Abstract: Statistical models of species distributions rely on data on species occupancy, or use, of sites across space and/or time. For rare or cryptic species, indirect signs, such as dung, may be the only realistic means of determining their occupancy status across broad spatial extents. However, the consequences of sign decay for errors in estimates of occupancy have not previously been considered. If signs decay very rapidly, then false-negative errors may occur because signs at an occupied site have decayed by the time it is surveyed. On the other hand, if signs decay very slowly, false-positive errors may occur because signs remain present at sites that are no longer occupied. We addressed this issue by quantifying, as functions of sign decay and accumulation rates: 1) the false-negative error rate due to sign decay and, 2) the expected time interval prior to a survey within which signs indicate the species was present; as this time interval increases, false-positives become more likely. We then applied this to the specific example of koala Phascolarctos cinereus occupancy derived from faecal pellet surveys using data on faecal pellet decay rates. We show that there is a clear trade-off between false-negative error rates and the potential for false-positive errors. For the koala case study, false-negative errors were low on average and the expected time interval prior to surveys that detected pellets indicate the species was present within less than 2-€“3 yr. However, these quantities showed quite substantial spatial variation that could lead to biased parameter estimates for distribution models based on faecal pellet surveys. This highlights the importance of observation errors arising from sign decay and we suggest some modifications to existing methods to deal with this issue.
The Consequences of Using Indirect Signs that Decay to Determine Species’ Occupancy

Jonathan R. Rhodes, Daniel Lunney, Chris Moon, Alison Matthews, Clive A. McAlpine

J. R. Rhodes (j.rhodes@uq.edu.au) and C. A. McAlpine, The University of Queensland, Centre for Remote Sensing and Spatial Information Science, School of Geography, Planning and Environmental Management, Brisbane, QLD 4072, Australia and The University of Queensland, The Ecology Centre, Brisbane, QLD 4072, Australia. - D. Lunney, C. Moon and A. Matthews, Department of Environment and Climate Change (NSW), P. O. Box 1967, Hurstville, NSW 2220, Australia. - D. Lunney, School of Biological Sciences and Biotechnology, Murdoch University, WA 6150, Australia. - A. Matthews, Institute for Land, Water and Society, Charles Sturt University, P. O. Box 789, Albury, NSW 2640, Australia.
Abstract

Statistical models of species’ distributions rely on data on species’ occupancy, or use, of sites across space and/or time. For rare or cryptic species, indirect signs, such as dung, may be the only realistic means of determining their occupancy status across broad spatial extents. However, the consequences of sign decay for errors in estimates of occupancy have not previously been considered. If signs decay very rapidly, then false-negative errors may occur because signs at an occupied site have decayed by the time it is surveyed. On the other hand, if signs decay very slowly, false-positive errors may occur because signs remain present at sites that are no longer occupied. We addressed this issue by quantifying, as functions of sign decay and accumulation rates: (1) the false-negative error rate due to sign decay and, (2) the expected time interval prior to a survey within which signs indicate the species was present. As the expected time interval prior to a survey that detected signs relate increases, false-positives become more likely. We then applied this to the specific example of koala *Phascolarctos cinereus* occupancy derived from faecal pellet surveys using data on faecal pellet decay rates. We show that there is a clear trade-off between false-negative error rates and the potential for false-positive errors. For the koala case study, false-negative errors were low on average and the expected time interval prior to surveys that detected pellets relate were mostly within 2-3 years. However, these quantities showed quite substantial spatial variation that could lead to biased parameter estimates for distribution models based on faecal pellet surveys. This highlights the importance of observation errors arising from sign decay and we suggest some modifications to existing methods to deal with this issue.
Introduction

Statistical models of species’ distributions are important tools for understanding spatial and temporal patterns in ecology (Guisan et al. 2006). These models often depend on data on species’ occupancy, or use, of sites across space and time that are often derived from direct observations of the species. However, the large sampling effort required for understanding broad spatial and temporal patterns using direct observations (e.g., Link and Sauer 1998) may be impractical for many species, especially for those that are cryptic or rare. An alternative is to identify species’ occupancy based on indirect, but easily observable, signs of the presence of the species (e.g., Kendall et al. 1992, Wilson and Delahay 2001, Stephens et al. 2006, McAlpine et al. 2008). However, indirect signs (e.g., dung or snow tracks) decay and disappear over time, resulting in two potential problems for their use in estimating occupancy. First, sign decay may lead to false-negative observation errors if a species occupies a site, but fails to be detected because the signs have disappeared by the time the site is surveyed. Second, the length of the time interval prior to the survey within which indirect signs indicates the species was present at least once will depend on the rate at which signs decay (Hiby and Lovell 1991). If this interval is long, then the species may no longer occupy a site even though signs are still present, resulting in false-positive errors. Although a number of statistical methods have recently been developed to account for observation error in occupancy models (MacKenzie et al. 2002, Tyre et al. 2003, Royle and Link 2006), the consequences of errors arising from the decay of indirect signs has not been considered.

Surveys of indirect signs record the presence of a species within a time interval prior to the survey, rather than only at the time of the survey. The probability that signs left at an occupied site have decayed by the time of the survey (i.e., the probability of a false-negative) will depend on the rate of sign decay. If signs decay rapidly, then the false-negative rate will be higher than if signs decay slowly. If the resulting observation errors, and their variation
among sites, are not accounted for in species’ distribution models biased parameter estimates can result (e.g., Simonetti 1989). However, the rate of sign decay also determines the time interval within which signs are a record of a species’ presence (Hiby and Lovell 1991). If signs decay slowly, on average, signs present at the time of a survey will relate to the presence of the species within a longer time interval than if signs decay rapidly. If the time interval is long enough that the occupancy status of the site has changed, then false-positive errors can also occur (i.e., the species did occupy the site, but no longer occupies the site). Consequently, signs that decay slowly will have low false-negative error rates, but may be prone to false-positive errors if the time interval to which the signs relate is long enough (Hone and Martin 1998).

Standard methods that account for observation errors in occupancy surveys rely on observations of species’ presence and absence from repeat surveys of the same sites over a short period of time (MacKenzie, et al. 2002, Tyre, et al. 2003, Royle and Link 2006). Observation errors are then estimated from the variation in recorded presences and absences at sites resulting from false-positive and/or false-negative errors in the recorded occupancy. However, if the occupancy status of a species is inferred from the presence or absence of indirect signs, repeat surveys of a site provides no information about errors that arise from the imperfect link between the presence of signs and the presence of the species. This is because, each repeat survey of a site, samples exactly the same signs. Therefore, any variation in the observed presence or absence of signs can only occur due to failures to detect the signs (false-negative) or due to the recording of signs in error (false-positive). Hence, this approach will only account for observation errors related to the imperfect observation of signs and not of the species. Therefore, there is a critical need to understand the consequences of sign decay for occupancy estimates and to develop methods for correcting the resulting bias in models of species’ distributions or habitat use.
In this paper we address this issue by quantifying the magnitude of false-negative errors that result from sign decay and the time interval prior to a survey that detected signs relate as functions of sign decay and accumulation rates. Then, we present an example of koala *Phascolarctos cinereus* occupancy determined from dung surveys, and quantify the spatial and temporal variation in false-negative error rates and time intervals using data from koala dung decay trials. We show that, by quantifying sign decay rates we can understand the potential magnitude of observation errors that arise from the decay process and develop simple strategies for reducing their effects. We conclude by suggesting some modifications to existing survey and analysis methods that may enable observation errors that arise from sign decay to be minimised, or explicitly accounted for in modelling species’ distributions.

**Methods**

Our focus is on observation errors that arise from the process of sign decay over time. In particular, we consider those errors that can arise from: (1) the absence of signs at an occupied site because the signs have decayed (false-negative), and (2) the presence of signs at a site that is currently unoccupied because the signs relate to a time when the site was occupied (false-positive). In doing so, we acknowledge that observation errors can also occur due to imperfect detection and misidentification of the signs themselves (false-negatives and false-positives) and the failure of a species present at a site to leave signs (false-negative). We believe that current approaches deal with the former case adequately (MacKenzie, et al. 2002, Royle and Link 2006), while in the latter case, we would expect for most practical signs (e.g., dung or snow tracks), that the probability of a species not leaving any signs, given that it is present to be negligible. Therefore we only focus on observation errors that arise directly from the process of sign decay.
We quantified false-negative error rates arising from sign decay by assuming that a site is occupied, simulating sign decay and accumulation through time and then calculating the probability that no signs remain at the time of a survey. A key assumption we made is that there has been no change in occupancy status over time. This assumption may break down if the time interval prior to the survey that the signs relate is long relative to the rate of change in occupancy status. If this is the case, then false-positive errors may arise. However, it is not possible to calculate the actual false-positive rate without information on the change in occupancy over time. As an alternative, we calculated the time interval prior to a survey that signs relate based on the expected age of signs that would be detected at an occupied site. This provided an indicator of the potential for false-positives to occur. We simulated these two quantities for a range of sign accumulation and decay rates. Then, we applied this framework to a case study of koala occupancy determined by faecal pellet surveys using data on faecal pellet decay rates.

**General Case**

Assume that a species occupies a site and leaves \(Y\) signs per day and that this is constant through time (we formulate the problem here in terms of a daily time interval, but any other suitable unit of time could be substituted). Also, assume that a survey of signs is conducted at time \(t\) and that \(\Pr(T > t \mid v)\) is the probability that a sign deposited on day \(v\) survives until least day \(t\). If \(s_u\) is the probability of surviving day \(u\), then \(\Pr(T > t \mid v) = \prod_{u=v}^{t} s_u\). Now, the probability that all signs at a site have decayed by time \(t\) (i.e., the probability no signs are detected, given the site is occupied; the false-negative rate) is

\[
\Pr(X = 0 \mid \text{occupies site}) = \prod_{v=t-d}^{t} \left(1 - \Pr(T > t \mid v)\right)^Y,
\]  

(1)
where $X$ is the number of signs found during the survey and $d$ is a period of time long enough that $\Pr(T > t \mid t - d)$ is very small, i.e. $\Pr(T > t \mid t - d) \approx 0$. Hence, the false-negative rate (eq. 1) is a function of the sign accumulation and decay rates. Further, the expected age of signs found at the time of a survey (i.e., the time interval prior to the survey that signs relate) is

$$E(t - \nu) = \frac{\sum_{t - d}^{t} \Pr(T > t \mid \nu)(t - \nu)}{\sum_{t - d}^{t} \Pr(T > t \mid \nu)} ,$$

(2)

where $t - \nu$ is the sign age. Note here that, because we assume $Y$ does not depend on $\nu$ (i.e., is assumed to be constant through time), the $Y$s cancel out in eq. 2 and the expected sign age only depends on the rate of sign decay. If $E(t - \nu)$ is high relative to the period of time over which occupancy is expected to change, then false-positive errors may occur. We evaluated the false-negative error rate and expected sign age for a range of sign survival and accumulation rates, while assuming both rates are constant through time and setting $d = 1,000,000$.

Case Study: Koala Faecal Pellet Surveys

The koala is a cryptic arboreal marsupial, often occurring at low densities in forests and it can easily be missed at a site even if it is present. In contrast, their distinctive dung (usually referred to as faecal pellets) can readily be found under trees they have occupied.

Consequently, pellet surveys have been used as a practical approach for determining the occupancy status of koalas across broad spatial extents (McAlpine et al. 2006, Rhodes et al. 2006, McAlpine, et al. 2008, Rhodes et al. 2008). In addition, pellet surveys have been used to determine preferences for tree species and habitat types (Lunney et al. 2000, Phillips et al. 2000) and counts of pellets have been used to provide abundance estimates (Sullivan et al. 2004). Much research and land-use planning for koalas now depends on this field technique,
and it increasingly underpins local government koala management plans (e.g., Lunney et al. 1999). Understanding the consequences of pellet decay for occupancy surveys of koalas is therefore crucial.

Based on the framework developed above, we investigated the potential for false-negative or false-positive errors in koala occupancy estimates determined from faecal pellet surveys. Bayesian models of pellet decay (survival models) were first developed using pellet decay trial data conducted in two study areas in eastern Australia. Then, using estimates of koala densities and defecation rates to calculate accumulation rates, we applied eqns 1 and 2 to estimate false-negative error rates and expected pellet ages.

Koala Faecal Pellet Decay Trials

During 1996 and 1997 koala pellet decay trials were conducted in two study areas in New South Wales, Australia: Coffs Harbour on the north coast and Port Stephens on the central coast. In each study area, trials were conducted across a range of koala habitats and seasons between April 1996 and March 1997. In Port Stephens, the trials were conducted in five plots within a single site. In Coffs Harbour, the trials were conducted within five sites, with three plots nested within each site. At each site, the plots were located in different topographic positions: one on a ridge, one on a mid-slope, and one in a gully (exceptions to this were that, in one site, all three plots were classified as gully and, in another site, there were two plots for each topographic position). Each month, a group of 10 fresh koala pellets was laid out in each plot and the number of remaining identifiable pellets was counted at approximately weekly intervals in Port Stephens and fortnightly intervals in Coffs Harbour. Detailed descriptions of the study sites and plots are given in the Supplementary material.
Survival Models

We developed Bayesian statistical models of koala pellet decay rates as functions of spatial and temporal explanatory variables. The spatial variables were categorical and consisted of “plot” for Port Stephens, and “site” and “topography” for Coffs Harbour (Table 1). The temporal variables were continuous and consisted of “pellet age”, “daily rainfall”, “daily mean humidity”, and “daily mean temperature” for both study areas (Table 1). Meteorological data were obtained from the Australian Bureau of Meteorology. The spatial and temporal variables (except pellet age) were chosen to represent variation in environmental conditions across space and time. Microclimatic conditions in each plot were not specifically measured, but site, plot and topography were used as proxies for spatial variation in environmental conditions. Pellet age was considered because dung decay rates have commonly been found to depend on age (Barnes and Barnes 1992, Laing et al. 2003).
Table 1. Descriptions of the explanatory variables.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site *</td>
<td>Categorical variable specifying the site (only applies to Coffs Harbour)</td>
</tr>
<tr>
<td>Plot *</td>
<td>Categorical variable specifying the plot (only applies to Port Stephens)</td>
</tr>
<tr>
<td>Topography *</td>
<td>Categorical variable (ridge, mid-slope or gully) specifying the topography of each plot (only applies to Coffs Harbour)</td>
</tr>
<tr>
<td>Age †</td>
<td>Pellet age (days)</td>
</tr>
<tr>
<td>Rainfall †</td>
<td>Daily rainfall (mm)</td>
</tr>
<tr>
<td>Humidity †</td>
<td>Daily mean humidity (%)</td>
</tr>
<tr>
<td>Temperature †</td>
<td>Daily mean temperature (°C)</td>
</tr>
</tbody>
</table>

* = spatial variables, † = temporal variables

We used a discrete-time survival model with a daily resolution and specified the daily pellet survival probability as a function of the spatial and temporal explanatory variables. The daily survival probability on day \( t \) was defined as the probability that a pellet survives day \( t \), given survival up to day \( t - 1 \), i.e., \( \Pr(T > t \mid T > t - 1) \). Given the length of time between data points (the sampling interval), a daily time resolution was considered to be sufficiently small to approximate the continuous process of pellet decay. Further, temporal explanatory variables (e.g., rainfall) were available at a daily resolution, so it did not make sense to try to model survival at a finer temporal resolution.

We specified the daily survival probability as a function of explanatory variables via a logit link function (sensu Cox 1972, Thompson 1977, Rotella et al. 2007), such that
\[
\ln \left( \frac{s_{ijt}}{1-s_{ijt}} \right) = \beta_0 + \beta'x_{ijt} + a_i,
\]

where \( s_{ijt} \) is the daily survival probability for day \( t \) in sampling interval \( j \) in pellet group \( i \); \( \beta_0 \) is the intercept; \( \beta \) is a vector of regression coefficients; \( x_{ijt} \) is a vector of explanatory variables for day \( t \) in sampling interval \( j \) in pellet group \( i \); and \( a_i \) is a random-effect for pellet group \( i \), with \( a_i \sim \text{Normal}(0, \tau_{\text{group}}) \), where “~” means “distributed as”. The random-effect term models unobserved differences between pellet groups and accounts for any within-group correlations (Pinheiro and Bates 2000, Congdon 2003). Such unobserved differences between groups is often referred to as “frailty” in the survival analysis literature (Congdon 2003). The product of the daily survival probabilities during each sampling interval then gives the probability that a pellet survives that interval, such that

\[
S_{ij} = \prod_{t=1}^{T_{ij}} s_{ijt},
\]

where \( S_{ij} \) is the probability that a pellet in group \( i \) survives sampling interval \( j \), given that it survived the previous interval, \( j - 1 \), and \( T_{ij} \) is the number of days in interval \( j \) for pellet group \( i \).

Given the interval survival probabilities, \( S_{ij} \), the number of pellets surviving each interval could be modelled as a binomial process. However, exploratory analysis revealed substantial overdispersion in the data and therefore we modelled the number of pellets surviving each interval with a beta-binomial distribution (Prentice 1986). The probability density function for the beta-binomial is

\[
\Pr(Y = y) = \binom{y}{n}p^y(1-p)^{n-y},
\]

\[p \sim \text{beta}(a,b)\]

where \( y \) is the number of successes (i.e., the number of pellets surviving the interval) from \( n \) trials (i.e., the number of pellets at the start of the interval); \( p \) is the expected probability of
success (i.e., the expected probability that a pellet survives the interval); and $a$ and $b$ are the parameters of the beta distribution. The beta-binomial distribution accounts for overdispersion by introducing extra-binomial variation into the binomial process.

We used a specific parameterisation of the beta-binomial model (see Prentice 1986) in which the marginal likelihood of the data is

$$
\Pr(y | n, S, \gamma) = \prod_{i=1}^{N} \prod_{j=1}^{M_i} \left[ \binom{n_{ij}}{y_{ij}} (S_{ij} + \gamma) \frac{\binom{n_{ij} - y_{ij}}{k}}{(1 - S_{ij} + \gamma)} \right] / \prod_{k=0}^{n_i-1} (1 + \gamma k),
$$

(6)

where $N$ is the number of pellet groups; $M_i$ is the number of sampling intervals for pellet group $i$; and $\gamma = 1/(a + b)$ is the overdispersion parameter. We constrained the parameter $\gamma$ to be greater than zero. The higher the value of $\gamma$, the more overdispersed the data, and as $\gamma \to 0$ the model approaches the standard binomial model. Although the overdispersion parameter, $\gamma$, can be formulated as a function of explanatory variables (Prentice 1986), we assumed that it was constant for all values of $S_{ij}$. We also assumed uninformative prior distributions on the model parameters, such that

$$
\beta_0 \sim \text{Normal}(0,1000) \\
\beta_i \sim \text{Normal}(0,1000) \\
\gamma \sim \text{Gamma}(0.1,0.1) \\
\tau_{\text{group}} \sim \text{Gamma}(0.1,0.1)
$$

(7)

where $\beta_i$ is component $i$ of the vector of regression coefficients, $\beta$.

For each study area we constructed a series of alternative models consisting of different combination of the explanatory variables. We included pellet age in all models to control for age and assumed that humidity and rainfall were alternative measures of moisture availability, so did not consider models that contained both these variables simultaneously. Also, to limit the number of alternative models to a manageable level, we did not consider interactions between variables. Otherwise, the alternative models consisted of all possible combinations of the explanatory variables. This resulted in 12 alternative models for Port
Stephens and 24 alternative models for Coffs Harbour. Prior to fitting these models we centred each continuous explanatory variable around its median value and checked for high levels of colinearity among variables. We used Markov chain Monte Carlo (MCMC), in WinBUGS version 1.4.1 (http://www.mrc-bsu.cam.ac.uk/bugs/), to estimate the parameter posterior distributions and the Deviance Information Criterion (DIC, Spiegelhalter et al. 2002) for each model. DIC is a Bayesian information criterion for comparing hierarchical models and can be used for model selection in a similar way to Akaike’s Information Criteria (AIC, Akaike 1973, Burnham and Anderson 2002). For each model, we ran three MCMC sequences and retained 50,000 samples per sequence after an initial burn-in of 20,000 samples per sequence had been discarded. Posterior distribution convergence was assessed using the Gelman and Rubin convergence statistic (Gelman and Rubin 1992), calculated with the package “coda” in R version 2.4.1 (http://www.r-project.org/). Convergence was considered satisfactory if the 97.5% quantiles of the potential scale reduction factors for all parameters were less than 1.1.

We ranked models by their DIC values and used the rule-of-thumb that all models within 7 DIC units of the best model had support. Similar rules-of-thumb have been proposed for AIC and these are also considered to apply to DIC (Burnham and Anderson 2002, Spiegelhalter, et al. 2002). For the most parsimonious models we assessed model adequacy using posterior predictive checks (Gelman et al. 2004). First, we conducted global goodness-of-fit tests, using the deviance as a measure of model fit (Hosmer and Lemeshow 2000). Second, we constructed empirical quantile-quantile plots of the residuals as a graphical assessment of model fit (Landwehr et al. 1984). See Supplementary material for full details of the procedures used to assess model fit.
**False-negative Error Rates and Expected Faecal Pellet Ages**

We combined koala pellet decay rates estimated from the survival models with estimates of koala densities and defecation rates to quantify false-negative error rates and expected pellet ages. We made the simplifying assumption that koala abundance, $A$, and the production rate of pellets per individual, $D$, at an occupied site are constant through time and calculated the false-negative error rates and expected pellet ages using eqns 1 and 2 and pellet survival rates derived from the survival models. In Port Stephens, koala population densities in occupied habitat have been estimated to range from 0.02 koalas ha$^{-1}$ to 0.75 koalas ha$^{-1}$ depending on the vegetation community (Lunney et al. 2007, D. Lunney unpublished data) and this probably represents the typical range of densities in Port Stephens and Coffs Harbour. Koala defecation rates have been estimated from in-care koalas in Coffs Harbour at around 80 pellets koala$^{-1}$ day$^{-1}$ (C. Moon unpublished data). Therefore, pellet accumulation rates (i.e., $A \times D$) in survey sites of 0.05 ha size (e.g., circular plots of 12.5 m radius) would range from 0.08 pellets day$^{-1}$ to 3 pellets day$^{-1}$ in the study areas, depending on koala densities. Previous studies have used circular plots of around 10-15 m radius to survey faecal pellets for koala occupancy (McAlpine, et al. 2008, M. Bowen personal communication). We calculated expected false-negative error rates and expected pellet ages (and 95% credible intervals) for the range of pellet accumulation rates and assuming surveys were conducted at each of the decay trial plots at the end of March, June, September, and December during 1996 (the year in which the decay trials were run). Survival rates were calculated from 1,000 posterior parameter samples from the most parsimonious model in each study area and actual meteorological records. In eqns 1 and 2, $d$ was set at 3,649 days (i.e., 10 years) because the probability of a pellet surviving longer than 10 years was very low, i.e., $\Pr(T > t \mid t - 3649) \approx 0$. 

15
Results

General Case

False-negative error rates declined rapidly as sign survival or sign accumulation rates increased (Fig. 1). However, the rate at which false-negative error rates declined with increasing accumulation rates was greatest when the survival rate was high, and the rate at which false-negative error rates declined with increasing survival rates was greatest when accumulation rates were high. These interactions mean that, when sign survival is high, the accumulation rate of signs does not need to be particularly high to ensure low false-negative rates. Consequently, for signs that decay very slowly, false-negative errors will tend to be low, even for low density populations where signs may only accumulate slowly. The expected sign age initially increased slowly with daily sign survival probability, but it showed a very rapid rate of increase once the daily sign survival probability was above around 0.95 (expected sign age > 20 days, Fig. 2). At a daily survival probability of 0.99, the expected sign age was 100 days, while at a daily survival probability of 0.999, the expected sign age was 1,000 days.
Figure 1. False-negative error rate as a function of the daily sign accumulation rate and the daily sign survival probability.

Figure 2. Expected sign age as a function of the daily sign survival probability.
Koala Faecal Pellet Surveys

For Port Stephens, the most parsimonious survival model contained plot, humidity, and temperature (Table 2). This model indicated that: (1) there was considerable variation in survival between plots; (2) survival decreased with increasing humidity and temperature; and (3) survival increased as pellets got older. However, there was considerable model uncertainty, with six out of the 12 models within 7 DIC units of the best model. All models within 7 DIC units contained plot, indicating strong support for spatial variation among plots. Hence, most model uncertainty was associated with which meteorological factors were important predictors of pellet survival. In fact, the model containing no meteorological predictors had a DIC within only 4 DIC units of the best model. Therefore, strong statements about the importance of meteorological predictors for pellet survival were not possible.

For Coffs Harbour, the most parsimonious survival model contained site, topography, and humidity (Table 3). This model indicated that: (1) there was considerable variation in survival between sites; (2) survival was higher on ridges compared to mid-slopes and gullies; (3) survival decreased with increasing humidity; and (4) survival increased as pellets got older. There was far less model uncertainty for Coffs Harbour than Port Stephens, with only four out of the 24 models within 7 DIC units of the best model. The top two models were also differentiated by about 6 DIC units from the next two, suggesting that the best two models were better supported by the data than the remaining models. The top two models differed by the inclusion, or omission, of topography, indicating some uncertainty in the importance of topography as a predictor of pellet survival. However, variation in survival with site and humidity had strong support.

The global, deviance-based, goodness-of-fit tests for the most parsimonious models revealed no significant lack of fit for either Port Stephens ($p = 0.12$), or Coffs Harbour ($p = 0.27$) at a 0.05 significance level. Inspection of the quantile-quantile plots revealed some
deviation from the expected 1:1 line but, in general, most points lay within the simulated 95% bounds (see Supplementary material). This indicated that the models fitted reasonably well.
Table 2. Port Stephens model rankings, DIC values and parameter posterior means for all models within 7 DIC units of the best model.

<table>
<thead>
<tr>
<th>Model rank</th>
<th>DIC</th>
<th>ΔDIC</th>
<th>β₀</th>
<th>β_{plot}</th>
<th>β_{age}</th>
<th>β_{rain}</th>
<th>β_{hum}</th>
<th>β_{temp}</th>
<th>σ_{row}</th>
<th>γ</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7864.23</td>
<td>0.00</td>
<td>5.34</td>
<td>-0.28, -0.46, -1.31, -1.42</td>
<td>1.28x10^{-3}</td>
<td>-0.020</td>
<td>-0.055</td>
<td>0.36</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>7865.79</td>
<td>1.56</td>
<td>5.31</td>
<td>-0.28, -0.44, -1.27, -1.45</td>
<td>1.17x10^{-3}</td>
<td></td>
<td>-0.055</td>
<td>0.37</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>7865.84</td>
<td>1.61</td>
<td>5.16</td>
<td>-0.29, -0.44, -1.28, -1.48</td>
<td>1.09x10^{-3}</td>
<td>0.20</td>
<td>-0.056</td>
<td>0.38</td>
<td>0.70</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>7866.39</td>
<td>2.16</td>
<td>5.36</td>
<td>-0.28, -0.47, -1.37, -1.47</td>
<td>3.32x10^{-4}</td>
<td>-0.02</td>
<td></td>
<td>0.37</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>7867.85</td>
<td>3.62</td>
<td>5.17</td>
<td>-0.28, -0.45, -1.36, -1.55</td>
<td>-1.53x10^{-4}</td>
<td>0.21</td>
<td></td>
<td>0.41</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>7867.95</td>
<td>3.72</td>
<td>5.34</td>
<td>-0.29, -0.46, -1.36, -1.53</td>
<td>9.54x10^{-6}</td>
<td></td>
<td></td>
<td>0.39</td>
<td>0.69</td>
<td></td>
</tr>
</tbody>
</table>

ΔDIC = difference between model DIC and model with the lowest DIC; β₀ = intercept; β_{plot} = coefficients for the plots; β_{age} = coefficient for pellet age; β_{rain} = coefficient for rainfall; β_{hum} = coefficient for humidity; β_{temp} = coefficient for temperature; σ_{row} = standard deviation of the group random-effect; and γ = overdispersion parameter. Continuous explanatory variables in the model were centred based on: median age = 106 days, median rainfall = 0 mm, median humidity = 71 %, and median temperature = 19.82 °C.
Table 3. Coffs Harbour model rankings, DIC values and parameter posterior means for all models within 7 DIC units of the best model.

<table>
<thead>
<tr>
<th>Model rank</th>
<th>DIC</th>
<th>ΔDIC</th>
<th>β₀</th>
<th>β₁site</th>
<th>β₂mid</th>
<th>β₃gully</th>
<th>β₄age</th>
<th>β₅rain</th>
<th>β₆hum</th>
<th>β₇temp</th>
<th>σ₁row</th>
<th>γ</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>17277.20</td>
<td>0.00</td>
<td>4.96</td>
<td>-1.71, 0.35, 0.89</td>
<td>-0.74</td>
<td>-0.74</td>
<td>7.49x10⁻³</td>
<td>-0.092</td>
<td>1.10</td>
<td>0.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>17277.90</td>
<td>0.70</td>
<td>4.45</td>
<td>-1.74, 0.10, 0.89</td>
<td></td>
<td></td>
<td>7.39x10⁻³</td>
<td>-0.092</td>
<td>1.13</td>
<td>0.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>17283.10</td>
<td>5.90</td>
<td>4.59</td>
<td>-1.73, 0.39, 0.93</td>
<td>-0.75</td>
<td>-0.75</td>
<td>6.41x10⁻³</td>
<td>-0.016</td>
<td>1.25</td>
<td>0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>17283.50</td>
<td>6.30</td>
<td>4.84</td>
<td>-1.66, 0.31, 0.89</td>
<td>-0.71</td>
<td>-0.71</td>
<td>1.03x10⁻²</td>
<td>-0.078</td>
<td>-0.087</td>
<td>1.01</td>
<td>0.33</td>
<td></td>
</tr>
</tbody>
</table>

ΔDIC = difference between model DIC and model with the lowest DIC; β₀ = intercept; β₁site = coefficients for the plots; β₂mid = coefficient for mid-slope; β₃gully = coefficient for gully; β₄age = coefficient for pellet age; β₅rain = coefficient for rainfall; β₆hum = coefficient for humidity; β₇temp = coefficient for temperature; σ₁row = standard deviation of the group random-effect; and γ = overdispersion parameter. Continuous explanatory variables in the model were centred based on: median age = 71 days, median rainfall = 0 mm, median humidity = 71.5 %, and median temperature = 19.4 °C.
For Port Stephens, the expected false-negative rate due to pellet decay were always close to zero (≤ 0.0171), regardless of survey location, time of year, or pellet accumulation rate. The false-negative rate was highest in summer/autumn (December and March) and lowest in winter/spring (June and September), although variation was much greater among plots than among different times of year. Expected pellet ages ranged from around 700 days to 75 days and depended on the site and time of year, although variation was greatest among sites (Fig. 3). For Coffs Harbour, the expected false-negative rate due to pellet decay was low (≤ 0.0006) when pellet accumulation rates were assumed to be 3.00 pellets day\(^{-1}\) (high density population). However, when pellet accumulation rates were assumed to be only 0.08 pellets day\(^{-1}\) (low density population) only site 4 (Bellingen) had a very low expected false-negative rate (< 0.004), while the expected false-negative rate at site 2 (Carson’s Road) was as high as 0.770 (Fig. 4A). The expected false-negative rates at sites 1 and 3 (Raleigh and Dutton’s Estate) were still reasonably low (< 0.197 and < 0.092 respectively), but not extremely low. Again, the false-negative rate was highest in summer/autumn and lowest in winter/spring, with much greater variation among sites than among different times of year. Expected pellet ages ranged from around 1,650 days to 4 days and depended on the site and time of year, although variation was again greatest among sites (Fig. 4B).
Figure 3. Expected pellet ages (for a survey occurring in September 1996 - the month with the lowest false-negative error rate) for Port Stephens. Error bars show the 95% credible intervals.
Figure 4. (A) Expected false-negative error rates (for a survey occurring in March 1996 - the month with the highest false-negative error rate), and (B) expected pellet ages (for a survey occurring in September 1996 - the month with the lowest false-negative error rate), for Coffs Harbour among the different sites and topographies and assuming a pellet accumulation rate of 0.08 pellets day$^{-1}$ (r = ridge, m = mid-slope, and g = gully). Error bars show the 95% credible intervals. Note that the ridge and midslope values for site 3 (Dutton’s Estate) are predictions assuming the existence of a ridge or midslope at that site.
Discussion

For cryptic or rare species, surveys of indirect signs can be preferable to direct observations because it can reduce detection errors (Jachmann 1991). However, this depends on the rate at which signs decay over time. Signs that decay very rapidly may still exhibit high false-negative error rates and signs that decay very slowly can have the effect of introducing other sources of error, such as false-positives. Both these sources of error can cause bias in parameter estimates for models of species’ distributions, or habitat use, based on surveys of indirect signs (Simonetti 1989, Gu and Swihart 2004). We found that false-negative error rates due to sign decay will be low, provided signs decay slowly enough, and this is true even under relatively low sign accumulation rates (Fig. 1). However, if signs decay very slowly, then the time interval prior to the survey to which the signs relate can be long (Fig. 2). If this time period is long relative to the time-scales over which occupancy changes can occur, then this may result in false-positive errors. This demonstrates the critical importance of quantifying the rate of sign decay and its spatial and temporal variation for understanding potential bias in models of species’ distributions based on indirect signs.

In general, dung decay rates have been found to vary spatially with habitat and microclimatic factors (Lehmkuhl et al. 1994, Prugh and Krebs 2004, Telfer et al. 2006). Prugh and Krebs (2004) show significant differences in snowshoe hare Lepus americanus pellet decay rates among habitat types. Similarly, Lehmkuhl et al. (1994) investigate both habitat type and topography and show that elk Cervus elaphus roosevelti pellets decay faster in clear-cut compared to forest habitats and in valley bottoms compared to slopes. In Coffs Harbour, the rapid decay rates at site 2 (Carson’s Road) could be attributed to the moist conditions at the site. Similarly, the slower decay rates on ridges than in gullies probably reflect the drier conditions on ridges. At a broader spatial scale we found that decay rates were more rapid in Coffs Harbour than in Port Stephens. This may be related to the fact that, during the study
period, Coffs Harbour experienced higher average humidity (72.66 % versus 70.14 %) and rainfall (5.59 mm day$^{-1}$ versus 2.81 mm day$^{-1}$) than did Port Stephens.

Previous studies that have developed koala distribution models based on faecal pellet surveys have generally assumed that errors due to pellet decay are small (e.g., McAlpine, et al. 2008, Rhodes, et al. 2008). We found that, on average, pellets decayed slowly enough to ensure low false-negative error rates. However, the high spatial variation in decay rates that we found could result in biased parameter estimates, especially if those sites with very rapid decay rates are associated with particular habitat types. Further, although we found that the time interval prior to the survey to which signs relate (expected pellet age) was generally less than 2-3 years, for some sites it was as much as 4.5 years (Figs 3 and 4). This may not be a major problem for landscapes or populations not subject to rapid change, especially for a long-live species like the koala, but for dynamically changing landscapes or populations, false-positive errors may be a real possibility.

False-negative errors can be reduced by sampling more intensively, or by having larger survey plots, in those habitats where error rates are expected to be high, or to avoid sampling at those times of year when decay rates are expected to be high (Johnson and Jarman 1987, Massei et al. 1998). However, a more efficient use of data is to use appropriate survey designs and statistical methods to correct for observation errors (MacKenzie, et al. 2002, Tyre, et al. 2003). Unfortunately, as we have already argued, standard methods to account for observation errors do not necessarily solve the problem for observation errors that arise from sign decay.

MacKenzie et al. (2005) suggest that an alternative to repeat surveys of the same site is to survey multiple sub-sites within a larger site. This may provide a means of accounting for false-negative errors that arise form sign decay because variation in observed occupancy status among repeat surveys of a site can then occur due to sign decay, as well as other
sources of detection error. This approach has been used for dung surveys (Buij et al. 2007). However, one concern here is that the closure assumption, which requires the true occupancy status of all sub-sites within a site to be the same at the time of the survey, may not be violated. For example, if the species only uses a proportion of a larger site, then the closure assumption will not hold. This is not necessarily a problem if habitat use and sign presence varies randomly between sub-sites, because then habitat use estimates remain unbiased (MacKenzie et al. 2004). However, different sources of observation error will not be distinguishable from each other and the estimated detection probability will consist of four confounded probabilities: (1) the probability that the species uses a sub-site, given that it uses the larger site; (2) the probability that signs are left at a sub-site, given the species uses the sub-site, (3) the probability that not all signs have decayed, given that signs have been left; and (4) the probability that a sign is detected, given that signs are present at the time of the survey. If habitat use and sign presence are non-randomly distributed within sites (e.g., due to spatially correlated habitat use) then occupancy estimates can be biased. Therefore, careful consideration needs to be given to whether these assumptions hold when using this approach.

In addition, spatial variation in decay rates, habitat and animal abundances makes accounting for variation in observation errors among sites crucial for surveys using this approach. One way to achieve this is to introduce covariates for the detection probabilities and/or model detection probabilities directly as functions of abundance (MacKenzie, et al. 2002, Royle and Nichols 2003).

Stanley and Royle (2005) develop a specific method to account for observation errors in indirect sign surveys that accounts for variation in detectability with abundance (Royle and Nichols 2003). Their approach relies on the ability to reset sites (i.e., clear sites of all signs) at the end of discrete survey intervals and an assumption that signs do not disappear during survey intervals. For many signs, including dung, this approach may be problematic because
they decay over time and/or it may be impossible to detect all signs at a site to ensure the site is cleared (e.g., this would be very difficult for koala pellets). However, if it can reasonably be assumed that all signs at a site can be detected, then applying this method with survey intervals short enough to ensure that signs do not decay may be a useful approach. In this case, *a priori* estimates of sign decay rates are required to set an appropriate interval length, e.g. using on a sign survival model. Clearing sites of dung and then counting their accumulation over a short time period so that it can be assumed no decay has occurred has commonly been used to estimate animal densities, but with varied success (Lehmkuhl, et al. 1994, Murray et al. 2005).

An alternative approach is to modify Stanley and Royle’s (2005) method so that sign decay is accounted for using ancillary data on decay rates. Approaches that adopt this idea are commonly used for estimating abundance from dung counts (Hiby and Lovell 1991, Barnes 1993). Stanley and Royle (2005) specify the probability of detecting a species at a site as

\[
 p = 1 - (1 - q)^{(t - d)D},
\]

where \( q \) is the probability of detecting the species per unit time; \( t - d \) is the length of the sampling interval; and \( A \) is the abundance of the species at the site (assumed constant over time). In this case, \( q \) is essentially the probability per unit time that an individual present at a site leaves signs. As an alternative, for a one-off sign survey, we could write

\[
 p = 1 - \prod_{v=d}^{t}(1 - f(t \mid v))^{AD},
\]

where \( D \) is the number of signs left per individual per unit time (assumed constant over time); \( f(t \mid v) \) is the probability that a sign created at time \( v \) survives until time \( t \); and \( d \) is a period of time long enough that \( f(t \mid t - d) \) is very small.

Here, we have replaced \( q \) with \( f(t \mid v) \) to account for sign decay and note the similarity between the second term of this formulation and eq. 1. This model could be fitted to suitable data provided we have *a priori* information about \( f(t \mid v) \), either through a survival model, or decay trials at each site, and we can assume a parametric distribution for \( AD \) (see Royle and
Nichols 2003, Stanley and Royle 2005). Such an approach is yet to be evaluated, but is likely
to be a fruitful area for future research.

One problem for dealing with false-positives that arise due to very slow sign decay is
that false-positive rates cannot be estimated unless we have information about the age of
detected signs and changes in occupancy status over time. For example, even if we can age
signs, so that we know when a site was occupied, we still need to know the probability that
the site is no longer occupied to estimate the false-positive rate. There is no way that this can
be determined from a one-off survey. If signs can be reliably aged, then one solution is to
exclude old signs from the data set, so as to reduce the risk of false-positives, and estimate
occupancy and false-negative rates based only on young signs. Methods have been developed
to reliably age koala pellets (Sullivan et al. 2002), but it is not at all clear that that this can be
reliably achieved for many signs. One simple alternative may be to identify those sites where
sign decay rates are likely to be sufficiently slow to potentially introduce false-positive errors
and then examine whether the exclusion of those sites has an impact on model parameter
estimates. If the exclusion of those sites does not have a significant impact on model
parameter estimates, this may be an indication that bias due to false-positive errors is small.
Similarly to false-negative errors, standard methods that account for both false-positive and
false-negative errors from repeat surveys (Royle and Link 2006) are unlikely to be
particularly helpful. Consequently, developing robust methods to deal with both false-
negative and false-positive errors is an important area of research for indirect sign surveys.

Models of sign decay are critically important for understanding the potential
consequences of their decay for models of species’ distributions derived from indirect sign
surveys. Provided information is available on sign decay and accumulation rates, relationships
among false-negative error rates/expected pellet ages and sign decay/accumulation rates can
be used to assess the extent to which observation errors due to sign decay are likely to be an
issue. In dealing with false-negative errors, spatial replicates may be suitable provided assumptions, such as the closure are not violated. False-positives are more difficult to deal with, although conducting sensitivity analyses with respect to those sites estimated to have very slow decay rates, or developing methods to reliably age signs will be helpful. None the less, there is significant potential to develop new methods that explicitly account for observation errors due to sign decay, in addition to the simple strategies that we recommend here. In developing and applying these methods, understanding the conditions under which the benefits of collecting data on sign decay and/or conducting repeat surveys (e.g., Field et al. 2005) exceeds the costs will be important.

Acknowledgements

Thank you to Anne Carey for carrying out the field work in Port Stephens. Thank you also to Jane Elith and one anonymous referee for constructive comments that helped to improve earlier versions of this paper. This work was initially presented at the International Statistical Ecology Conference at the University of St. Andrews in 2008.

References


Figure 1

Daily sign survival probability

Daily sign accumulation rate
Figure 2

Expected sign age (days)

Daily sign survival probability
Figure 3

Expected pellet ages (days)

Plot

0 1 2 3 4 5

0 500 1000 1500
Decay Trial Study Area and Site and Plot Descriptions

The Port Stephens study area was located within a 4,000 ha area known as the Tomago Sandbeds, managed as a water catchment, containing large forest fragments. The forest communities include swamp forest, dry forest, low forest and woodlands, dominated by eucalypts, including swamp mahogany \textit{Eucalyptus robusta}, blackbutt \textit{E. pilularis}, as well as broad-leaved paperbark \textit{Melaleuca quinquenervia}. The Coffs Harbour study area is dominated by moist open and closed eucalypt forests with a coastal sclerophyll complex and dry open eucalypt forest to the north and rainforest to the southwest. Most of the fertile river valleys and coastal plains have been cleared for agriculture and urban development, while the elevated slopes remain largely forested.

In Port Stephens there were five plots. These were located: (1) at the base of a mature swamp mahogany \textit{E. robusta} tree just above the high water mark of the swamp, with 100% leaf litter in an ecotone woodland; (2) at the edge of open woodland under a mature scribbly gum \textit{E. signata} tree, with a thick grassy understory in an ecotone open forest; (3) at the base of a large smooth-barked apple \textit{Angophora costata} tree at the base of a dune that gave way to a swamp, with thick understory and 10% leaf litter in a tall open forest ecotone; (4) at the base of a large blackbutt \textit{E. pilularis} tree on an elevated position on south side of a large dune with 100% litter cover in a tall open forest ecotone; (5) in a dry swamp with no understory except sparse bracken fern on thick, moist leaf litter in a broad-leaved paperbark \textit{M. quinquenervia} / swamp mahogany association. Plots were generally a few hundred meters apart.

In Coffs Harbour there were four sites: (1) Raleigh; (2) Carson’s Road, (3) Dutton’s Estate; and (4) Bellingen. Then, within each site, there were three plots, each in a different topographical location: one on a ridge, one on a midslope, and one in a gully. Exceptions to
this were that, at Dutton’s Estate, all three plots were classified as gully, and at Bellingen two plots were located within each topographical type, giving a total of six plots there. At the Raleigh site (site 1), the ridge plot was in dry, partially cleared forest, the midslope plot was in moist, shaded, south-east facing flooded gum *E. grandis* forest with ground litter, and the gully plot was in moist, shaded, grassy, south-east facing flooded gum forest. At the Carson’s Road site (site 2), the ridge plot was in moist tallowwood *E. microcorys* forest, with ground leaf litter, open to the north and west, the midslope plot was in very moist, south facing, closed flooded gum forest with ground leaf litter, and the gully plot was in very moist, south facing brush box *Lophostemon confertus* / flooded gum closed forest with ground leaf litter. All three plots at the Dutton’s Estate site (site 3) were in flat, moist, closed mixed forest with ground leaf litter. At the Bellingen site (site 4), the ridge plots were on exposed and grassy to bare ground, with tall moist forest to the south and east, and the midslope and gully plots were in moist, tall mixed forest, with leaf litter ground layers. Sites were generally several kilometres apart, while plots within sites were between fifty and a few hundred meters apart.

**Procedures for Assessing Model Fit**

Posterior predictive checks were conducted by generating simulated predictions from the posterior parameter distributions and comparing these to actual data. First, we conducted global goodness-of-fit tests, using the deviance as a measure of model fit (Hosmer and Lemeshow 2000) and all 150,000 samples from the posterior parameter distributions. For each parameter sample, we calculated the deviances for the actual and simulated data and then calculated the proportion of parameter samples where the deviance for the actual data was greater than the deviance for the simulated data. This provided a posterior predictive *p*-value indicating whether the actual deviances were a likely realisation of the deviances that would arise if the model were true (Gelman et al. 2004). Second, we constructed an empirical
quantile-quantile plot of the residuals, \( r_i = (\hat{y}_i / n_i) - S_i \), based on the approach described by Landwahr et al. (1984). However, instead of generating the simulated quantiles and bounds from a single set of parameter values, we generated them from 3,000 samples of the posterior parameter distributions. If the model adequately describes the data, then the quantile-quantile plot should lie close to the 1:1 line. Deviations from the 1:1 line can indicate the presence of outliers, or inadequacies in model structure and distributional assumptions (Landwehr, et al. 1984).
Figure S1. Quantile-quantile plots for: (A) the most parsimonious Port Stephens model and (B) the most parsimonious Coffs Harbour model. Points show the observed quantiles for a
single set of (randomly chosen) posterior parameter values, solid lines show the 95% credible
intervals for the simulated quantiles, and the dotted line shows the 1:1 line.

References


