Anales de Biología 33: 149-160, 2011 ARTICLE

Effects of population variability on the accuracy of detection probability estimates

Alejandro Ordóñez[1,2], Emiel van Loon[2] & Willem Bouten[2].

1 Nelson Institute Center for Climatic Research (CCR). 1225 W. Dayton St. 53706-1695 Madison –WI, USA.

2 Institute for Biodiversity and ecosystem Dynamics IBED, Computational Bio – ecology Group. University of Amsterdam.

Correspondence
A. Ordóñez
E-mail: ordonezglori@wisc.edu
Phone: +1 (608) 263-7655

Received: 6 September 2011
Accepted: 29 November 2011
Published on-line: 23 December 2011

Resumen

Efectos de la variabilidad en parámetros poblacionales en predicciones de probabilidad de detección

Observar una fracción constante de la población a través del tiempo, lugares, o especies es una tarea difícil de realizar, de modo que, la cuantificación de este porcentaje (*i.e.*, la probabilidad de detección) es una tarea importante en estudios poblacionales. A través del uso de simulaciones, se evaluó el efecto de la variabilidad en parámetros poblacionales en la exactitud de estimadores de probabilidad de detección. Estos resultados muestran de forma consistente como diferentes metodologías de muestreo y estimadores, sobrepredicen la probabilidad de detección. Comparaciones entre estimadores y métodos de muestreo mostraron diferencias significativas entre ellos (*i.e.*, estimadores que toman en cuenta la heterogeneidad en parámetros poblacionales producen predicciones más precisas). El tamaño poblacional fue el factor que más influyo en la incertidumbre y la precisión de las predicciones. Nuestros resultados muestran la necesidad de incluir características de la población (ya sea como una función de corrección o factores en un modelo de observación) al estimar las probabilidades de detección. El estudio concluye sugiriendo dos métodos para el uso de características de la población para estimar las probabilidades de detección.

Palabras clave: Probabilidad de detección, Captura-recaptura, Tamaño poblacional, Remoción, Sensitividad, Incertidumbre

Abstract

Observing a constant fraction of the population over time, locations, or species is virtually impossible. Hence, quantifying this proportion (i.e. detection probability) is an important task in quantitative population ecology. In this study we determined, via computer simulations, the effect of population characteristics on estimates of detection probability. Simulation results showed a consistent and significant over-prediction of detection probability across sampling methodologies and estimators. Comparisons between estimators and sampling methods showed significant differences amongst them (estimators accounting for heterogeneity are the most accurate). Population size was the most important factor influencing the uncertainty and accuracy of the estimates. Our results show the need to include population characteristics (either as a correction function or as factors in the observation model) when estimating detection probabilities. The study concludes by suggesting two methods for using population characteristics to estimate detection probabilities.

Key words: Detection probability, Mark-recapture, Population size, Removal, Sensitivity, Uncertainty

Introduction

Quantitative population ecology models are important tools to prioritize conservation efforts, land management decisions and policy-making strategies. Additionally, the study of variation in abundance and occurrence has become a recurrent topic in population, community or meta-community ecology. In this perspective, identifying the main sources of uncertainty when estimating abundance and occurrence as well as establishing the sensitivity of these estimates is paramount for effective conservation planning.

Two important factors determine the quality abundance estimates: sample size and detection probability. The most common way to deal with these difficulties is the use of statistical descriptions of both the sampling (observation) and occurrence (state) processes The goal with this approach is to accurately estimate the variable of interest by including relevant covariates (e.g. population size, abundance, density, the spatial distribution of the species and the role of ecological and biological dynamics/interactions).

Classical approaches to estimate site occupancy and/or abundance are based on sampling protocols where independent and replicate observations (in time or by several observers) are made at a series of sample locations. This allows the simultaneous estimation of occurrence/abundance and detection probability. The main limitation of this approach is the failure to fully incorporate the two types of possible observational "zeros" : true absence at particular sampling (also known as true zeros) and failure to detect an individual (also known as false negatives).

More recent methods to estimate site occupancy/abundance have been developed to account for a variety of problems in the observation process. These include variation in occurrence and detection among seasons or species, unobserved sources of variation in detection among locations and the possibility of both false negative and false positive errors. Although the relevance of each one of these complexities is indisputable, the way in which variability in population characteristics (such as age, size, morphological distinctiveness, and level of exposure in the environment) influence false negative errors is a topic still to be explored.

This work focuses on the problem to estimate detection probabilities by investigating how population characteristics (e.g., population size, age-size structure and morphological distinctiveness) influence the accuracy and uncertainty of the estimated detection probabilities and therefore the estimation of population size and occurrence rates. Here we define uncertainty as the set of possible outcomes of an estimate where a probability of occurrence is assigned; and accuracy as the degree of veracity of an estimate

The objective of this work is to assess how population characteristics influence the estimation of detection probability. To do so, first we determined the effects of population characteristics (i.e. population size, age-size structure, morphological distinctiveness, and level of exposure in the environment) on the accuracy and uncertainty of detection probability estimates. Second, we formulate an observation model. Thirdly, we determine the sensitivity of the predictions by the observation model to variability in the population parameters.

Material and methods

In this study the influence of population variables on the accuracy and uncertainty of detection probability estimates are explored using computer simulations. A set of populations is generated using a specific combination of population variables (i.e. population size, age – size structure, morphological distinctiveness and level of exposure) defined by a particular mean and range of variation. Each of these populations is then sampled using both a removal (RMV) and a mark–recapture (MRC) methodology. Individual detection probabilities are subsequently estimated using classical and modified implementations of the MRC and RMV estimators of detection probability. The results of these experiments are analysed with a linear-mixed model to describe the accuracy of the detection probabilities predicted by MRC and RMV estimators, as a function of population characteristics and sampling methods. Finally, the sensitivity of the detection probability to population characteristics is investigated. A detailed description of these steps is included as supplementary information (Appendix S1).

Generating the test populations and estimating detection probabilities

Test populations with 10 and 100 individuals

where generated. These population sizes were selected for computational reasons (larger populations increased exponentially the computational time). The characteristics of each of these were determined using different means as well as variances for population age, size, morphological distinctiveness and exposure. Details on how the test populations were generated, and summary of the characteristics of each test population is presented in Appendix S1. We call each unique combination of population size, sexual dimorphism, age-size, morphological distinctiveness and exposure structure a population class (i.e., a unique combinations of each of these parameters). For each population class a total of 100 realizations were generated. Each of these was then sampled 100 times using both a removal (RMV) and a mark–recapture (MRC) approach.

Using the generated observation histories it was possible to determine, for a specific population/sample, the detection probabilities using a statistical description of the observation process (as described in Appendix S1). To make this calculation, four types of estimators were implemented, based on Borchers et al. (2002): MRC_0/RMV_0, MRC_t /RMV_t, MRC_{h1}/RMV_{h1} and MRC_{h2}/RMV_{h2}. The MRC_0 and RMV_0 models assume a homogenous population with respect to capture probability meaning that all animals are considered equally catchable (the subscript 0 stands for no heterogeneity). The MRC_t and RMV_t models assume that capture probability varies between capture events but that all individuals within a sampling occasion are equally catchable (the subscript t stands for heterogeneity depending on time). Last, the $MRC_{h1\text{-}2}$ and $RMV_{h1\text{-}2}$ models assume that capture probability differs between individuals but remains constant over all capture occasions. The difference between h1 and h2 is the inclusion of sampling effort (measured as the number of observers in h2 estimations) in the estimation process.

Evaluating the estimates of detection probability

The estimated mean detection probability for each combination of sampling strategy (i.e. MRC or RMV) and estimator (i.e. Method 0, Method t, or Method h.1 or Method h.2) was compared to the known "real" mean detection probability (i.e., the mean probability used to build the full population). A paired-T-test as well as a mixed linear model (with estimator as a fixed effect and the 100 replicas, nested within the estimator, as a random effect) was used for this comparison. Additionally, for the $MRC_{h1\text{-}2}$ and $RMV_{h1\text{-}2}$ models a two sample Kolmogorov–Smirnov test was used to evaluate the differences between the frequency distributions of estimated and real detection probabilities. This test allowed determining the impact of specific population parameters on the level of agreement between estimated and population "true" detection values.

Last, a linear model, using the mean population characteristics (estimated from the sample) as predictors, was build to describe the accuracy of the predicted detection probabilities (i.e., observed-known detection probability differences). This approach was used as a first order description of the prediction bias, and to correct the estimates of detection probability. Overall model quality and parameter relevance was evaluated using respectively the adjusted R^2 values and the significance of model coefficients.

Evaluating the influence of population parameters

Using the detection probability estimates of both the MRC and RMV methods; a logistic observation model was generated to determine the probability of detecting an individual given its individual level characteristics (i.e. sex, age and size class, morphological distinctiveness and exposure level).

To evaluate how the uncertainty in the estimation of detection probability can be partitioned between different sources of variability a variance decomposition global sensitivity analysis was used. Variance decomposition methods are "model free" approaches, meaning that its application does not rely on special assumptions on the behaviour of the model. These are based on the ranking of the factors according to the amount of variance removed from the prediction when it is fixed to its "expected value". Variance based measures are generally estimated numerically using different methodologies. From these, SOBOL and the Fourier Analysis Sensitivity Test (FAST) methods are the most commonly used. Both of these methods allow a simultaneous computation of the first and total effect indices for a given factor and hence the impact of fixing it on the output vari-

ance. We applied both SOBOL and FAST for variance decomposition. Both methods give first order and total order sensitivities for each parameter. First order effects (S_1) measure the individual and linear effects of a particular parameter on the variability of a prediction while the other variables remain constant at their means. Total order effects (S_t) measure the effects of the interaction between a particular parameter (held constant at its mean value) and the remaining predictors (left free to vary within their variation range).

Results

The mean real and estimated detection probabilities, in addition to test determining the reliability of detection probabilities are presented in Table 1. A significant over prediction (predicted>real) by both sampling methodologies and estimators was observed (5 to 51% for MRC estimators and 5 to 33% for RMV estimators as shown in Fig. 1). There is a significant differentiation between the estimators (0, t, h.1 and h.2) as pointed out by linear-mixed models (MRC: $F_{(3,800)} = 5.9$; $p<0.001$ and RMV: $F_{(3,800)} = 30.312$; $p<0.001$). Simple estimators (MRC_0, RMV_0, MR_{Ct} and RM_{Vt}) had significantly different detection probability estimates than those methods considering individual level detection probabilities ($MRC_{h1\text{-}2}$ and $RMV_{h1\text{-}2}$ models).

When evaluating the drivers of estimates uncertainty, population size had the strongest influence. This trend was consistent across estimators and sampling methodologies. Observed trends on predictions uncertainty showed how estimates from small size populations had consistently larger, although no significantly different, ranges of variation (that is 95% trustable intervals) than its larger population size counter part (MRC: $F_{(3,800)} = 0.0356$; $p = 0.99$ and RMV: $F_{(3,800)} = 0.0293$; $p = 0.993$). When the level of variability in the population parameters was incorporated in the analysis (Fig 2.), ranges of variation became consistently larger and the accuracy of the predictions decreased.

Contrasts between sampling methodologies indicated how RMV estimates are on average significantly ($F_{(3,800)} = 434.68$; $p < 0.001$) closer to the real detection probability than MRC estimates (Fig. 1). When sampling methodologies were compared across different population sizes and levels of variability in population parameters (Fig. 1), differences between estimates increased with increasing population variability, but remained constant across the same population size class.

Accuracy for $MRC_{h1\text{-}2}$ and $RMV_{h1\text{-}2}$ was significantly influenced by population size (the most important component determining estimation accuracy as shown in Table 2). While detection probability estimates from large populations consistently differed from the real frequency distribution; estimations from population with fewer individuals agreed with the real frequency distribution on average 19 to 65% of the comparisons. This trend was persistent for comparisons across sampling methodologies, and across levels of variability in population factors.

Given the consistent overestimation of detection probabilities by all analysed estimators; the need to develop a methodological approach to correct these inaccuracies becomes evident. For this a linear model was build using the analysed population variables as predictors, and the discrepancy between real value and estimate as the dependent variable.

When the patterns of deviation of detection probability estimates were analysed (Fig. 1) difference on the influence from population variables was clear. In particular, simple estimators (MRC/RMV_0 and MRC/RMV_t) had a stochastic behaviour (as population heterogeneity and sampling error were not evaluated). Meanwhile, estimators that consider individual heterogeneity ($MRC/RMV_{h1\text{-}2}$) showed a systematic overestimation of detection probability. Defining an adequate correction function that uses the population variables was only possible for simple estimators (as adjusted R^2 and coefficients indicated, Table 2). The use of this correction functions significantly improved the accuracy and reduced the uncertainty of detection probability estimations.

When analysing the sensitivity of all the models predicting detection probability to the variability in the population parameters, there was an equal contribution of each parameter to the uncertainty of the variance on detection probability (Fig. 2). On average, each factor accounted for 23% of the variance on detection probability (23.22–23.91% for MRC methods and 23.67–23.67% for RMV methods). The influence of each factor, measured by both first (S_i) and total order indices (S_t) are very close for both FAST (Fig. 2) and SOBOL (results not shown) indicating the consistency of this equal partitioning of variability

across all the parameters factor as the most important in determining the variability on the detection probability estimation.

Discussion

As population and metapopulation studies focus on abundance and occurrence, there is a clear motivation for establishing a functional link between these variables and the observation process. Royle et al. (2005) showed the importance of this link, and stated how estimation of the parameters in most ecological models is limited by imperfect detection. This work pursued this idea aiming to establish and explicitly link between the effects of population variability and detection probability estimates.

	Estimator	Detection probability (Mean ± SD)	T-test	Linear mixed model ANOVA	Kolmogorov-Smirnov
MRC	Method 0	0.559±0.118	t = 151.53 **	$F_{(99,1600)}$ = 23703.211 **	D = 1 **
	Method t	0.559±0.118	t = 155.2 **	$F_{(99,4800)}$ = 9637.176 **	D = 1 **
	Method h.1	0.561±0.138	t = 79.81 **	$F_{(99,45807)}$ = 1267.932 **	D = 1 **
	Method h.2	0.561±0.138	t = -30.33 **	$F_{(99,45807)}$ = 60.42 **	D = 1 **
RMV	Method 0	0.562±0.117	t = 15.63 **	$F_{(99,1600)}$ = 124.576 **	D = 0.89 **
	Method t	0.562±0.117	t = 51.81 **	$F_{(99,4800)}$ = 1053.683 **	D = 1 **
	Method h.1	0.572±0.136	t = 44.65 **	$F_{(99,41439)}$ = 255.52 **	D = 1 **
	Method h.2	0.572±0.136	t = -31.67 **	$F_{(99,41439)}$ = 51.846 **	D = 1 **

Tabla 1. Resumen de la media de probabilidad de detección real y estimada por métodos de captura-recaptura (MRC) y extracción (RMV). Los valores promedios se compararon mediante un T-test pareado para determinar la significación de la desviación de la estima de la probabilidad de detección. Adicionalmente, las predicciones y los valores reales se compararon con un modelo mixto, donde se utiliza el estimador (i.e., Método 0, Método t, Método h.1 o Método h.2) como de efectos fijos y réplica (anidado dentro del estimador) como un efecto aleatorio. Diferencias significativas marcadas como p <0.001 (***), p <0.01 (**), p <0.05 (**), y P> 0.5 (NS).

Table 1. Summary of mean real and estimated detection probability for mark recapture (MRC) and removal (RMV) sampling strategies. Mean values were compared using a paired-T-test to determine the deviation of the estimation to the real population detection probability. Additionally, predictions and real values were compared using a mixed design, where the estimator (i.e. Method 0, Method t, or Method h.1 or Method h.2) is used as fixed effect and replica (nested within the estimator) is used as a random effect. Significant differences marked as p<0.001 (***), p<0.01 (**), p<0.05 (*), and p>0.5 (N.S.).

	Estimator	Intercept	Age class	Size class	Exposure	Morphological variability	Adjusted R^2
MRC	Method 0	0.146±0.053 **	-0.095±0.024 ***	-0.028±0.025 NS	-0.072±0.059 NS	-0.016±0.06 NS	0.234
	Method t	0.285±0.135 *	-0.042±0.06 NS	-0.069±0.064 NS	-0.13±0.148 NS	0.02±0.152 NS	0.007
	Method h.1	0.114±0.221 NS	-0.014±0.098 NS	0.109±0.105 NS	-0.122±0.244 NS	0.192±0.25 NS	-0.012
	Method h.2	0.183±0.152 NS	-0.04±0.067 NS	-0.055±0.072 NS	-0.228±0.167 NS	-0.246±0.171 NS	0.008
RMV	Method 0	-0.058±0.318 NS	0±0.141 NS	-0.016±0.15 NS	-0.445±0.35 NS	0.303±0.359 NS	0
	Method t	0.194±0.25 NS	-0.212±0.111 NS	0.131±0.118 NS	-0.178±0.275 NS	0.019±0.282 NS	0.001
	Method h.1	0.319±0.203 NS	-0.07±0.09 NS	0.036±0.096 NS	-0.206±0.223 NS	-0.202±0.229 NS	-0.024
	Method h.2	-0.249±0.146 NS	-0.191±0.065 **	0.026±0.069 NS	0.128±0.161 NS	0.208±0.165 NS	0.084

Tabla 2. Resumen de los modelos de regresión comparando la desviación de estimados MRC_{h1-2} y RMV_{h1-2} (precedida menos la probabilidad de detección real) en función de parámetros poblacionales específicos (rango de edad, rango de tamaño, exposición y variabilidad morfológica). Los datos representan la influencia de cada parámetro de nivel de población en la precisión de la estimación. Significación de los coeficientes de regresión marcada como p <0.001 (***), p <0.01 (**), p <0.05 (**), y P> 0.5 (NS).

Table 2. Summary of regression models comparing the deviation in MRCh1-2 and RMVh1-2 estimations (predicted – real detection probability) to particular population parameters (Age class, size class, exposure and morphological variability). Data represent the influence of each population level parameter on the estimation accuracy. Significance of regression coefficients marked as p<0.001 (***), p<0.01 (**), p<0.05 (**), and p>0.5 (N.S.).

As our results showed, estimates of detection probability are strongly influenced by population variables determining an individual "detectability" (i.e., the probability of observing a specific organisms in a surveyed area) regardless of the used sampling methodology or estimator. In particular, it is clear that actual population size, and the level of variability in the population parameters have a strong effect on the accuracy of the estimation.

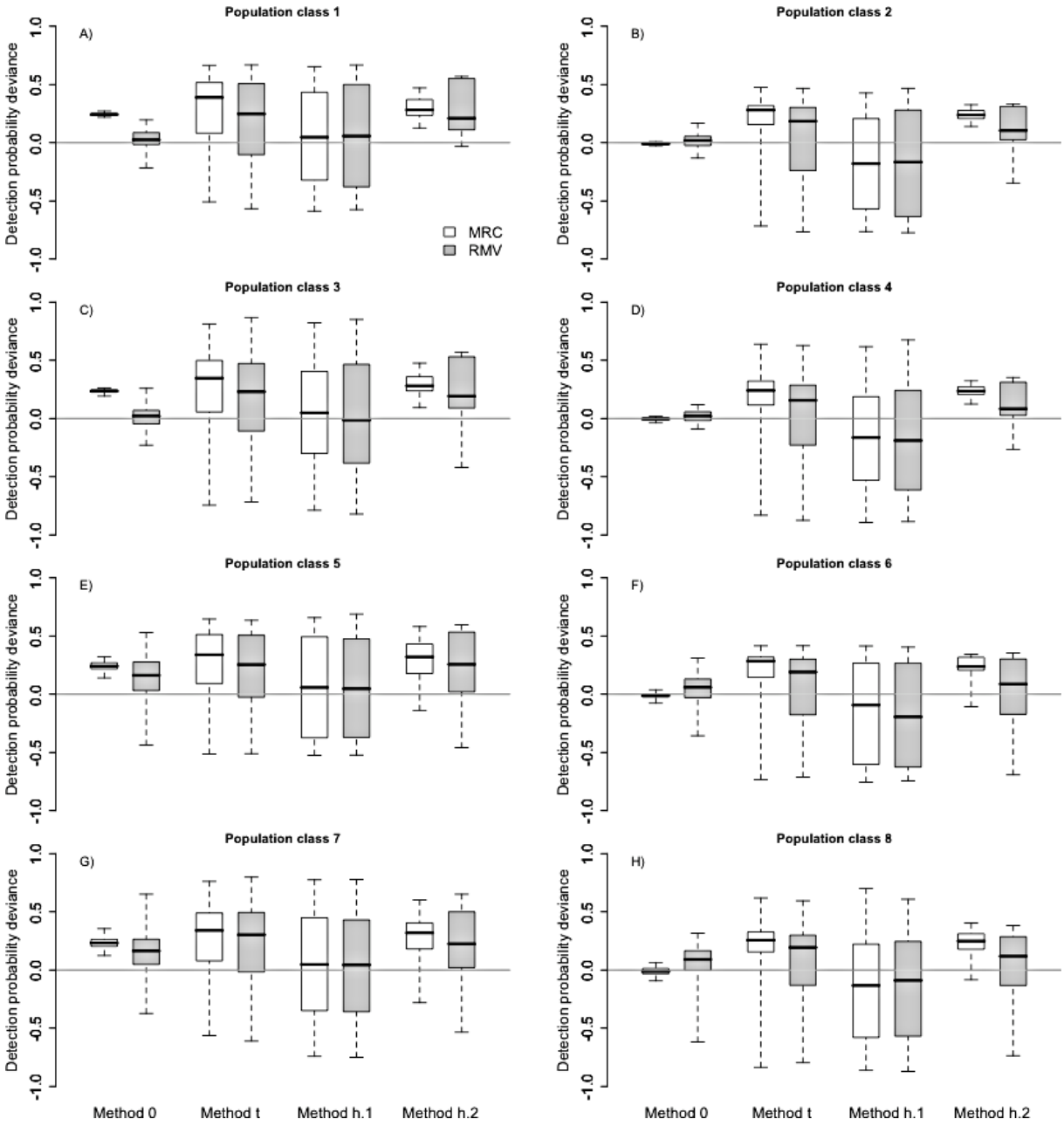

Figura 1. Las diferencias entre la probabilidad de detección predicha por estimadores MRC y RMV, y la probabilidad de detección real; estas diferencias muestran si un individuo se muestreado o no (es decir, la probabilidad de detección "real"). La línea horizontal gris indica que no hay una desviación significativa. Caja muestran la variabilidad intequantil y las líneas discontinuas del rango de los datos. Símbolos blancos representa las estimaciones MRC y grises estimaciones RMV.

Figure 1. Differences between predicted detection probability using MRC RMV estimations, and the known detection probability used to specify if a given individual was sampled or not (i.e., the "real" detection porbabiity). Horizontal grey line indicates no deviation from the population mean real value. Box are inter-quintile variability and dashed lines the maximum-minimum deviation range. White box represent MRC estimations and grey symbols RMV estimations.

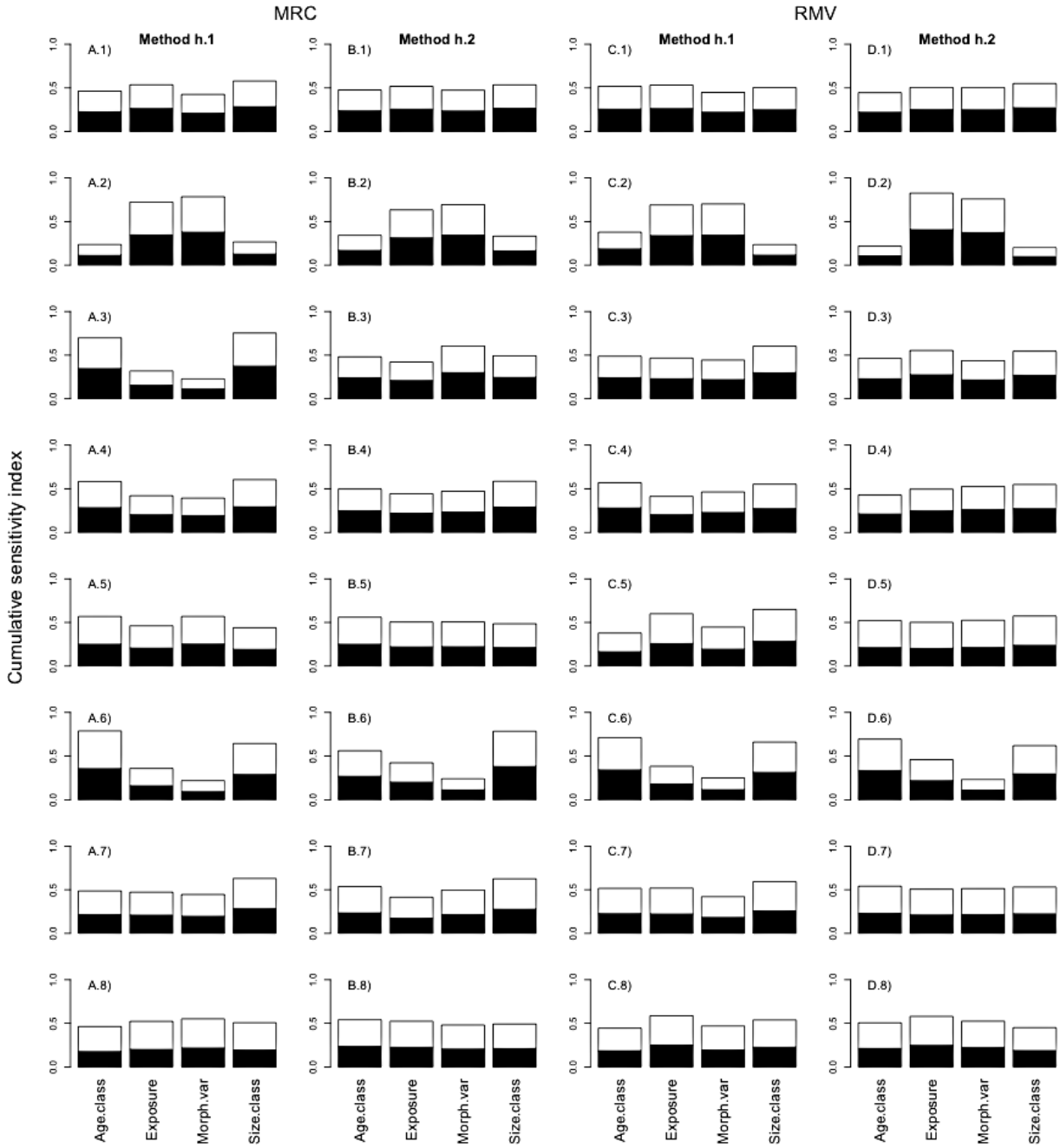

Figura 2. Mediciones de la sensibilidad del modelo de observación en la variabilidad en los parámetros de la población. Barras representan el efecto acumulativo de cada variable (índices de 1er orden - negro) y de la interacción entre factores (orden total - blanco) en las predicciones de cada modelo. Paneles organizados en columnas de acuerdo a la metodología de muestreo (MRC y RMV), y el estimador (Método h.1 y h.2 método, véase el texto para más detalles); filas representan el tamaño de la población (véase el texto para más detalles). Índices ilustrados (i.e., 1er y total) son los resultados de un análisis de descomposición de la varianza utilizando el método FAST. Tamaños poblaciones (filas) de arriba a abajo son 1, 2, 3, 4, 5, 6, 7 y 8. Columnas de izquierda a derecha son: $MRC_{h.1}$, $MRC_{h.2}$, $RMV_{h.1}$ y $RMV_{h.2}$.

Figure 2. Measurement of sensitivity of the observation model to the variability on population parameters. Staked bars represent the cumulative effect of the individual (1st order index-black) and the interaction variables (total order-white) on model predictions. Panels organized in columns according to sampling methodology (MRC and RMV) and estimator (Method h.1 and Method h.2); rows represent population class (see text for details). Plotted indices (i.e. first and total order) are the results of a variance decomposition analysis using the FAST methods. Rows form top to bottom are population 1, 2, 3, 4, 5, 6, 7 and 8. Columns form left to right are: $MRC_{h.1}$, $MRC_{h.2}$, $RMV_{h.1}$ and $RMV_{h.2}$.

Additionally, it was found that there are not single most important population parameters determining the detection probability estimate accuracy. Nevertheless, it is important to emphasize the relevance of certain parameters (e.g. exposure and morphology for low population variability and age and size for high population variability) if we aim to determine the most important factors shaping the detection function. Additionally, understanding how population parameter(s) variability influences the detection function demands an extensive knowledge of the auto ecology of the studied species.

It is also of importance to highlight the minor influence of the sampling protocol (MRC versus RMV) on the accuracy of the predictions. Based on our results, it is evident that there are no clear benefits, regarding only the accuracy of the estimation, of choosing one sampling protocol over the other. Therefore, selecting a sampling methodology should be based on the imposed constrains of resource availability and time. An important issue to emphasize here is that our evaluations only took into account two of the most commonly used sampling methods (mark recapture and removal sampling) hence extrapolation to other sampling strategies should be done with caution.

Our results are in line with Dorazio (2007), who established how the population available to be sampled should be considered in analyses of site occupancy given the interaction between site-specific abundance and detection frequency. Other works have also found such a strong inverse association between population size and detection frequencies (that is the realization of the observation process given the individual detection probabilities). All of them explain the low detection frequencies as a result of either (or both) practical limitations in the spatial extent of the survey or the variability on individual detection probabilities due to population heterogeneity.

So these studies point to the idea that probabilities of animal detection and occurrence could be estimated more accurately if the models used in analysis accounted for heterogeneity in population parameters and population size. Given this, and the levels of accuracy and uncertainty on the estimates of detection probability reported in this work, the need to correct any estimates of this variable is evident. This becomes of special relevance for estimators that do not consider individual level heterogeneity.

From the formulated correction models, only those for estimators that do not include population variability (MRC/RMV_0 and MRC/RMV_t) did adequately increase the estimation accuracy. In the case of estimations where individual detection probabilities are predicted ($MRC_{h1\text{-}2}$ and $RMV_{h1\text{-}2}$), the formulation of an observation model did prove to be the most adequate approach to increase the accuracy of the detection probability prediction. It is important to emphasize here that our observation model formulation does not include all possible sources of variability in the observation process. A complete observation model should include, as Borchers et al. (2002) proposed, a series of survey level parameters (e.g. number of observers, area cover, sampling intensity) in addition to the population characteristics analysed here.

Although, the notion that detection probability should be included in the abundance/occurrence estimation process has been generally proposed, just a few studies have actually focused on the role of population parameters in this context. This work focuses on this idea, and explicitly shows the effects of population variability on detection probability estimates. In particular, it shows how the variability on population variables (i.e. age, size, morphological distinctiveness, and level of exposure in the environment) influence the rate of "false negative" errors. From the evaluated factors, population size proves to be the most relevant factor shaping the accuracy and uncertainty of the estimates. Additionally, two methods are proposed to correct for the errors in estimated detection probabilities by using population variables.

The results from this study support, jointly with results from several other studies, the need to incorporate all possible information regarding the observation process (i.e. population level parameters and survey level characteristics) in the construction of an observation model. Such observation models improve the detection probability estimates considerably, which in return helps to obtain correct estimates of animal abundance and occurrence.

Acknowledgements

Thanks to the University of Groningen (Netherlands) for financial support through an Ubbo Emmius scholarship. This study was supported by the

EcoGRID project of the University of Amsterdam.

References

Barry S & Elith J. (2006) Error and uncertainty in habitat models. Journal of Applied Ecology 43: 413-423.

Bayley PB & Peterson JT. (2001) An approach to estimate probability of presence and richness of fish species. Transactions of the American Fisheries Society 130: 620-633.

Borchers D, Buckland ST. & Zucchini W. (2002) Estimating Animal Abundance: Closed Populations.

Brooks T. da Fonseca GAB & Rodrigues ASL. (2004) Species, data, and conservation planning. Conservation Biology 18: 1682-1688.

Chefaoui RM, Hortal J & Lobo JM. (2005) Potential distribution modelling, niche characterization and conservation status assessment using GIS tools: a case study of Iberian Copris species. Biological Conservation 122: 327-338.

Dorazio R & Royle J. (2005) Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. Journal of the American Statistical Ass 100: 389-398.

Dorazio RM. (2007) On the choice of statistical models for estimating occurrence and extinction from animal surveys. Ecology 88: 2773-2782.

Drosg M. (2007) Dealing with uncertainties: a guide to error analysis. Springer, Berlin.

Feria TP & Peterson A. T. (2002) Prediction of bird community composition based on point-occurrence data and inferential algorithms: a valuable tool in biodiversity assessments. Diversity and Distributions 8: 49-56.

Gaston KJ, Borges PAV, He FL & Gaspar C. (2006) Abundance, spatial variance and occupancy: arthropod species distribution in the Azores. Journal of Animal Ecology 75:, 646-656.

He FL & Gaston KJ (2003) Occupancy, spatial variance, and the abundance of species. American Naturalist 162: 366-375.

MacKenzie DI. (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier.

MacKenzie DI & Kendall WL. (2002) How should detection probability be incorporated into estimates of relative abundance? Ecology 83: 2387-2393.

MacKenzie DI, Nichols JD, Hines JE, Knutson MG & Franklin AB. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84: 2200-2207.

Rabinovich S. (2005) Measurement Errors and Uncertainties: Theory and Practice. Springer, Berlin.

Royle JA. (2006) Site occupancy models with heterogeneous detection probabilities. Biometrics 62: 97-102.

Royle JA & Dorazio RM. (2008) Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Academic Press Inc

Royle JA & Link WA. (2006) Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87, 835-841.

Royle JA, Nichols JD & Kery M. (2005) Modelling occurrence and abundance of species when detection is imperfect. Oikos 110: 353-359.

Saltelli A. (1999) Sensitivity analysis: Could better methods be used? Journal of Geophysical Research-Atmospheres 104: 3789-3793.

Saltelli A. (2002) Sensitivity analysis for importance assessment. Risk Analysis 22: 579-590.

Saltelli A, Ratto M, Tarantola S, Campolongo F, Commission E & Ispra JRC. (2006) Sensitivity analysis practices: Strategies for model-based inference. Reliability Engineering & System Safety 91: 1109-1125.

Saltelli A & Tarantola S. (2002) On the relative importance of input factors in mathematical models: Safety assessment for nuclear waste disposal. Journal of the American Statistical Association 97: 702-709.

Saltelli A, Tarantola S & Campolongo F. (2000) Sensitivity analysis as an ingredient of modeling. Statistical Science 15: 377-395.

Smith LL, Barichivich WJ, Staiger JS, Smith KG & Dodd CK (2006) Detection probabilities and site occupancy estimates for amphibians at Okefenokee National Wildlife Refuge. American Midland Naturalist 155: 149-161.

Tyre AJ, Tenhumberg B, Field SA, Niejalke D, Parris K & Possingham HP. (2003) Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. Ecological Applications 13: 1790-1801.

Walther BA & Moore JL. (2005) The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28: 815-829.

Zar JH. (1999) Biostatistical Analysis. Prentice-Hall Inc, Upper Saddle River, NJ.

Appendix: Supplementary material: Extended description of the simulation, sampling and estimation procedure

Generating a test population: Population parameters: five population parameters were selected to determine the detection probability of an individual; these where: sex, age, size, morphological distinctiveness and exposure. These parameters have a known, and strong, influence on individual detection probabilities; this is as they represent key population, ecological and behavioural aspects that shape the detection function (Borchers et al., 2002;MacKenzie and Kendall, 2002;Royle and Nichols, 2003;Dorazio, 2007).

As age and size are factors known to be associated in live individuals (that is, older individuals have larger sizes), these two variables where modelled as correlated normally distributed variables drawn form a multi-normal distribution. For all generated populations the level of correlation between variables was set to 0.5; and three preselected levels of variables mean (-1,0,1) and standard deviations (0.1,1,10) were determined. This allowed the evaluation of different age and size population structures and variable levels of variation.

Morphological distinctiveness describes the degree at which the morphology of a given individual fits the species "type phenotype" (given by the species description). This was modelled as a function of age and was represented with a value in the range between 0 and 1 (with 1 meaning a complete agreement). The idea of modelling this a function of age arises from the conception that the "type description" of an individual is usually given for a sexually mature and reproductive active individual, meaning that younger non-reproductive active (e.g. they may not have the sexual ornaments needed for court ship and mating) and old individuals (e.g. degradation of the ornaments) may not fit this physical description of the specie. To model this value a normal distribution centered in the mean population age and with a variable standard deviation (set to 3 levels: 0.1,1 and 10) was assumed to represent the behaviour of the spread of morphological variability in the modelled population.

Exposure level was assumed to represent the level of visibility of an individual as a result of both its behavioural (determined by age) and morphological characteristics (determined by size). Size was assumed to be the best variable to capture both factors and used to determine the level of exposure as the probability of being seen given it's size. This variable was modelled by assuming that the process had a normal probability density function (PDF) with mean 0 and three possible levels of standard deviation (0.1,1 and 10).

Determining individual detection probabilities: After generating the individual level characteristics, based on the specified population level variables (as specified on the previous section) an individual detection probability was determined based on the linear combination, without interactions, of the individual generated parameters in a logistic function (see Eq(a)).

Eq(a) $$p_i = \frac{e^{x_i \theta}}{1 - e^{x_i \theta}}$$

here p_i represent the detection probability if individual i given it's population level variables, x_i is the vector of population level characteristics (i.e. age, size, morphological distinctiveness, exposure) for the i individual, and θ represents the individual contribution of each parameter to the detection function (or function parameters). Is clear that many other options are possible to model the detection probability (e.g. normal exponential, gamma beta, etc.) and the selection of a particular one depends on the context and type of survey. Here a logistic function was selected as the functional form to model individual detection probabilities.

The contribution of each parameter to the detection probability estimation was established a priori so the lineal combination of function parameters added up to one. All possible combinations of five possibilities (i.e. 0, 0.25,0.5,0.75,1) that summed up to one were evaluated. This allowed determining the effects of differential weights of the evaluated parameters, on the estimation of detection probability. In the text only the results of equal weighs (that is a 0.25 contribution of each parameter) was analysed and discussed.

Sampling process: As described in the methods section, two spatial implicit approaches (e.g. MRC and RMV) were used both to sample and determine the detection probability of the target population.

Here MRC sampling was modelled as a series of independent random binomial process (each sampling event is considered as unrelated processes and individuals are observed independently of one form another) determined by the individual detection probability. For RMV experiments, the capture process was modelled as a series of independent binomial process for each individual, but for each of them it was a binomial process conditional on the fact that the individual was not seen on a previous event (individual detection probabilities where kept constant until an individual was observed; at this point the detection probability of that particular individual was set to 0 for the subsequent sampling events).

Detection probability estimation: If the set of individuals detected on a particular sample occasion constitute a representative sub-population of known size, the proportion of observed individuals (and the ratio of recapture in MRC) is an obvious estimator of the probability of observing an individual. Obviously the assumption of representatively is stringent, but regardless of this, it was decided to be uses as it is implemented in most population census surveys and the most commonly used software packages (White and Burnham, 1999;Thomas et al., 2006).

The conceptual framework for the estimation of detection probability using either a RMV or MRC approach fundament is the idea that the complete sampling process can be modelled as a multinomial process (with each sampling event being a binomial process) where neither population size (N) or detection probability (p) are known (Borchers et al., 2002).

For both the MRC and RMV method the same general the basic likelihood functions can be used to describe the observation process (in literature this is described as the observation model). When no consideration is taken on the sampling history, and only the detection frequencies are considered Eq(b) describes the observation process, where the estimation of detection probability (and abundance) is based on the number of removals or observations on each sampling event:

Eq(b) $$L(N_{pop}, p) = \prod_{s=1}^{s} \binom{N_s}{n_s} p^{n_s} (1-p)^{N_s - n_s}$$

here N_{pop} represent the total population size (estimated as the total number of observed individuals (N_{tot}) plus the total missed individuals (n_0) in the surveyed area); n_s is the number of individuals detected; N_s are the number of individuals on survey event s (this number is constant in MRC surveys but changes in RMV experiments as individuals are observed and removed); p represents the overall detection probability for all individuals in all sampling events (e.g. a mean value of detection probability) and s are the number of survey events.

Is important to highlight that the calculation of N_{tot} differs between RMV and MRC approaches so that:

If sampling RMV

$$N_{tot} = \sum_{s=1}^{s} n_s$$

$$N_s = N_{tot} - \sum_{s=1}^{s} n_s = N_{tot} - \sum_{s=1}^{s} r_s$$

where r_s is the number of removed individuals in sample event s

If sampling MRC

$$N_{tot} = N_s$$

$$N_s = \sum_{s=1}^{s} m_s$$

where m_s is the number marked individuals on sample event s

An alternative approach for the estimation of the detection probability is evaluating the process individually for each sampling event. This allows estimating a detection probability for each sampling occasion. A likelihood function to describe this process is presented in Eq(c), where the estimation of sampling event detection probabilities (p_s) is based on the sampling event history of event s (this is the w_s vector). The sampling history vector w_s is a vector of 1 and 0 of length N_s, in which 1 represent that animal i was captured in the evaluated sampling event.

Eq(c) $$L(N_{pop}, p_s) = \prod_{s=1}^{s} \binom{N_s}{n_s} p_s^{w_s} (1 - p_s)^{1 - w_s}$$

A more complex approach is based on the idea of detection heterogeneity between individuals within a study area. Equation Eq(d) describes a maximum likelihood on which individual capture histories (that is w_{is}, a vector of 1 and 0 of length s, in which 1 represent that animal i was captured in the sampling event s) are used to determine the individual detection probabilities' (p_i) of the observed individuals.

Eq(d) $$L(N_{pob}, p_i) = \prod_{i=1}^{N_{tot}} p_i^{w_{is}} (1 - p_i)^{1 - w_{is}}$$

using the estimates of p_i is possible to determine the influence of a set of population parameters, vector θ in Eq(a), in determining the individual detection probabilities. The vector θ was estimated using a generalized lineal model (i.e. a logistic regression) using the individual level characteristics of the observed individuals and the estimated p_i individual detection probabilities.