

## Estimating abundance of cryptic but trappable animals using trapping point transects: a case study for Key Largo woodrats

Joanne M. Potts<sup>1\*†</sup>, Stephen T. Buckland<sup>1</sup>, Len Thomas<sup>1</sup> and Anne Savage<sup>2</sup>

<sup>1</sup>Centre for Research into Ecological and Environmental Modelling, University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, Fife KY16 9LZ, UK; <sup>2</sup>Disney's Animal Kingdom®, Education and Science Department, Lake Buena Vista, FL 32830, USA

### Summary

1. Obtaining robust abundance or density estimates is problematic for many rare or cryptic species. We combine elements of capture–recapture and distance sampling, to develop a method called trapping point transects (TPT), and we applied this method to estimate the abundance of the endangered Key Largo woodrat (*Neotoma floridana smalli*).

2. Trapping point transects requires two separate surveys to be held concurrently in space and time. In the *main survey*, the encounter rate (number of animals caught per trap per session) is measured. In the *trial survey*, animals whose locations are known prior to opening traps are used to estimate the detection function  $g(r)$  (the probability of capturing an animal given it is distance  $r$  from a trap when it is set), so the effective trapping area in the main survey can be estimated. It is assumed animals in the trial survey are a representative sample of all animals in the population. Individual heterogeneity in trappability is accommodated using random effects in  $g(r)$ .

3. Performance of two TPT estimators was assessed by simulation. Generally, when underlying capture probabilities were high [ $g(0) = 0.8$ ] and between-individual variation was small, modest survey effort (360 trap nights in the trial survey) generated little bias in estimated abundance (*c.* 5%). Uncertainty and relative bias in population estimates increased with decreasing capture probabilities and increasing between-individual variation. Survey effort required to obtain unbiased estimates was also investigated.

4. Given the challenges of working with cryptic, sparse or nocturnal species, we tested the validity of this method to estimate the abundance of the Key Largo woodrats between 2008 and 2011.

5. Trapping point transects was found to be an effective monitoring method yielding annual estimates of the extant wild population of 693, 248, 78 and 256 animals, with CVs of 0.45, 0.55, 0.82 and 0.43, respectively. The TPT method could be adapted to a range of species that are otherwise very difficult to monitor.

**Key-words:** abundance estimation, capture–recapture, distance sampling, Key Largo, *Neotoma floridana smalli*, rodents, small mammals, woodrat

### Introduction

In many ecological studies, the primary parameter of interest is population density ( $D$ ) or abundance ( $N$ ). Distance sampling (Buckland *et al.* 2001) and capture–recapture (Pollock *et al.* 1990) can be effective approaches to estimate such parameters, but when animals are sparsely distributed or cryptic, they are

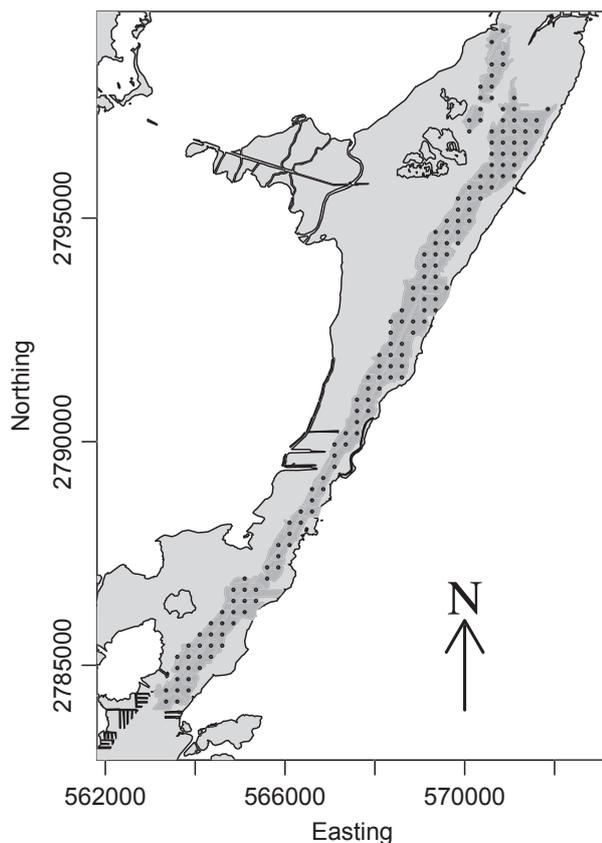
problematic. For example, in distance sampling surveys of cryptic animals, probability of detection is often low even at zero distance from the transect, violating a fundamental assumption. Capture–recapture approaches are prone to problems with heterogeneity in capture probability caused by unequal access to traps (Otis *et al.* 1978; Seber 1992). Research has consequently focused on methods that combine trapping studies with distance sampling theory, leading to the development of trapping webs (Lukacs, Anderson & Burnham 2005), spatially explicit capture–recapture (SECR, Borchers & Efford 2008; Royle & Young 2008) and trapping point transects (TPT, Buckland *et al.* 2006).

\*Correspondence author. E-mail: potts@unimelb.edu.au

†Present address: Australian Centre of Excellence for Risk Analysis, School of Botany, University of Melbourne, Parkville 3010, Australia.

We were challenged to develop an effective method to estimate the abundance of Key Largo woodrats (*Neotoma floridana smalli*). The species is restricted solely to the tropical hardwood hammock on northern Key Largo, FL, USA (Fig. 1) and is subject to a recovery plan that identifies potential threats and describes management actions to be undertaken (US FWS 1999). A reliable population abundance estimate, together with an associated measure of uncertainty, is essential to evaluate management decisions for the woodrat population. Because woodrats are nocturnal, cryptic and sparsely distributed, standard population monitoring methods do not work well (e.g. require unrealistic investment of survey effort; Winchester 2007). Thus, we chose to evaluate the use of TPT in estimating the abundance of Key Largo woodrats.

Trapping point transects require two surveys. Data collected during the *trial survey* are used to estimate the detection function,  $g(r)$ , the probability of detecting an animal in a trap, given the animal was distance  $r$  from the trap when the trap was set. Then, for each animal detected during a separate *main survey*, its probability of detection is predicted using the detection function fitted to the data collected during the trial survey. A Horvitz–Thompson-like estimator (Borchers *et al.* 1998) is



**Fig. 1.** Map showing the main survey design. 137 sample points were distributed throughout the suitable habitat (shaded dark grey) based on a randomly placed systematic grid with a 250-m trap spacing (black dots). Traps were not placed in unsuitable habitats of water (white) and mangrove swamp (light grey).

used to estimate overall abundance. An advantage of TPT is that in the main survey, traps can be widely spaced, for example using a systematic random design, and hence, a large study area can be sampled at low cost relative to trapping webs and SECR, which both require clusters of closely spaced traps. This advantage, however, is offset by the need for the trial survey to estimate detectability, and we return to this issue later in the paper.

Buckland *et al.* (2006) proposed the TPT method and used it to estimate abundance of the Scottish crossbill (*Loxia scotica*). In their main survey, a lure (a tape of excitement calls) was initiated at a systematic random set of points in the study area and flocks of crossbills that responded to the lure and were detected by the observer were recorded. For the trial survey, one observer located flocks, and another observer initiated the lure at pre-determined distances. Detection probability was estimated from the outcomes using logistic regression. Earlier, Turchin & Odendaal (1996) had adopted a similar strategy to estimate the effective sampling area of a pheromone trap for a species of beetle, although they used a simple linear regression of log capture proportion on log distance from the trap instead of logistic regression. Acosta & Perry (2000) used a similar method for crayfish. In all of these examples, for the trial survey, only one trial was performed per flock or individual. This is not efficient if significant effort is required to obtain a sample of animals for the trials. For example, if animals are highly cryptic, it may be possible to trap and radiocollar a sample of animals, so that their location can be determined conveniently and then perform multiple trials over a period of time on the same individuals. This strategy was used by Legare *et al.* (1999) to estimate density of black rails (*Laterallus jamaicensis*). They used logistic regression to fit the detection function from the trials, but ignored individual variation in animals and assumed each trial observation was independent. Here, we extend the approach presented by Buckland *et al.* (2006) to allow multiple trials on the same individuals, using a hierarchical logistic model to account for individual heterogeneity in trappability as a function of known explanatory variables (covariates) and also a between-individual random effect. We conduct a simulation study to investigate (i) the properties of two abundance estimators that accommodate random effects in the detection function; (ii) the trade-off between the number of trials per individual and the number of individuals in the trial survey; and (iii) two different strategies for selecting the distances at which to perform trials.

We use the TPT method to estimate abundance of the endangered Key Largo woodrat (*N. f. smalli*). The TPT survey design allowed the entire population to be surveyed at moderate cost. We provide a robust estimate of the population but also acknowledge the variance of the resulting abundance estimates was high. We provide recommendations on how the variance could be reduced, whilst still keeping required survey effort within feasible bounds. Thus, TPT provides a robust method for estimating Key Largo woodrat abundance and can be applied to other cryptic but trappable species.

## Materials and methods

### TRAPPING POINT TRANSECTS

#### Survey design

In the *main survey*, traps are set on a systematic grid throughout the survey region. Trap separation is sufficient that we can assume that whether an animal is trapped at one location is independent of capture events at other locations. It is not necessary to individually mark animals in the main survey, but recording covariate information (e.g. sex) of detected animals may be useful at the analysis stage.

In the *trial survey*, an animal is located, and a trap is set at some pre-determined distance and random direction from that location. Subsequently, the trap is checked to see whether or not the animal was captured. This is repeated for many trial distances on the same individual and across numerous individuals. Thus, a binomial response variable is recorded for each trial (1 for capture, 0 otherwise), together with the distance of the initial location from the trap.

#### Data analysis

A detection function,  $g(r|z)$ , specifying the probability of capturing an animal initially at distance  $r$  from a trap location given a set of covariates  $z$ , can be estimated using the binomial response data collected from the trial surveys. Buckland *et al.* (2006) presented the statistical methods for the simpler situation when only one trial is conducted per individual, and here, we extend their analysis using generalized linear mixed models (GLMMs) to account for the non-independence in trial observations when multiple trials are conducted on the same individual. Such models are also known as hierarchical models, because they include between-individual and within-individual effects. If a logit link function is used in the binary regression, then the general form of the detection function is

$$g(r|z, b) = \text{logit}(\alpha + \beta_0 r + \sum_{j=1}^J \beta_j z_j + b) \quad \text{eqn 1}$$

where  $\alpha$  is the intercept,  $\beta_0$  is the coefficient (slope) for the explanatory variable distance ( $r$ ),  $\beta_j$  are the coefficients for each of  $J$  additional explanatory variables ( $z_j$ ), and  $b$  represents a random effect assumed normally distributed with mean 0 and variance  $\sigma_b^2$ . We can use, for example, Akaike's Information Criterion (AIC, Burnham & Anderson 2003) to select explanatory variables.

Using the fitted detection function, the estimated probability of capturing each animal observed in the main survey,  $p_i$ , given that the animal is at some unknown distance  $r < w$  from the sample point, can be calculated (Buckland *et al.* 2006). A value of  $w$  is chosen so that the probability of capturing an animal that is initially at least a distance  $w$  from the trap is zero to a good approximation. To calculate  $\hat{p}_i$  for each animal detected in the main survey, we condition on the observed values of each explanatory variable  $z_{ij}$ . Given random trap placement and no edge effects (effects caused by sample points near the edge of the study area, Buckland *et al.* 2001), the probability density of available animals as a function of distance (the availability function),  $\pi_r(r)$ , is triangular on  $(0, w)$ . To correct for edge effects, the availability function may be calculated as:

$$\pi_r(r) = \frac{rq(r)}{\int_0^w rq(r)dr}$$

where  $q(r) = [\sum_{k=1}^K q_k(r)]/K$ , for  $0 \leq r \leq w$  and  $q_k(r)$  is the proportion of the circumference of a circle of radius  $r$  centred on the

point  $k$  that lies within the survey region, and  $K$  is the number of points in the main survey (Buckland *et al.* 2006). We write  $\hat{p}_i = p(r, b; z_{i1}, \dots, z_{iJ})$ , for  $0 \leq r \leq w$ .

The estimated probability of detecting the  $i$ th animal captured in the main survey unconditional on its distance from the trapping sample point,  $\hat{P}(b; z_{i1}, \dots, z_{iJ})$ , can be estimated by integrating over the unknown  $r$ :

$$\hat{P}(b; z_{i1}, \dots, z_{iJ}) = E_r[\hat{p}(r, b; z_{i1}, \dots, z_{iJ})] = \int_0^w \pi_r(r) \hat{p}(r, b; z_{i1}, \dots, z_{iJ}) dr$$

The random effect term,  $b$ , in  $\hat{P}(b; z_{i1}, \dots, z_{iJ})$  must also be integrated out. Here, we do this by simulation, taking 10,000 samples of  $\hat{P}(b; z_{i1}, \dots, z_{iJ})$  from the distribution of  $b_i$  for each individual  $i$  detected in the main survey (thus implicitly including uncertainty in the estimate of the variance of the random effect). Given the resulting estimates of detection probability conditional on observed covariates, a Horvitz-Thompson-like abundance estimator (Borchers *et al.* 1998) is given by

$$\hat{N} = \frac{A}{A_c} \sum_{i=1}^n \frac{1}{E_b[\hat{P}(z_{i1}, \dots, z_{iJ})]} = \frac{A}{A_c} \sum_{i=1}^n \frac{1}{\int_0^w \pi_b(b) \hat{P}(z_{i1}, \dots, z_{iJ}) db} \quad \text{eqn 2}$$

where  $A$  is the area of the survey region,  $A_c$  is the area of the covered region and  $\pi_b(b)$  is the pdf of the random effects distribution.

Variance in the estimated abundance has two sources. First, there is a variance associated with the encounter rate (i.e. animals caught per trap) in the main survey, and secondly, variance associated with estimating the detection function in the trial survey. We suggest a nonparametric bootstrap approach, as follows (Manly 2007). First, generate a random resample with replacement of the trap locations in the main survey. Secondly, generate a random resample with replacement of the individuals in the trial survey. Fit a new detection function model to the trials data, repeating the model selection procedure used in the original analysis (e.g. selecting the model from the candidate set with the lowest AIC) and thereby incorporating model uncertainty into the variance estimation (Buckland, Burnham & Augustin 1997). Third, use the new detection function in conjunction with the new main survey data to generate a new ('bootstrap') abundance estimate using eqn 2. Steps 1–3 are repeated a large number of times (e.g. 999 in total), and the sample variance of the bootstrap estimates of abundance is taken as an estimate of the variance of the estimator  $\hat{N}$ . Approximate confidence intervals for abundance may be obtained, for example, using the percentile method (Buckland 1984).

### SIMULATION STUDY

We used a simulation study to first assess the percentage bias (%bias) and root-mean square error (RMSE) of our abundance estimator. We also considered a second estimator, but it was found to have poor properties. We present that estimator in the Supporting Information, so that other developers of estimators are aware of its shortcomings.

Secondly, we examined the trade-off between the number of individual animals used in the trial survey and the number of repeat trials on each individual, for a fixed level of survey effort. We also investigated how much trial survey effort was required before  $\hat{N}$  became approximately unbiased.

Thirdly, we investigated two alternative strategies ('uniform' and 'adaptive') for selecting distances at which to perform trials in the trial survey. For the 'uniform' method, trial distances were selected uniformly between 0 and  $w$  metres. For the 'adaptive' method, half the trial survey effort was allocated uniformly, and a preliminary

detection function was fitted. The remaining survey effort was then allocated between 0 and  $w$  metres, according to the cumulative distribution function (cdf) of detection distances, estimated using the data from the initial uniform trials. Values systematically distributed between 0 and 1 were back-transformed through the fitted cdf to generate trial distances. This has the effect of allocating more trials to distances where more detections are expected to occur – we anticipated that this might lead to more precise estimates of the detection function for a given level of trial survey effort.

Each animal in the main and trial survey was allocated a unique detection function, drawn randomly from an underlying ‘true’ mean detection function with a specified random variation about the intercept term (i.e. probability of detecting the animal if a trap is placed 0 m from its location).

The probability of a successful response (i.e. capturing the radio-collared animal,  $y_{iig} = 1$ ) for trial  $t$  on each individual  $i$  in group  $g$  ( $g = 1, 2, \text{ or } 3$ ) was modelled as:

$$\text{logit}(E[y_{iig}]) = \text{logit}(p_{iig}) = \alpha_g + \beta r_{iig} + b_{ig}$$

where  $\alpha_g$  is the intercept for an individual in group  $g$ ,  $\beta$  is the coefficient (slope) for the explanatory variable distance  $r$  and  $b_{ig}$  is a random effect because of individual  $i$  in group  $g$  with an independent normal distribution with mean 0 and variance  $\sigma_g^2$ .

Three detection function scenarios were investigated (see Table S1 in the Supporting Information). The first scenario contained a single group of animals with a ‘high’ average probability of detection. The second scenario contained two groups of animals, one with a ‘high’ average probability of detection and the other with a ‘medium’ average probability of detection. Scenarios 1 and 2 assume between-individual variation is relatively small. The third scenario also contained two groups of animals, one with a ‘high’ average probability of detection, and the other ‘low’. The between-individual variation in the third scenario is relatively large (see Table S1 in the Supporting Information). Scenarios 2 and 3 are intended to mimic two groups of animals within the population, such as males and females, where one sex can have a substantially lower probability of detection than the other. Scenario 3 was designed to be close to that of the Key Largo woodrat case study, where between-individual variation was found to be relatively large (see below). The underlying true detection function from which data in the trial survey were sampled was assumed to be unknown during the analysis.

In the first simulation, the amount of survey effort available in the trial survey was fixed at 360 trap nights, as this was believed to be a realistic amount of survey effort two people could achieve during an 8-week field season to conduct a TPT survey on the Key Largo woodrat. The number of trials conducted per individual varied: 6, 10, 18, 24, 40 and 60 trials (thus forcing the number of individuals in the trial survey to be 60, 30, 20, 15, 9 and 6, respectively). In the second simulation, the number of trials conducted per individual was the same as the first simulation (i.e. 6, 10, 18, 24, 40 and 60), but the number of individuals in the survey was changed such that the total trial survey effort was 720, 1080 and 1440 trap nights (i.e. when 18 trials were conducted per individual, trials were performed on 40 individuals if the total survey effort was 720 trap nights). In the second simulation, only the ‘adaptive’ method of selecting trial distances was investigated.

The main survey consisted of a true population size of 2000 individuals randomly located on a survey area (dimensions 3000 by 4300 m). The main survey was a 10-by-15 grid of trap locations (250-m inter-trap spacing), each sampled once. If multiple groups were present in the population (i.e. the second and third scenarios), 50% of individuals were randomly allocated a detection function with a ‘high’ average probability of detection, and the remainder were allocated to the

other group (‘medium’ or ‘low’ average detection probabilities, see Table S1 in the Supporting Information).

The simulation was run 999 times, and abundance was estimated using data obtained for each iteration of the trial and main surveys, either by assuming underlying heterogeneity (i.e. group membership) was known (e.g. an observable covariate such as sex) or by unknown (e.g. an unobservable covariate, in which case a pooled detection function was fit to all data). Percentage bias and RMSE were calculated. Further details regarding the simulation study are presented in Potts (2011).

## CASE STUDY: APPLYING TPT TO THE KEY LARGO WOODRAT

### *Species and survey area*

The Key Largo woodrat is one of the six recognized subspecies of the eastern woodrat (*Neotoma floridana*). It has a highly restricted geographic range, occupying extant, tropical hardwood hammock on northern Key Largo, Florida, USA (Fig. 1). Key Largo covers c. 21 km<sup>2</sup> (US FWS 1999). Although tropical hardwood hammock was once the dominant vegetation type across Key Largo, because of urbanization, approximately one-third remains within two protected reserves. Despite its protected status, the remaining tropical hardwood hammock is highly fragmented with roads, tracks and abandoned developments. Woodrats typically occupy home ranges of c. 0.23 ha, forage at night and rest in one of the several nests within their home range during the day (US FWS 1999).

### *Survey methodology*

Trapping point transects surveys of the Key Largo woodrat were undertaken during the same season (February to April) in each of 4 years, 2008–2011. The *main survey* comprised a randomly placed systematic grid of 136 sample points with a 250-m trap spacing throughout suitable habitat within the range of the subspecies (Fig. 1). The large trap spacing was used so that detection events at neighbouring sample points could be assumed independent. The distance was chosen based on the home range size of the woodrat.

In 2011, additional investment of survey effort allowed the main survey to be repeated three times within the 10-week field season. To ensure the assumption that neighbouring sample points were independent, the original 136 points were surveyed and then traps were moved 125 m east and the survey was repeated (142 points), and then traps were moved 125 m north and the survey was repeated again (142 points). In total, 420 main survey points were trapped in 2011.

The large trap spacing also meant that the whole study area could be surveyed with moderate effort. Two vented Sherman traps with raccoon-proof door latches (c. 10.2 × 11.4 × 38.1 cm in size, model PXL15, H. B. Sherman Traps Inc., Tallahassee, FL, USA) were placed within a metre of one another at each trap location and were set in the afternoon using whole oat bait. Each main survey trap location was trapped for three consecutive nights. All woodrats captured in the 3-day period were double-marked with passive integrated transponder (PIT) tags (AVID, Norco, CA, USA) and #1005 Monel ear tags (National Band and Tag, Newport, KY, USA). Sex was recorded.

To conduct the *trial survey*, radio transmitters were attached to a subset of woodrats captured during the main survey and during additional dedicated trapping. Because the woodrat is nocturnal, radiocollared individuals were located during the daytime at their

nesses. An individual trial was conducted on a radiocollared woodrat by setting two trial traps (as in the main survey) at some pre-determined distance and random direction away from the nest. The trial traps then checked the following morning, and captured animals were released at point of capture. The trial survey recommenced immediately if the woodrat was not recaptured, or after a rest period of typically 2 days otherwise.

Each woodrat was exposed to trial surveys at various distances. Typically, three trials were performed at each 5-m interval between 5 and 60 m. Some trials were performed at very long distances for which capture was believed to be extremely unlikely (up to 320 m), to ensure the tail of the detection function (i.e. large distances,  $r$ , where  $g(r) \approx 0$ ) would be accurately estimated. Some woodrats were exposed to numerous, very short trial distances (1 m), to retrieve the collar.

### Data analysis

Separate detection functions of the GLMM form presented in eqn 1 were fitted to the trial survey data collected on male and female woodrats. Owing to small sample sizes collected during the trial survey on male woodrats, data were pooled across year, and a simple detection function was fitted that assumed average probability of detection depended only on distance from trap ( $dist$ ) and a random effect about the intercept term. Covariates considered during model selection of the detection function fitted to the female trial survey data included distance from trap ( $dist$ ) and year of survey ( $year$ ). A simple random effect about the intercept term was assumed, and distance was centred by the group mean (Kreft, de Leeuw & Aiken 1995). Forward model selection based on AIC was used (Burnham & Anderson 2003).

All GLMM modelling was completed using the 'glmer' function within the 'lme4' package (v0.999375-37, Bates & Maechler 2009) of the statistical software R (v2.12.0, R Development Core Team 2010). Maximum likelihood estimates of the parameters in the detection function were approximated using adaptive Gaussian quadrature (Lesaffre & Spiessens 2001). To decrease computation time in fitting the models, but maintain sufficient accuracy in estimating the likelihood, 10 quadrature points were used for all models fitted (Lesaffre & Spiessens 2001).

Observed values of each explanatory variable  $z_{i1}, \dots, z_{ij}$  were substituted into the fitted detection function for each woodrat captured in the main survey. We estimated the availability function,  $\pi_r(r)$ , by taking 10 points evenly distributed between 0 and  $w$  m (i.e. every 12.5 m), laid along each of the four cardinal (N, S, E and W) and four intercardinal (NE, SE, SW and NW) directions of the compass. Thus, 80 surrounding points were checked for each main survey trap location to determine whether or not they fell in woodrat habitat. A binary logistic regression model was then fitted to define habitat availability as a function of distance from the main survey trap location.

Estimates of woodrat abundance were calculated by sex and year, using the Horvitz–Thompson-like estimator presented in eqn 2. A nonparametric bootstrap, as described earlier, was used to estimate variance in abundance, with 95% confidence intervals.

## Results

### SIMULATION STUDY RESULTS

Detailed results for simulating the trial and main surveys are presented in the Supporting Information and Potts (2011). In

the first simulation, percentage bias of  $\hat{N}$  was lowest when the adaptive method was used to select trial distances, and 18 trials were conducted on each individual (c. 4%, Fig. S1 in Supporting information). Percentage bias and RMSE for both estimators decreased until at least 10 trials were conducted per individual, after which results plateaued if more trials were conducted per individual. With decreasing average probability of detection, more trials were required per individual to achieve unbiased results. When underlying individual heterogeneity in detection probability was ignored, the adaptive method used to select trial distances typically had lower percentage bias and RMSE of population estimates compared with the uniform method (see Fig. S2 in the Supporting Information).

As with the first simulation, in the second simulation increasing the number of trials conducted on each individual to more than c. 10 did not increase precision in  $\hat{N}$ , regardless of total survey effort (see Fig. S3 in the Supporting Information). However, as would be expected, percentage bias and RMSE of  $\hat{N}$  decreased when total survey effort increased (regardless of whether the effort was allocated to more trials or more individuals). However, this increase in precision came at considerable survey cost: doubling survey effort from 360 to 720 trap nights when 18 trials were performed on each individual,  $\hat{N}$  decreased approximately a third (see Supporting Information).

When group-heterogeneity was accounted for, percentage bias in  $\hat{N}$  decreased with increasing survey effort, and the lowest percentage bias (= 0.95%) was achieved when 40 trials were conducted on 36 individuals (1440 trap nights); however, this bias was comparable with that obtained for simulations with less sampling effort. For example, the bias when 40 trials were conducted on 27 individuals (1080 trap nights) was 1.06%, and when 18 trials were conducted on 40 individuals (720 trap nights), the bias in  $\hat{N}$  was 1.57%. Similar results were obtained when group-heterogeneity was ignored, but the magnitude of the bias was larger (see Supporting Information and Potts (2011) for a more detailed assessment of these results).

### CASE STUDY RESULTS

The capture rate of female and male woodrats (per 100 trap nights) declined substantially between 2008 and 2010 and then increased slightly in 2011 (Table 1). In 2010, only a single male and female were caught in the 816 trap nights of effort in the main survey (Table 1).

In total, 1190 individual trials were conducted on 34 female (645 trials) and 22 male (545 trials) woodrats between 2008 and 2011. Of these trials, 176 (66 trials on males and 110 on females) were successful (Table 2). The maximum trial distance for which a radiocollared woodrat was recaptured was 80 and 60 m for a female and male woodrat, respectively (Table 2). Trial surveys were conducted on an additional two female and one male woodrat; however, these three woodrats were found predated by feral cats soon after radiocollars were attached. Trials from these individuals were omitted from the data analysis because date of death was unknown, so that we could not distinguish between an unsuccessful trial on a live animal and an attempted trial on a dead animal.

**Table 1.** The total number of unique female and male woodrats captured, and the capture rate per 100 trap nights (given in parentheses), in the main survey. Two traps were placed at each main survey point and set for three consecutive nights (e.g. 136 main survey points equated to 816 trap nights). Main survey effort in 2011 was trebled

Year	Female	Male	No. main survey points
2008	6 (4.4)	8 (9.5)	136
2009	4 (2.9)	2 (1.5)	136
2010	1 (0.7)	1 (0.7)	136
2011	6 (2.4)	7 (2.6)	420

For females, the detection function model with lowest AIC was that with trial distance and an individual-level random effect. The model with the next-lowest AIC included a year-effect, but was found to be non-significant ( $\Delta\text{AIC} = 4.07$ ), hence abundance estimates were based only on the model that included trial distance. For males, the detection function was dependent on trial distance, and a random individual-level effect model was fitted. The detection functions fitted to the female and male trial data are shown in Fig. 2a,b. The availability function took account of edge effects, and so increased less quickly than a triangular availability distribution.

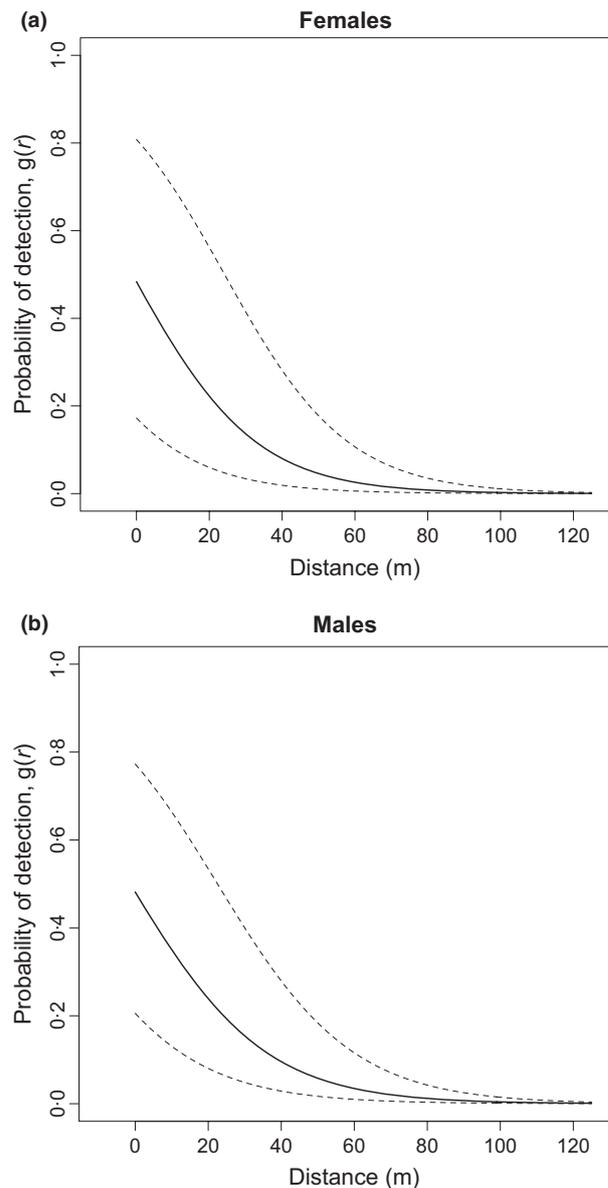
Estimated abundance for both male and female woodrats declined between 2008 and 2010, with some evidence of population increase in 2011 (Table 3). However, uncertainty for sex-specific abundance estimates was disappointingly large, especially when capture rates were low (for example, in 2010, when only one male and female woodrat were captured, CVs for female and male woodrats were 1.19 and 1.11, respectively, Table 3). Uncertainty for the abundance estimates of the entire population ranged between 0.43 in 2011 when substantial survey effort was undertaken and 0.82 in 2010 when capture rates were especially low (Table 3).

## Discussion

To date, all trapping point transect studies (Buckland *et al.* 2006) and variants (Turchin & Odendaal 1996; Legare *et al.* 1999; Acosta & Perry 2000) either performed single trials on individuals or performed multiple trials on individuals but failed to account for individual variation. The innovative aspect of this research is accounting for individual variation in

**Table 2.** The number of individuals for which radiocollars were attached and trial surveys performed (Ind.), along with the total number of trials (Trials), the percentage of trials that were successful (Success) and the maximum distance of a successful trial (Max. dist.) for female and male woodrats in the 4-year survey period

Year	Females				Males			
	Ind.	Trials	Success (%)	Max. dist. (m)	Ind.	Trials	Success (%)	Max. dist. (m)
2008	11	119	23	41	4	69	22	30
2009	7	169	12	40	5	148	7	60
2010	5	117	18	80	5	120	17	36
2011	11	240	18	64	8	208	8	30



**Fig. 2.** Mean detection function plot (solid line) corresponding to the best model for the female (Panel A,  $b_0 = -0.065$ ,  $b_1 = -0.059$ ) and male (Panel B,  $b_0 = -0.073$ ,  $b_1 = -0.054$ ) trial data that had the lowest Akaike's Information Criterion (AIC) value of all the models fitted (where a year-effect was not included in the model). Dashed lines indicate the 2.5th and 97.5th percentiles (as calculated based on 10,000 samples of the estimated random effects distribution).

**Table 3.** Abundance estimates, 95% percentile intervals and coefficients of variation for female, male and total population of woodrats between 2008 and 2011 using abundance estimator  $\hat{N}$  (eqn 1)

Year	$\hat{N}_F$	$\hat{N}_M$	$\hat{N}_T$	$CV_F$	$CV_M$	$CV_T$
2008	235 (63, 623)	458 (83, 1164)	693 (253, 1462)	0.65	0.59	0.45
2009	177 (28, 422)	71 (0, 201)	248 (60, 538)	0.67	0.84	0.55
2010	43 (0, 169)	35 (0, 139)	78 (0, 233)	1.19	1.11	0.82
2011	130 (29, 341)	126 (31, 273)	256 (94, 518)	0.65	0.52	0.43

capture probability using random effects. By radiocollaring animals, we were able to obtain multiple trial observations on each animal to estimate the detection function using GLMMs.

Using a simulation study, we found percentage bias of  $\hat{N}$  (eqn 1) was low (*c.* 5%) with modest levels of survey effort (360 trap nights in the trial survey). Uncertainty and relative bias in population estimates increased with decreasing capture probabilities and increasing between-individual variation. Another estimator we investigated (results shown in the Supporting Information) was found to have a large bias and is generally not recommended. We recommend that the adaptive method be used to select trial distances. For the detection function scenarios we investigated, *c.* 20 trials per individual proved satisfactory, after which additional survey effort should be invested in radiocollaring more individuals, rather than conducting more trials on the same individuals.

A key advantage of the TPT method over other commonly implemented methods (e.g. capture–recapture) is uncertainty can be partitioned into its components. Here, uncertainty can be due to estimating the encounter rate in the main survey and estimating detectability in the trial survey. By partitioning the variance in this manner, one may choose to invest more survey effort into one or other of the surveys to reduce the overall uncertainty, whilst also ensuring bias in  $\hat{N}$  remains at a satisfactorily low level. We demonstrated using a bootstrap to estimate the variance, but the delta method could have also been used (Fewster *et al.* 2009).

We used TPT to estimate abundance of the Key Largo woodrat. Between 2008 and 2010, the TPT method required *c.* 1000 trap nights per field season, which equated to *c.* 960 person-hours (a four-person field team working full time for *c.* 8 weeks). In 2011, the main survey was repeated three times and required an additional 1704 trap nights. Abundance estimates for both males and females steadily declined between 2008 and 2010, before increasing again in 2011 (Table 3). The lowest abundance estimates were in 2010 when only two woodrats were captured during the main survey. However, uncertainty in the abundance estimates for each sex was disappointingly large (CVs ranging between 0.52 and 1.19, Table 3) with the greatest uncertainty occurring in 2010 when capture rates were especially low (i.e. only one male and female woodrat was captured in 816 trap nights in the main survey, Table 1). In years when capture rates are low, greater survey effort is required to obtain useful abundance estimates. Should the TPT survey be implemented in future years, more survey effort should be implemented in both the main and trial survey to decrease uncertainty. Simulation studies presented in the Supporting Information and in Potts (2011) show that once

*c.* 20 trials are conducted on each individual, trial survey effort should be aimed at radiocollaring more individuals, and in the main survey, more grids can be set, as long as trapping points can be considered independent (here, 250 m apart).

We discuss each of the assumptions of the TPT method and the consequences of these assumptions for the Key Largo woodrat case study:

**1** Capture events at one location in the main survey are assumed independent of capture events at other locations. To meet this assumption, separation of main survey points needs to be sufficiently large. Here, the spacing of traps used in the main survey was 250 m, based on the estimates of home range size of woodrats. We did not capture any woodrats at more than one main survey point. In the case of nomadic males that can roam large distances between nest locations, it is possible that a woodrat might be captured in more than one main survey trap location, but this would represent only a minor violation of the assumption.

**2** The detection function model fitted to the trial survey data is assumed to apply to the animals captured in the main survey, and incorporating covariates in the detection function (e.g. sex) can help. The best way to achieve this is if the main and trial surveys are held concurrently in space and time, and the same field methods (i.e. the same trap design and layout) are used in the main and trial survey. In the woodrat case study presented here, because of logistical constraints, the trial survey was performed either shortly before or shortly after the main survey was completed (with a maximum difference of 3 weeks), and both were conducted in the same study region. The discrepancy of up to 3 weeks was not sufficient for substantial changes in trappability arising from seasonal differences.

In addition to space and time variation, it is possible that there is a behavioural response to the trapping processes, which was not accounted for in this study. Standard capture–recapture models have been developed to incorporate behavioural response to the capture experience, and the TPT method could be extended to include these types of models. In the case study presented here, individuals in the trial survey had already been trapped at least once (to attach the radiocollar). We therefore implicitly assume the trappability of woodrats after first capture when the radiocollar is attached does not change. As with all capture–recapture studies, unmodelled heterogeneity in capture probability will cause an upward bias in estimated detection probability.

**3** We modelled individual differences in catchability using a random effect, which was assumed normal on the logit scale.

The most expensive aspect of the TPT survey implemented in this study was the initial purchase of radiocollars and the

field time taken to locate radiocollared woodrats. However, radiocollaring woodrats enabled auxiliary information to be gathered, in addition to the estimation of trapping probability from the trial survey. First, nest locations were identified and nesting behaviour observed. Secondly, numerous predation events by invasive species were observed. This includes the discovery of Burmese pythons (*Python molurus bivittatus*) in Key Largo, the first of which was found because it had consumed a radiocollared woodrat (Greene *et al.* 2007). Also during the 2011 survey, four of the 22 radiocollared woodrats in the trial survey were predated by feral cats. Predation by feral cats and introduced non-native species may be a contributing factor to any decline in Key Largo woodrat abundance during the survey period.

The cost of implementing the TPT survey can be reduced, if the radiocollaring aspect of the method can be omitted. It may be possible to use the point of release after a capture event as the starting position of a trial (Potts 2011). That is, an animal is captured (and released) at point  $R$ , and upon release, it is assumed to return to its nest ( $C$ ). A trial trap is set some distance ( $T$ ) away from the release point  $R$ . Because the location of  $C$  is unknown, the distance of an individual trial,  $d$ , is estimated as the distance between the animal's point of release ( $R$ ) and the location of the trial trap ( $T$ ). However, the 'true' trial distance is actually  $D$ , the distance between the animal's start point ( $C$ ) when the trial trap was set, and the location of the trial trap  $T$ . Whether the discrepancy between  $d$  and  $D$  causes bias in population estimates needs to be explored. This point-of-release approach could be viewed as a combination of TPT and SECR, in that the location of traps in the SECR survey are moved each night, in response to where the animal was being captured (centred on its home range). This approach could be used for species that are too small to attach radiocollars (e.g. the Key Largo cotton mouse, *Peromyscus gossypinus allapaticola*) and should be investigated.

Analysis of genetic samples taken from animals captured in the survey period also suggests there are five genetically distinct subpopulations of Key Largo woodrats (T. King, USGS, unpublished data). Woodrat population recovery will be multifaceted. The construction of supplemental nest structures that provide safe refuges for woodrats (Winchester, Castleberry & Mengak 2009) will serve as a conduit to join subpopulations. In addition, captive bred individuals can supplement the wild population (Alligood *et al.* 2009), and the removal of feral cats and Burmese pythons that increase predation pressure of a threatened species will aid population recovery.

Winchester (2007) also concluded that a standard capture–recapture survey to estimate Key Largo woodrat abundance was likely to be cost-prohibitive to implement as a long-term monitoring programme, because of the large survey effort required and low recapture rates of individuals. We found the TPT method to be practical to implement in the field and relatively cost-effective (also see Potts (2011) for a comparison of TPT with SECR). The TPT method offers considerable flexibility to adapt to a range of species that are otherwise very difficult to monitor. Because the method can be applied without physically capturing animals, provided it is possible to

conduct trials on known-location animals, many different methods might be used to trap or detect animals at the sample point. Buckland *et al.* (2006) used recordings of excitement calls of Scottish crossbills to lure birds in. Various other types of lure might be used. Baits might be successful, for example for surveys of fish, predators or carrion eaters. Camera traps are an option if individuals are identifiable, for example through natural markings. We anticipate that TPT surveys may see wide usage for estimating population abundance of cryptic but trappable species.

## Acknowledgements

Data collection was assisted by staff at the Disney's Animal Kingdom® Wildlife Tracking Center and the Animal Operations Night Team; the University of St Andrews, and Friends and Volunteers of Refuges. Particular thanks to Christy Alligood, Rob Carlson, Martin Cox, Andy Daneault, Clay and Ralph DeGayer, Sarah DeWees, Steve Klett, Laura Marshall, Britta Muiznieks, Sandra Sneckenberger and Lindsay Scott-Hayward. Funding was provided by Disney's Animal Programs, U.S. Fish and Wildlife Service and the University of St Andrews. Fieldwork was permitted by the U.S. Fish and Wildlife Permit #TE139405-2, Florida Fish and Wildlife Conservation Commission #WV08573 and Florida Department of Environmental Protection #5-11-03. We thank three anonymous reviewers for their comments and suggestions, which led to a much improved paper.

## References

- Acosta, C.A. & Perry, S.A. (2000) Effective sampling area: a quantitative method for sampling crayfish populations in freshwater marshes. *Crustaceana*, **73**, 425–431.
- Alligood, C.A., Wheaton, C.J., Daneault, A.J., Carlson, J.K. & Savage, A. (2009) Behavioral predictors of copulation in captive Key Largo woodrats (*Neotoma floridana smalli*). *Behavioural Processes*, **81**, 337–342.
- Bates, D. & Maechler, M. (2009) *Package 'lme4': Linear Mixed-effects Models Using Eigen and S4* (v0.999375-34). <http://lme4.r-forge.r-project.org/>.
- Borchers, D.L. & Efford, M.G. (2008) Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, **64**, 377–385.
- Borchers, D.L., Buckland, S.T., Goedhart, P.W., Clarke, E.D. & Hedley, S.L. (1998) Horvitz-Thompson estimators for double-platform line transect surveys. *Biometrics*, **54**, 1221–1237.
- Buckland, S.T. (1984) Monte Carlo confidence intervals. *Biometrics*, **40**, 811–817.
- Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997) Model selection: an integral part of inference. *Biometrics*, **53**, 603–618.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling*. Oxford University Press, Oxford.
- Buckland, S.T., Summers, R.W., Borchers, D.L. & Thomas, L. (2006) Point transect sampling with traps or lures. *Journal of Applied Ecology*, **43**, 377–384.
- Burnham, K.P. & Anderson, D.R. (2003) *Model Selection and Multi-model Inference – A Practical Information-theoretic Approach*. Springer, USA.
- Fewster, R.M., Buckland, S.T., Burnham, K.P., Borchers, D.L., Jupp, P.E., Laake, J.L. & Thomas, L. (2009) Estimating the encounter rate variance in distance sampling. *Biometrics*, **65**, 225–236.
- Greene, D.U., Potts, J.M., Duquesnel, J.G. & Snow, R.W. (2007) Geographic distribution: *Python molurus bivittatus* (Burmese python). *Herpetological Review*, **38**, 355.
- Kreft, I.G.G., de Leeuw, J. & Aiken, L.S. (1995) The effect of different forms of centering in hierarchical linear models. *Multivariate Behavioral Research*, **30**, 1–21.
- Legare, M.L., Eddleman, W.R., Buckley, P.A. & Kelly, C. (1999) The effectiveness of tape playback in estimating Black Rail density. *The Journal of Wildlife Management*, **63**, 116–125.
- Lesaffre, E. & Spiessens, B. (2001) On the effect of the number of quadrature points in a logistic random-effects model: an example. *Applied Statistics*, **50**, 325–335.
- Lukacs, P.M., Anderson, D.R. & Burnham, K.P. (2005) Evaluation of trapping web designs. *Wildlife Research*, **32**, 103–110.

- Manly, B.J. (2007) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, **62**, 1–135.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990) Statistical inference for capture–recapture experiments. *Wildlife Monographs*, **107**, 1–97.
- Potts, J.M. (2011) *Estimating Abundance of Rare, Small Mammals: A Case Study of the Key Largo Woodrat (Neotoma floridana smalli)*. PhD thesis, University of St Andrews, UK.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Royle, J.A. & Young, K.V. (2008) A hierarchical model for spatial capture–recapture data. *Ecology*, **89**, 2281–2289.
- Seber, G.A.F. (1992) A review of estimating animal abundance 2. *International Statistical Review*, **60**, 129–166.
- Turchin, P. & Odendaal, F.J. (1996) Measuring the effective sampling error of a pheromone trap for monitoring population density of southern pine beetle (Coleoptera: Scolytidae). *Environmental Entomology*, **25**, 582–588.
- US FWS (1999) Multi-species recovery plan for South Florida – the Key Largo woodrat. Technical Report, United States Fisheries and Wildlife Service.
- Winchester, C. (2007) *An Evaluation of Habitat Selection and An Abundance Estimate for the Endangered Key Largo Woodrat*. Master's thesis, University of Georgia, Georgia.
- Winchester, C., Castleberry, S.B. & Mengak, M.T. (2009) Evaluation of factors restricting distribution of the endangered Key Largo woodrat. *The Journal of Wildlife Management*, **73**, 374–379.

Received 4 October 2011; accepted 10 March 2012  
Handling Editor: David Warton

## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Plots of percentage bias estimates (left axis, solid line) and RMSE (right axis, dashed line) for both  $\hat{N}$  (left column, plots A, C, and E) and  $\hat{N}_3$  (right column, plots B, D, and F) when the allocation

of total trial survey effort (360 trap nights) changes for detection function scenarios 1 (plots A and B), 2 (plots C and D) and 3 (plots E and F), when underlying heterogeneity in detection probability was accounted for. RMSE for scenario 3 (plots E and F) is not plotted, see text for explanation.

**Fig. S2.** Plots of percentage bias estimates (left axis, solid line) and RMSE (right axis, dashed line) for both  $\hat{N}$  (left column, plots A and C) and  $\hat{N}_3$  (right column, plots B and D) when the allocation of total trial survey effort (360 trap nights) changes for detection function scenarios 2 (plots A and B) and 3 (plots C and D), when underlying heterogeneity in detection probability was ignored.

**Fig. S3.** Plots of percentage bias estimates (left axis, solid line) and RMSE (right axis, dashed line) for both  $\hat{N}$  (left column, plots A and C) and  $\hat{N}_3$  (right column, plots B and D) when the total trial survey effort changes for detection function scenario 2 (medium detectability) when underlying heterogeneity is accommodated (plots A and B) and ignored (plots C and D).

**Table S1.** Input parameters for the three detection function scenarios, where  $\alpha_g$  is the intercept term for an individual in group  $g$  ( $g = 1, 2, \text{ or } 3$  for individuals in the ‘high’, ‘medium’ and ‘low’ groups, respectively),  $\beta$  is the coefficient (slope) parameter for the explanatory variable distance  $r$ , and  $b_{ig}$  is a random effect due to individual  $i$  in group  $g$ .

**Appendix S1.** The simulation study.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.