



Location matters: Using spatially explicit occupancy models to predict the distribution of the highly mobile, endangered swift parrot



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ABSTRACT

Occupancy modelling using data collected by repeatedly sampling sites is a common approach utilised by land managers to understand species distributions and trends. Two important factors that can complicate interpretation of these models are imperfect detection and spatial autocorrelation. We examine the effect of these potential errors using a multi-year data set on the distribution of the migratory and endangered swift parrot (*Lathamus discolor*). We simultaneously account for these effects by extending a zero-inflated Binomial (ZIB) framework to allow the inclusion of semiparametric, smooth spatial terms into both the occupancy and detection component of the model, in a maximum likelihood framework easily implemented in common software. This approach also has the advantage of relatively straightforward model selection procedures. We show that occupancy and detectability were strongly linked to food availability, but the strength of this relationship varied annually. Explicitly recognising spatial variability through the inclusion of semiparametric spatially smooth terms in the ZIBs significantly improved models in all years, and we suggest this predictor is an effective proxy for unmeasured environmental covariates or conspecific attraction. Importantly, the spatially explicit ZIBs predicted fewer occupied sites in more defined areas compared to non-spatial ZIBs. Given the importance of predicted distributions in land management, habitat protection and conservation of swift parrots, these models serve as an important tool in understanding and describing their ecology. Our results also reinforce the need for designing surveys that capture the underlying spatial structure of an ecosystem, especially when studying mobile aggregating species.

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1. Introduction

Effective population monitoring is fundamental to threatened species management and conservation planning (Martin et al., 2007; Sanderson et al., 2006). The importance of developing effective monitoring designs and analytical approaches has generated considerable discussion (Reynolds et al., 2011; Rhodes and Jonzén, 2011; Wintle et al., 2010), particularly regarding the need to identify and account for sources of error. When the results of monitoring identify the need for management responses that are contentious, expensive or impact on industry, accounting for error becomes especially important (Martin et al., 2007).

Highly mobile, rare or cryptic species can be difficult and expensive to monitor. Because resources are often limited, collecting detection/non-detection data from a sample of sites to be analysed within an occupancy-modelling framework is a popular approach among land management agencies (Kéry et al., 2013). Consequently, occupancy models and the relationship between occupancy and abundance, have been used extensively to estimate species density, distributions and habitat associations (e.g. Gaston et al., 2000; Hui et al., 2006). Estimating and accounting for false negative error rates or detection probability is fundamental to improving the reliability of occupancy models (MacKenzie et al., 2002; Martin et al., 2005; Royle and Nichols, 2003; Tyre et al., 2003; Wintle et al., 2004). The most common approach involves repeatedly sampling sites to estimate detection probability p , defined as the probability a species will be detected in a single site visit given that it occupies that site (MacKenzie et al., 2002). The

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detection process is commonly influenced by the behaviour and abundance of the target species (Gu and Swihart, 2004; McCarthy et al., 2013), and if there is spatial or temporal heterogeneity in p , establishing its relationships with environmental variables can reduce bias in parameter estimators and improve sampling strategies (e.g. Bailey et al., 2004; Gibson, 2011; Lahoz-Monfort et al., 2014).

Errors in interpreting ecological relationships can also arise if spatial autocorrelation (SAC) is ignored, or not accounted for in the distribution of the target species (Dormann, 2007; Hawkins, 2012; Legendre, 1993). Generally, SAC originates from either an autocorrelated environment (i.e. where nearby locations are more similar than more distant ones) or through processes like conspecific attraction and limited dispersal ability of the target species (Lichstein et al., 2002). Importantly, recognition and analysis of SAC can provide insights into ecological processes that may otherwise be overlooked (Bini et al., 2009; Hawkins, 2012) and the effect of spatial structure has been recognised as an important component in modelling the occupancy-abundance relationship (Hui et al., 2006).

Recently, considerable attention has focused on improving statistical methods to account for either SAC or imperfect detection; however, relatively few studies have formally accounted for these processes simultaneously (but see Aing et al., 2011; Bled et al., 2011; Johnson et al., 2013; Royle et al., 2007). Some studies have accounted for spatial correlation in discrete spatial domains (Johnson et al., 2013; Royle et al., 2007; Wintle and Bardos, 2006), while others have focused on the detection process in transect based or cluster sampling designs (Aing et al., 2011; Guiller-Arroita et al., 2010, 2012; Hines et al., 2010). Other approaches model spatial variability through the inclusion of spatially correlated random fields (Diggle et al., 1998; Post van den Burg et al., 2011). Most of these studies, and other occupancy models that contain autocorrelation structure adopt a hierarchical Bayesian perspective (see also Gardner et al., 2010; Hoeting et al., 2000; Sargeant et al., 2005).

In this study, we use the endangered swift parrot (*Lathamus discolor*) to illustrate the importance of accounting for SAC and detection when modelling the distribution of mobile, cryptic and threatened species. Swift parrots are a migratory nectarivorous species seriously threatened by anthropogenic habitat loss throughout their range (Higgins, 1999). Their breeding range is restricted to the island of Tasmania, Australia, where they nest in tree hollows and rely on the erratic flowering of the Tasmanian blue gum (*Eucalyptus globulus* subsp. *globulus*) and black gum (*Eucalyptus ovata*) for food (Webb et al., 2012). However, there are few empirical data that quantify the relationship between nectarivores and flowering at macroecological scales. The very specific nesting and food requirements of the swift parrot, and the need for hollows and flowering to occur in the same area, make the species highly vulnerable to the effects of continuing habitat degradation and loss (Webb et al., 2012).

A key question for land managers is: how much habitat needs to be protected to conserve the species? Approximately one-third of the swift parrots potential breeding habitat is afforded varying levels of protection through the Comprehensive, Adequate and Representative (CAR) Reserve System (see Commonwealth of Australia, 1992). However, conservation (or protection) of non-reserved land (e.g. private land, production forest) that contains breeding habitat is highly contentious (Allchin et al., 2013) and can have serious economic implications for stakeholders. In this context, the relative importance of a particular area to swift parrots is often heavily scrutinised, especially where information is limited. Accurate, annual spatiotemporal information on the distribution of swift parrots, and the availability of their nesting and feeding habitat, is required to identify ecologically relevant spatial scales of

management, prioritise key sites or regions, develop and inform off-reserve management actions, and set spatially explicit thresholds for habitat loss.

Given the dependence of swift parrots on flower for food, its use as a key explanatory variable was a logical starting point for our analyses. However, it is likely that other environmental or behavioural factors also influence occupancy and detection. From a logistical or economic perspective, it is often difficult to identify or measure these factors. We hypothesised that explicitly incorporating a smoothed spatial covariate in the occupancy and/or detectability component of zero-inflated Binomial models (ZIB) in a generalised additive model (GAM) framework, should help explain a large proportion of the variation due to these unknown or unmeasured factors. Our approach models the autocorrelation through smoothed functions of spatial coordinates where space is viewed as inherently continuous. This is in contrast to approaches that discretize space into regions or sites, and model spatial correlation through correlated random effects defined over sites in a Bayesian hierarchical framework (e.g. Bled et al., 2011; Johnson et al., 2013 and references therein; Wintle and Bardos, 2006). Our approach is more similar to geostatistical models in which spatial variability is modelled as spatially correlated random fields (e.g. Diggle et al., 1998; Post van den Burg et al., 2011). However, by modelling spatial variability through smooth functions of spatial coordinates rather than correlated random fields, our models can be fitted with standard maximum likelihood methods avoiding the need for complex Markov Chain Monte Carlo techniques.

Here we describe the design and implementation of a monitoring program, and associated analytical techniques, to better understand the spatial ecology of swift parrots and inform a landscape-scale conservation management strategy. We fitted Binomial models (with perfect detection), and zero-inflated Binomial models (that accounted for imperfect detection) with and without a smooth spatial covariate in GAM and generalised linear model (GLM) frameworks respectively, to test our hypothesis about the importance of spatial location. Using these models, we mapped the predicted distribution of swift parrots to illustrate dramatic spatiotemporal variation in their occurrence and detectability, while highlighting the importance of accounting for SAC. We also used simulated spatially structured data to form more generalised insights from our models.

2. Methods

2.1. Study area and sampling regime

We sampled across the known breeding range of the swift parrot (broadly defined by the natural range of *E. globulus*), which is restricted to Tasmania and covers approximately 10,000 km² (Fig. A1, Webb et al., 2012). Swift parrot detection/non-detection data were collected by repeatedly sampling a number of distinct sites over a three-week period in October 2009–2012 (number of sites ranged from 771 to 1034). A site was defined as a 200 m radius around a fixed point and the number of site visits, across all years, ranged from one to eight with a mean of 2.4 (see Appendix A for detailed sampling protocols). Flowering intensity (0–4 scale) was also recorded during these visits. Minimizing the amount of time taken for each annual survey reduced the likelihood of changes in detectability and violation of the assumption of closure, which is inherent in the models utilised (MacKenzie et al., 2006; Rota et al., 2009). A small subset of sites ($n = 16$) from the north-west of Tasmania that were geographically distinct from the rest of the sites (Fig. A1) was not used in the analyses to reduce their disproportionate impact as spatial outliers.

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