

Population abundance, size structure and sex-ratio in an insular lizard

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ABSTRACT

Estimating population size and understanding its variation is a fundamental, yet complicated, aim of many ecological studies. We considered the problem of estimating spring and autumn population abundance, size-dependent population structure and sex-ratio of the endemic Balearic Lizard, *Podarcis lilfordi* from a three occasions capture-recapture study. We used a Bayesian formulation of individual covariate models to incorporate individual sex, size and trap-response. We first considered a set of simulated data with a medium-to-low probability of recapture and individual recapture heterogeneity to evaluate potential problems in model fitting and selection. Results from simulated data indicated a low performance in parameter estimation and model selection when probability of detection was low (0.15–0.30). We found a negative permanent trap response and a positive effect of size on detection probability in the spring survey but not in the autumn one. The estimated mean densities varied from about 800 to 1000 lizards ha⁻¹, a high value when comparing with mainland lizard populations. The observed increase in abundance was probably due to a drop in territorial behaviour and the immigration of females into the area sampled. As a consequence, sex-ratio changed from nearly even in June (mean posterior, 95%CRI; 0.928, 0.676–1.167) to a female-skewed population in October (0.612, 0.478–0.772).

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1. Introduction

The distribution of individuals over time and space is a central theme in evolutionary and ecological theories (Begon et al., 1990), but robust estimates of population size are notoriously difficult to obtain (Kendall, 1999, see review in Seber, 1982, 1992; Schwarz and Seber, 1999). Exhaustive counts are not possible and the number of individuals should be inferred from a partial sampling of the population using appropriate statistical models (Seber, 1982; Skalski et al., 2005b; Williams et al., 2002). Capture-mark-recapture (CMR) models, based on multiple observations of marked individuals, are now common methods to estimate animal abundance (Seber, 1982; Schwarz and Anderson, 2001; Williams et al., 2002). These models rely on the assumption that all individuals are independent and equally likely to be captured. Nevertheless, this is not always verified. In a study on elk *Cervus elaphus* population abundance, Skalski et al. (2005a) found that the probability of being marked covaried

with herd size, so that animals from the same herd tend to have the same encounter history. Heterogeneity in detection probability might also be due to individual characteristics, such as size or sex. The recapture probability of the sessile Pen Shell *Pinna nobilis* for example, depends on shell width and assuming equal detection would lead to underestimation of recruitment rate (Kéry and Schaub, 2011; Hendriks et al., 2012). Unequal catchability also rises when recapture probability at a given time depends on whether an animal was captured before or not. This trap-response can be positive, when captured animals are more likely to be captured again or negative, when captured animals are less likely to be captured in the future (Pollock et al., 1990). Trap-response might be common in studies with baited traps or in which animals have to be physically recaptured. Unequal catchability across individuals typically tends to underestimate the true animal abundance (Pollock et al., 1990).

Probably the most widely used method for modelling individual covariates in closed population models is the Huggins-Alho procedure (Huggins, 1989; Alho, 1990). The method is based on the so-called “conditional likelihood” (i.e. the likelihood for the data conditional on capture) and is built into freely available software such as program MARK (White and Burnham, 1999). The Huggins' estimator is an ad hoc solution to the problem and it might be favoured in practice because it is “design-based”, and should

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consequently be robust to model assumptions (but see [Little, 2004](#)). Here we adopted an alternative approach, a fully model-based formulation that considers the joint distribution of the encounter history observations and the individual covariate, by prescribing a probability distribution for the latter ([Royle, 2009](#)). The fully model-based approach has several advantages compared to classical estimation procedure. It allows (i) inferences on the population distribution of the covariate while the ‘classical’ methods are conditional to the observed data, (ii) handling missing values in the covariates, and making explicit inferences about their values (in the case of spatial capture-recapture models; e.g. [Royle and Young, 2008](#)), and (iii) estimating proper variances for population size N directly, avoiding the use of the delta approximation. Moreover, Huggins’ conditional approach prevents the modelling of N directly, which is often the focus of the inference.

Here we used the fully model-based approach to estimate population size and size-dependent population structure in the Balearic Lizard *Podarcis lilfordi*, a lizard endemic to the Balearic archipelago (Spain) using three-occasions capture-recapture data. The method permits incorporation of heterogeneity of recapture due to individual characteristics, as well as trap-response, and has recently been extended to include between-occasion survival parameters ([Gardner et al., 2010a](#)).

Potential problems in model fitting and selection can arise from the analysis of small or sparse datasets, gathered during few sampling occasions and/or in the presence of a low probability of detection and individual heterogeneity. Among the expected problems we can mention a low precision in parameter estimates, the underestimation of population size, and model selection uncertainty. Simulation of scenarios that mimic the own setting is a practice suggested to evaluate and anticipate potential problems in model fitting and selection (e.g. [Marques et al., 2010](#)). To this end, we first used sets of simulated data with a medium-to-low probability of recapture and individual recapture heterogeneity, i.e. size-dependent recapture and trap-response. We then applied the approach to real data and extended the method to the simultaneous analysis of males and females, contrasting hypotheses on adult sex-ratio (ASR) and sex-by-size population structure. ASR is a crucial demographic parameter affecting the viability of vertebrate populations and it is of particular interest in some reptile species due to environmental sex-determining mechanisms. It figures also amongst the determining factors in calculations of both demographic and genetic effective population sizes (e.g. [Le Galliard et al., 2005b](#)). Estimates of ASR in the presence of imperfect detection can be potentially biased by differences between the sexes in the detection probability. We exploited a fully model-based formulation of individual covariate models to estimate ASR while accounting for potential sources of detection heterogeneity, and to explore the variation of ASR between two seasons.

2. Materials and methods

2.1. Model formulation

We refer to the classical closed population situation in which a population of N individuals is sampled J times, yielding encounter histories on $n \leq N$ individuals. If we assume that detection probability does not vary over J occasions we can consider the capture frequencies of the sample of n unique individuals, where individuals $i = 1, 2, \dots, n$ were captured $\{y_i\}_{i=1}^n$ times. An auxiliary individual variable (x_i , in this case body length) is thought to influence the detectability of individuals. We assumed that captures are independent and identically distributed (i.i.d.) Bernoulli trials with parameter $p(x_i; \theta_1) \equiv p_i$, with $\text{logit}(p_i) = \alpha + \beta x_i$, where the parameter θ_1 is the vector $\theta_1 = (\alpha, \beta)$. We adopted a Bayesian formulation of

the individual covariate model based on parameter-expanded data augmentation (e.g. [Royle and Dorazio, 2011](#)). The general concept is to augment the observed data set with a fixed, known number, say $M - n$, of “all zero” capture-recapture histories, and to analyze the augmented dataset (of size M) with a new model. Given the augmented dataset, we introduced a set of latent variables z_i for $i = 1, 2, \dots, M$ which are Bernoulli trials with the parameter ψ . This parameter is the inclusion probability, that is the probability that an individual from the augmented data list is an element of the exposed population. Thus, $1 - \psi$ is the zero-inflation parameter, quantifying the number of excess zeros in the augmented data list. Parameter ψ is related to N in the sense that $N \sim \text{Binomial}(M, \psi)$ under the model for the augmented data. Conceptually, M represents the size of a super-population of “pseudo-individuals” that potentially could belong to the real population (of size N) exposed to sampling. If $z_i = 0$, then individual i (from the super-population of size M) does not correspond to an individual in the population exposed to sampling, whereas if $z_i = 1$ individual i is a member of the population of size N ([Royle and Dorazio, 2008](#)). We assert that M is sufficiently large so that the posterior of N was not truncated (this can be achieved by trial and error with no philosophical or practical consequence; [Royle and Young, 2008](#)). Under data augmentation, population size is a derived parameter $N = \sum_{i=1}^M z_i$, and the estimation problem is converted from one of estimating N to one of estimating the parameter ψ and summaries of the latent variables z .

The model for the augmented data is composed of three components:

1. $z_i \sim \text{Bernoulli}(\psi)$;
2. $[y_i | p(x_i)] \sim \text{Binomial}(J, z_i p(x_i))$, with $\text{logit}(p_i) = \alpha + \beta x_i$;
3. $[x_i] \sim \text{Normal}(\mu_x, \sigma_x^2)$

where the conventional “bracket notation” $[\cdot]$ represents the probability density function (pdf), or the conditional pdf $[\cdot | \cdot]$ of the related term.

We further extended the model to account for a behavioural effect due to a possible permanent trap response ([Royle and Dorazio, 2008](#)), so that the detection model is

$$\text{logit}(p_{ij}) = \alpha_0(1 - x_{1,ij}) + \alpha_1 x_{1,ij} + \beta x_{2,i}. \quad (1)$$

The covariate $x_{1,ij}$ indicates if the individual i was captured at some previous time ($x_{1,ij} = 1$ if the individual was captured previous to sample j), and $x_{2,i}$ is the body length covariate. In this model parametrisation, α_0 is the mean for individuals that have not previously been captured, and α_1 is the mean for previously captured individuals. We reparametrised the model in Eq. (1) by expressing α_0 as the product of a trap response parameter (tr) and α_1 , which gives the following linear predictor:

$$\text{logit}(p_{ij}) = tr \alpha_1 (1 - x_{1,ij}) + \alpha_1 x_{1,ij} + \beta x_{2,i}. \quad (2)$$

Expressing α_0 as a function of α_1 allowed us to save one parameter when modelling real data using sex-specific detection probabilities (see below the “Case study” section), assuming that the degree of trap response was equal for males and females. In fact, instead of having four sex-specific parameters, two for both α_0 and α_1 , their number is reduced to three in the new parametrisation (tr , $\alpha_{1,males}$ and $\alpha_{1,females}$).

For estimation by data augmentation, the observed data set containing information on individual sex was subjected to two distinct data augmentations by introducing, for each sex u , a fixed number ($M_u - n_u$) of “all zero” capture-recapture histories, missing covariate values $\{x_i\}_{i=n_u+1}^{M_u}$, sex indicator values $\{sex_i\}_{i=n_u+1}^{M_u}$, and a set of latent indicator variables $\{z_{iu}\}_{i=1}^{M_u}$ that are observed ($z_{iu} = 1$) for $i = 1, 2, \dots, n_u$ and unobserved for $i = n_u + 1, \dots, M_u$.

2.2. Simulated data

We simulated a population of $N=200$ individuals along with their standardized normally distributed body length and subjected them to sampling considering detection probability positively affected by body length (with a covariate coefficient $\beta=0.5$ on the logit scale) and two different levels for the mean detection probability ($p=0.3$ and $p=0.6$, respectively) without any random noise added. In addition, we considered a negative behavioural response after initial capture (trap shyness) again for two distinct levels of detection probability. More specifically, we fixed the mean probability of being detected for the first time, p_0 , as twice the probability at next occasions, p_1 . We generated four sets of data considering three sampling occasions. Simulated data were modelled with and without a trap-response and the individual covariate (the full linear predictor is reported in Eq. (1)) to investigate the consequences of fitting a wrong model. For each of the four scenarios, we simulated 50 datasets to which the specific model was fitted. Summaries of the mean across the 50 replicates of the Bayesian point estimate (of each posterior statistic) are reported, for each scenario and parameter, in Appendix B (Tables B.1 and B.2). In addition we provided the percentage of 95% posterior intervals that contained the true value of each parameter.

2.3. Case study

Lizards were captured using pit traps positioned along and within the bushes over an area of c. 0.25 ha, in a five hectares islet off the southern coast of Mallorca Island (Balearic Islands, Spain). Captured lizards were measured and sexed by the inspection of femoral pores. Recent work has shown that individuals of *Podarcis muralis* can be recognized by the highly variable and individually unique pattern of pectoral scales (Sacchi et al., 2010). In a pilot study conducted during the period 2007–2008, we ascertained that individual identification of Balearic lizards can be achieved based on the same criterion (results not shown). Each captured lizard was measured and photographed using a digital camera prior to release at the same trap where it was captured. Individuals were identified from their pectoral scale patterns using the computer aided APHIS procedure (Moya et al. in preparation). For the analyses we used the capture-photo-recapture data collected during three consecutive days in June (130 lizards, 64 males and 66 females) and October 2010 (130 lizards, 49 males, 81 females).

We initially considered four potential sex-independent models. Model 1, denoted by $M(\cdot)$, assumed p constant across individuals and time; Model 2, $M(b)$, in which p is affected only by a possible permanent behavioural effect; Model 3, $M(h)$, in which there is heterogeneity among the capture probabilities of individuals that depends on their body length, and Model 4, $M(b, h)$, in which p is influenced by both trap response and individual heterogeneity. For the analyses, the body length covariate was centred by subtracting the mean.

We then extended the best supported model for each of the two datasets considering sex-specific parameters and selected the best model from which to estimate population sex-ratio (see Appendix A for further details). Sex-ratios were then derived, together with their estimate of uncertainty, as $(N_{males}/N_{females}) =$

$$\left(\sum_{i=1}^M Z_{i,males} / \sum_{i=1}^M Z_{i,females} \right).$$

Pit traps selected lizards above a certain size and thus able to reach and fall into the trap. This sampling deficiency affects the interpretation of parameter estimates, which is only referred to individuals in the population that have some nonzero probability of being detected.

2.4. Model selection and checking

The Bayesian variable selection procedure of Kuo and Mallick (1998, see Appendix A for further details) was tested for each replicate simulated dataset to evaluate its performance in selecting the correct model (Appendix B, Table B.3). The same method was then applied to real data (Appendix A). Sensitivity of posterior model probabilities to prior specification was tested by repeating the model selection for three different priors for all linear predictor coefficients, assumed drawn from $N(0, \sigma^2)$ with $\sigma^2 \in \{10, 100, 1000\}$ (Appendix A, Tables A.1 and A.2; Appendix B, Table B.3).

We tested goodness-of-fit of the Normal model for the individual covariate using a standard Bayesian p -value approach (Meng and Wong, 1994). To do this we (i) generated new realizations of the data set from the posterior distribution (x^{rep}), (ii) split both observed (x) and predicted body length data into 10 classes $(-\infty, -4, -3, -2, -1, 0, 1, 2, 3, 4, \infty)$, (iii) computed the probabilities of being in each class for each of the posterior samples of the Normal distribution parameters, (iv) computed a test statistic for both observed ($D(x, \theta)$) and simulated samples ($D(x^{rep}, \theta)$), (v) derived the Bayesian p -value as the proportion of times the discrepancy function based on predictive data is higher than the observed discrepancy, $P(D(x^{rep}, \theta) > D(x, \theta) | x)$. The Freeman–Tukey statistic (Freeman and Tukey, 1950) was used as discrepancy function.

2.5. Bayesian estimation and size-dependent population structure

We augmented both simulated and real data with $M - n = 500$ observations of $y=0$, and corresponding missing covariates. Models with sex-specific parameters were run on a single dataset previously augmented of 200 zeros for each sex. Posterior masses for the estimates of population size N were located well away from the upper bounds, indicating that sufficient data augmentation was used. As in Royle (2009), we adopted conventional default priors which, ostensibly, express little prior information about the model parameters (Appendix A, Table A.3, Fig. A.1). The models were implemented in JAGS (Plummer, 2003) through the R2jags package (Su and Yajima, 2012). Data and an R (R Core Team, 2012) script for the sex-specific model are provided as a supplement. Summaries of the posterior distribution were calculated from three independent Markov chains initialized with random starting values, run 50,000 times after a 20,000 burn-in and re-sampling every 20 draws for simulated data. For modelling real data 100,000 iterations, a 50,000 burn-in and a thinning rate of 30 were used. We computed the Brooks–Gelman–Rubin convergence diagnostic (\hat{R} ; Brooks and Gelman, 1998) for which values near 1.0 indicate convergence. For our data, the \hat{R} for each parameter was less than 1.009.

From the super-population of latent variables z_i we can extract and tabulate data for individuals that are members of the population of N individuals exposed to sampling (those with $z=1$). From this sample we summarized size dependent population structure for the whole sample of individuals (males and females) in the study area.

3. Results

3.1. Simulated data

Models that contain the effects considered when data were simulated, in this case an individual heterogeneity and the presence/absence of a behavioural response, led to good estimates of N and other parameters of interest (Appendix B, Table B.1). As expected, precision was lower in the presence of a trap response and a low detection probability ($p_0=0.3$, $p_1=0.15$). When data generated without trap response were modelled considering a

Table 1

Posterior summaries of model parameters under the best model. For June, the model included permanent behavioural response and individual heterogeneity on detection probability. A constant detection probability was modelled for October. N is the estimated population size, the parameters p_0 and p_1 are the mean detection probabilities (on the probability scale) for the first capture event and subsequent occasions respectively, β is the coefficient on body length, μ_x and σ_x are respectively the centred mean and SD of population body length, ψ is the 'zero-inflation' parameter associated with data augmentation.

Parameter	Mean	SD	2.5%	Median	97.5%
<i>June</i>					
N	179.141	32.155	145.000	171.000	259.000
p_0	0.415	0.072	0.265	0.420	0.548
p_1	0.264	0.036	0.197	0.263	0.335
β	0.774	0.263	0.291	0.760	1.314
μ_x	-0.132	0.105	-0.370	-0.122	0.037
σ_x	0.696	0.052	0.606	0.693	0.808
ψ	0.285	0.054	0.216	0.275	0.416
<i>October</i>					
N	242.530	29.849	194.000	239.000	310.000
p	0.231	0.032	0.172	0.231	0.295
ψ	0.385	0.051	0.300	0.380	0.497

permanent trap response effect, precise estimates were obtained only for a moderate-to-high mean detection probability ($p=0.6$). Conversely, when data simulated with a negative trap response were analysed without any behavioural effect, parameter estimates were imprecise, regardless of the mean value of detection probability. The effect of individual heterogeneity on detection probability (β) was correctly estimated with or without a behavioural response. Furthermore, parameter estimates were relatively close to the reference values when the model did not take individual heterogeneity into account (Appendix B, Table B.2).

The model selection procedure performed well in selecting the correct model in presence of a moderate-to-high mean detection probability ($p=0.6$). On the contrary, it was poor in the scenario with a trap-response and a low detection probability ($p_0=0.3$, $p_1=0.15$). Posterior model probabilities were fairly stable under the different prior sets, with an expected performance loss under more vague priors, especially in the presence of a low detection probability (Appendix B, Table B.3).

3.2. Case study

With the June data, the best supported model included both a behavioural response and an effect of body length ($M(b, h)$), with a low sensitivity of posterior model probabilities on prior assumptions. In contrast, for the October data set the model with a constant detection probability received the largest posterior probability (Appendix A, Table A.1). Posterior summaries of parameter estimates, from the most supported model for each season, are given in Table 1. June population size was estimated to be about 30% less than in October (posterior median, 95% CRI; $N_{June}=171$, 145–259; $N_{October}=239$, 194–310).

Posterior distributions of p_0 , p_1 , and β were concentrated above zero in the June data. Thus, the results indicate a decrease in detection probability once an individual is captured, and a positive effect of size on the detection probability (Fig. 1). The estimated population mean and standard deviation of the body length covariate indicate that the sample of measured covariate values (mean = 6.42 cm, SD = 0.66) was slightly biased towards greater values. The positive bias of sampled body length values is consistent with positive values of β . Back-transforming the posterior mean of the estimate for μ gave a population mean $E[x]=6.29$ cm, with $SD[x]=0.70$ (Fig. 2). The proportion of lizards with body length lower than the sample mean was estimated to be 13% higher than that derived by the sampled data. Goodness-of-fit p -value (0.89)

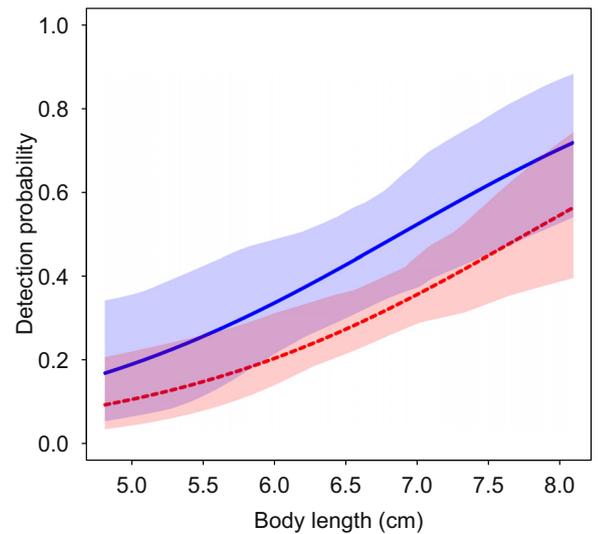


Fig. 1. Spring relationship between detection probability p and body length in *Podarcis lilfordi* from Mallorca (Spain). The blue solid line denotes first captured Balearic lizards, the red dotted line stands for lizards captured at least once in the previous occasions. Shaded areas represent 95% CRI. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

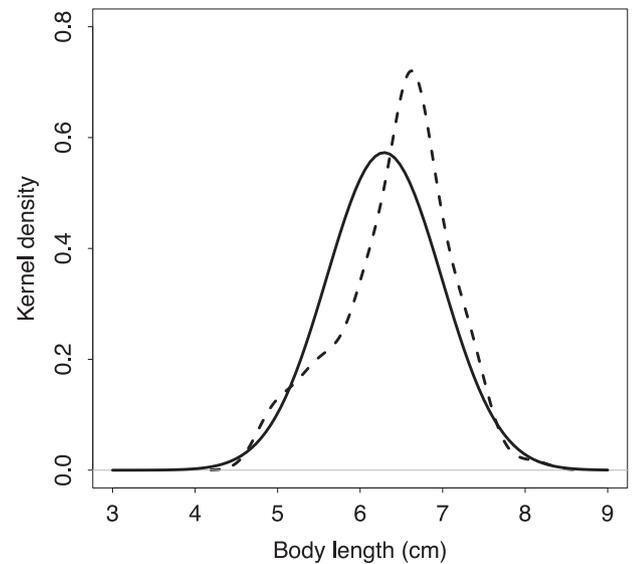


Fig. 2. Spring size dependent population structure of *Podarcis lilfordi* in Mallorca (Spain). Population structure as density of individuals in relation to body length, for sampled Balearic lizards (dashed line) and for population estimates (solid line).

indicated that the fit of the Normal model for body length was adequate (i.e., p -value was between 0.05 and 0.95) and the assumption provides an adequate description of the individual covariate data. For the autumn season the most supported model did neither include a trap-response effect nor an effect of body length on the detection probability (Table 1).

We extended the best supported models to males and females, considering sex-specific probabilities of detection and of being in the population (ψ) for both seasons (Appendix A). A sex-independent β received the larger posterior probability using the June data, whereas a sex-independent detection probability was mainly supported by the October data (Appendix A, Table A.2).

The estimates indicated a change in the sex-ratio over the summer, from an even sex-ratio in June (mean posterior, 95% CRI;

Table 2

Posterior summaries of model parameters under the best sex-dependent model. For June, the model included sex-specific permanent behavioural response and common individual heterogeneity on detection probability. A constant detection probability was modelled for October. N_m and N_f denote the estimated number of males and females respectively. N_m/N_f denotes the estimated sex-ratio. For sex u , the parameters $p_{0,u}$ and $p_{1,u}$ are the sex-specific mean detection probabilities (on the probability scale) for the first capture event and subsequent occasions respectively, β is the coefficient on body length, μ_x and σ_x are respectively the centred mean and SD of population body length, ψ_u is the sex-specific 'zero-inflation' parameter associated with data augmentation.

Parameter	Mean	SD	2.5%	Median	97.5%
<i>June</i>					
N_m	92.521	22.104	71.000	86.000	153.000
N_f	101.338	27.774	73.000	93.000	182.000
N_m/N_f	0.928	0.121	0.676	0.932	1.167
$p_{0,m}$	0.401	0.073	0.236	0.410	0.526
$p_{0,f}$	0.375	0.087	0.192	0.381	0.532
$p_{1,m}$	0.287	0.050	0.196	0.286	0.388
$p_{1,f}$	0.239	0.046	0.157	0.236	0.337
β	0.866	0.332	0.274	0.838	1.592
μ_x	-0.147	0.119	-0.448	-0.128	0.026
σ_x	0.652	0.051	0.565	0.647	0.764
ψ_m	0.352	0.088	0.247	0.332	0.589
ψ_f	0.382	0.108	0.255	0.355	0.689
<i>October</i>					
N_m	93.144	13.938	71.000	91.000	125.000
N_f	153.095	20.601	120.000	151.000	200.000
N_m/N_f	0.612	0.075	0.478	0.607	0.772
p	0.228	0.032	0.168	0.227	0.292
ψ_m	0.375	0.063	0.267	0.370	0.516
ψ_f	0.545	0.078	0.412	0.538	0.718

0.928, 0.676–1.167) to an uneven sex-ratio in October following an increase in the number of females (0.612, 0.478–0.772; Table 2 and Fig. 3). Results for June indicate lower detection probabilities for females and a positive effect of individual size on detection probability for both sexes (Table 2).

4. Discussion

4.1. Testing model performance

The use of CMR models to estimate animal abundance in closed populations relies on the validity of model assumptions, the main ones being that population is closed, marks are not lost and individuals are independent and equally capturable. In some cases, results

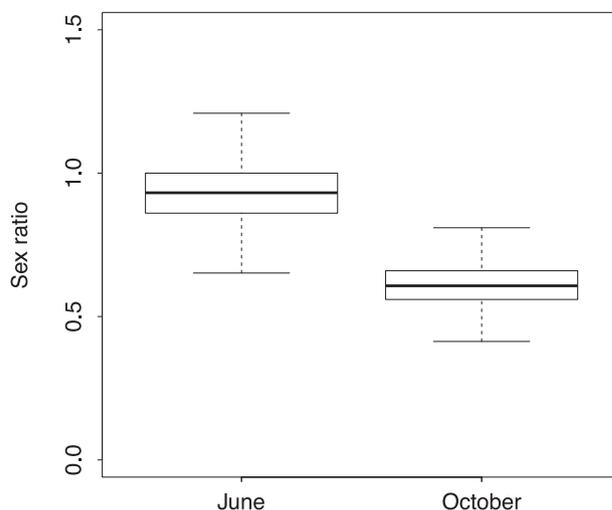


Fig. 3. Population sex-ratio (males/females) of *Podarcis lilfordi* in the island of Mallorca (Spain).

are robust to deviation from these assumptions and assessing the performance of CMR models in different situations would provide important guidelines for survey design (e.g. Skalski et al., 2005a) and to anticipate potential problems related to model performance (Marques et al., 2010). In this paper we used individual covariate models in a Bayesian formulation to estimate population abundance and sex-ratio in the Balearic lizard, pre-emptively evaluating method performance by means of simulated scenarios that mimic our setting.

Results from simulated data showed that under the correct model, estimates of population size, population structure and recapture probabilities were close to those used in the simulations. Interestingly using a model different from the one used to simulate the data, did not always result in biased estimates. A general model including an 'unnecessary' trap-response effect, for example, performed well when the recapture probability was moderately high ($p=0.6$), but not when it was moderately low ($p=0.30$). Applying this model to data would be 'playing safe' only when capture probability is high. The opposite was never true; simpler models, i.e. with no trap-response, were never adequate when trap-response was present, and population size tended to be overestimated. A low recapture probability could also influence the ability to select the correct model by means of the employed Bayesian variable selection procedure (Kuo and Mallick, 1998), in particular in the presence of both behavioural response and individual heterogeneity.

4.2. Population size, sex-ratio and size structure

Pérez-Mellado et al. (2008) used line transect methods (Buckland, 2001) to estimate the density of the Balearic lizard in 41 islands of the Balearic archipelago. They found that late spring density varies across the islets of the archipelago from a minimum of 32 to a maximum of about 8000 lizards ha^{-1} with most islands having a density lower than 1000 ha^{-1} (median = 717; Table 1 in Pérez-Mellado et al., 2008). The reason of this variability is not fully known and it is likely to be the result for multiple factors such as island vegetation structure, density compensation and predation relaxation (Pérez-Mellado et al., 2008; Salvador, 2009). We estimated a mean June density of about 800 lizards ha^{-1} , close to the median density in the archipelago but a third of the density found by Pérez-Mellado et al. (2008) for the same island. In October the lizard population was estimated to be slightly denser than in spring (c. 1000 lizards ha^{-1}). Part of the difference between our estimates and those reported may be due to the natural fluctuations of the population from one year to the next. However, the difference might arise, in part, from the systematic biases of the two methodologies. In habitat with dense vegetation, where animals are more difficult to detect, robust density estimates by line transect are hardly achievable. Capture-mark-recapture methods are thought to be more accurate than visual methods for monitoring elusive species (Wanger et al., 2009). However, in our case the capture method selects for individuals large enough to reach and fall into the traps (body length ≥ 4.8 cm). This might lead to underestimating total population size, depending on the presence and proportion of very small individuals. In June, we found that recapture probability covaried positively with lizard size so that the estimated population is more skewed toward smaller sizes than the observed sample. The goodness-of-fit test based on the Bayesian p -value suggested that the assumption of a normally, and hence symmetrically, distributed covariate provides an adequate description of the data. Finally, we have shown how capture-recapture models of the ordinary sense, but analysed using a Bayesian formulation with data augmentation, can be extended to the simultaneous analysis of multiple (two, in our case) groups. This approach can be applied for estimating latent frequencies of other

Table A.1

Summaries of posterior model probabilities under different prior sets, for sex-independent models applied to the two seasonal datasets. Model notation indicates the inclusion, in the detection function, of a constant term $M(\cdot)$, a term for behavioural response $M(b)$, a term for body size effect $M(h)$, or the latter two together $M(b, h)$. Results are related to three different priors for linear predictor coefficients (assumed drawn from $N(0, \sigma^2)$ with a varying σ^2).

Model	June			October		
	$\sigma^2 = 10$	$\sigma^2 = 100$	$\sigma^2 = 1000$	$\sigma^2 = 10$	$\sigma^2 = 100$	$\sigma^2 = 1000$
$M(\cdot)$	0.000	0.000	0.000	0.444	0.750	0.895
$M(b)$	0.035	0.102	0.047	0.435	0.211	0.090
$M(h)$	0.000	0.000	0.000	0.065	0.033	0.013
$M(b, h)$	0.965	0.898	0.953	0.056	0.007	0.002

Table A.2

Summaries of posterior model probabilities under different prior sets, for sex-dependent models applied to the two seasonal datasets. Model notation is as in Table A.1, with the additional term “sex” in case of sex-specific parameters. As above, results are related to three different priors for linear predictor coefficients (assumed drawn from $N(0, \sigma^2)$ with a varying σ^2).

Model	June			Model	October		
	$\sigma^2 = 10$	$\sigma^2 = 100$	$\sigma^2 = 1000$		$\sigma^2 = 10$	$\sigma^2 = 100$	$\sigma^2 = 1000$
$M(b_{\text{sex}}, h)$	0.800	0.995	0.822	$M(\cdot)$	0.625	0.840	0.987
$M(b_{\text{sex}}, h_{\text{sex}})$	0.200	0.005	0.178	$M(\cdot, \text{sex})$	0.375	0.160	0.013

categorical individual covariates (e.g. colour and pattern polymorphisms) and distributions of individual covariates within a population (e.g. parasite load or weight). The method we used allowed the estimation of lizard sex-ratio taking advantage of the parameters shared between groups (see also Gardner et al., 2010b for another example with spatial capture-recapture models). In our case, an even sex-ratio at late spring was followed by an uneven autumn sex-ratio, with an increase in the estimated number of females in the sampled population. Adult sex-ratio in lizards is often reported to be female biased, as expected in polygynous vertebrates (Massot et al., 1992; Le Galliard et al., 2005a; Buckley and Jetz, 2007). However this varies substantially in time and space (Massot et al., 1992; Galán, 2004). Schoener and Schoener (1980) proposed a mechanistic model in which the number of females changed with per capita resource availability while the number of males depended on habitat quality. The interaction between resource availability and habitat quality would generate spatio-temporal changes in the sex-ratio. Indeed, biased adult sex-ratio can arise temporally due to the interaction between ephemeral resources and despotic behaviour (Pérez-Mellado, personal communication) or can be due to a lower detection or higher mortality probability of one of the two sexes (Schoener and Schoener, 1980; M'Closkey et al., 1998; Galán, 2004). In June we found that recapture probability was slightly lower in females, but once corrected for this difference, the estimates of female number was only slightly higher than the estimated number of males. In Schoener and Schoener's (1980) model this would correspond to a high level of per capita resources. The area surveyed is sheltered from the sea storms and limited by a small beach regularly visited by tourists during the summer. It is possible that the extra food provided by tourists or the sheltered character of the vegetation increases the per capita resources. On the other hand, the loss of male territorial behaviour during autumn might be responsible for a larger number of females migrating into the area at the end of the summer. At the moment we do not have enough elements to explain the observed shift in adult sex-ratio, but if temporal resources and female movements are the proximal causes, we expect another change in the sex-ratio before the spring.

5. Conclusions

In summary, we tackled the issue of estimating population size from capture-mark-recapture data for an endemic lizard. A fully model-based formulation of individual covariate models

was used after testing its performance in simulated scenarios that mimic our setting. We accounted for heterogeneity of recapture due to individual characteristics and behavioural trap response while exploring the variation between two seasons in population size, size-dependent population structure, and adult sex-ratio.

The estimated increase in population abundance, from June to October, was probably linked to both an increase in the number of individuals available for sampling, i.e. larger than a threshold dimension, and to a drop in male territorial behaviour with the resulting immigration of females into the sampling area. As our results suggest, recruitment of small individuals into the sampling population would not necessarily affect the sex-ratio which changed from nearly even to female-skewed. Sex-ratio is a crucial demographic parameter affecting the viability of vertebrate populations, and the size of the latter represents perhaps their key descriptor. Thus, special care must be taken to obtain less biased estimates, and the method we adopted accomplishes this task.

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Table A.3

Prior sets assumed for sensitivity analysis of posterior parameter estimates.

Parameter	Prior set 1	Prior set 2	Prior set 3
α	$N(0, 1000)$	$U(-10, 10)$	$U(-10, 10)$
tr	$N(0, 1000)$	$U(-5, 5)$	$U(-10, 10)$
β	$N(0, 1000)$	$U(-10, 10)$	$U(-10, 10)$
μ_x	$N(0, 1000)$	$U(-10, 10)$	$U(-10, 10)$
$\tau_x = 1/\sigma_x^2$	$Ga(0.01, 0.01)$	$Ga(0.01, 0.01)$	$Ga(0.01, 0.01)$
ψ	$U(0, 1)$	$U(0, 1)$	$U(0, 1)$

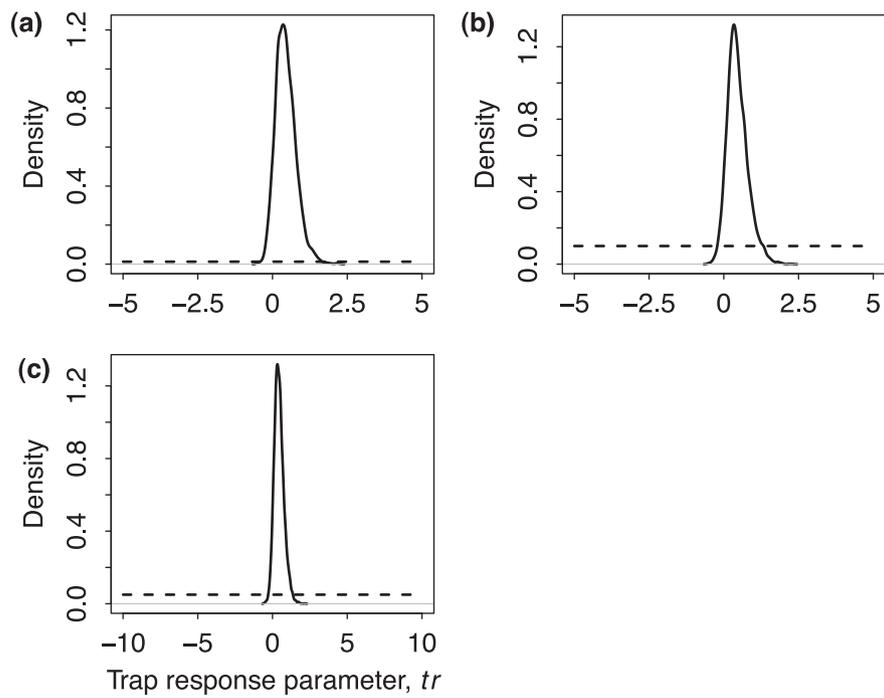


Fig. A.1. Prior (dashed line) and posterior (solid line) distributions of parameter for trap response (tr). Sensitivity analysis gave similar posterior mean and 95%CRI for tr under different priors [posterior mean (95%CRI), under $N(0, 1000)$: 0.357 (–0.271 to 1.237), panel a; under $U(-5, 5)$: 0.350 (–0.291 to 1.243), panel b; under $U(-10, 10)$: 0.351 (–0.270 to 1.241), panel c. The probabilities that tr was positive are 0.925, 0.935, and 0.936, respectively.

Appendix A. Model selection and prior assumptions for sensitivity analysis on posterior distributions

We performed Bayesian model selection using the method developed by [Kuo and Mallick \(1998\)](#) and followed by [Royle \(2009\)](#)

to calculate posterior model probabilities in a very similar case. Examples of implementation are reported in [Royle \(2008\)](#), [Royle and Dorazio \(2008\)](#). For a performance comparison of this and other variable selection methods see [O'Hara and Sillanpää \(2009\)](#). For each real data set, we selected the four (sex-independent) models

Table B.1

Posterior summaries of parameters for models containing only standardized body length as a covariate on detection probability (p) or the length effect plus a permanent behavioural response (p_0, p_1). All detection probability values are given in probability scale. For each scenario and parameter, the mean across the 50 replicates of the Bayesian point estimate (of each posterior statistic) is reported, together with the percentage of 95% posterior intervals that contained the true value of each parameter (CI).

Simulated data	Model	Mean	SD	2.5%	Median	97.5%	CI
$p = 0.30$	N	217.874	31.853	172.887	212.120	297.217	0.94
	p	0.288	0.036	0.219	0.288	0.360	0.96
	β	0.548	0.177	0.210	0.547	0.902	0.92
	N	269.244	80.330	169.461	249.570	471.009	0.92
	p_0	0.256	0.071	0.126	0.254	0.399	0.94
	p_1	0.286	0.038	0.214	0.285	0.363	0.06
$p = 0.60$	β	0.558	0.175	0.221	0.557	0.904	0.90
	N	201.975	6.470	191.439	201.190	216.632	0.98
	p	0.599	0.025	0.549	0.600	0.648	0.98
	β	0.508	0.117	0.286	0.506	0.742	0.98
	N	204.645	10.073	190.307	202.890	229.187	0.98
	p_0	0.589	0.048	0.490	0.591	0.676	0.94
$p_0 = 0.30$ $p_1 = 0.15$	p_1	0.610	0.030	0.551	0.611	0.668	0.00
	β	0.528	0.118	0.302	0.526	0.762	0.96
	N	341.290	71.437	234.047	330.140	507.253	0.10
	p	0.167	0.031	0.113	0.166	0.232	0.00
	β	0.526	0.213	0.106	0.528	0.933	0.94
	N	278.706	82.956	172.113	259.380	477.347	0.94
$p_0 = 0.60$ $p_1 = 0.30$	p_0	0.254	0.071	0.129	0.251	0.397	0.90
	p_1	0.147	0.030	0.093	0.145	0.210	0.98
	β	0.594	0.204	0.200	0.593	0.997	0.94
	N	280.355	28.779	236.796	276.100	347.863	0.00
	p	0.348	0.030	0.290	0.348	0.406	0.00
	β	0.606	0.137	0.345	0.604	0.876	0.92
	N	204.502	10.124	190.028	202.740	228.988	0.94
	p_0	0.589	0.048	0.490	0.591	0.676	0.92
	p_1	0.294	0.028	0.239	0.293	0.350	0.94
	β	0.542	0.123	0.305	0.540	0.786	0.96

Table B.2

Posterior summaries of parameters for models with a constant detection probability (p) or a permanent behavioural response (p_0, p_1). Unlike models reported in Table B.1, individual heterogeneity (β) was here never modelled. All detection probability values are given in probability scale. For each scenario and parameter, the mean across the 50 replicates of the Bayesian point estimate (of each posterior statistic) is reported, together with the percentage of 95% posterior intervals that contained the true value of each parameter (CI).

Simulated data	Model	Mean	SD	2.5%	Median	97.5%	CI
$p = 0.30$	N	188.740	15.653	162.786	187.210	223.394	0.94
	p	0.331	0.033	0.268	0.331	0.397	0.84
	N	232.200	68.125	156.538	212.280	417.957	1.00
	p_0	0.290	0.079	0.139	0.291	0.440	0.98
	p_1	0.340	0.037	0.270	0.339	0.414	0.00
$p = 0.60$	N	195.653	4.306	188.348	195.280	204.951	0.80
	p	0.610	0.024	0.563	0.611	0.656	0.88
	N	196.899	6.574	187.060	195.840	212.385	0.94
	p_0	0.596	0.045	0.502	0.598	0.678	0.98
	p_1	0.613	0.029	0.556	0.613	0.669	0.00
$p_0 = 0.30$ $p_1 = 0.15$	N	289.284	44.207	218.631	283.860	391.060	0.26
	p	0.189	0.030	0.134	0.188	0.251	0.06
	N	224.912	61.326	155.364	208.690	385.627	0.96
	p_0	0.315	0.078	0.163	0.316	0.460	0.92
	p_1	0.183	0.030	0.129	0.182	0.245	0.82
$p_0 = 0.60$ $p_1 = 0.30$	N	241.278	13.672	217.718	240.200	271.053	0.02
	p	0.382	0.028	0.328	0.382	0.436	0.00
	N	198.009	6.672	188.168	197.040	213.992	0.92
	p_0	0.596	0.045	0.503	0.598	0.678	0.96
	p_1	0.324	0.028	0.271	0.323	0.379	0.92

by specifying a set of two indicator variables, w_k for the k th effect, having a Bernoulli (0.5) prior distribution:

$$w_k = \begin{cases} 1 & \text{if covariate } k \text{ is included in the linear predictor} \\ 0 & \text{if covariate } k \text{ is not included in the linear predictor} \end{cases}$$

with the expanded linear predictor specified as:

$$\text{logit}(p_{ij}) = \alpha_0 (1 - x_{1,ij}) + w_1 \alpha_1 x_{1,ij} + w_2 \beta x_{2,i}. \quad (\text{A.1})$$

The four possible models are indexed by the binary sequence (w_1, w_2) , where w_1 and w_2 represent the (persistent) behavioural response and the effect of body size respectively. Posterior model probabilities, for each of the four possible models, were computed using the MCMC samples, and taking the ratio between the number

of iterations giving this model over the total number of iterations (Table A.1).

The best supported (sex-independent) model, for each of the two datasets, was then extended with sex-specific parameters. We selected between two (sex-dependent) candidate models for each data set, by expanding the linear predictor with the indicator variable w_1 . This led to the following model formulations, for individual i of sex u :

- $z_{iu} \sim \text{Bernoulli}(\psi_u)$;
- $[y_i | p(x_i)] \sim \text{Binomial}(J, z_{iu} p(x_i))$, expanded linear predictor for the June data set: $\text{logit}(p_{iju}) = \text{tr} \alpha_{1,u} (1 - x_{1,ij}) + \alpha_{1,u} x_{1,ij} + w_1 \beta x_{2,i} + (1 - w_1) \beta_{1,u} x_{2,i}$, expanded linear predictor for the October data set: $\text{logit}(p_{iju}) = w_1 \alpha_1 + (1 - w_1) \alpha_{1,u}$;

Table B.3

Summaries of posterior model probabilities based on Monte Carlo simulation of 50 replicate datasets under four different scenarios and different prior sets. The mean and median across the replicates of the Bayesian point estimate (posterior model probability) are reported, together with the proportion of times that the correct model received the largest posterior probability (%). Scenarios were simulated as above, always with individual heterogeneity $\beta = 0.5$. The model notation indicates the inclusion, in the detection function, of a constant term $M(\cdot)$, a term for behavioural response $M(b)$, a term for body size effect $M(h)$, or the latter two together $M(b, h)$. For each scenario, the correct model is highlighted in bold. Results are related to three different priors for linear predictor coefficients (assumed drawn from $N(0, \sigma^2)$ with a varying σ^2). For further details see Appendix A.

Simulated data	Model	$\sigma^2 = 10$			$\sigma^2 = 100$			$\sigma^2 = 1000$		
		Mean	Median	%	Mean	Median	%	Mean	Median	%
$p = 0.30$	$M(\cdot)$	0.258	0.129	0.26	0.295	0.129	0.30	0.528	0.549	0.56
	$M(b)$	0.056	0.019	0.00	0.045	0.013	0.02	0.024	0.012	0.00
	$M(h)$	0.566	0.694	0.72	0.594	0.714	0.66	0.431	0.414	0.44
	$M(b, h)$	0.121	0.115	0.02	0.066	0.041	0.02	0.018	0.009	0.00
$p = 0.60$	$M(\cdot)$	0.025	0.001	0.00	0.080	0.001	0.06	0.120	0.000	0.10
	$M(b)$	0.004	0.000	0.00	0.003	0.000	0.00	0.003	0.000	0.00
	$M(h)$	0.851	0.899	0.98	0.874	0.959	0.94	0.853	0.978	0.90
	$M(b, h)$	0.121	0.079	0.02	0.042	0.026	0.00	0.023	0.009	0.00
$p_0 = 0.30$ $p_1 = 0.15$	$M(\cdot)$	0.184	0.113	0.20	0.259	0.172	0.30	0.468	0.504	0.54
	$M(b)$	0.137	0.077	0.06	0.109	0.042	0.08	0.091	0.024	0.10
	$M(h)$	0.392	0.343	0.54	0.463	0.400	0.50	0.340	0.184	0.28
	$M(b, h)$	0.287	0.217	0.20	0.170	0.083	0.12	0.101	0.018	0.08
$p_0 = 0.60$ $p_1 = 0.30$	$M(\cdot)$	0.000	0.000	0.00	0.002	0.000	0.00	0.005	0.000	0.00
	$M(b)$	0.027	0.000	0.00	0.060	0.000	0.02	0.187	0.001	0.16
	$M(h)$	0.006	0.000	0.00	0.025	0.000	0.00	0.042	0.000	0.02
	$M(b, h)$	0.966	1.000	1.00	0.913	0.999	0.98	0.766	0.888	0.82

3. $[x_i] \sim \text{Normal}(\mu_x, \sigma_x^2)$.

For the June data set, the two candidate models had in common a sex-specific detection probability and differed in the coefficient (sex-dependent or not) for body length effect. Thus, the model with a sex-independent effect of body size on p occurs if $w_1 = 1$, while a sex-specific effect of body size is selected if $w_1 = 0$.

In contrast, the competing models for the October data set differed only in the constant detection probability (sex-specific or not corresponding with $w_1 = 0$ or $w_1 = 1$; Table A.2).

We tackled the well known issue of sensitivity of posterior model probabilities to the prior specification (e.g. O'Hara and Sillanpää, 2009) by repeating the model selection for three different priors for all linear predictor coefficients, assumed drawn from a $N(0, \sigma^2)$ with $\sigma^2 \in \{10, 100, 1000\}$ (Tables A.1 and A.2).

Posterior model probabilities were calculated from three independent Markov chains run 1,000,000 times, with a burn-in of 500,000 and a thinning rate of 20.

The Kuo and Mallick (1998) method, as in Eq. (A.1), was also applied to the replicate simulated data. Posterior model probabilities (Appendix B; Table B.3) were calculated from one Markov chain run 150,000 times, with a burn-in of 50,000 and thinned every 50 iterations.

Appendix B. Posterior model parameters and probabilities for replicated datasets.

Posterior summaries of model parameters and probabilities for 50 replicate simulated datasets. The latter were derived from different detection probabilities (indicated in the first column of the tables) both in presence (p_0, p_1) or absence (p) of behavioural response, but always with individual heterogeneity $\beta = 0.5$, and starting from a population size $N = 200$.

Appendix C. Supplementary material

Supplementary data and model script associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2013.07.015>.

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