonic responses (i.e., quadratic), because using PRCC assumes that all responses will be monotonic, although not necessarily linear.

RESULTS

Population dynamics

The population size reached a quasistationary state well within the maximum time of 200 yr (Fig. 4). The population dynamics roughly follow logistic growth. The primary cause of density dependence is the limitation to one animal per territory. This leads to an increase in dispersal mortality with density, which reach-

es 40–50% at the quasistationary state (Tyre et al. 1998). This increase in dispersal mortality arises from competition between migrating individuals and residents. When the landscape is fully occupied, this competitive effect forces migrating individuals to travel greater distances, and therefore incur increased mortality risks.

Explanatory power

Two example habitat occupancy analyses for the greater glider by VERA are shown in Fig. 5. They provide an indication of the range of data collected by the virtual ecologist. They are the replicates with the median receiver operating characteristic (ROC) curve areas for each scenario. There are two points to highlight from these analyses. First, territories in high-quality areas are sometimes unoccupied, because individuals die and replacement does not happen instantaneously. Second, habitat quality can influence the probability of occupancy even when active habitat selection behavior is weak. In Fig. 5A, $\alpha = 1$ (very close to a random walk), yet there is a significant effect of habitat quality on the probability of occupancy. This arises because of the localized nature of the random walk and spatial correlations in habitat quality. Occupied good-quality territories seed the neighboring territories, because individuals search nearby territories first.

Overall, there is little difference between the two scenarios in the quality of models produced (Fig. 6). The median ROC curve area is slightly lower when the habitat variable affects survival, and the worst replicates are all from the survival scenario. The most important point from this figure is that ROC curve areas for habitat models under perfect conditions will rarely exceed 0.95; any habitat model that comes close to this under real conditions is performing extremely well.

Table 2 has the partial rank correlation coefficients (PRCC) for each of the input variables against population size and ROC curve area for each scenario. We examine the effect of variation in input parameters on population size first. Population size tends to be lower when dispersal mortality is higher and when survival

⁵ URL: <http://www.mayo.edu/hsr/Sfunc.html>

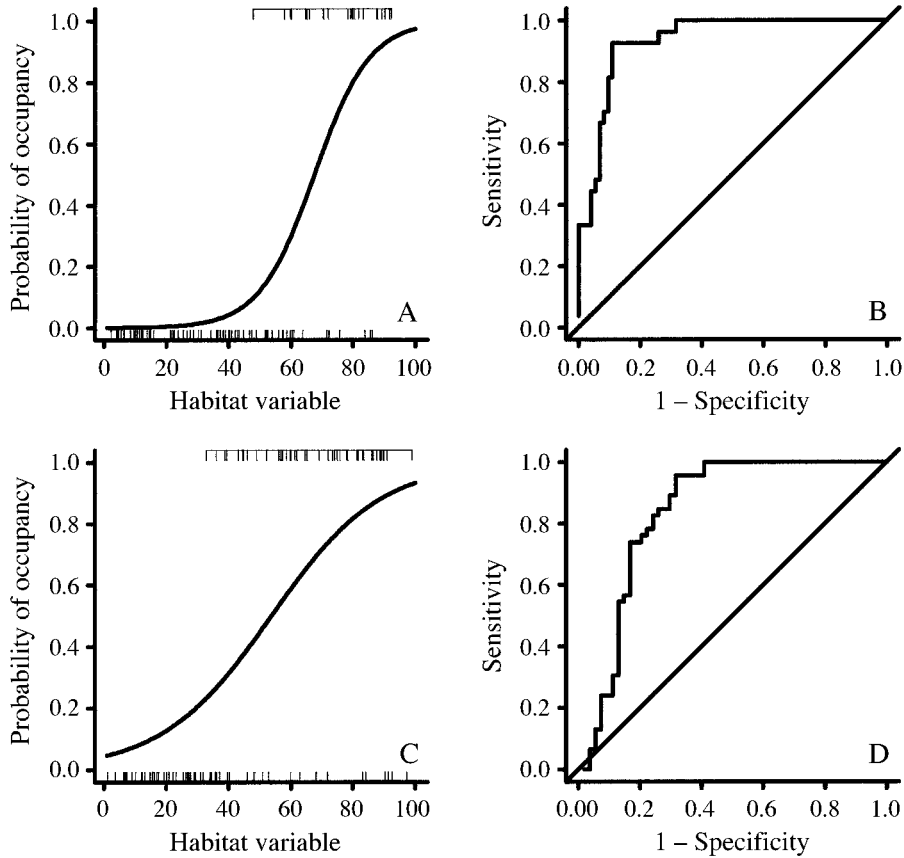


FIG. 5. Two example logistic regressions for habitat occupancy by greater gliders, $\bar{Q} = 90$. (A and C) The solid line is the predicted probability of occurrence. High-density bars indicate the frequency distribution of observed occupied (top of figure) and unoccupied (bottom of figure) home ranges. (B and D) Receiver operating characteristic curves for each model; see *Habitat modeling* for definition of “sensitivity” and “specificity.” (A) Fecundity scenario: $H = 2.4$, $d = 0.005$, $\alpha = 1$, $S_{1,2} = 0.845$, $F_2 = 0.4$, (C) Survival scenario: $H = 2.6$, $d = 0.008$, $\alpha = 5$, $S_{1,2} = 0.855$, $F_2 = 0.48$. See Table 1 for variable ranges.

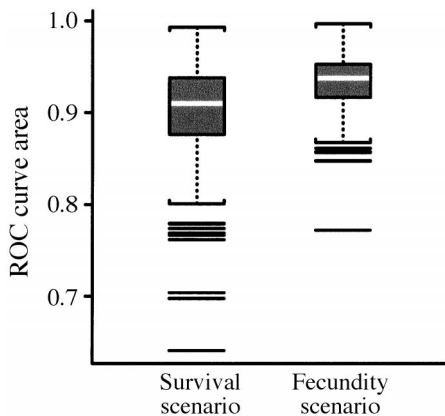


FIG. 6. Box plots of receiving operator characteristic (ROC) curve area for all replicates in each of the two scenarios. White bars are the medians, the boxes show the interquartile range (i.e., 25th–75th percentiles), and the whiskers show the range of the data. Points $>1.5\times$ the interquartile range from the median are shown as lines.

or birth rates are lower. The effect of dispersal mortality is not statistically significant in the survival scenario. Population size also tends to be lower on landscapes with higher fractal dimensions.

One surprising result is that high levels of habitat selectivity lead to lower population sizes (Fig. 7), although the effect is not strong. This result is quite general for a range of other dispersal rules (Tyre et al. 1997, 1998), and arises because selective individuals concentrate themselves into the highest quality areas at an increased cost of mortality during dispersal. Therefore the density-dependent dispersal mortality increases faster at lower population sizes.

The significant relationships between input parameters and population size suggest that population size should be controlled for when examining the effect of input parameters on ROC curve area. When population size was controlled for, the ROC curve area was not sensitive to variation in landscape fractal dimension or dispersal mortality in either scenario. In the fecundity scenario, ROC curve area increased slightly with in-

TABLE 2. Partial rank correlation coefficients (PRCC) for each of the variable input parameters against population size and receiving operator characteristic (ROC) curve area.

Input parameter	Fecundity scenario		Survival scenario	
	Population size	ROC curve area	Population size	ROC curve area
H	-0.23**	-0.16	-0.20*	-0.01
d	-0.24**	0.02	-0.17	0.09
α	-0.44***	0.15*	-0.56***	0.29***
$S_{1,2}$	0.84***	-0.01	0.83***	-0.22**
F_2	0.81***	-0.22**	0.46***	-0.19*
Population size	...	-0.01	...	-0.25**

Note: Population size becomes an input parameter in the calculation for ROC curve area, thus the effect of variation in population size is controlled in the effects of parameters on ROC curve area.

* $P \leq 0.1$; ** $P \leq 0.05$; *** $P \leq 0.001$.

creased habitat selectivity (Fig. 8). This was not unexpected; if animals are better at finding good habitat, then habitat models should be better predictors of animal distributions. The weakness of the effect was unexpected. Receiver operating characteristic area decreases with increasing birth rate; this is over and above any effect of increased population size, which has been statistically controlled for. This effect arose because,

at high birth rates, variation introduced by habitat quality had a relatively smaller effect across the landscape.

In the survival scenario, ROC curve area responded similarly to habitat selectivity (α) and birth rate (F_2 , Fig. 9A, B), and for the same reasons. In addition, an increase in baseline survival rate or population size leads to a decrease in ROC curve area (Fig. 9C, D).

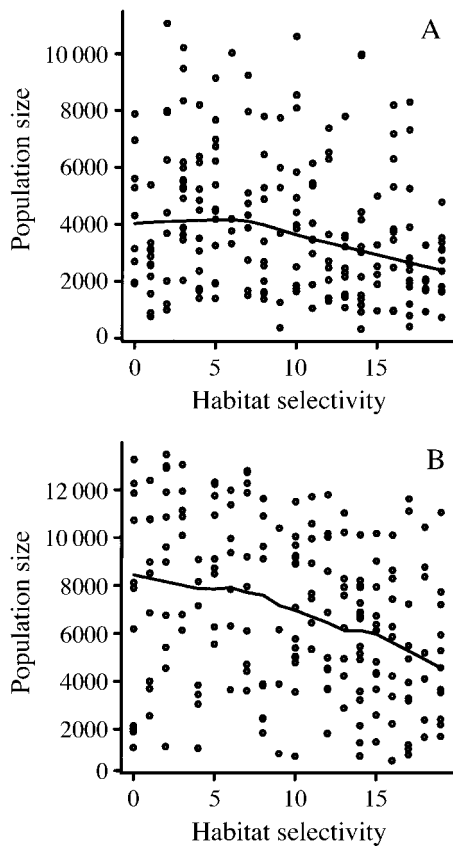


FIG. 7. Scatter plots of population size vs. α , the habitat selectivity for all replicates in both scenarios: (A) fecundity scenario; (B) survival scenario. The lines are smoothed through the points to highlight the weak trend. See Table 1 for range of α .

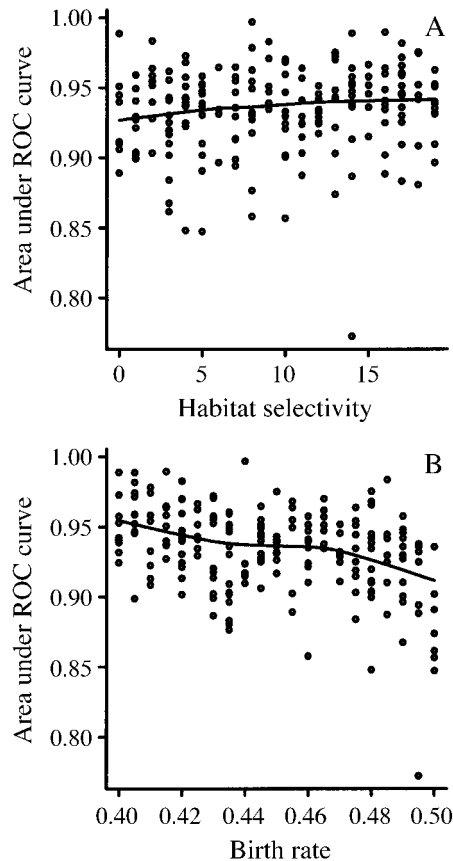


FIG. 8. Scatter plots of ROC curve area vs. (A) α and (B) F_2 for the fecundity scenario. We show plots only for those input parameters with partial rank correlation coefficients (PRCC) significant at $P \leq 0.1$. Lines are smooth fits through the points to highlight the trend. See Table 1 for variable ranges.

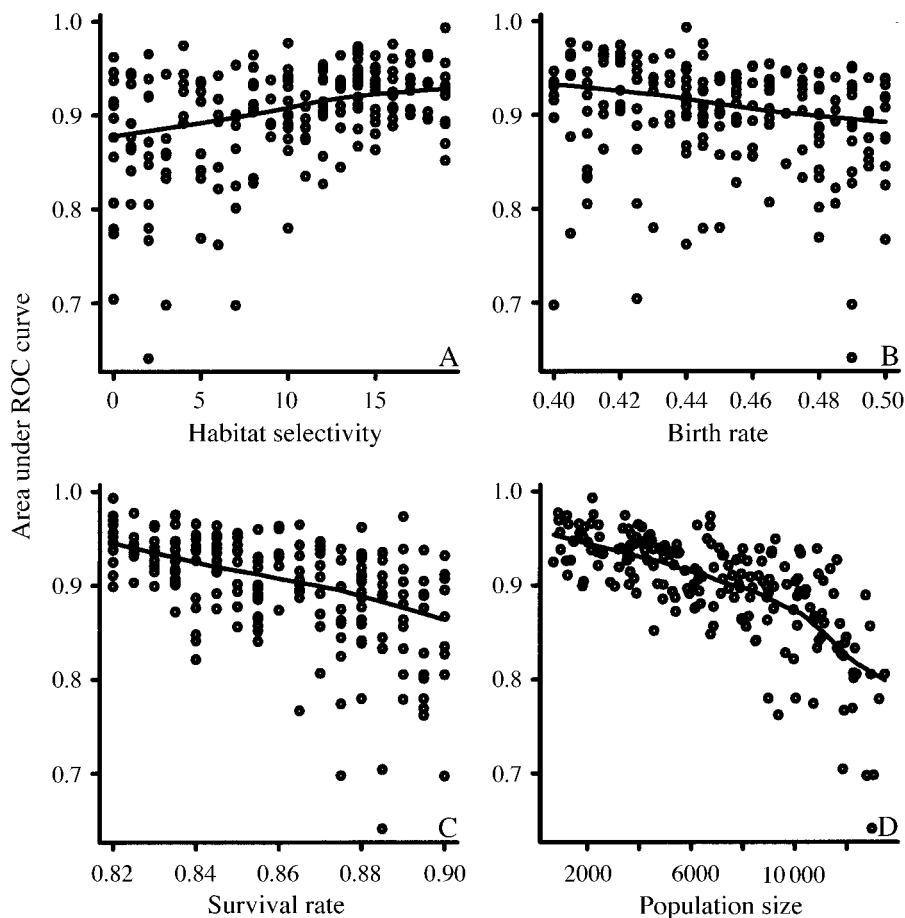


FIG. 9. Scatter plots of ROC curve area vs. (A) α , (B) F_2 , (C) $S_{1,2}$, and (D) population size for the survival scenario. We show plots only for those input parameters with partial rank correlation coefficients (PRCC) significant at $P \leq 0.1$. Lines are smooth fits through the points to highlight the trend. See Table 1 for variable ranges.

These effects were stronger than for the fecundity scenario, because the population growth rate is in general much more sensitive to variation in survival than variation in fecundity.

Overall, the sensitivity analysis reveals no surprises; the model behaves much as expected. The most important contribution of this section is the observation that ROC curve area is unlikely to exceed 0.95, and not infrequently is as low as 0.8, even under perfect conditions. This provides a useful upper boundary against which to benchmark empirical models.

What can pattern tell us about process?

The ultimate test of a static habitat model is whether or not it also provides information about population processes. In this case, the processes of interest were birth and death rates of individuals in the population. Is there a simple relationship between birth and death rates and the effect a habitat quality variable has on the probability of territory occupancy? This is important if we are to infer something about population processes from patterns of distribution and abundance.

In the fecundity scenario, habitat influences only the birth rate, and the survival rate is simply constant over all habitat qualities. As might be expected, the birth rate increases monotonically with an increasing probability of occupancy. However, the exact nature of that increase is quite variable with a wide range of possible relationships between the estimated probability of occupancy and the local birth rate (Fig. 10A). This variation appears to be driven primarily by the population size at the time of the sample. When landscapes are relatively crowded, more individuals are found in habitats with lower quality, and the curve is pushed well below the 1:1 line (lower curve). When the population size is low, the vast majority of individuals are found in relatively high-quality habitats, and the local birth rates are very high and constant in territories with high predicted probabilities of occupancy (upper curve). At intermediate population sizes, the predicted probability of occupancy almost directly reflects variation in local birth rates (center curve). This relationship breaks down when the predicted probability of occupancy exceeds 0.5. So the output of a static habitat model can

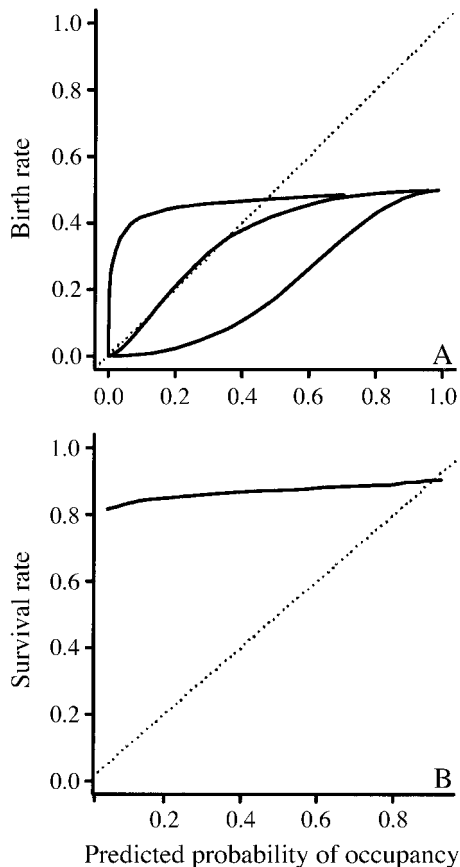


FIG. 10. (A) Local birth rate or (B) survival rate vs. the predicted probability of occupancy in some example replicates from the fecundity and survival scenarios, respectively. The dotted lines indicate equality between the rates and the predicted probability.

reflect variation in local birth rates, but only at “intermediate” population sizes.

Fecundity is constant in the survival scenario, so the predicted probability of occupancy should only reflect variation in local survival rates. Across the landscape as a whole, variation in survival in this scenario is still quite low (Fig. 10B), much lower than variation in the predicted probability of occupancy. There is little variation in the shape of this relationship among replicate runs in this scenario. Again, a higher predicted probability of occupancy indicates a higher survival rate, but there would appear to be no simple translation from one to the other.

These results present a conundrum: *something* is varying on the landscape that leads to variation in the predicted probability of occupancy, but in both the fecundity and survival scenarios the habitat-induced variation in local process rates seems to be too small to account for the variation in territory occupancy. The analysis so far has considered only local processes influenced by habitat quality. However, the neighborhood will also affect the probability that a site is occupied,

because it is dispersers from neighboring sites that will occupy an empty territory. We evaluated this effect by measuring two process rates directly from the artificial landscape: the survival probability and the recolonization probability.

We called the rate at which occupied territories remain occupied, p_{11} . We refer to this as the “survival probability.” Likewise, we can determine the rate at which empty territories become occupied, p_{01} . This is a combination of both the number and fecundity of other individuals in the local area, and the probability of mortality during dispersal. p_{01} includes the possibility that a territory was colonized and the individual died before sampling took place, because the transitions are sampled after mortality occurs. We will refer to this as the “recolonization probability.” We assessed the ability of a habitat model to provide information about these process rates by correlating the observed process rate at each site with the predicted probability of occupancy for that site. We first examine in detail the results for the same pair of replicates considered earlier, and then look at the broader pattern of correlations in the two scenarios.

In the median replicate from the fecundity scenario (as measured by ROC curve area), the recolonization probability increases with increased probability of occupancy, while the survival probability does not (Fig. 11A, B). The explanation for this result is that habitat with a high probability of occupancy occurs in areas with higher birth rates, and consequently more dispersing individuals will encounter empty sites. Therefore, we expect that survival probability should be related to predicted probability of occupancy in replicates from the survival scenario. However, this is not the case (Fig. 11C, D). The recolonization probability is still strongly related to the predicted probability of occupancy, while the survival probability is only weakly related, if at all. The small change that is present is entirely consistent with the effect of the habitat variable on survival.

In addition, it would appear that the predicted probability of occupancy forms a rough upper boundary on the true probability of recolonization. This can be seen in Fig. 11, C by noting that there are few or no points above the 1:1 line.

Inspecting all replicates in both scenarios (Fig. 12) reinforces this pattern. Correlations between the predictions of the habitat model and recolonization probability are high in both scenarios. Correlations between the predictions of the habitat model and survival probability are essentially nonexistent in the fecundity scenario, as expected. Many correlations between habitat model predictions and survival probability in the survival scenario are significantly different from zero, however the magnitude of these correlations is much lower than that for the recolonization probability.

The magnitude of the correlations between process rates and habitat model predictions are weakly sensitive

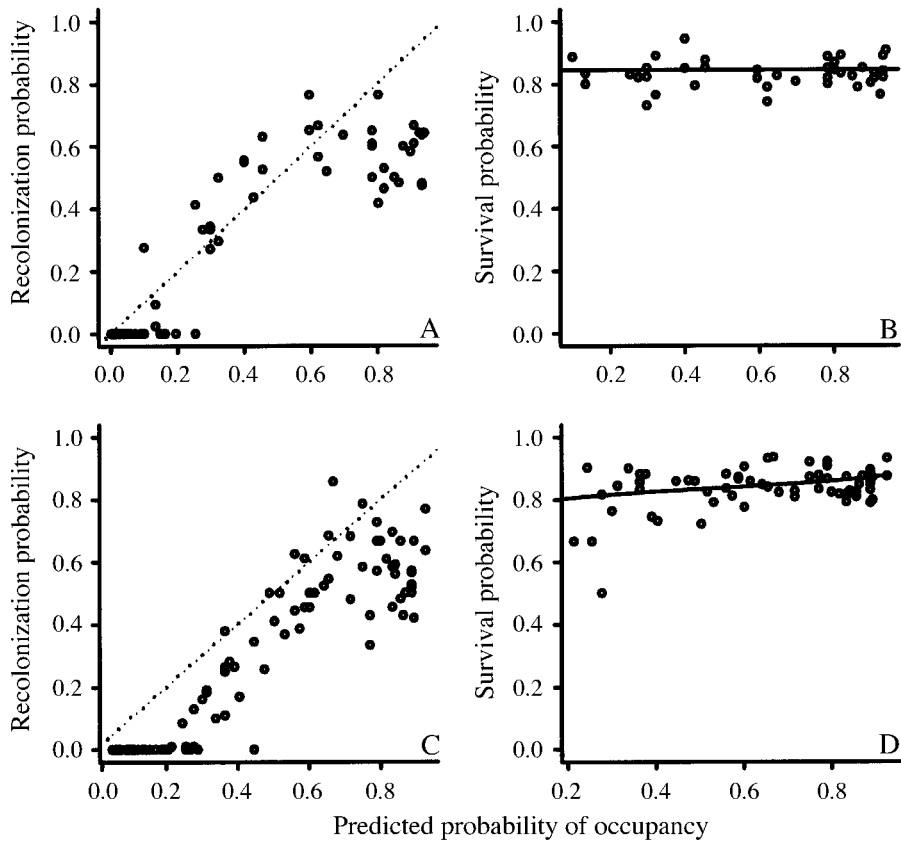


FIG. 11. Scatter plots of the recolonization (A and C) and survival probabilities (B and D) against the predicted probability of occupancy from the habitat model for the median replicate run in the fecundity (A and B) and survival (C and D) scenarios. The dashed lines in (A) and (C) indicate where the predicted probability and the recolonization probability would be equal. (B and D) The lines are not smooth fits, but rather the predicted changes in survival probability due to the effect of habitat for these two replicate landscapes. The Kendall's τ values for each plot are (A) 0.52, (B) 0.01, (C) 0.66, and (D) 0.11.

to variation in some input parameters (Table 3). The PRCC for survival probabilities are generally low and nonsignificant, except for the effect of baseline survival in the survival scenario, where higher baseline survival

means a better correlation between survival probabilities and habitat model predictions. The correlation between recolonization probabilities and habitat model predictions are sensitive to baseline survival in the survival scenario, and baseline fecundity in the fecundity scenario. This suggests that the effect of the habitat variable on process rates is reflected in the recolonization probability, regardless of which scenario is being considered. There are weak landscape structure and habitat quality effects in the survival scenario.

DISCUSSION

The first main outcome of this work was that habitat occupancy analysis frequently has less-than-perfect discrimination, even under ideal conditions. Residual variance will persist, irrespective of the number of habitat variables measured, the accuracy of methods to survey animals in the field, or the number of samples taken. In the current simulation, the single source of variability in population process rates was perfectly measured, and there was no error in occupancy measurement. Imperfect discrimination in habitat models is often attributed to unmeasured variables. Our work

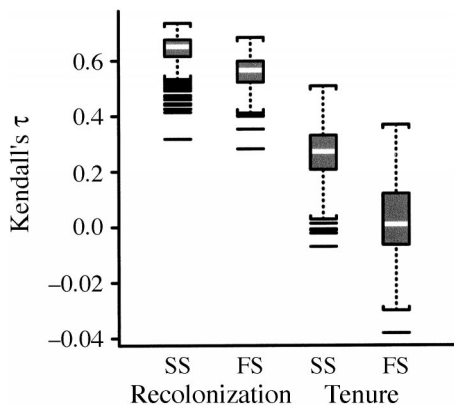


FIG. 12. Box plots of Kendall's τ for all replicates for both process rates in each of the two scenarios: SS, survival scenario; FS, fecundity scenario. Box plot structures are the same as in Fig. 6.

TABLE 3. Partial rank correlation coefficients (PRCC) for each of the variable input parameters and population size against recolonization and survival probabilities.

Input parameter	Recolonization probability		Survival probability	
	Survival scenario	Fecundity scenario	Survival scenario	Fecundity scenario
H	0.15**	0.13*	0.09	0.07
D	0.13**	0.07	0.08	-0.05
α	-0.05	0.16**	-0.09	0.00
$S_{1,2}$	0.20**	0.11	0.16**	0.05
F_2	0.10	0.24***	0.09	0.11
Population size	0.01	0.11	0.07	-0.05

* $P \leq 0.1$; ** $P \leq 0.05$; *** $P \leq 0.001$.

shows that demographic stochasticity alone can contribute large amounts of variation that will be unexplainable in terms of habitat quality.

Unexplained deviance in the logistic regression model is the sum of the residuals between the model predictions and the actual observations. The two biggest contributors to residual deviance in a habitat model are unoccupied territories with high predicted probabilities of occupancy, and occupied sites with low predicted probabilities of occupancy. In what follows, we refer to these as false positive and false negative predictions, consistent with the terminology in common use when fixed prediction thresholds are employed. The changes in the model output that we have described can be understood in the context of processes leading to these two kinds of residuals.

When an individual dies in a high-quality territory, that territory is a potential false positive prediction. When adult mortality is relatively high, as with the greater gliders, the probability that an otherwise good territory is observed to be vacant is higher than if mortality was relatively lower. If survival were the only component that contributed to errors of this kind, then habitat models should predict best when survival is high and not variable.

The likelihood that an otherwise high-quality territory is found to be empty is not only a function of average survival. It is also increased if the lag between the site becoming unoccupied and being recolonized is greater. This lag is a function of imperfect information on the part of individuals inhabiting the landscape; they do not know the location of unoccupied, high quality-habitat. If habitat patches had boundaries, biased random walkers would not cross them before exhausting the possibilities within the current patch. This helps to explain why habitat model quality decreases as landscapes become patchier (i.e., as H increases; Table 2), although the effect is weak.

The other source of unexplained deviance results from territories expected to be empty that are in fact occupied (false negatives). The main population process responsible for these errors is local competition for space. If a dispersing individual cannot locate unoccupied habitat by looking "uphill" on the quality gradient, it gradually switches to looking anywhere.

The likelihood of encountering a marginal site near a good site is increased on landscapes with $H = 2.9$, because of increased patchiness (e.g., Fig. 1). Increased use of marginal habitats in the vicinity of high-quality habitat has been found in other theoretical work incorporating continuous variation in habitat quality (Milne et al. 1989, Gustafson and Gardner 1996). However, individuals that are selecting habitat will tend to avoid the occasional poor-quality territory interspersed among otherwise good territories. Thus, the discriminatory power of habitat models decreases with landscape fractal dimension and increases with habitat selectivity.

These relationships between false negative and positive observations and overall quality of the statistical model might permit a general statement of how different life history characteristics influence the potential quality of a habitat model. As we have described, high survival reduces false positive predictions. The residuals created by false positives are likely to occur right up to the very best habitat available (i.e., at the extremes of the habitat variable distribution), because regions of high-quality habitat tend to be heavily occupied. High survival simultaneously increases false negative predictions, because, once a poor home range is occupied, it is more likely to remain occupied. The residuals created by false negative predictions are more likely to occur in the middle of the habitat quality distribution because individuals tend to avoid the regions of poorest habitat. Therefore, the residuals from false negative predictions will tend to have less impact on the results of the regression than the residuals from false positive predictions, and consequently species with high survival should, all else being equal, make better targets for statistical habitat modeling.

The second major outcome of this work was that habitat occupancy models provide information about some population process rates. The main information provided is an upper bound on the probability that an unoccupied home range becomes occupied. This probability is a combination of natal dispersal ability and the proximity of occupied good habitat. This recolonization probability varies substantially across the landscape, regardless of what population process is influenced by habitat quality. A more accurate interpre-

tation of a significant effect of habitat on occupancy is that it indicates a high probability that the species occurs in the vicinity of sites with those characteristics, and is able to disperse there. Habitat models appear to be quite insensitive to variation in survival rates. This lack of information about survival rates is unfortunate, because population extinction or quasiextinction risk is especially sensitive to variation in survival (McCarthy et al. 1994, Letcher et al. 1998).

Clearly, the simulation did not include all processes that might have influenced habitat occupancy. Including processes such as succession, patch structure, or multispecies interactions would make relationships harder to quantify, not easier. For example, the simulation landscape is static. Real landscapes change according to processes like succession, disturbance, and human perturbation. If such processes alter the landscape slowly at spatial scales related to dispersal distance, then temporal variation in habitat quality should not influence the relationship between occupancy and quality. This is because populations will track these changes. Problems will arise when succession or disturbance, particularly human perturbations, occur faster on larger scales. Essentially, this leads to fragmentation of the landscape, blocking dispersal to other patches of suitable habitat. Wiens et al. (1987) observed this failure to track habitat changes in the course of their regional-scale study of bird responses to habitat structure.

In this paper we have developed a new concept of experimenting with models that transcends traditional power analysis: the "virtual ecologist." This concept has considerable potential value in conservation biology and other ecological disciplines where empirical experiments are impossible because of the temporal and spatial scales involved (Turner et al. 1995). Many studies in these disciplines rely on "snapshots" at single points in time to understand processes that cannot be measured easily. This critical assessment of the conditions under which snapshot data, like occupancy patterns in a heterogeneous landscape, can be extrapolated to understand processes is timely. We have found that snapshot data provides little or no information about key process rates such as birth and death—the rates that are needed to make management decisions.

ACKNOWLEDGMENTS

This manuscript benefited from ongoing discussions with Ian Ball, Steve Ball, Brigitte Tenhumberg, and other members of the Possingham HyperLab discussion group. Leonore Fahrig, Mark Burgmann, Scott Field, Steve Trombulak, and Thorsten Wiegand made critical comments. Francis Pantus generated the graphics for Fig. 1. The work was supported by a National Sciences and Engineering Research Council Post Graduate Scholarship B (NSERC PGS B) to A. J. Tyre and Australian Research Council grants to H. P. Possingham and D. B. Lindenmayer.

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