

Point transect sampling with traps or lures

STEPHEN T. BUCKLAND,* RON W. SUMMERS,† DAVID L. BORCHERS*
and LEN THOMAS*

*Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 9LZ, UK; and †Royal Society for the Protection of Birds, North Scotland Office, Etive House, Beechwood Park, Inverness IV2 3BW, UK

Summary

1. The ability to monitor abundance of animal populations is becoming increasingly important, in light of growing concerns over the loss of biodiversity through anthropogenic changes. A widely used tool for such monitoring is distance sampling, in which distances of detected animals from a line or point are modelled, to estimate detectability and hence abundance. Nevertheless, many species still prove problematic to survey. We have developed two extensions to point transect sampling that potentially allow abundance to be estimated for a number of species from diverse taxa for which good survey methods have not previously been available.

2. For each method, the primary survey comprises a random sample of points, or more usually a systematic grid of points, through the region of interest. Animals are lured to a point, or trapped at a point, and the number of animals observed at each point is recorded. A separate study is conducted on a subset of animals, to record whether they respond to the lure or enter the trap, for a range of known distances from the point. These data are used to estimate the probability that an animal will respond to the lure or enter the trap, as a function of its initial distance from the point. This allows the counts to be converted to an estimate of abundance in the survey region.

3. We illustrated the methods using a lure survey of crossbills *Loxia* spp. in coniferous woodland in Scotland.

4. *Synthesis and applications.* Two extensions of point transect sampling that use the same statistical methodology, lure point transects and trapping point transects, have been developed. Lure point transects extend the applicability of distance sampling to species that can be lured to a point, while trapping point transects potentially allow abundance estimation of species that can be trapped, with fewer resources needed than trapping webs and conventional mark–recapture methods.

Key-words: distance sampling, logistic regression, *Loxia scotica*, lure point transects, point transect sampling, trapping point transects, trapping webs

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Introduction

At the 2002 World Summit on Sustainable Development in Johannesburg, political leaders agreed to strive for ‘a significant reduction in the current rate of loss of biological diversity’, by the year 2010. The first necessary step to achieve this is to develop adequate monitoring methods, to allow quantification of the rate

of loss of biodiversity. With such methods in place, the success of management actions can be assessed by their impact on the rate of change of biodiversity. A common strategy is to estimate smoothed trends in abundance for each of a number of species (Siriwardena *et al.* 1998; Fewster *et al.* 2000) from which biodiversity changes may be quantified (Buckland *et al.* 2005). Distance sampling (Buckland *et al.* 2001) provides a flexible set of tools for estimating abundance of a wide variety of species, from which trends can be quantified.

Point transects, a form of distance sampling, are widely used for songbird surveys, and occasionally for other

types of populations such as spotlight surveys of nocturnal mammals (Ruelle, Stahl & Albaret 2003). The observer visits each of a set of randomly located points, and records the distance from the point to all animals detected within some truncation distance, w . Not all animals within distance w will be detected; instead the distribution of observed distances is used to estimate the detection function (i.e. the probability of detection of an animal as a function of distance from a point), and hence the average probability of detection of animals within the surveyed circles. This estimate is used to correct for animals missed. Buckland *et al.* (2001) describe the method in detail, and Buckland (2006) discusses implementations of the method for songbirds.

Point transect methods work well for many species, but some species are insufficiently visible or noisy to allow adequate numbers of detections by observers standing at random points. This has led to the development of methods that combine trapping studies with point transect sampling. The standard method for this is the trapping web (Anderson *et al.* 1983; Lukacs, Franklin & Anderson 2004). A single web typically contains 90 or more traps, which are arranged rather like a circular spider's web, with a higher density of traps at the centre than at the edges. Conceptually, the point of the point transect is at the centre of the web, and trapping density is sufficient to be certain of trapping any animals located at or near the web centre.

There are two major shortcomings of trapping webs. First, they are resource demanding: each point of the design requires at least 90 traps, and a minimum of 15 points (webs) is required to draw reliable inference on population abundance (Lukacs, Franklin & Anderson 2004). Secondly, if animals move over a wide area, or have large home ranges relative to the separation distance between traps, then too many captures tend to occur close to the centre of the web, where trap density is greatest. This leads to upwards bias in density estimates (Lukacs, Franklin & Anderson 2004).

Trapping web methods do not utilize mark–recapture data. Efford (2004), Efford, Dawson & Robbins (2004) and Efford *et al.* (2005) developed inverse prediction methods that use the information in recaptures on the trapping web to allow for movement, and hence provide abundance estimates. D. L. Borchers & M. Efford (unpublished data) developed similar methods based on maximum likelihood. Their approach is based on a design in which trap locations remain fixed from one sampling occasion to the next, and a movement model is used to fit the resulting heterogeneity in capture probabilities. This heterogeneity arises at least in part because a trap that lies within the home range of a particular animal on one sampling occasion is also likely to lie within it on the next occasion, so that animals caught previously are more likely to be caught again. The methods allow estimation of the effective size of the sampled plots simultaneously with animal density.

We propose a design in which there is just a single trap at each sample point. The difficulty with such a design

is that we do not know the size of the plot that we have sampled, because we do not know how far a trapped animal has travelled before encountering the trap, so we cannot convert our count of animals trapped to an estimate of density or abundance. If we were able to record for each trapped animal its location when the trap was first set, we could use standard point transect methods to estimate abundance.

In this study, we developed point transect sampling methods for occasions when it is possible to run an experiment alongside the point transect trapping survey, in which the location of animals relative to the trap location is known at the time the trap is set. The data from this experiment are used to estimate the detection function, the probability of trapping an animal as a function of its distance from the point, using logistic regression.

Our methods are also appropriate when a lure is set at the sample point. Lures are often used to attract species that are otherwise difficult to survey. Examples are deep sea fish attracted to a bait (Priede & Merrett 1998), benthic organisms attracted to a baited trap (Taggart *et al.* 2004), mammals and reptiles caught in traps (Parmenter *et al.* 2003), birds and primates responding to recorded calls (Reid, Horn & Forsman 1999; Klavitter, Marzluff & Vekasy 2003) and insects attracted by a pheromone lure (Dahlsten *et al.* 2004). By conducting trials on animals at known locations and recording whether they respond to the lure, we can use the resulting data to estimate the detection function.

The methods of this paper were developed to allow estimation of the number of Scottish crossbills *Loxia scotica* Hartert in Britain. The Scottish crossbill is Britain's only endemic bird species, and is a Red List species (Gregory *et al.* 2002). A national survey is proposed for 2007, and we used data from pilot surveys of two forests, Abernethy and Glenmore, together with trial data for estimating the detection function model, to illustrate the methods.

Traditional distance sampling methods do not work well with crossbills. Birds are often recorded in flight; inclusion of such detections may cause substantial upwards bias in standard line and point transect sampling estimates (Buckland *et al.* 2001), exclusion leads to downwards bias unless a correction is made for proportion of time in flight (Buckland *et al.* 2001). Further, crossbills often remain quiet in the tops of trees, so they are overlooked; that is, detection at the line or point is uncertain, contrary to the assumptions of standard point transect sampling (Buckland *et al.* 2001). The methods of this study do not assume certain detection at the point. A tape of excitement calls is played at the point, which elicits a response from most flocks close to the point, many of which would not be detected using conventional distance sampling methods.

In the point transect lure survey, numbers of flocks detected are recorded for each point, together with flock sizes. Distances of flocks from the point prior to response are unknown, so unrecorded. Therefore, it is necessary to carry out an additional study to estimate the detection

function. Flocks are located, and one observer remains with the flock while a second moves a predetermined distance from the flock. The second observer then initiates the lure, and records whether or not the flock responds in a way that makes it detectable from the point. The first observer provides an additional check, in case there is more than one flock in the vicinity.

Methods

FIELD METHODS

Point transect trapping surveys comprise a main survey, in which numbers of animals captured are recorded, and separate experimental trials, for which a subset of animals have known initial locations with respect to the traps. For the main survey, the trapping locations should be determined by an appropriate randomized design as for a normal point transect survey (Strindberg, Buckland & Thomas 2004). For example, a systematic grid of points, randomly superimposed over the survey region, might be used.

Conceptually we take a 'snapshot' of where animals are located at a single point in time (corresponding to when traps are set) and choose trap locations that are independent of the animal locations at the snapshot moment. However, if trap separation is such that at most one trap is accessible to a given animal, the snapshot moment can be different for each trap. The time interval from the snapshot moment to the checking of traps should be the same in the experimental trials as for the main survey.

For the trials, animals do not need to be located independently of trap locations, but they should have a representative spread of distances over which capture is possible. If it is feasible to radio-tag perhaps 40 or more animals, then this provides a means of locating a subset of animals on which to conduct trials when traps are set. If animal behaviour is believed not to change after being trapped, the same animal might be used for more than one trial, with traps at different locations within its home range. (Differences in trappability between first and subsequent captures could be tested for.)

In the absence of radio-tagged animals, the same traps might be used both for catching animals for the trials and for the main survey. In this case, an initial sample of animals should be caught and marked, and their initial location is the location of the trap that caught them (assuming release at that location). The traps should then be relocated according to a randomized scheme, as otherwise animals are likely to be recaptured at zero distance from first capture, and a markedly non-representative set of distances obtained. At most one of the two sample occasions should use a systematic grid of points, as otherwise the trap separations (and hence distances for estimating the detection function) from the trials will be poorly distributed.

The danger of using the same trapping method for marking a sample of animals as for the main survey is

that some animals may be inherently more catchable than others, or animals may become trap-shy after capture. In these circumstances, it would be preferable to have a totally different method of catching animals for the trials than for the main survey.

In the case of lures, it is first necessary to locate a subset of animals. If the animals stay at that location, one observer can wait while a second observer moves to a predetermined distance and sets the lure. The second observer records whether or not there is a response; the first observer verifies that it is the located animal that responds. If animals do not stay put, it may be necessary to have the two observers searching simultaneously some distance apart. When one locates an animal, the other sets the lure and, again, the observers determine whether or not there is a detectable response.

For either lures or traps, if covariates can be recorded that correlate with how detectable an animal is, then bias arising from heterogeneity in detectability will be reduced. Provided animals at or near the point are certain to be detected or trapped, and using a flexible model for the detection function, then the pooling robustness property ensures that estimation is asymptotically unbiased, even if such heterogeneity is not modelled (Burnham *et al.* 2004).

MODELLING OF THE DATA

In the following development, we consider the case that animals occur in clusters (e.g. flocks). This is very often likely to be the case when lures are used, but only rarely for trapping surveys. If animals do not occur in clusters, cluster sizes in the following development should all be set to unity. The terminology below assumes that we are conducting a survey using lures; the same formulae apply for point transect trapping surveys.

For the point transect trapping or lure survey, let:

K = number of points,

n_k = number of clusters detected from point k ,

$k = 1, \dots, K$,

s_{ik} = size of cluster i detected from point k , $i = 1, \dots, n_k$,

$n = \sum_{k=1}^K n_k$ = total number of clusters detected.

For the trial data from which the detection function is to be modelled, let:

m = number of trials (i.e. number of clusters tested)

$$y_i = \begin{cases} 0, & \text{cluster } i \text{ is not detected from the point} \\ 1, & \text{cluster } i \text{ reacts to lure, allowing detection} \\ & \text{from the point,} \end{cases}$$

r_i = initial distance of cluster i from lure, $i = 1, \dots, m$,

z_{ij} = value of covariate j for cluster i , $i = 1, \dots, m$, $j = 1, \dots, J$.

Note that r_i cannot be observed for the n clusters detected during the main survey. We assume that covariates z can all be recorded for these clusters. One of these J covariates is likely to be cluster size.

We can model the probability of detection by fitting a generalized linear model (McCullagh & Nelder 1989) or generalized additive model (Hastie & Tibshirani 1990) for binary data to the observations y_i . Distances r_i should be included as a covariate, and other covariates z_{ij} might be tested for inclusion. If we use standard logistic regression, then:

$$E(y_i) = p_i \text{ say} = \frac{\exp\left(\alpha + \beta_0 r_i + \sum_{j=1}^J \beta_j z_{ij}\right)}{1 + \exp\left(\alpha + \beta_0 r_i + \sum_{j=1}^J \beta_j z_{ij}\right)} \quad \text{eqn 1}$$

with the corresponding fitted values \hat{p}_i .

We now use this fitted model to estimate the probability of detection of those clusters detected in the main survey. For each of these detections, we can readily substitute values z_{ij} into the fitted model, but we do not know r_i . Thus \hat{p}_i is a function of the unknown r_i : $\hat{p}_i \equiv \hat{p}(r; z_{i1}, \dots, z_{iJ})$ for $0 \leq r \leq w$, where w is some large distance at which a reaction to the lure is believed to be very unlikely. We therefore estimate the probability of detection of cluster i unconditional on its distance from the point by integrating over the unknown r :

$$\hat{P}(z_{i1}, \dots, z_{iJ}) = \int_0^w \pi(r) \hat{p}(r; z_{i1}, \dots, z_{iJ}) dr \quad \text{eqn 2}$$

where $\pi(r)$, $0 \leq r \leq w$, is the probability density function of distances of clusters (whether detected or not) from the point. In conventional point transect sampling, clusters within one of the circles of radius w are assumed to be randomly positioned in the circle, so that $\pi(r) = 2r/(w^2)$. This assumption is assured through random point placement (or, more usually, a systematic grid of points, randomly located). Edge effects caused by some circles extending beyond the survey region, where cluster density may differ, are addressed by one of two ways. The first is 'plus sampling', in which points beyond the survey region boundary, but within w of it, are sampled, and animals detected from such points are recorded only if they are inside the survey region (Strindberg, Buckland & Thomas 2004). This option is unsatisfactory in the current context because traps or lures set outside the survey region boundary may be in unsuitable habitat, and therefore fail to attract animals, or, if they are in suitable habitat, we will be unable to distinguish whether detected animals were originally within the survey region or not.

The second way of addressing the problem in conventional point transect sampling is to ignore the edge effect. In effect, this means that we model the product of detectability and availability, that is $\pi(r) \hat{p}(r; z_{i1}, \dots, z_{iJ})$ in the above notation. The pooling robustness property (Burnham *et al.* 2004) ensures that this does not bias abundance estimates. Thus if no animals occur beyond the survey region boundary, the reduction in detections

at points close to the boundary is compensated for by the reduction in the apparent probability of detection, caused by the reduced availability. This compensation does not occur in the current context, because we model detectability as a separate exercise. There are two possible solutions to this difficulty. First, if few of the sampled points lie within w of the survey region boundary, or if cluster density is similar either side of the survey region boundary, then bias will be small if we ignore the problem, and assume $\pi(r) = 2r/(w^2)$.

Secondly, it can be noted that, given random point placement and assuming that animals do not occur beyond the survey region boundary, the availability function is:

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

where $q_k(r)$ is the proportion of the circumference of a circle of radius r centred on point k that lies within the survey region, for $0 \leq r \leq w$, and $q(r) = [\sum_{k=1}^K q_k(r)]/K$, $0 \leq r \leq w$. If this proportion is always 1, then $\pi(r) = 2r/(w^2)$ as expected.

The multiple covariate distance sampling estimators of Marques & Buckland (2003) use equation 2 together with $\pi(r) = 2r/(w^2)$.

Estimation of abundance now proceeds using a Horvitz–Thompson-like estimator (Borchers *et al.* 1998). The estimated number of animals in the covered region is:

$$\hat{N}_c = \sum_{i=1}^n \frac{s_i}{\hat{P}(z_{i1}, \dots, z_{iJ})} \quad \text{eqn 3}$$

and estimated abundance in the entire survey region of size A is:

$$\hat{N} = \frac{A}{A_c} \hat{N}_c \quad \text{eqn 4}$$

where A_c is the size of the covered region. The covered area within distance w of point k is:

$$2\pi \int_0^w rq_k(r) dr,$$

so that:

$$A_c = 2\pi \sum_{k=1}^K \int_0^w rq_k(r) dr = 2\pi K \int_0^w rq(r) dr.$$

If $q(r)$ is always one, then $A_c = K\pi w^2$.

If animals do not occur in clusters, s_i is set to 1 in equation 3 for each detection. This also gives the estimated abundance of clusters for clustered populations.

Analytic variances for \hat{N}_c and \hat{N} may be obtained by adapting the results of Borchers *et al.* (1998). Let $\mathbf{Y} = (y_1, \dots, y_m)$ be the set of binary data from the experiment and $\Delta = (\delta_1, \dots, \delta_{N_c})$ the set of binary data from the main survey, where $\delta_i = 1$ if cluster i was detected and $\delta_i = 0$ otherwise, $i = 1, \dots, N_c$. Then:

$$\text{var}(\hat{N}_c) = E_{\Delta}[\text{var}_Y(\hat{N}_c | \Delta, \mathbf{Y})] + \text{var}_{\Delta}(E_Y[\hat{N}_c | \Delta, \mathbf{Y}])$$

The expression $E_{\Delta}[\text{var}_Y(\hat{N}_c | \Delta, \mathbf{Y})]$ may be estimated by:

$$\hat{E}_{\Delta}[\text{var}_Y(\hat{N}_c | \Delta, \mathbf{Y})] = \left(\frac{d\hat{N}_c(\beta)}{d\hat{\beta}} \bigg|_{\hat{\beta}} \right)^T \hat{\mathbf{I}}(\hat{\beta})^{-1} \left(\frac{d\hat{N}_c(\beta)}{d\hat{\beta}} \bigg|_{\hat{\beta}} \right)$$

where $\hat{\beta} = (\alpha, \beta_0, \beta_1, \dots, \beta_j)$ and $\hat{\mathbf{I}}(\hat{\beta})$ is the estimated information matrix from the logistic regression.

Further $\text{var}_{\Delta}(E_Y[\hat{N}_c | \Delta, \mathbf{Y}])$ can be estimated by:

$$\text{var}_{\Delta}(E_Y[\hat{N}_c | \Delta, \mathbf{Y}]) = \sum_{i=1}^n \frac{(1 - \hat{P}(z_{i1}, \dots, z_{ij}))s_i^2}{(\hat{P}(z_{i1}, \dots, z_{ij}))^2}$$

Then:

$$\text{var}(\hat{N}) = \left(\frac{A}{A_t} \right)^2 [\hat{E}_{\Delta}[\text{var}_Y(\hat{N}_c | \Delta, \mathbf{Y})] + \text{var}_{\Delta}(E_Y[\hat{N}_c | \Delta, \mathbf{Y}])] \tag{eqn 5}$$

An approximate confidence interval for N may be found assuming log-normality (Buckland *et al.* 2001).

Perhaps a more robust way to estimate variance of n is to treat the n_k as independent observations on the expected number of detections per point. This suggests a bootstrap approach: a resample corresponding to the main survey is obtained by sampling with replacement the K points along with their data, and a resample corresponding to the experiment for fitting the detection function is obtained by resampling the m clusters from the experiment. The above methods are applied to these resampled data, and bootstrap estimates of N_c and N are obtained. This is repeated a large number of times, and the sample variance of the bootstrap estimates of a parameter provides the required variance estimate. This approach also allows uncertainty over which model to use for the detection function to be incorporated into the variance, by re-evaluating for each sample which model fits the data best (Buckland, Burnham & Augustin 1997). For example, Akaike's information criterion (AIC) can be evaluated for each model, and the model with the smallest AIC selected as the best approximating model for the original data, and similarly for each of the bootstrap resamples.

CROSSBILL SURVEYS

To illustrate the methods, we used data pooled across sexes and species of crossbill, and obtained estimates of abundance of crossbills at two sites for which pilots of the point transect lure survey were conducted: Abernethy Forest (57°15' N, 3°40' W, 34.1 km²) and Glen-

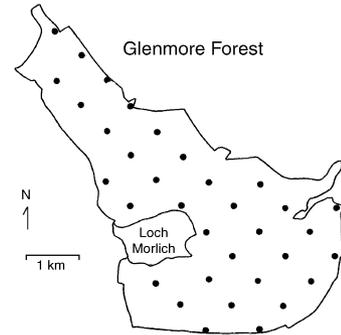
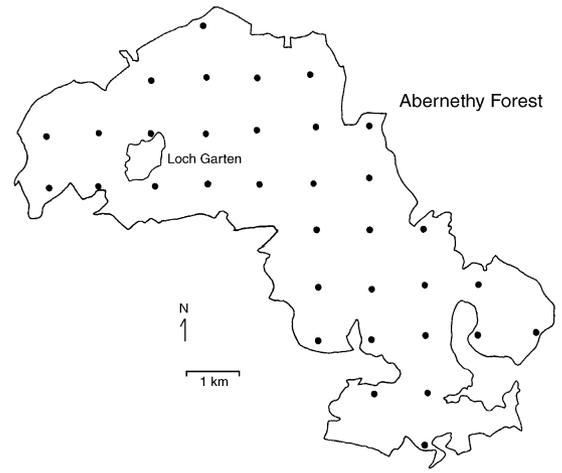


Fig. 1. Survey design for the pilot surveys of Abernethy Forest (top) and Glenmore Forest.

more Forest (57°10' N, 3°40' W, 18.5 km²) in the central highlands of Scotland (Fig. 1). For the main survey, separate estimates will be obtained for males and females, as many females will be incubating at the time of the survey, and these are unlikely to respond to the lure. Further, it will be necessary to estimate abundance separately for the three species, Scottish crossbill *L. scotica*, common crossbill *Loxia curvirostra* Linn. and parrot crossbill *Loxia pytyopsittacus* Borkhavsén. For reliable identification of the three species, calls will be recorded for subsequent computer analysis (Summers *et al.* 2002). For the analyses presented here, we ignore these issues.

In order to determine the probability of response to the lure, trials were conducted during 2002–05 at a number of sites throughout northern Scotland. Several detection function models were fitted to the data from 152 trials. AIC resulted in selecting the model in which probability of a response is a function of distance from the point alone (Table 1). The fitted model is illustrated in Fig. 2; its functional form is:

$$\hat{p} = \frac{\exp(2.28 - 0.0120r)}{1 + \exp(2.28 - 0.0120r)}$$

The model fits the observations well, as judged from the close proximity of the plotted response means by

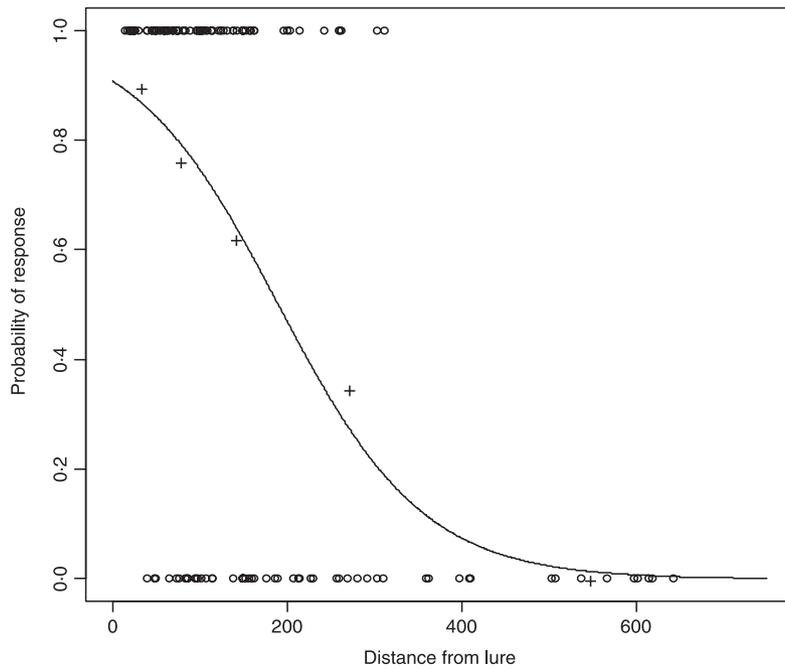


Fig. 2. Plot of response (1 = birds responded; 0 = no response) against distance of birds from the point for 152 trials. Also shown is the estimated probability of a response, as a function of distance from the point. The mean response is shown by '+', plotted at the mean distance of responses from the point, for each of the following distance intervals: 0–50 m, 50–100 m, 100–200 m, 200–400 m, 400–750 m.

Table 1. Logistic regression models fitted to the crossbill trial data ($n = 152$). D represents distance from the point, Y is days from 1 January, S is size of flock, B a behavioural factor with three levels, and H a habitat factor with two levels. Model D corresponds to a logistic regression of response on distance from the point, $D + S$ indicates a logistic regression of response on distance and flock size, etc. At each step, the variable selected for elimination corresponded to the largest reduction in AIC. Time of day was not recorded for some records, so is not included in this table. Its coefficient did not differ significantly from zero

Model	AIC	Δ AIC
$D + Y + S + B + H$	158.4	2.6
$D + S + B + H$	157.4	1.6
$D + S + B$	156.4	0.6
$D + S$	156.0	0.2
D	155.8	0.0
Null	202.1	46.3

interval to the fitted curve; the residual deviance of the model is 151.8 with 150 degrees of freedom, also indicating a good fit.

A truncation distance of $w = 1$ km was selected, beyond which probability of a response was deemed to be zero; estimation was insensitive to this choice for values above $c. 700$ m. It was estimated that 5.8% of birds within the circular plots of radius 1 km responded to the lure; this equates to an effective radius of detection of around 240 m, and an effective area surveyed around each point of about 18 ha. Almost all birds that respond are estimated to have been within 500 m of the lure, so that the 1-km separation of points in Abernethy ensures that the assumption of independence between points

is likely to be reasonable. For Glenmore, separation between points was around 700 m (Fig. 1), so that it is possible that a few birds were lured away from their initial location, and hence unavailable to detection from the next point, when initially they may have been within responding range. Given the pooling robustness property of distance sampling estimators (Burnham *et al.* 2004), the resulting bias is likely to be slight, as birds very close to one point will be around 700 m from the next nearest point, and so very unlikely to be lured away (Fig. 2).

For the favoured model, $\hat{P}(z_{i1}, \dots, z_{ij}) = \hat{P}$, independent of the covariates other than distance. The function $q(r)$, representing the average proportion of land within distance r of a point that is within woodland, was estimated as follows. For each point in each site, additional points were located at 125-m intervals out to 1000 m, to the north, south, east and west. The initial points were recorded as 1 (i.e. inside the region) and the additional points were recorded as 1 or 0, depending on whether they were inside the survey region or outside. A logistic regression was then used to estimate $q(r)$, separately for Abernethy and Glenmore. Uncertainty in these estimates was allowed for by bootstrapping the initial points in each site, along with their associated additional points. Estimation error in $q(r)$ could be avoided by digitizing the boundaries and points and using a geographical information system to evaluate $q(r)$.

There were just 35 points in the pilot survey of Abernethy, for which 16 birds in 11 clusters were detected. For Glenmore, there were 34 points, and 54 birds in 31 clusters were detected. Application of equations 3 and 4 gave abundance estimates of 95 crossbills in Abernethy

(corresponding density estimate 2.8 birds km⁻²), and 182 crossbills in Glenmore (9.8 birds km⁻²). Corresponding bootstrap standard errors based on 3999 resamples were 40 and 64, respectively, and 95% percentile confidence intervals were (37, 193) birds for Abernethy and (90, 339) birds for Glenmore. For comparison, the standard errors obtained from equation 5 were 37 birds for Abernethy and 57 birds for Glenmore, suggesting slight underestimation of variance by the analytic method. If the edge effect is ignored ($q(r) = 1$ for $0 \leq r \leq w$), the abundance estimate is around 10% lower for both Abernethy and Glenmore. In this case, there is fairly substantial bias if the edge effect is ignored.

The national survey will have several hundred survey points, so that the component of variance for encounter rate will be much smaller than in these pilot surveys. However, precision of the estimated detection function is dictated by the number of trials conducted, and this component of variance can only be reduced by conducting more trials. For our pilot surveys, just over 60% of the variance in the Abernethy abundance estimate was because of estimating the detection function, and for Glenmore it was just over 40%.

Discussion

Biodiversity monitoring tends to concentrate on species and species communities that are easy to survey. Quantification of trends is problematic and bias-prone for species where survey data are limited to presence–absence data. Even for those for which relative abundance indices are available, detectability typically differs within species across habitats, or between species, or even over time at the same locations for the same species, because of time-varying factors such as habitat succession, background traffic noise and changes of observer. This generates bias in estimated trends in abundance, and hence in measures of biodiversity change (Buckland *et al.* 2005). New methodologies are therefore needed, to allow estimation of abundance of a wider number of species, and hence more reliable quantification of biodiversity change. The methods of this paper allow the commonly used technique of distance sampling to be applied to a wider range of species.

In conventional point transect sampling, it is assumed that animals at the point are detected with certainty. The methods of this paper do not make this assumption, although individual heterogeneity in the probability of detection may become problematic if probability of detection at the point is not close to unity. An important advantage of the data gathered from the experiment from which the detection function is estimated is that we observe whether each of a sample of animals (or clusters) is trapped (or responds) or not, whereas in conventional point transect sampling we cannot observe distances to undetected animals.

The logistic form for the detection function may be found to be too inflexible for some data sets. Borchers *et al.* (1998) show how to transform the recorded dis-

tances to fit other parametric forms for the detection function, while still using logistic regression software to fit the model.

The truncation distance w should be sufficiently large that few if any recorded animals in the main survey were initially further than w from the point at which they were detected or caught. If w is chosen to be very large, then the $\hat{P}(z_{i1}, \dots, z_{id})$ of equation 2 will tend to be small. The Horvitz–Thompson-like estimator can be badly biased if there are relatively large errors in estimates of small detection probabilities. However, by integrating out r in equation 2, we substantially reduce the variability in the detection probabilities, which can be expected to lead to smaller errors in their estimation; equation 3 may therefore prove satisfactory even for large values of w , provided the $P(z_{i1}, \dots, z_{id})$ are not highly variable. If bias is a concern, the bootstrap may be used to correct for it (Efron & Tibshirani 1993); for the crossbill abundance estimates, bootstrap estimates of bias were four birds for Abernethy and seven birds for Glenmore, giving adjusted abundance estimates of 91 and 175, respectively.

If animals occur in clusters, it is possible that part of the cluster will react to the lure or enter the trap and part not. In the study for estimating the detection function, such clusters should be recorded as two separate clusters. (For the crossbills, there were 11 such clusters out of 141, resulting in 152 ‘trials’ for analysis.) This is because, in the main survey, only the animals that respond or are trapped are detected when recording the cluster size, so we need to estimate their probability of response from the recorded cluster size, not the size of the cluster before the lure or trap was set.

We must assume that the detection function model fitted to the trials (lure point transects), or to the animals whose locations are known when the traps are set (trapping point transects), applies in the main survey. If, for example crossbill density in the main survey is higher than when the trials were conducted, or if the trials were conducted in unrepresentative habitat, then the detection function model may yield a biased estimate of the probability of a response, and hence of abundance. Ideally, such bias would be avoided through design, by ensuring that the trials are conducted on a representative subset of clusters, spread through the survey region, and throughout the duration of the main survey. Similarly for trapping point transects, the animals whose location are known would ideally be a random sample of the animals in the population of interest.

In the case of trapping surveys, it may not be possible to catch more than one animal in a single trap. Provided this applies to both the marked animals and the unmarked equally, and provided animals initially close to a trap are nearly certain to be captured in it, this does not invalidate the method for estimating overall abundance. Even though detectability (i.e. capture probability) will be lower in high-density areas because occupied traps will be encountered, pooling robustness (Burnham *et al.* 2004) ensures that the overall abundance

estimate is asymptotically unbiased. However, if the trials show that a significant proportion of animals that are initially close to a trap are not subsequently caught, then bias can be anticipated. Appropriate survey design (greater frequency of checking traps, higher trap density, setting of multiple traps at each point) will reduce or eliminate this bias.

Point transect trapping surveys also suggest the possibility of methods designed for multiple capture occasions. The methods of Efford (2004), Efford, Dawson & Robbins (2004), Efford *et al.* (2005) and D.L. Borchers & M. Efford (unpublished data) may be readily adapted for the analysis of such data.

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References

- Anderson, D.R., Burnham, K.P., White, G.C. & Otis, D.L. (1983) Density estimation of small-mammal populations using a trapping web and distance sampling methods. *Ecology*, **64**, 674–680.
- 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. (in press) Point transect surveys for songbirds: robust methodologies. *Auk*, **123**.
- 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, UK.
- Buckland, S.T., Burnham, K.P. & Augustin, N.H. (1997) Model selection: an integral part of inference. *Biometrics*, **53**, 603–618.
- Buckland, S.T., Magurran, A.E., Green, R.E. & Fewster, R.M. (2005) Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society of London, Series B*, **360**, 243–254.
- Burnham, K.P., Buckland, S.T., Laake, J.L., Borchers, D.L., Marques, T.A., Bishop, J.R.B. & Thomas, L. (2004) Further topics in distance sampling. *Advanced Distance Sampling* (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 307–392. Oxford University Press, Oxford, UK.
- Dahlsten, D.L., Six, D.L., Rowney, D.L., Lawson, A.B., Erbilgin, N. & Raffa, K.F. (2004) Attraction of *Ips pini* (Coleoptera: Scolytinae) and its predators to natural attractants and synthetic semiochemicals in Northern California: implications for population monitoring. *Environmental Entomology*, **33**, 1554–1561.
- Efford, M. (2004) Density estimation in live-trapping studies. *Oikos*, **106**, 598–610.
- Efford, M.G., Dawson, D.K. & Robbins, C.S. (2004) DENSITY: software for analysing capture–recapture data from passive detector arrays. *Animal Biodiversity and Conservation*, **27**, 217–228.
- Efford, M.G., Warburton, B., Coleman, M.C. & Barker, R.J. (2005) A Field Test of Two Methods for Density Estimation. *Wildlife Society Bulletin*, **33**, 731–738.
- Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, London, UK.
- Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology*, **81**, 1970–1984.
- Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Procter, D., Gibbons, D.W. & Galbraith, C.A. (2002) The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, **95**, 410–448.
- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. Chapman & Hall, London, UK.
- Klavitter, J.L., Marzluff, J.M. & Vekasy, M.S. (2003) Abundance and demography of the Hawaiian hawk: is delisting warranted? *Journal of Wildlife Management*, **67**, 165–176.
- Lukacs, P.M., Franklin, A.B. & Anderson, D.R. (2004) Passive approaches to detection in distance sampling. *Advanced Distance Sampling* (eds S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas), pp. 260–280. Oxford University Press, Oxford, UK.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, London, UK.
- Marques, F.F.C. & Buckland, S.T. (2003) Incorporating covariates into standard line transect analyses. *Biometrics*, **59**, 924–935.
- Parmenter, R.R., Yates, T.L., Anderson, D.R., Burnham, K.P., Dunnun, J.L., Franklin, A.B., Friggens, M.T., Lubow, B.C., Miller, M., Olson, G.S., Parmenter, C.A., Pollard, J., Rexstad, E., Shenk, T.M., Stanley, T.R. & White, G.C. (2003) Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. *Ecological Monographs*, **73**, 1–26.
- Priede, I.G. & Merrett, N.R. (1998) The relationship between numbers of fish attracted to baited cameras and population density: studies on demersal grenadiers *Coryphaenoides (Nematomurus) armatus* in the abyssal NE Atlantic Ocean. *Fisheries Research*, **36**, 133–137.
- Reid, J.A., Horn, R.B. & Forsman, E.D. (1999) Detection rates of spotted owls based on acoustic-lure and live-lure surveys. *Wildlife Society Bulletin*, **27**, 986–990.
- Ruette, S., Stahl, P. & Albaret, M. (2003) Applying distance-sampling methods to spotlight counts of red foxes. *Journal of Applied Ecology*, **40**, 32–43.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, **35**, 24–43.
- Strindberg, S., Buckland, S.T. & Thomas, L. (2004) Design of distance sampling surveys and geographic information systems. *Advanced Distance Sampling* (eds S.T. Buckland, D.R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers & L. Thomas), pp. 190–228. Oxford University Press, Oxford, UK.
- Summers, R.W., Jardine, D.C., Marquiss, M. & Rae, R. (2002) The distribution and habitats of crossbills *Loxia* spp. in Britain, with special reference to the Scottish crossbill *Loxia scotica*. *Ibis*, **144**, 393–410.
- Taggart, S.J., O’Clair, C.E., Shirley, T.C. & Mondragon, J. (2004) Estimating dungeness crab (*Cancer magister*) abundance: crab pots and dive transects compared. *Fishery Bulletin*, **102**, 488–497.

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