

SHORT COMMUNICATION

Estimating population growth rates from tracking tunnels

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Abstract: Tracking tunnels are widely used for monitoring small mammal populations, but inference on population size is hindered by the non-linear relationship between frequency of detection and abundance. The detection-abundance relationship can be used to relate the probability of a tunnel being tracked to the abundance of animals in the population and the population growth rate. We describe equations that show that a complementary-log-log link transformation for analysis of presence-absence tracking data allows estimation of small mammal population growth rates and proportional differences in abundance at different sites or under different treatments, as well as estimation of the rate at which animals pass through tunnels. We demonstrate the utility of this type of model to long-term temporal monitoring data of rat irruptions during beech mast seeding events, and show that the results are similar to theoretical growth rates of rat populations under such scenarios. This form of analysis yields biologically interpretable parameters and thus is an improvement on most current analytical techniques; however, it still requires the assumption that the probability of detection remains constant or is independently modelled, and it can still not be used to make inference on absolute population size.

Keywords: tracking tunnels; estimating population growth rates; generalised linear models

Introduction

Indices are widely used field methods for monitoring animal populations (Whisson et al. 2005). However, estimating abundance from indices and estimating changes in abundance in time and space are confounded by the non-linear relationship between detection and abundance. They are further confounded by probabilities of detection which can vary in time and space (Conn et al. 2004). In New Zealand, small mammals, particularly rodents, are most commonly index monitored with tracking tunnels (Gillies & Williams 2013). Indices from tracking tunnels are most commonly presented as the percentage frequency of detection (i.e. the percentage of tunnels with detections - hereinafter “tracking rate”), since distinguishing individuals on tracking cards is not reliable (Russell et al. 2009). Furthermore, these tracking rates are rarely calibrated with independent studies of population abundance (see Brown et al. 1996). This is particularly problematic for conservation managers trying to assess the population growth rates of pest animals, and the effectiveness of pest animal control programmes. The obvious measure of pest control efficiency, for example, percentage of pest animals killed, is not easily extracted from tracking rates. The non-linear relationship between tracking rates and abundance means that a decrease in a tracking rate from (for example) 80% to 40% does not represent the same percentage reduction in abundance as a change from 40% to 20%.

Presence-absence data such as tracking tunnel data are often analysed using generalised linear models (“glms”) with logistic link functions (logistic regression) (Hosmer & Lemeshow 2000). Such analyses model the relationship between the odds of detection and a suite of covariates, but

the parameter estimates produced by these models are often not readily interpretable when applied to tracking rates. For example, a logistic regression parameter estimate associated with time might erroneously be regarded as a population growth rate, but it is in fact the log of the rate of change of the odds of detection.

The relationship between species detection and abundance can be used to estimate animal abundance from detection data (MacKenzie et al. 2002, Royle & Nichols 2003, Cruz et al. 2013) but these models require repeated sampling during each survey; an approach not possible with baited tracking tunnels, as animals become habituated to regularly offered bait.

Caughley (1977) described the relationship between presence and absence of animals in detection devices and their abundance, based on properties of the Poisson distribution, and showed that so long as absolute population size estimates are not required, robust relative estimates of population size among sites, and its change over time, are possible. Caughley’s technique makes the important assumptions that the animals behave randomly and independently, and that their detectability does not change in time and space. Recent advances in both computational power and generalised linear modelling (“glm”) methods enable easy application of Caughley’s idea.

Here we show how detection data from tracking tunnels can provide estimates of relative population change in time and space using glms with complementary-log-log (“cloglog”) link functions (see also Appendix 1 of Getzlaff et al. 2013).

To demonstrate the utility of this approach we use glms with cloglog links with rat tracking data collected during population irruptions in beech forests in New Zealand and estimate population growth rates.

Model

It is reasonable to assume that in the absence of resource constraints animal populations grow exponentially. Thus:

$$N_{t+\Delta t} = N_t \times \lambda^{\Delta t} \quad (1)$$

Where:

N is the number of rats in the environment
 t is time
 λ is the finite rate of population increase

Or alternatively:

$$N_{t+\Delta t} = e^{(\log(N_t) + \Delta t \log(\lambda))} \quad (2)$$

The number of animals that leave tracks in a tracking tunnel, c , will be related to their population size N , and their probability of detection, p , thus:

$$c_t = pN_t \quad (3)$$

Without an independent calibration study for an index, probability of detection and population size are confounded. However, in the absence of any other information we might as well assume that the number of animals that leave tracks in tracking tunnels is linearly proportional to their abundance (i.e. as population size increases so does the number of animals passing through tunnels), thus:

$$c_t \propto N_t \quad (4)$$

It is not possible to determine how many animals have passed through a tracking tunnel, we can only say whether any have passed through the tunnel (i.e. presence or absence of tracking). However, we know from the Poisson distribution that given a density N , the probability of a sample including no animals is given by:

$$p_{no\ animals} = e^{-N_t} \quad (5)$$

Thus the probability of a sample including at least one animal is given by:

$$\begin{aligned} p_{at\ least\ 1\ animal} &= 1 - p_{no\ animals} \\ &= 1 - e^{-N_t} \end{aligned} \quad (6)$$

Applying this relationship to tracking tunnel data, the probability of tracking any animals, f_t , is related to the number passing through the tracking tunnel by the following:

$$f_t = 1 - e^{-c_t} \quad (7)$$

and

$$f_{t+\Delta t} = 1 - e^{-(c_t \times \lambda^{\Delta t})} \quad (8)$$

To linearise this relationship, we can re-arrange it as follows:

$$f_{t+\Delta t} = 1 - e^{-(\log(c_t) + \Delta t \log(\lambda))} \quad (9)$$

and

$$\log(-\log(1 - f_{t+\Delta t})) = \log(c_t) + \Delta t \log(\lambda) \quad (10)$$

The term on the left of Eqn 10 is the cloglog function which is available as a link function in many generalised linear modelling packages, such as R (R Core Team, 2016). Thus, if one used the tracking results for each tunnel in a tracking tunnel survey and expressed the results as 1 when tracked and 0 when not tracked, one can estimate the parameters $\log(c_t)$ and $\log(\lambda)$ in R using:

```
glm(tracks~time, family=binomial(link='cloglog'))
```

The intercept term $\log(c_t)$ provides an estimate of the number of animals passing through a tracking tunnel but cannot be used to make inference on population size N_t due to the inescapable confounding effect of detectability (p), which is inestimable. However, the slope parameter estimate associated with “time” will be the maximum likelihood estimate of $\log(\lambda)$, i.e. the instantaneous population growth rate, r .

This formulation is a regression of cloglog transformed tracking rates against time. The cloglog link function transforms tracking rates such that the linear predictors are not constrained between 0 and 1. This facilitates linear modelling, and fortuitously provides theoretically plausible estimates of population growth rates.

As for any regression model, co-varying factors can be included as covariates to factor out their influence. This is particularly important where such factors might be correlated with the probability of detection.

Similarly, any random variation among transect lines can be accounted for using mixed effects models. Using the package lme4 in R (Bates et al. 2015), for example, a model estimating growth rates from tracking tunnel data grouped by tunnel within transect lines, could be specified by

```
glm(tracks~time+(1|transect/tunnel), family=binomial(link='cloglog'))
```

The relative abundance of animals between sites can be compared using a model that would be specified in R by

```
glm(tracks~site, family=binomial(link='cloglog'))
```

and the parameter estimates associated with the site terms can be interpreted in much the same way as growth rates. That is the intercept parameter $\log(site_0)$ is an estimate of the average number of animals passing through a tracking tunnel at the reference site, and parameters $\log(site_1)$ to $\log(site_n)$ are estimates of the relative abundance of animals at sites 1 to n compared to the abundance at site 0.

Again, using the same logic, a Before-After-Control-Impact (BACI) experimental design might be analysed using a model specified by

```
glm(tracks~site+time+site:time, family=binomial(link='cloglog'))
```

where *time* is before or after treatment, and the parameter *site:time* is the log of the effect of the treatment on abundance.

Example

We used the analytical framework described above to estimate population growth rates of ship rats (*Rattus rattus*) monitored with tracking tunnels in southern beech (Nothofagaceae) forest

of New Zealand. In New Zealand beech forests, populations of ship rats sometimes increase irruptively following the mast seeding of beech trees (King & Moller 1997). We used rat tracking data from five beech forest sites in Otago, Southland and North Canterbury where tracking tunnel data have been collected in the year following beech mast. Tracking data were collected using the methods of Gillies & Williams (2013). Tracking tunnels were placed along transects of 10 tunnels at 50 m intervals. There were between 60–100 tracking tunnels at each of the five sites, and inked tracking cards were placed in the tunnels for one night once every 1–3 months. Tunnels were baited with peanut butter placed at both ends of the tunnels.

The dataset comprised 2040 records for individual tracking tunnels each with three variables:

- site* - the site at which the data were collected
- tracks* - the presence (1) or absence (0) of tracking in a tunnel when it was checked
- days* - days since 1 January in the year of the beech mast

Visual inspection of the data (Fig. 1) show that rat tracking rates increased following beech mast at the five sites.

We used AICc (Burnham & Anderson 2002) to compare three generalised linear models: one with a common growth rate and intercept for all sites (Model 1), one with a common growth rate but separate intercepts for the sites (Model 2), and one with separate growth rates and intercepts for the sites (Model 3) (Table 1). AICc values suggest that the model with separate growth rates and intercepts (Model 3) was best.

Model 1 estimated a common growth for all the sites of 1.0103 per day, while Model 3 estimated rates ranging from 1.0071 to 1.0191 at each of the sites.

To determine whether the rates of population growth estimated by the GLMs are biologically plausible we combined data from three sources to estimate the maximum possible growth rate of rats in New Zealand. Estimates of litter size came from Innes et al. (2001), while estimates of breeding frequency, age at first breeding and survival came from Tompkins & Veltman (2006). Sweetapple & Nugent (2007) and Innes et al. (2001) provided estimates of the proportion of females that were breeding. We populated a Leslie matrix with the data from these sources that would give the maximum possible growth rate and estimated the growth rate from the dominant eigenvalue of the matrix. This provided an estimated

Table 1. AICc values for three different GLMs of rat population growth during periods of rapid population growth following beech mast.

Model		AICc	Δ AICc
3	$\text{glm}(\text{tracks} \sim \text{days} * \text{site}, \text{family} = \text{binomial}(\text{link} = \text{'cloglog'}))$	154.98	0.00
2	$\text{glm}(\text{tracks} \sim \text{days} + \text{site}, \text{family} = \text{binomial}(\text{link} = \text{'cloglog'}))$	183.64	28.66
1	$\text{glm}(\text{tracks} \sim \text{days}, \text{family} = \text{binomial}(\text{link} = \text{'cloglog'}))$	475.15	320.17

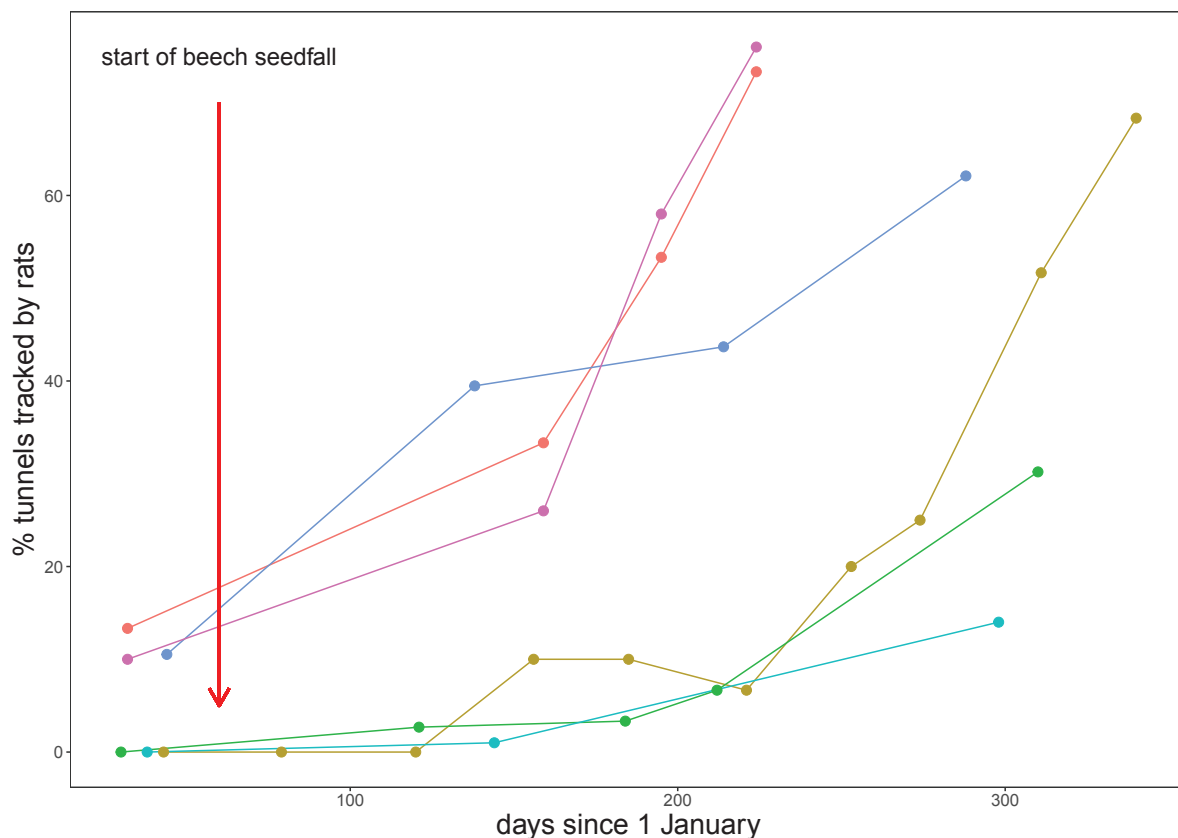


Figure 1. Rat tracking rates following six beech masts at five beech forest sites.

maximum daily growth rate of 1.0103, remarkably similar to the estimates from the tracking tunnels.

Discussion

The analytical framework we describe makes important assumptions: that animals behave randomly and independently of each other (a Poisson process) and that the detectability of animals is constant among comparisons in time and space. We have no good reason to assume that these assumptions are met, but in the absence of other information they are the most parsimonious assumptions we can make. Tracking tunnel data have no power to detect non-random animal behaviour or changes in detectability: such information will have to come from studies not involving tracking tunnels.

Presence-absence data are often analysed using logistic generalised linear models, using the logit link and analyses using the logit and cloglog links often produce similar results. The important difference when analysing tracking tunnel data is that slope parameters in logistic generalised linear models estimate the rate of change in the odds of detection, whereas slope parameters in a cloglog generalised linear model can be interpreted as estimates of the rate of change in the number of animals passing through tunnels, or changes in abundance.

The estimate of the average daily population growth rate of ship rats after beech mast provided by the GLMs was almost exactly equal to estimates derived from population studies of rats in New Zealand. This does not necessarily indicate that tracking rates accurately reflect changes in rat population size because it is possible that the changes in our tracking tunnel indexes reflected changes in behaviour rather than a real population increase, but it is at least encouraging. The prediction of rat irruptions and the control of rats have become important tools in the conservation management of endangered species in New Zealand (Elliott & Suggate 2007, Elliott & Kemp 2016). Determining the relative importance of population growth and detectability on changes in the rate at which animals are detected in tracking tunnels could have significant impact on rat control in New Zealand.

The analytical framework we describe here can be generalised to any presence-absence detector, such as chew cards, wax-tags (Whisson et al. 2005, Sweetapple & Nugent 2011) or even traps. When analysed appropriately, index data can provide robust information on animal population dynamics.

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References

Brown KP, Moller H, Innes J, Alterio N 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *New Zealand Journal of Ecology* 20: 271–275.

Bates D, Machler M, Bolker BM, Walker SC 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.

Burnham KP, Anderson DR, 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York, Springer Verlag. 488 p.

Caughley G 1977. Analysis of vertebrate populations. London, John Wiley and Sons. 234 p.

Conn PB, Bailey LL, Sauer JR 2004. Indexes as surrogates to abundance for low-abundance species. In: Thompson WL ed. Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Washington, Island Press. 15 p.

Cruz J, Glen AS, Pech RP 2013. Modelling landscape-level numerical responses of predators to prey: The case of cats and rabbits. *PLoS ONE* 8(9): e73544.

Elliott G, Kemp J 2016. Large-scale pest control in New Zealand beech forests. *Ecological Management and Restoration* 17: 200–209.

Elliott G, Suggate R, 2007. Operation Ark. Three year progress report. Christchurch, Department of Conservation. 84 p.

Getzlaff CL, Sievwright KA, Hickey-Elliott AB, Armstrong DP 2013. Predator indices from artificial nests and tracking tunnels: do they tell the same story? *New Zealand Journal of Ecology*: 232–239.

Gillies C, Williams D, 2013. DOC tracking tunnel guide v2.5.2: Using tracking tunnels to monitor rodents and mustelids. Hamilton, Department of Conservation. 14 p.

Hosmer DW Jr, Lemeshow S 2000. Applied logistic regression. 2nd edn. New York. John Wiley and Sons. 374 p.

Innes JG, Flux M, King CM, Kimberley MO 2001. Population biology of the ship rat and Norway rat in Pureora Forest Park. *New Zealand Journal of Zoology* 28: 57–78.

King CM, Moller H 1997. Distribution and response of rats *Rattus rattus*, *R. exulans* to seedfall in New Zealand beech forests. *Pacific Conservation Biology* 3: 143–155.

MacKenzie DI, Lachman GB, Nichols JD, Droege S, Royle JA, Langtimm CA 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83: 2248–2255.

Nathan HW, Clout MN, Murphy EC, MacKay JW 2013. Strategies for detection of house mice on a recently invaded island. *New Zealand Journal of Ecology* 37: 26–32.

R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle JA, Nichols JD 2003 Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84: 777–790.

Russell JC, Hasler N, Klette R, Rosenhahn B 2009. Automatic track recognition of footprints for identifying cryptic species. *Ecology* 90: 2007–2013.

Sweetapple P, Nugent G 2011. Chew-track-cards: a multiple-species small mammal detection device. *New Zealand Journal of Ecology* 35: 153–162.

Tompkins DM, Veltman CJ 2006. Unexpected consequences of vertebrate pest control: predictions from a four-species community model. *Ecological Applications* 16: 1050–1061.

Whisson DA, Engeman RM, Collin, K 2005. Developing relative abundance techniques (RATS) for monitoring rodent populations. *Wildlife Research* 32: 239–244.

White GC 2005. Correcting wildlife counts using detection probabilities. *Wildlife Research* 32: 211–216.

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