

Optimizing Presence–Absence Surveys for Detecting Population Trends

JONATHAN R. RHODES,^{1,2} School of Geography, Planning and Architecture, The University of Queensland, Brisbane, QLD 4072, Australia

ANDREW J. TYRE, School of Natural Resource Sciences, University of Nebraska-Lincoln, Lincoln, NE 68583-0819, USA

NICLAS JONZÉN,² The Ecology Centre, The University of Queensland, Brisbane, QLD 4072, Australia

CLIVE A. McALPINE, School of Geography, Planning and Architecture, The University of Queensland, Brisbane, QLD 4072, Australia

HUGH P. POSSINGHAM, The Ecology Centre, The University of Queensland, Brisbane, QLD 4072, Australia

Abstract

Presence–absence surveys are a commonly used method for monitoring broad-scale changes in wildlife distributions. However, the lack of power of these surveys for detecting population trends is problematic for their application in wildlife management. Options for improving power include increasing the sampling effort or arbitrarily relaxing the type I error rate. We present an alternative, whereby targeted sampling of particular habitats in the landscape using information from a habitat model increases power. The advantage of this approach is that it does not require a trade-off with either cost or the $\Pr\{\text{type I error}\}$ to achieve greater power. We use a demographic model of koala (*Phascolarctos cinereus*) population dynamics and simulations of the monitoring process to estimate the power to detect a trend in occupancy for a range of strategies, thereby demonstrating that targeting particular habitat qualities can improve power substantially. If the objective is to detect a decline in occupancy, the optimal strategy is to sample high-quality habitats. Alternatively, if the objective is to detect an increase in occupancy, the optimal strategy is to sample intermediate-quality habitats. The strategies with the highest power remained the same under a range of parameter assumptions, although observation error had a strong influence on the optimal strategy. Our approach specifically applies to monitoring for detecting long-term trends in occupancy or abundance. This is a common and important monitoring objective for wildlife managers, and we provide guidelines for more effectively achieving it. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):8–18; 2006)

Key words

koala, Markov model, monitoring, observation error, occupancy, optimization, population trends, presence–absence surveys, statistical power.

Decisions about how to manage wildlife often rely on information about whether populations are increasing or decreasing. Therefore, understanding our ability to detect population trends is a primary interest (e.g., Jassby and Powell 1990, James et al. 1996, Shea and Mangel 2001). If frequentist hypothesis tests are used to detect these trends, 2 types of possible errors may be encountered: 1) identifying a trend when no trend exists, known as a type I error, and 2) failing to detect a trend when a trend exists, known as a type II error. Statistical power is the probability of detecting a trend when a trend exists and is $1 - \Pr\{\text{type II error}\}$. As such, quantifying and setting specific targets for the $\Pr\{\text{type I error}\}$ and the $\Pr\{\text{type II error}\}$ is important for the design of long-term wildlife monitoring programs (Gerrodette 1987, Peterman 1990, Mapstone 1995, Field et al. 2004).

Due to financial and other constraints, presence–absence surveys are regularly employed to make indirect inferences about trends in abundance (e.g., Buckland and Elston 1993, Lindenmayer et al. 2000, Miller and Franklin 2002, Reunanen et al. 2002). Although empirical evidence suggests that occupancy–abundance relationships are generally positive, the form of this relationship can depend on factors such as mean occupancy rate and the temporal and spatial variation in abundances (Gaston et al. 2000). The link between abundance and occupancy patterns can also depend on processes such as habitat selection, density dependence, and dispersal (e.g., Fretwell and Lucas 1970, Pulliam and Danielson

1991, Morris 1994). These factors will affect our ability to detect trends in abundance from presence–absence data.

Previous studies have demonstrated that presence–absence surveys lack effectiveness in detecting temporal trends in occupancy, unless the effect size is large (Kendall et al. 1992, Strayer 1999). Kendall et al. (1992; grizzly bears) and Strayer (1999; unionid mussels) found that, apart from increasing the $\Pr\{\text{type I error}\}$, power could be increased most effectively by adding sites rather than increasing sampling effort per site. The only other option that has been considered for improving the power of presence–absence surveys is increasing the $\Pr\{\text{type I error}\}$, with the increased risk of falsely inferring a trend (Strayer 1999).

Of considerable interest is how one might optimize the power of presence–absence surveys to detect trends for a fixed sampling effort (cost), other than by increasing the $\Pr\{\text{type I error}\}$. One way may be to concentrate sampling in those parts of the landscape that result in a maximization of power. Although this has not been investigated for presence–absence surveys, it has been considered for surveys of abundance. For example, Bowers (1996) used a simulation approach to show that the power of abundance surveys to detect population declines was often maximized by surveying poor-quality habitats in a spatially structured landscape. Similarly, it has been shown that for a simple source–sink model, the power to detect population declines is often higher if the sink, rather than the source, is sampled, even if the decline is caused by a reduction in reproductive output in the source (Jonzén et al. 2005).

The koala is a cryptic species that is distributed, often at low densities, across eastern Australia (Sullivan et al. 2002). These characteristics make abundance estimates difficult and costly.

¹ E-mail: jonathan.rhodes@csiro.au

² Present address: CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, TAS 7000, Australia

Therefore, presence–absence surveys (e.g., fecal pellet surveys) are often the preferred monitoring method (e.g., Reed et al. 1990, Lunney et al. 2000, Sullivan et al. 2002). Hence, how to optimize our ability to detect temporal trends in abundance using these survey methods is an important issue for koala managers.

In this paper, we use a spatially explicit simulation model of koala population dynamics to investigate sampling strategies for optimizing the power of presence–absence surveys to detect trends in occupancy caused by a change in abundance. Alternative sampling strategies differ in the habitat qualities they target, and the monitoring process is simulated by sampling from the output of the population model (e.g., Berger et al. 1999, Grimm et al. 1999, Tyre et al. 2001). The power to detect a trend is estimated by simulating changes in abundance and fitting a statistical model to the data recorded by the simulated monitoring process. One strength of this approach is that it allows the effect of population dynamics on the power of the presence–absence surveys to be explicitly assessed.

Two issues have emerged that we aim to address. First, it is unclear as to what degree targeting particular habitat qualities with survey effort can improve the power of presence–absence surveys to detect temporal occupancy trends, especially when observation error is present. Second, how demographic and spatial population processes affect the power of presence–absence surveys to detect trends is also unclear. Consequently, our specific goals are to quantify how power changes in response to 1) sampling effort and effect size, 2) targeting particular habitat qualities with sampling effort, 3) observation error, 4) dispersal assumptions, and 5) landscape fragmentation.

Methods

Model of Population Dynamics

We used a spatially explicit individual-based population model to simulate koala population dynamics on random fractal landscapes (Tyre et al. 2001). Individual-based models allow processes that naturally occur at the level of the individual to be modeled in a realistic way. This makes the approach particularly appropriate for modeling populations in complex landscapes where landscape structure influences individual behavior. The model was a slightly modified version of that used by Tyre et al. (2001) and is described below.

The landscape upon which the simulated population resides was assumed to be a 50×50 grid of equal-area square home ranges. Each home range had an associated habitat quality, Q , arbitrarily scaled from 0 to 99. We regarded Q as a relative measure of the resource availability in each home range. For each simulation, a random landscape of fractal dimension, D , was constructed by assigning habitat qualities to each home range using a midpoint displacement algorithm (Saupe 1988). This approach allowed random landscapes to be constructed with varying degrees of spatial correlation. Spatial correlation was controlled by the parameter D , which could take any value between 2 and 3. High values of D created landscapes with low spatial correlation and vice-versa for low values (Tyre et al. 2001, fig. 1). Landscapes with low spatial correlation were more highly fragmented than landscapes with high spatial correlation. These fractal landscapes

provided an advantage over using real landscapes because their spatial properties could be tightly controlled.

The size of the landscape was chosen to approximately represent the area of a typical planning unit for koalas in the coastal areas of Australia in New South Wales and Queensland. Planning for koalas in these areas typically occurs at the local-government scale (e.g., Lunney et al. 1998, 1999). Mean home-range size estimates for female koalas in these areas range from around 15 to 50 ha in size (White 1999; J. R. Rhodes, The University of Brisbane, unpublished data). Therefore, each artificial landscape represented an area of around 40,000–125,000 ha.

The individual-based population model consisted of a set of rules that determined the fate of each individual each year. Only females were modeled, and it was assumed that each individual exclusively occupied (except for undispersed offspring) a single home range in the landscape. The model rules are described below in the order in which they were applied each year.

Reproduction.—Each individual had an age-specific annual probability of giving birth to a single individual. The annual $\Pr\{\text{giving birth}\}$ varied with habitat quality, Q , through a logistic relationship (Tyre et al. 2001). The probability, $f_{x,i}$, that an individual of age i , in a home range, x , of quality Q_x , gave birth in a given year was determined by the relationship

$$\ln\left(\frac{f_{x,i}}{1-f_{x,i}}\right) = \ln\left(\frac{f_i}{1-f_i}\right) + b\left(\frac{Q_x}{\tilde{Q}} - 1\right) \quad (1)$$

where b determined the slope of the fecundity-habitat quality relationship, \tilde{Q} was the 90th percentile habitat quality in the landscape, and f_i was the probability that an individual of age class i in a home range of quality \tilde{Q} gave birth. By scaling fecundity relative to \tilde{Q} , we corrected for differences in the distribution of habitat quality between landscapes. By choosing \tilde{Q} to represent the 90th percentile habitat quality, 10% of each landscape had fecundities greater than f_i , regardless of the exact landscape configuration. The value of f_i therefore represented the fecundity rate in the ninetieth percentile habitat quality. Assuming the sex ratio at birth was 1:1 led to a probability of giving birth to a female of $0.5f_{x,i}$.

Survival.—Each individual of age i had an age-specific probability, s_i , of surviving to age $i + 1$, up to the maximum age, A_{max} . This survival probability was assumed to include mortality due to age, disease, predation, and human-induced mortality, such as vehicle collisions.

Dispersal.—The understanding of dispersal processes for koalas and other arboreal marsupials is limited. Therefore, rather than speculate about the exact nature of koala dispersal behavior we used a generic model of dispersal that has been used previously for simulating dispersal in other arboreal marsupials (Tyre et al. 2001).

Each undispersed individual of age i had an annual age-specific probability of dispersing, d_i , and the dispersal process took place just prior to the following year's breeding season. All dispersing individuals simultaneously took consecutive dispersal steps until they had successfully dispersed or suffered a mortality event (see *Dispersal Mortality* section). Each dispersal step consisted of the individual choosing a move to one of the 8 immediately adjacent home ranges. The probability, m_x , of moving to a home range, x , was defined as

$$m_x = \frac{Q_x^\gamma}{\sum_{i=1}^8 Q_i^\gamma} \quad (2)$$

where $i = 1, \dots, 8$ represented the immediately adjacent home ranges, and γ was the dispersal selectivity index. The dispersal selectivity index controlled how much more the probability of selecting a higher-quality home range was than the probability of selecting a lower-quality home range. Once an individual reached a vacant home range it had successfully dispersed and so stopped. If an encountered home range was occupied by a younger or same-age individual, the resident individual was displaced with a probability of 0.5. If a displacement event occurred, the dispersing individual took up residence of that home range and the displaced individual continued dispersal. Only home ranges within the landscape confines were available (i.e., the probability of moving outside the landscape was zero).

If $\gamma = 0$, the probabilities of moving to any of the adjacent home ranges were the same. Conversely, if $\gamma = 1$, the probability of moving to an adjacent home range was proportional to its habitat quality, relative to the other 7 home ranges. As γ increased further, the probability of moving to better-quality home ranges, relative to poorer-quality home ranges, increased. For a given difference in Q , the difference in selection probabilities was greater in low-quality habitats than in high-quality habitats.

Dispersal mortality.—Each dispersing individual experienced a per-step probability of mortality, c , over and above age-specific mortality, due to other factors. The implication was that because they had to move further to find a vacant home range, dispersing individuals incurred higher mortality in crowded landscapes compared to less-crowded landscapes. This introduced a form of density-dependence into the model.

Monitoring Model

We used a model, which we refer to as the virtual ecologist, to simulate presence-absence monitoring surveys of the landscape (Berger et al. 1999, Grimm et al. 1999, Tyre et al. 2001). This has become a popular technique for assessing both the sampling process itself (e.g., Tyre et al. 2001) and model performance against real data (e.g., Wiegand et al. 1998). The approach attempts to mimic the process of real-world sampling from a model system.

The virtual ecologist selected a number of home ranges, n , on the landscape and then “surveyed” the same sites for presence-absence of koalas once a year for m years. We subsequently refer to these surveys as the monitoring surveys. Surveys occurred just after dispersal in year t and just prior to the breeding season in the following year. If a site was occupied at the time of a survey, it was recorded as present with probability g . If the site was unoccupied, then it was recorded as unoccupied without error. The value of g represented the probability of correctly recording the species as present, given that the home range was truly occupied (Tyre et al. 2003). The probability of recording a false-negative was $1 - g$. In real systems, detection probabilities can vary across space and time, especially with respect to a species’ abundance (Royle and Nichols 2003). However, if sampling were conducted at the home-range scale, as we assumed here, abundance would be of minor importance for detectability because an occupied home range

would always have the same abundance of 1 adult individual. Therefore, we made the reasonable assumption that g was constant and did not depend on habitat quality.

The selection of sites for the monitoring surveys was assumed to follow 1 of 2 selection strategies, described below.

(1) **Global monitoring strategy.**—Sites were chosen from the entire landscape and range of habitat qualities using simple random sampling (Thompson 1992).

(2) **Targeted monitoring strategy.**—Monitoring sites were chosen from a subset of the landscape, based on estimates of the probability that each home range was occupied. In reality, this would only be possible if we had some information about occupancy patterns. Therefore, a habitat-modeling process was initially simulated before sites were selected for the monitoring surveys. The resulting habitat model was then used as a basis for site selection.

Habitat modeling was based on a separate presence-absence survey conducted by the virtual ecologist, which coincided with the first year of monitoring surveys. We subsequently refer to these as habitat surveys. Sites for each habitat survey were chosen using a protocol that we called extensive-random sampling (Tyre et al. 2001). Extensive-random sampling stratified sites across the full range of habitat qualities, placing approximately equal numbers of sites in each stratum. Habitat surveys were also assumed to be subject to false-negative errors, with probability $1 - g$. Data from the habitat survey were then used to construct a logistic regression habitat model with the presence-absence data as the dependent variable and Q as the explanatory variable (Hosmer and Lemeshow 2000). In doing so, we assumed that Q was measured without error. This habitat model then provided an estimate of the probability of occupancy, $\hat{\pi}$, for each home range. The logistic regression model we used did not account for observation error in the presence-absence data, but this could be achieved by conducting repeat visits to each site, thereby improving the habitat models (MacKenzie et al. 2002, Tyre et al. 2003). In this study, we assumed only 1 visit per site because habitat models are often built with data of this type, and understanding the effect of observation error for these standard modeling approaches was an important objective.

After habitat modeling, we chose sites for the monitoring surveys using simple random sampling, but for this strategy the choice of sites was restricted to those home ranges where $\hat{\pi}$ was between a specified value S and $S + 0.5$ (Fig. 1). When $S = 0$, sites were only chosen from those home ranges where $\hat{\pi} < 0.5$. As S increased from 0 to 0.5, the proportion of sites chosen from those home ranges with $\hat{\pi} \geq 0.5$ increased until, when $S = 0.5$, sites were only chosen from home ranges with $\hat{\pi} \geq 0.5$. The sampled range of habitats expanded when $S \rightarrow 0$ or $S \rightarrow 0.5$ because of the nonlinear nature of the logistic habitat model (Fig. 1). These simulated strategies provided a realistic model of how we might vary sampling strategies between sampling only good-quality habitats ($\hat{\pi} \geq 0.5$, $S = 0.5$), poor-quality habitats ($\hat{\pi} < 0.5$, $S = 0.0$), or intermediate-quality habitats. Numerous other strategies were possible, but the strategies proposed here allowed us to quantify the independent effect of sampling a narrow range of habitat qualities.

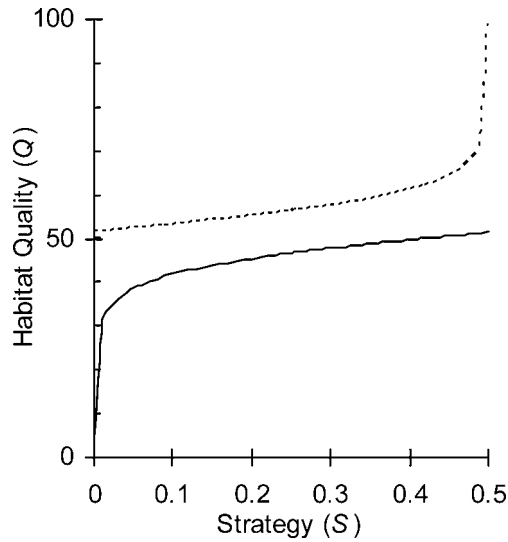


Figure 1. Intervals of habitat qualities from which sites were selected for different targeted strategies, S . Graph shows the minimum (solid line) and maximum (dashed line) habitat qualities defining the interval, for a logistic model of the form $\text{logit}(\hat{\pi}) = -11.7991 + 0.229457Q$, where, $\hat{\pi}$ is the probability of occupancy and Q is the habitat quality. The logistic model was derived from the presence-absence of each home range in the landscape at year 200 for a single simulation, with fractal dimension, $D = 2.5$ and the ninetieth percentile habitat quality, $\hat{Q} = 79$. Other parameters were as in Table 1.

Model Parameters

Baseline life-history parameters, except for dispersal, were taken from Penn et al. (2000) for the Springsure population in Queensland, Australia (Table 1). Female koalas reach sexual maturity around the end of their second year (Eberhard 1972, Gall 1980, Martin and Handasyde 1990, Melzer 1995), and we assumed that dispersal occurred at the same time. This is also broadly consistent with observed ages at dispersal (Dique et al. 2003). Tyre et al. (2001) used a per-step dispersal mortality of 0.005 when modeling movement in greater gliders (*Petauroides volans*), another folivorous arboreal marsupial. We used the same value for the koala in the absence of a more specific parameter estimate. We also assumed that the probability of a koala moving

Table 1. Baseline model parameters.

Parameter	Symbol	Value
Maximum age	A_{max}	12 ^a
Pr{survival}: age 0 to 1	s_0	0.7 ^a
Pr{survival}: age 1 to 2	s_1	0.8406 ^a
Pr{survival}: ages 2 to 3, 3 to 4, ..., 11 to 12	s_2, \dots, s_{11}	0.9153 ^a
Pr{giving birth}: age 0	f_0	0 ^a
Pr{giving birth}: age 1	f_1	0 ^a
Pr{giving birth}: ages 2 to 12	f_2, \dots, f_{12}	0.69 ^a
Pr{dispersal}: age 0 to 1	d_0	0
Pr{dispersal}: age 1 to 2	d_1	1
Dispersal selectivity index	γ	1
Pr{mortality per dispersal step}	c	0.005 ^b
Slope of fecundity-habitat quality relationship	b	5
Pr{recorded as occupied home range is occupied}	q	1
Landscape fractal dimension	D	2.5

^a Penn et al. (2000).

^b Tyre et al. (2001).

to a given home range during dispersal was proportional to its relative habitat quality, thus $\gamma = 1$. The parameter b was set so that when the population reached a quasi-equilibrium, roughly half the landscape was occupied. Simulations were run on landscapes with an intermediate fractal dimension of 2.5, which was varied from 2.1 to 2.9 in the sensitivity analysis. It is uncertain what the false-negative detection probability might be for surveys of koalas. Therefore, in the absence of further information, we initially assumed there was no observation error (i.e., $q = 1$), but explored the effect of this parameter in the sensitivity analysis.

Statistical Model and Power Analysis

The demographic model was used to simulate replicate trends in population size (see *Simulations and Scenarios* section). The power to identify the resulting trends in occupancy was then estimated from data generated by the virtual ecologist. To enable this, we fitted a first-order Markov model to each replicate of the simulated survey data (Muenz and Rubinstein 1985). Then, a likelihood ratio test was used to determine whether a significant trend in occupancy had been observed for each replicate (Hilborn and Mangel 1997). A trend was deemed to have been correctly identified if it was both significant and in the right direction. The power to detect a given trend was then estimated as the proportion of replicate simulations in which the real trend was correctly identified.

The Markov model assumed that each site, $i = 1, 2, \dots, n$, at time $t = 0, 1, \dots, m$, is in state y_{it} , such that

$$y_{it} = \begin{cases} 0 & \text{if species was absent at site } i \text{ at time } t \\ 1 & \text{if species was present at site } i \text{ at time } t \end{cases}$$

and the transition matrix was

$$P = \begin{bmatrix} p_{00} & p_{01} \\ p_{10} & p_{11} \end{bmatrix} \quad (3)$$

where, p_{jk} was the probability of going from state j to state k with the constraint $p_{00} = 1 - p_{01}$ and $p_{11} = 1 - p_{10}$.

Since we were particularly interested in trends in these transition probabilities over time, we introduced time, t , as a covariate on p_{01} and p_{10} , such that

$$p_{01}^{(t)} = \frac{\exp(\phi_{01} + \vartheta_{01}t)}{1 + \exp(\phi_{01} + \vartheta_{01}t)} \quad (4)$$

$$p_{10}^{(t)} = \frac{\exp(\phi_{10} + \vartheta_{10}t)}{1 + \exp(\phi_{10} + \vartheta_{10}t)} \quad (5)$$

where $p_{01}^{(t)}$ and $p_{10}^{(t)}$ were the transition probabilities from time t to time $t + 1$ and the unknown parameters of the model were ϕ_{01} , ϑ_{01} , ϕ_{10} , ϑ_{10} (Muenz and Rubinstein 1985).

Following this, the negative log-likelihood of the data, y_{it} , given the Markov model was

$$L = - \sum_{i=1}^n \sum_{t=0}^{m-1} \left[y_{i(t+1)} \ln p_{01}^{(t)} + (1 - y_{i(t+1)}) \ln (1 - p_{01}^{(t)}) \right] (1 - y_{it}) \\ + \sum_{i=1}^n \sum_{t=0}^{m-1} \left[(1 - y_{i(t+1)}) \ln p_{10}^{(t)} + y_{i(t+1)} \ln (1 - p_{10}^{(t)}) \right] y_{it} \quad (6)$$

where $p_{01}^{(t)}$ and $p_{10}^{(t)}$ were defined as in equation (5). This model

could be extended to include the likelihood of the initial observations at $t = 0$, but since we were only concerned with trends in transition probabilities it was not required. The derivation of the likelihood function and this extension is given in Appendix 1.

Maximum-likelihood parameter estimates for this model were obtained by minimizing equation (6) using Powell's method for multidimensional minimization (Press et al. 1992). We then tested whether the parameters ϑ_{01} and ϑ_{10} were simultaneously significantly different from zero using a likelihood ratio test and a critical $\Pr\{\text{type I error}\} = \alpha$ (Hilborn and Mangel 1997). A significant trend was deemed to be in the right direction if the predicted change in occupancy from the Markov model was in the same direction as the actual change in occupancy.

Simulations and Scenarios

For each replicate simulation, we located 1,000 individuals randomly on the landscape and allowed the model to run for 200 years to ensure that the population size and distribution had reached a quasi-equilibrium. Reducing or increasing mortality rates for all age classes linearly over a 10-year period then created different population trend scenarios. A 50% increase in mortality from our baseline parameters over 10 years equated to a mean population-size decline of around 30% over this period. This matches the IUCN criteria for a vulnerable listing (IUCN, <http://www.redlist.org>) and therefore was deemed to be an appropriate effect size. However, lower effect size scenarios (25% and 10% increases in mortality, resulting in population size declines of 15% and 6% over 10 years, respectively) were also considered. Similarly, population recovery scenarios were simulated by 50, 25, and 10% declines in mortality rates, which resulted in 22, 12, and 5% increases in population size over 10 years, respectively.

For each scenario, we simulated a global monitoring strategy and a series of targeted strategies between $S = 0$ and $S = 0.5$ in steps of 0.05. The first monitoring survey and the habitat survey were simulated immediately prior to the start of the perturbation, and subsequent monitoring surveys occurred annually over the 10-year period. Sampling effort for presence-absence surveys using fecal pellet searches for a koala management plan might typically be around 50 sites per year (e.g., Port Stephens Council 2001). We therefore set our baseline monitoring sampling effort to 50 sites per year. For the habitat surveys, we assumed 100 sites were sampled, which is a realistically attainable sampling effort for mapping koala habitat at the scale considered in this study (e.g., Lunney et al. 1998). Each scenario was replicated 500 times using a different random landscape for each replicate but the same 500 random landscapes between scenarios. For each strategy within each scenario, the power to detect the real trend in occupancy was estimated, using a critical $\alpha = 0.05$.

In order to estimate the optimal strategy, we ideally required a continuous functional relationship between power and S . However, because power was only estimated at discrete intervals of S , a functional relationship between the two was derived from the power results. This was achieved by fitting a least-squares, second-order polynomial regression to the power estimates, with S as the explanatory variable. The strategy at the maximum predicted power, P_{opt} , of this curve then determined the estimated optimal strategy, S_{opt} .

We tested the sensitivity of the optimal strategy and optimal power to a number of model parameters. In doing so, variation in the parameters q , γ , c , and D were considered because these were expected, a priori, to have a strong influence on occupancy patterns and therefore on optimal strategies.

Results

Statistical Model Fit

The Markov model, including a term in the likelihood for the observations in the first year of monitoring (see Appendix 1), had far more support when fitted to the simulated survey data than a standard logistic regression model with time, t , as an explanatory variable. For example, using a global monitoring strategy and a decline in population size (+50% mortality), the mean Akaike's information criterion (AIC) from 100 replicates for a logistic model was 717.87 (coefficient of variation = 0.069), while for the Markov model was 261.97 (coefficient of variation = 0.216). This provides overwhelming support for the Markov model relative to the standard logistic regression model (Burnham and Anderson 2002). This occurs because the Markov model takes into account the temporal dependence between years in the state of each site, while the logistic regression model falsely assumes independence between successive observations. Further, estimated changes in the probability of occupancy derived from the Markov model were not significantly biased when compared to actual changes ($P > 0.05$, Fig. 2).

Sampling Effort and Effect Size

The power to detect declines in occupancy was generally low, unless sampling effort or effect size was large. For example, a global monitoring strategy, with $\alpha = 0.05$ and a large population size decline (+50% mortality), required between 250 sites (10% of the landscape) and 500 sites (20% of the landscape) per year to obtain power greater than 0.8. If the effect size was lower (+10% mortality) then, even with half the landscape sampled per year, power was only 0.27 (95% CI = 0.23, 0.31). Very similar power versus sample-size relationships were observed for detecting increases in occupancy. Interestingly, sampling effort in the habitat surveys made very little difference to optimal targeted monitoring strategies or optimal power.

Optimal Strategies

Power analysis for the range of targeted strategies showed that, at least when the effect size was high, the optimal strategy had substantially greater power than a global strategy with the same sampling effort (Fig. 3). In addition, there were clear differences between optimal strategies for detecting declines compared to detecting increases in occupancy. For declines in occupancy, with large effect size (+50% mortality), the optimal strategy was achieved by only sampling from those home ranges with $\hat{\pi} \geq 0.5$, i.e., $S = 0.5$ (Fig. 3A). For increases in occupancy, with a large effect size (-50% mortality), the optimal strategy was achieved by sampling from those home ranges with $\hat{\pi}$ between 0.27 and 0.77, i.e., $S = 0.27$ (Fig. 3B). The optimal strategy varied slightly with effect size. However, when the effect size was low (10% change in mortality), power varied little between the global and any of the targeted monitoring strategies.

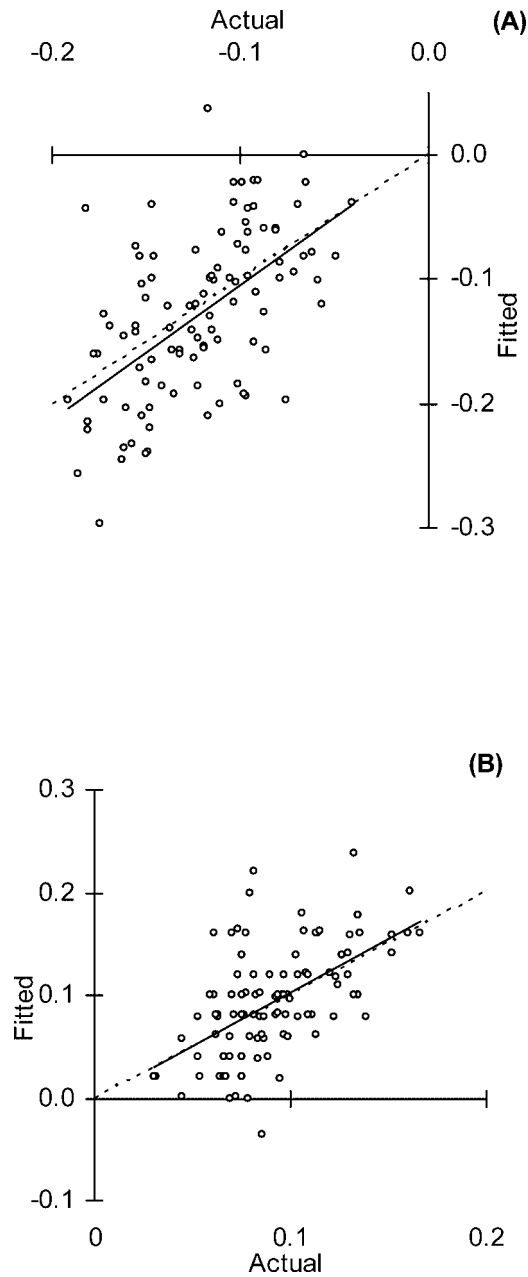


Figure 2. Actual simulated change in the probability of occupancy versus change in the probability of occupancy estimated from a Markov model fitted to (A) a decline in occupancy (+50% mortality over 10 years), and (B) an increase in occupancy (−50% mortality over 10 years). Circles show the actual simulated data points for 100 replicates and a global monitoring survey of 50 sites per year. The solid line is a linear regression through the points and the dashed line is a line through the origin with slope 1. The linear regressions have intercepts not significantly different from 0 (A: $t = 0.149$, $df = 98$, $P = 0.882$ and, B: $t = -0.091$, $df = 98$, $P = 0.928$) and slopes not significantly different from 1 (A: $t = 0.501$, $df = 98$, $P = 0.618$ and, B: $t = 0.235$, $df = 98$, $P = 0.815$). Other parameters were as in Table 1.

Sensitivity Analysis

Observation error.—With increasing observation error, the optimal monitoring strategy for detecting either declines or increases, changed towards sampling home ranges with lower $\hat{\pi}$ (Fig. 4A). Optimal power declined with increasing observation error (Fig. 4B), as did power for the equivalent global monitoring strategies.

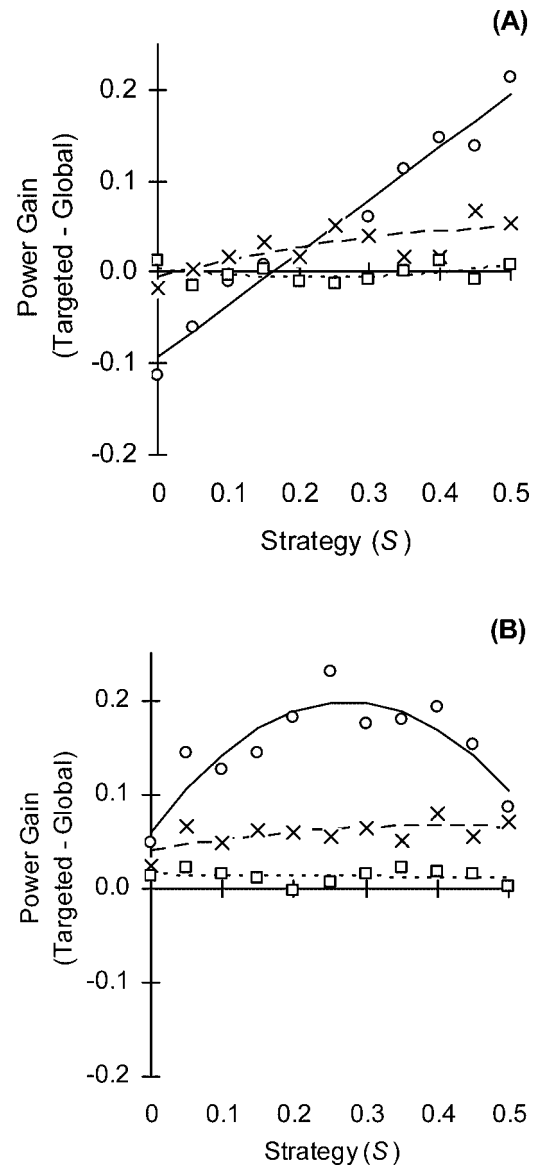


Figure 3. Estimated power of targeted, relative to global, monitoring strategies with the same sampling effort for (A) declines in occupancy, and (B) increases in occupancy. Points show the difference in power between the targeted strategy, S , and the global strategy for 50% (circles), 25% (crosses), and 10% (squares) changes in mortality over 10 years. Lines are the second-order polynomials fitted to these points. The power of the global strategies were 0.21, 0.08, and 0.05 to detect declines in occupancy, and 0.16, 0.05, and 0.04 to detect increases in occupancy for 50%, 25%, and 10% changes in mortality, respectively. Monitoring survey sampling effort was 50 sites per year, 100 sites were sampled for the habitat surveys, $\alpha = 0.05$, and 500 replicates were used. Other parameters were as in Table 1.

Dispersal mortality.—As ϵ was increased, the optimal monitoring strategy for detecting an increase in occupancy changed marginally towards sampling those home ranges with a higher $\hat{\pi}$ (Fig. 5A). There was no impact on the optimal strategy for detecting declines. Optimal power declined as ϵ increased (Fig. 5B), as did power for the equivalent global monitoring strategies.

Dispersal selectivity.—As γ changed, there was very little impact on the optimal monitoring strategy for detecting declines or increases in occupancy (Fig. 5C). Optimal power declined as γ

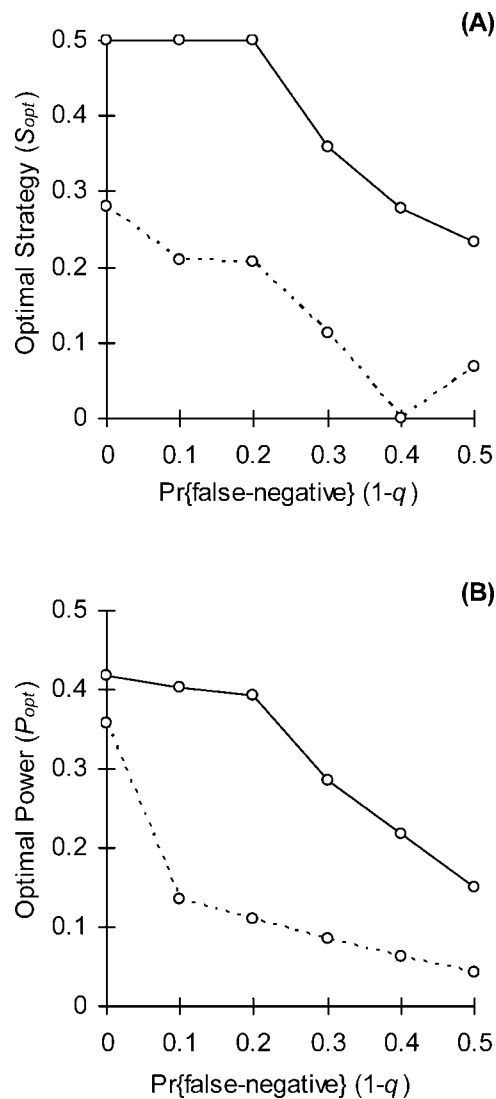


Figure 4. (A) Estimated optimal strategy, and (B) estimated optimal power for different values of false-negative error rate, $1 - q$. Graphs show results for detecting a decline in occupancy (+50% mortality over 10 years, solid line) and an increase in occupancy (-50% mortality over 10 years, dashed line). Monitoring survey sampling effort was 50 sites per year, 100 sites were sampled for the habitat surveys, $\alpha = 0.05$, and 500 replicates were used. Other parameters were as in Table 1.

increased (Fig. 5D), as did power for the equivalent global monitoring strategies.

Landscape fragmentation.—As D changed, there was little change in the optimal monitoring strategy for detecting declines or increases in occupancy (Fig. 6A). Optimal power declined as D increased (Fig. 6B). However, this decline in power was almost entirely due to a decline in the benefit of adopting a targeted monitoring strategy relative to a global strategy. For the equivalent global strategy, as D increased, power remained constant for detecting declines in occupancy and even improved for detecting increases in occupancy.

Discussion

We have investigated a method for optimizing the power of presence-absence surveys to detect population trends by targeting particular habitat qualities. We have also quantified the sensitivity

of the optimal strategies and power to observation error, dispersal parameters, and landscape fragmentation. For changes in population size of 20–30% over 10 years, a substantial improvement in power was achieved by targeting high-quality habitat to detect declines and intermediate-quality habitat to detect increases. However, targeting habitat when population size changes were small produces less improvement in power.

Changes in Occupancy and Abundance

In our study, optimal power was achieved by targeting the habitats that exhibited the largest changes in the probability of occupancy. Some studies have demonstrated that power to detect declines in abundance is maximized when poor quality habitats are surveyed preferentially because this is where population sizes change most rapidly (Bowers 1996, Jonzén et al. 2005). This may be because, if survivorship falls, poor-quality habitats will reach the point where mortality exceeds births sooner than good-quality habitats (Bowers 1996). Our results suggest that this is not necessarily the case for presence-absence data. In our simulations, the largest exponential rates of decline in abundance did indeed occur in poor-quality habitats, but, in contrast, the largest changes in the log-odds of the probability of occupancy occurred in good-quality habitats. Also, in poor-quality habitats few home ranges are occupied; therefore, the number of sites recording a transition from present to absent will be low. For standard logistic regression, a low number of events per variable leads to low power (Peduzzi et al. 1996), and this is also probably true for the Markov model. Therefore, presence-absence surveys may not detect declines in poor-quality habitat, even if this is where the largest rates of decline in abundance occur.

Sensitivity Analysis

As observation error increases, power is reduced and the optimal strategy changes to sampling habitats with lower estimated probabilities of occupancy. This is the result of 2 processes. First, false-negative errors mean that the habitat model underestimates the overall probability of occupancy. Therefore, when there are false-negative errors, in order to sample habitats with a particular true probability of occupancy, a lower estimated probability of occupancy must be targeted. Second, false-negative errors in the monitoring surveys tend to obscure the real trend in occupancy, leading to lower power.

Although we observed some change in optimal strategy for detecting increases in occupancy as dispersal parameters were changed, the effect was small. This insensitivity was somewhat surprising, but it may be because the habitat models, upon which the monitoring decisions are made, already capture some of the effects of dispersal. Tyre et al. (2001) showed that logistic regression models tend to measure the ability of individuals to reach areas, rather than birth and death processes. If this is the case, differences in dispersal parameters will intrinsically be accounted for in the occupancy patterns predicted by the habitat models, leading to little variation in optimal strategy.

Optimal monitoring strategies were also insensitive to the fractal dimension of the landscape, but the power benefit of adopting a targeted, over a global, monitoring strategy was reduced as the fractal dimension increased. This is because changes in occupancy occur more uniformly across different habitat types in the high

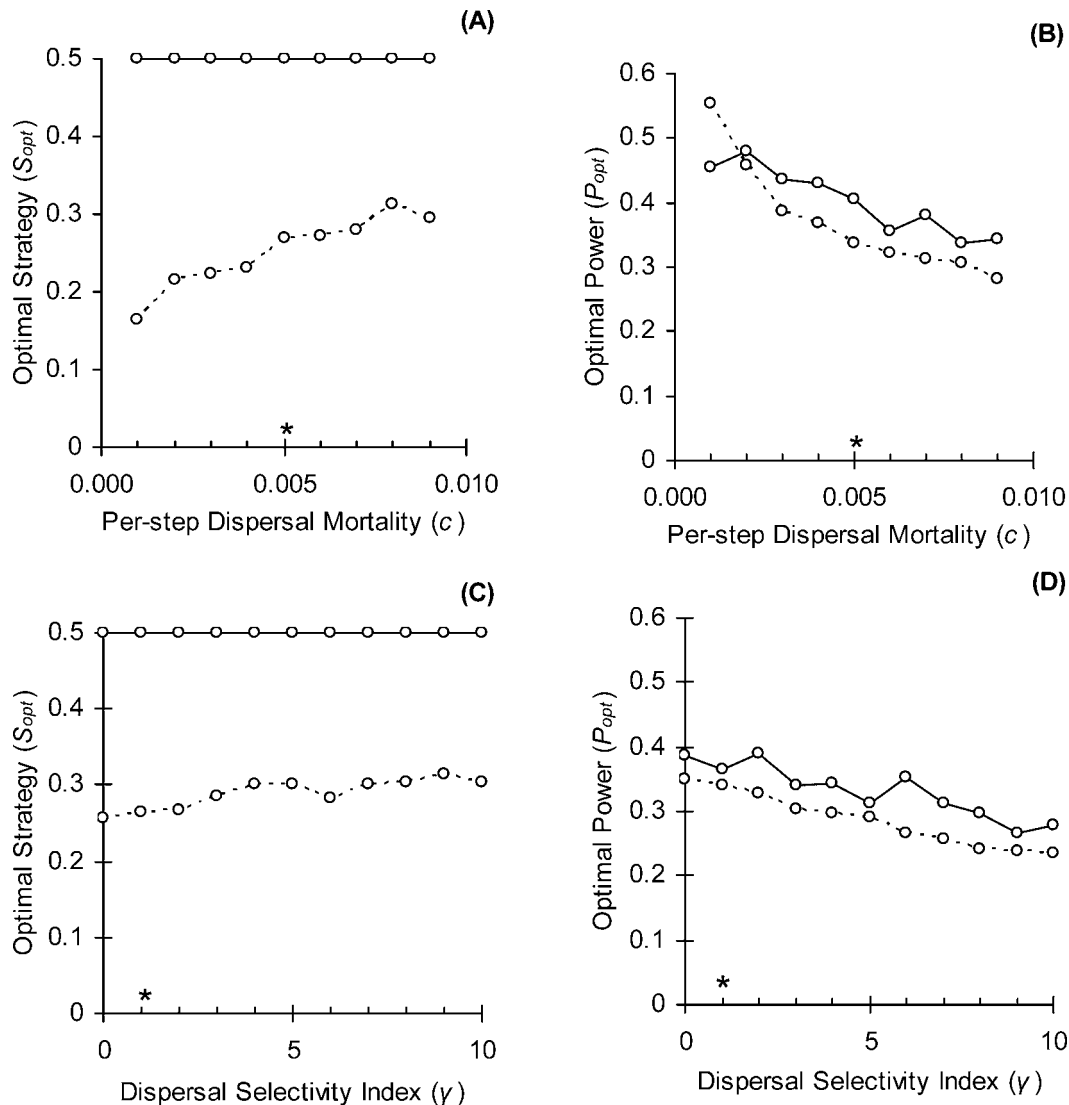


Figure 5. Estimated optimal strategy and optimal power for different values of (A, B) per-step dispersal mortality probability, c , and (C, D) dispersal selectivity index, γ . Graphs show results for detecting a decline in occupancy (+50% mortality over 10 years, solid line) and an increase in occupancy (–50% mortality over 10 years, dashed line). Monitoring survey sampling effort was 50 sites per year, 100 sites were sampled for the habitat surveys, $\alpha = 0.05$, and 500 replicates were used. Other parameters were as in Table 1 and * is the baseline parameter value.

fractal dimension landscapes (i.e., those with high levels of fragmentation). Therefore, this approach may be less useful in landscapes that are highly fragmented.

The Statistical Approach

We have demonstrated the use of a statistical framework for detecting trends in occupancy (also see MacKenzie et al. 2003). This approach performs better than standard statistical methods, such as logistic regression, that do not account for temporal correlation in the data. In addition to quantifying trends in occupancy, the Markov model also allows the estimation of colonization and extinction probabilities. This may be particularly useful in helping to identify the cause of trends in occupancy. The model can also easily be extended to include other parameters, such as habitat variables, if required (e.g., Muenz and Rubinstein 1985, MacKenzie et al. 2003).

The sensitivity of the optimal strategy and power to observation error may be problematic for the application of our method. However, statistical methods using mixture distributions that

incorporate false-negative errors have recently been applied in ecological contexts similar to ours (MacKenzie et al. 2002, 2003, Tyre et al. 2003). These methods offer a distinct advantage, especially when the false-negative error rates are expected to be high or are unknown. Using this approach would reduce the sensitivity of the optimal strategy to observation error and increase power to detect trends. However, these methods usually require a greater survey effort to estimate the false-negative error rates, although using a Bayesian approach (with prior information about the false-negative error rates) may avoid this necessity.

We presented the decision problem in a null-hypothesis framework because this is still the most commonly used approach. However, information-theoretic or Bayesian frameworks may be more useful, informative methods of making wildlife management decisions (Johnson 1999, Anderson et al. 2000). Therefore, application of these statistical methods to problems of the type we have addressed would be an important advance. However, when a frequentist null-hypothesis framework is used, as we did here, the

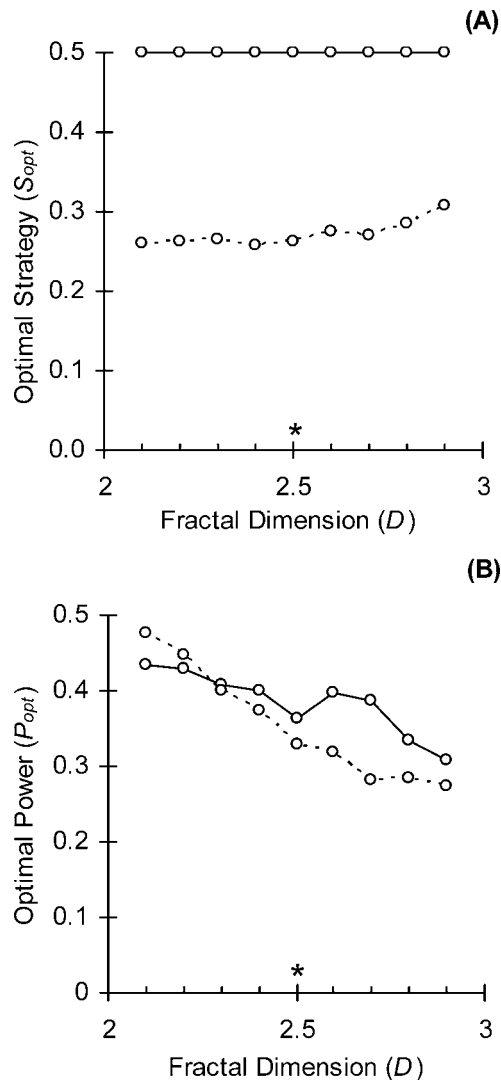


Figure 6. (A) Estimated optimal strategy, and (B) estimated optimal power for different landscape fractal dimensions, D . Graphs show results for detecting a decline in occupancy (+50% mortality over 10 years, solid line) and an increase in occupancy (–50% mortality over 10 years, dashed line). Monitoring survey sampling effort was 50 sites per year, 100 sites were sampled for the habitat surveys, $\alpha = 0.05$, and 500 replicates were used. Other parameters were as in Table 1 and * is the baseline parameter value.

$\Pr\{\text{type I error}\}$ and $\Pr\{\text{type II error}\}$ should be considered carefully. This is particularly important for presence–absence surveys because our simulations show very low power when the $\Pr\{\text{type I error}\}$ is set at 0.05. We have assumed the traditional $\Pr\{\text{type I error}\}$ of 0.05, but unless the cost of committing a type I error is much greater than committing a type II error, a larger value would be more appropriate. An appropriate solution is to set the $\Pr\{\text{type I error}\}$ and $\Pr\{\text{type II error}\}$ so that their ratio is the same as the reciprocal ratio of the costs of the errors (Mapstone 1995) or, preferably, so that the overall expected cost of the errors is minimized (Field et al. 2004).

Limitations and Future Research

An obvious drawback to implementing a monitoring strategy based on a habitat model is the requirement for a habitat model. For many species, distribution data are available and habitat modeling is a relatively common practice (e.g., Lunney et al. 1998,

Lindenmayer et al. 1999, Reunanen et al. 2002). In fact, it is common for the initial objective of wildlife management plans to be the development of a habitat model (e.g., Port Stephens Council 2001). Although we have assumed that habitat modeling coincides with the first year of monitoring, this need not necessarily be the case; the model could be based on data from a different time, or even a different area. If a habitat model were not available, an application of the proposed approach would require collection of data to build such a model, incurring additional costs, and leaving fewer resources for the monitoring surveys. However, we found that reducing the monitoring sampling effort by approximately 10% and investing this in a habitat survey still substantially increased power relative to the alternative global strategy (results not shown). So, even in the absence of a preexisting habitat model, it still appears to be worthwhile to collect the required data.

A caveat is that we have assumed we have a good habitat model, except where we have introduced observation error. The area under the receiver operating characteristic (ROC) curve averaged around 0.9 for our habitat models, which indicates good ability to discriminate between presence and absence (Pearce and Ferrier 2000). The simplifying assumption that only one variable determines the habitat quality of a home range and that this is measured without error means that models are obtained with good discrimination ability, even when only a few sites are sampled. In reality, habitat models can exhibit substantial mis-ordering of sites, and it is unclear how bad a habitat model can be before the optimal strategies are unreliable. Therefore, our results may only apply when a good habitat model is available. An important area for future research will be to assess the generality of these results for less-reliable habitat models.

Our assumptions about model structure and sampling design are important. In particular, we have implicitly assumed a 1:1 occupancy–abundance relationship. This arises from assuming that sampling occurs at the scale of single home ranges, with no change in home-range size or overlap as abundance changes. Therefore, we have only tested our method on the case in which single individuals, such as for territorial species, occupy sample sites. In other cases, occupancy–abundance relationships, although normally positive, may take a variety of nonlinear forms (Gaston et al. 2000). Without supplemental information about the form of this relationship, extrapolation to more general situations should be avoided. However, incorporating different occupancy–abundance relationships would be an important future extension.

Management Implications

The rules of thumb developed in this paper provide a useful, simple tool for designing presence–absence surveys aimed at maximizing their power to detect population trends. Our proposed approach requires a habitat model and therefore may be particularly useful in situations in which habitat models have already been developed. However, even if a habitat model does not exist, the efficiency gained by building the habitat model can more than compensate for the cost of its development.

Managers using presence–absence surveys for monitoring will often only realistically be concerned with detecting large changes in occupancy because power for detecting small changes is so low. However, our results suggest that, by optimizing power for

detecting large effect sizes (50% change in mortality), the outcome for detecting small effect sizes (10% change in mortality) will never be much worse than the optimal strategy for the small effect size anyway. This is a particularly useful additional result for wildlife managers who aim to detect a range of effect sizes. This is because they may only need to concentrate on achieving the optimal strategy for large effect sizes.

We have addressed a specific monitoring objective, which was to determine whether a trend in occupancy or abundance has occurred. However, monitoring is commonly conducted for a variety of reasons, including obtaining landscape-wide estimates of the magnitude of population change and investigating why a change has occurred (Bart and Klosiewski 1989, Shea et al. 2002). If monitoring strategies are designed to optimize the power to detect trends, as outlined in this paper, then strategies may be sub-

optimal for achieving other objectives. This should be an important further consideration for wildlife managers designing presence-absence monitoring programs.

Acknowledgments

We thank B. Lubow, B. Wintle, and 1 anonymous reviewer whose constructive and insightful comments improved earlier versions of this paper substantially. J. R. R. was funded by the Australian Research Council and the Australian Koala Foundation. N. J. is grateful to The Swedish Foundation for International Cooperation in Research and Higher Education (STINT) for financially supporting his postdoctoral visit to The Ecology Centre at The University of Queensland. This paper is a contribution of the University of Nebraska Agricultural Research Division, Lincoln, NE 68583, Journal Series No. 14400.

Literature Cited

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Bart, J., and S. P. Klosiewski. 1989. Use of presence-absence to measure changes in avian density. *Journal of Wildlife Management* 53:847–852.
- Berger, U., G. Wagner, and W. F. Wolff. 1999. Virtual biologists observe virtual grasshoppers: an assessment of different mobility parameters for the analysis of movement patterns. *Ecological Modelling* 115:119–127.
- Bowers, M. A. 1996. Species as indicators of large-scale environmental change: a computer simulation model of population decline. *Ecoscience* 3:502–511.
- Buckland, S. T., and D. A. Elston. 1993. Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* 30:478–495.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, New York, USA.
- Dique, D. S., J. Thompson, H. J. Preece, D. L. de Villiers, and F. N. Carrick. 2003. Dispersal patterns in a regional koala population in south-east Queensland. *Wildlife Research* 30:281–290.
- Eberhard, I. D. 1972. *Ecology of the koala, Phascolarctos cinereus* (Goldfuss), on Flinders Chase, Kangaroo Island. Dissertation, The University of Adelaide, Adelaide, Australia.
- Field, S. A., A. J. Tyre, N. Jonzén, J. R. Rhodes, and H. P. Possingham. 2004. Minimizing the cost of environmental management decisions by optimizing statistical thresholds. *Ecology Letters* 7:669–675.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Gall, B. C. 1980. Aspects of the ecology of the koala, *Phascolarctos cinereus* (Goldfuss), in Tucki Tucki Nature Reserve, New South Wales. *Australian Wildlife Research* 7:167–76.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. *Journal of Applied Ecology* 37:39–59.
- Gerrodette, T. 1987. A power analysis for detecting trends. *Ecology* 68:1364–1372.
- Grimm, V., T. Wyszomirski, D. Aikman, and J. Uchmanski. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. *Ecological Modelling* 115:275–282.
- Hilborn, R., and M. Mangel. 1997. *The ecological detective. Confronting models with data*. Princeton University Press, Princeton, New Jersey, USA.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. Second edition. John Wiley & Sons, New York, New York, USA.
- James, F. C., C. E. McCulloch, and D. A. Wiedenfeld. 1996. New approaches to the analysis of population trends in land birds. *Ecology* 77:13–27.
- Jassby, A. D., and T. M. Powell. 1990. Detecting changes in ecological time series. *Ecology* 71:2044–2052.
- Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:763–772.
- Jonzén, N., J. R. Rhodes, and H. P. Possingham. 2005. Trend detection in source-sink systems: when should sink habitats be monitored? *Ecological Applications* 15:326–334.
- Kendall, K. C., L. H. Metzgar, D. A. Patterson, and B. M. Steele. 1992. Power of sign surveys to monitor population trends. *Ecological Applications* 2:422–430.
- Lindenmayer, D. B., R. B. Cunningham, M. L. Pope, and C. F. Donnelly. 1999. The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecological Applications* 9:594–611.
- Lindenmayer, D. B., M. A. McCarthy, K. M. Parris, and M. L. Pope. 2000. Habitat fragmentation, landscape context, and mammalian assemblages in southeastern Australia. *Journal of Mammalogy* 81:787–797.
- Lunney, D., A. Matthews, C. Moon, and S. Ferrier. 2000. Incorporating habitat mapping into practical koala conservation on private lands. *Conservation Biology* 14:669–680.
- Lunney, D., C. Moon, A. Matthews, and J. Turbill. 1999. Coffs Harbour City koala plan of management. Part A. The plan. NSW National Parks and Wildlife Service, Hurstville, Australia.
- Lunney, D., S. Phillips, J. Callaghan, and D. Coburn. 1998. Determining the distribution of koala habitat across a shire as a basis for conservation: a case study from Port Stephens, New South Wales. *Pacific Conservation Biology* 4:186–196.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- Mapstone, B. D. 1995. Scalable decision rules for environmental impact studies: effect size, type I, and type II errors. *Ecological Applications* 5:401–410.
- Martin, R., and K. Handasyde. 1990. Population dynamics of the koala (*Phascolarctos cinereus*) in southeastern Australia. Pages 75–84 in A. K. Lee, K. A. Handasyde, and G. D. Sanson, editors. *Biology of the koala*. Surrey Beatty & Sons, Chipping Norton, Australia.
- Melzer, A. 1995. Aspects of the ecology of the koala, *Phascolarctos cinereus* (Goldfuss, 1817), in the sub-humid woodlands of central Queensland. Dissertation, University of Queensland, St. Lucia, Australia.
- Miller, J., and J. Franklin. 2002. Modeling the distribution of four vegetation alliances using generalized linear models and classification trees with spatial dependence. *Ecological Modelling* 157:227–247.
- Morris, D. W. 1994. Habitat matching: alternatives and implications to populations and communities. *Evolutionary Ecology* 8:387–406.
- Muenz, L. R., and L. V. Rubinstein. 1985. Markov models for covariate dependence of binary sequences. *Biometrics* 41:91–101.
- Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225–245.
- Peduzzi, P., J. Concato, E. Kemper, T. R. Holford, and A. R. Feinstein. 1996. A simulation study of the number of events per variable in logistic regression analysis. *Journal of Clinical Epidemiology* 49:1373–1379.
- Penn, A. M., W. B. Sherwin, G. Gordon, D. Lunney, A. Melzer, and R. C. Lacy. 2000. Demographic forecasting in koala conservation. *Conservation Biology* 14:629–638.
- Peterman, R. M. 1990. Statistical power analysis can improve fisheries

research and management. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2–15.

Port Stephens Council. 2001. Port Stephens Council comprehensive koala plan of management. Part 1: the CKPoM. Port Stephens Council, Raymond Terrace, Australia.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in C. The art of scientific computing. Second edition. Cambridge University Press, Cambridge, United Kingdom.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137:S50–S66.

Reed, P. C., D. Lunney, and P. Walker. 1990. A 1986–1987 survey of the koala *Phascolarctos cinereus* (Goldfuss) in New South Wales and an ecological interpretation of its distribution. Pages 55–74 in A. K. Lee, K. A. Handasyde, and G. D. Sanson, editors. *Biology of the koala*. Surrey Beatty & Sons, Chipping Norton, Australia.

Reunanen, P., A. Nikula, M. Mönkkönen, E. Hurme, and V. Nivala. 2002. Predicting occupancy for the Siberian flying squirrel in old-growth forest patches. *Ecological Applications* 12:1188–1198.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790.

Saupe, D. 1988. Algorithms for random fractals. Pages 71–136 in H. Peitgen, and D. Saupe, editors. *The science of fractal images*. Springer-Verlag, New York, New York, USA.

Shea, K., and M. Mangel. 2001. Detection of population trends in threatened coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:375–385.

Shea, K., H. P. Possingham, W. W. Murdoch, and R. Roush. 2002. Active adaptive management in insect pest and weed control: intervention with a plan for learning. *Ecological Applications* 12:927–936.

Strayer, D. L. 1999. Statistical power of presence-absence data to detect population declines. *Conservation Biology* 13:1034–1038.

Sullivan, B. J., G. S. Baxter, and A. T. Lisle. 2002. Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-east Queensland. I. Faecal pellet sampling protocol. *Wildlife Research* 29:455–462.

Thompson, S. K. 1992. *Sampling*. John Wiley & Sons, New York, New York, USA.

Tyre, A. J., H. P. Possingham, and D. B. Lindenmayer. 2001. Inferring process from pattern: can territory occupancy provide information about life history parameters? *Ecological Applications* 11:1722–1737.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* 13: 1790–1801.

White, N. A. 1999. Ecology of the koala (*Phascolarctos cinereus*) in rural south-east Queensland, Australia. *Wildlife Research* 26:731–744.

Wiegand, T., J. Naves, T. Stephan, and A. Fernandez. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs* 68:539–570.

Associate Editor: Lubow.

Appendix 1. The Markov Model Likelihood Function.

We can write the properties of the Markov chain relating to equations (3), (4), and (5) as

$$p_{01}^{(t)} = \Pr\{Y_{t+1} = 1 | Y_t = 0\}$$

and

$$p_{10}^{(t)} = \Pr\{Y_{t+1} = 0 | Y_t = 1\} \quad (A.1)$$

Therefore, at any given site, i , and for the observation $y_{i(t+1)}$, at time $t+1$, if the observation y_{it} at time t , is zero, then the contribution to the log-likelihood is

$$y_{i(t+1)} \ln p_{01}^{(t)} + (1 - y_{i(t+1)}) \ln(1 - p_{01}^{(t)}) \quad (A.2)$$

and if the observation y_{it} at time t , is 1, then the contribution to the log-likelihood is

$$(1 - y_{i(t+1)}) \ln p_{10}^{(t)} + y_{i(t+1)} \ln(1 - p_{10}^{(t)}) \quad (A.3)$$

Summing the log-likelihood contributions over $t = 0, \dots, m-1$, for any given site, i , we get the negative log-likelihood function

$$L_i = - \sum_{t=0}^{m-1} \left[y_{i(t+1)} \ln p_{01}^{(t)} + (1 - y_{i(t+1)}) \ln(1 - p_{01}^{(t)}) \right] (1 - y_{it}) \\ - \sum_{t=0}^{m-1} \left[(1 - y_{i(t+1)}) \ln p_{10}^{(t)} + y_{i(t+1)} \ln(1 - p_{10}^{(t)}) \right] y_{it} \quad (A.4)$$

If we then assume that the y_{it} are independent identically distributed across sites, then the negative log-likelihood in equation (A.4) can be summed over all sites, $i = 1, \dots, n$, to obtain equation (6)

$$L = - \sum_{i=1}^n \sum_{t=0}^{m-1} \left[y_{i(t+1)} \ln p_{01}^{(t)} + (1 - y_{i(t+1)}) \ln(1 - p_{01}^{(t)}) \right] (1 - y_{it}) \\ - \sum_{i=1}^n \sum_{t=0}^{m-1} \left[(1 - y_{i(t+1)}) \ln p_{10}^{(t)} + y_{i(t+1)} \ln(1 - p_{10}^{(t)}) \right] y_{it} \quad (A.5)$$

Since we were only interested in estimating transition probabilities we did not include a term in the negative log-likelihood function for the probability of the observations at $t = 0$, but the model can easily be extended to include such a term (Muenz and Rubinstein 1985). The full negative log-likelihood of the model in this case is

$$L = - \sum_{i=1}^n y_{i0} \ln(\pi) + (1 - y_{i0}) \ln(1 - \pi) \\ - \sum_{i=1}^n \sum_{t=0}^{m-1} \left[y_{i(t+1)} \ln p_{01}^{(t)} + (1 - y_{i(t+1)}) \ln(1 - p_{01}^{(t)}) \right] (1 - y_{it}) \\ - \sum_{i=1}^n \sum_{t=0}^{m-1} \left[(1 - y_{i(t+1)}) \ln p_{10}^{(t)} + y_{i(t+1)} \ln(1 - p_{10}^{(t)}) \right] y_{it} \quad (A.6)$$

where, π is the probability of occupancy at $t = 0$. The first term in equation (A.6) is the likelihood of the initial observations.

ERRATA

CONROY, M. J., P. BEIER, H. QUIGLEY, and M. R. VAUGHAN. 2006. Improving the use of science in conservation: lessons from the Florida panther. *Journal of Wildlife Management* 70:1–7.

Beier et al. (2006), the companion paper cited throughout the article, is missing from the literature cited. Citations in the online article incorrectly point to Beier et al. (undated). The correct citation is:

BEIER, P., M. R. VAUGHAN, M. J. CONROY, and H. QUIGLEY. 2006. Evaluating scientific inferences about the Florida panther. *Journal of Wildlife Management* 70:236–245.

Beier et al. (2003) is incorrectly listed in the literature cited as Beier et al. (undated). The correct citation is:

BEIER P., VAUGHAN M. R., CONROY M. J., QUIGLEY H. 2003. An analysis of scientific literature related to the Florida panther. Final report. Florida Fish and Wildlife Conservation Commission, Tallahassee, USA.

JWM apologizes to the authors for this error.

RHODES, J. R., A. J. TYRE, N. JONZÉN, C. A. McALPINE, and H. P. POSSINGHAM. 2006. Optimizing presence-absence surveys for detecting population trends. *Journal of Wildlife Management* 70:8–18.

Equation (1) on page 9 should read:

$$\ln\left(\frac{f_{x,i}}{1-f_{x,i}}\right) = \ln\left(\frac{f_i}{1-f_i}\right) + b\left(\frac{Q_x}{\bar{Q}} - 1\right)$$

JWM apologizes to the authors for this error.