CSIRO PUBLISHING

Wildlife Research, 2013, **40**, 552–560
http://dx.doi.org/10.1071/WR13127

Estimating lizard population density: an empirical comparison between line-transect and capture–recapture methods

J. Ruiz de Infante Anton[A], *A. Rotger*[A], *J. M. Igual*[A] *and G. Tavecchia*[A,B]

[A]Population Ecology Group, IMEDEA (CSIC–UIB), c. M. Marques 21, 07190, Esporles, Spain.
[B]Corresponding author. Email: g.tavecchia@uib.es

Abstract

Context. In most natural populations, exhaustive counts are not possible and estimates need to be derived from partial sampling by using analytical methods that account for biological processes, sampling errors and detection probability. The methods available have contrasting pitfalls and payoffs in relation to the assumptions made but are seldom contrasted on the same population.

Aims. We compared density estimates derived by different sampling methods. Despite the real density being unknown, the 'soft' validation of density estimates might help to better understand the possible pitfalls and payoffs of each method. This was done in three closed populations and with three different habitat typologies to disentangle the effects of different capture-detection processes to those introduced by the method itself.

Methods. We considered the problem of estimating population density of the endemic Balearic lizard, *Podarcis lilfordi*, in three island populations. We compared estimates derived by distance sampling (LT) in three types of habitat with those calculated from a simultaneous 3-day capture–mark–recapture study. Capture histories of marked individuals were used to estimate density using spatially explicit capture–recapture models (SECR) and a capture–mark–recapture model without spatial data (CMR). Moreover, we empirically assessed the influence of survey duration by extending the survey in the largest island to five occasions. The real population density was unknown and absolute accuracy of each method cannot be assessed; nevertheless, relative estimates might be informative.

Key results. LT estimates had the greatest coefficient of variation in vegetated habitats, corresponding to possible departures from model assumptions. SECR estimates differed among islands and were from 12% to 37% lower than those derived by LT but only in the largest islands with high and dense vegetation. CMR estimates depended on the number of occasions whereas SECR did not and showed lower variance. LT and SECR estimates showed differences across islets.

Conclusions. Line-transect and capture–recapture methods gave comparable results but the interaction between recapture processes and habitat types should be considered when inferring density to the whole area. We found density estimates between 1500 and 2500 individuals ha^{-1}, being a higher value than those found for lizards in continental regions.

Implications. Pitfalls and payoffs of each method are discussed to optimise experimental design in estimating population density.

Additional keywords: detection, distance sampling, habitat, island, SECR.

Received 19 February 2013, accepted 7 November 2013, published online 18 December 2013

Introduction

The distribution of individuals over space and time is a central theme in ecological theory. Yet, how to obtain a robust measure of population abundance (N), or density (D), is still an open field of research (Buckland *et al.* 2001; Seber 2002; Williams *et al.* 2002; Tavecchia *et al.* 2009). The problem has its root in the scientific method itself. When exhaustive counts are not possible, estimates have to be derived from partial sampling by using analytical methods that account for biological processes, sampling errors and detection probability. A first step to reduce problem complexity is to conduct surveys over a short period of time so that the population can be assumed to be closed to emigration, immigration, birth and death and only detection probability has to be considered (Otis *et al.* 1978; Seber 2002; Williams *et al.* 2002). An estimate of the population density, $\hat{D}$, defined as the number of individuals per unit area is generally preferred over an estimate of population size, $\hat{N}$, because it allows comparisons across species and over space and time. The two estimates are related by the area surveyed, A, so that $\hat{D} = \hat{N}/A$. As a consequence, population density models have typically two components, one to account for the detection process and a second to estimate A. The two sets of methods commonly used for the estimate of population density are line-transect (LT) and capture–mark–recapture methods (CMR). In LT, observers count the number of animals while moving along a transect line and measure, or give an estimate of, the distance from transect line at which each individual has been seen (Buckland *et al.* 2001). In CMR studies, animals are captured, marked and recaptured (or resighted) and an estimate of population abundance can be derived from individual capture histories (Schwarz and Anderson 2001; Seber 2002; Williams *et al.* 2002). Population density can be then derived using an estimate of A, which is typically based on the relative positions of detectors (Sutherland 2006) or on animal movements, such as average home-range size (Seber 2002) or mean maximum distance moved (Wilson and Anderson 1985). These add-on methods are only partially satisfactory. Spatially explicit capture–recapture models (SECR; Efford 2004) incorporate an estimate of A with an underlying model of animal home-range based on the movement of marked animals between detectors (traps). This solution should be preferred to the conventional CMR approach because in SECR models, the estimations of $\hat{D}$ and A occur simultaneously and density estimates or realised population size are less biased (see Borchers and Efford 2008; Noss *et al*. 2012; Efford and Fewster 2013 for more detailed on advantages of SECR).

At a first look, LT and capture–recapture methods differ only in the way recapture processes are treated. However, they have different pitfalls and payoffs in relation to the assumptions made and the system under study. Detection processes in LT are assumed to have the following three characteristics: (1) the detection probability decreases with the distance from the transect line, (2) individuals on the transect line are detected with certainty, and (3) individuals are detected at their initial location and their distance from the transect line is exact (Buckland *et al.* 2001). Capture–recapture methods assume that recapture events are independent, that marks are not lost, that individuals are homogeneous in their capture probability and that previous captures do not influence the following encounter history. Non-spatial explicit model further assumes geographic closure, hence, the need to estimate the sampled area. SECR models do not assume geographic closure, but assume that animal home-range is approximately circular and have a fix central location (Efford 2004). In some systems, LT provides a quick and not expensive way to obtain robust estimates of population density or abundance (Aars *et al.* 2009). In other cases, CMR and SECR methods might be more suitable because animals are difficult to detect or LT model assumptions are not met (Hendriks *et al.* 2012).

We considered the problem of estimating population density of the Balearic lizard, *Podarcis lilfordi* (Squamata, Lacertidae; Günther, 1874), in three island populations. The isolated character of island populations, the reduced species diversity and the relatively small number of interactions across species alter the balance of environmental and ecological control on population dynamics (MacArthur and Wilson 1967; Wright 1980). Because of this ecological setting and the low energetic costs, lizards on islands have potential to reach exceptionally high densities following predator release, diet change and competitor release, a phenomenon referred to as 'density compensation' (MacArthur *et al.* 1972; Olesen and Valido 2003). Buckley and Jetz (2007) found that lizards on islands occur at densities about an order of magnitude higher than those recorded on mainland. Within the Mediterranean basin, the Balearic Islands (Spain) are one of the regions in which endemic lizards attain very dense populations (Salvador 1986; Pérez-Mellado 1989, 1998); however, the exact density value has seldom been estimated (but see Pérez-Mellado *et al*. 2008). Reptile populations are notoriously difficult to measure because of the small body size of the animals, secretive behaviour, habitat preferences and fast unpredictable activity (Turner 1977). Despite these constraints, there is a long tradition of using transect sampling to estimate population densities of herpetofauna (Iverson 1978; Cassey and Ussher 1999; Germano *et al.* 2003; Reisinger *et al.* 2006; Pérez-Mellado *et al.* 2008). In some species of reptiles, however, individuals are difficult to detect and tend to be seen during movements, rather than before as assumed by LT models. The violation of model assumptions leads to biased estimates of density, to the point that some authors discourage the use of visual counts in estimating lizard density (Smolensky and Fitzgerald 2010). Other authors used capture–recapture methods to estimate population density and abundance (Ballinger and Congdon 1981; Kwiatkowski and Sullivan 2002); however, few have compared the two methodologies (Kacoliris *et al.* 2009; see also Funk *et al*. 2003; Smolensky and Fitzgerald 2010). Kacoliris *et al*. (2009) suggested that capture–recapture data might lead to less biased estimates; however, this might depend on animal behaviour and habitat characteristics (V. Pérez-Mellado, pers. comm.).

We compared lizard density estimates derived by (1) distance sampling (Buckland *et al.* 2001), (2) spatially explicit capture–recapture models (Efford and Fewster 2013) and (3) capture–recapture without spatial data (Seber 2002). The real density of lizards was unknown, but the 'soft' validation of density estimates (*senus* Rodda and Campbell 2002) might help better understand the possible pitfalls and payoffs of each method. We did this in three closed populations and with three different habitat typologies to disentangle the effects of different capture–detection processes to those introduced by the method itself.

Materials and methods

Species and study area

The Balearic lizard is an endemic lizard of the Balearic archipelago (Spain). It is considered endangered by the IUCN criteria (Pérez-Mellado and Martínez-Solano 2009), and vulnerable at the regional level (Viada 2006). Its distribution is currently confined to the islets of Mallorca and Menorca and to the Cabrera archipelago. We estimated lizard density in the following three islets in the south coast of Mallorca: Es Caragol (0.29 ha, named 'CA' hereafter), Na Guardia (1.98 ha, named 'GU' hereafter) and Na Moltona (5.09 ha, named 'MO' hereafter). Vegetation richness and structure changed with islet size, with 'CA' having a low and less diverse vegetation and 'MO' with a high and more diverse one. We recognised four main habitat categories and characterised each island on the basis of their occurrence (Table 1). The first habitat type, named 'A', was characterised by a vegetation higher than 50 cm, including mainly shrubs of genera *Pistacia* and *Phillyrea*, the second one, 'B', was

Table 1. Islet area, proportions of habitat type in the islet, number of transects and characteristic of trap-arrays

A = high vegetation, B = low vegetation, C = shore and scattered plants, D = rocks, nTD = nearest-neighbour distance between traps, W = average maximum distance between detections pooled over individuals, A = array area estimated by the minimum convex polygon (MCP), and A(nTD) = area of the array obtained by adding a boundary strip of constant width of 0.5 nTD. Note that Habitats A and B in GU are combined

Parameter	Es Caragol (CA)	Na Guardia (GU)	Na Moltona (MO)
Total area of the islet (ha)	0.29	1.98	5.06
High vegetation (Type A)	–	0.43	0.53
Low vegetation (Type B)	0.69		0.18
Shore (Type C)	–	0.11	0.29
Rocks (Type D)	0.31	0.46	–
Number of transects per day	3	5	7
Number of day	3	3	5
Number of traps	26	25	31
Trap array perimeter (m)	118	157	181
nTD (m)	5.9	8.1	6.3
W (m)	5.6	5.7	8.0
A(nTD) (ha)	0.125	0.233	0.270
A (ha)	0.088	0.164	0.210
Total number of lizards observed or captured			
Line transect	164	379	1507 (881^{A})
Capture in grid	232	188	397 (254^{A})
Recapture in grid	80	35	94 (36^{A})

^{A}Three days only.

characterised by vegetation less than 50 cm (i.e. *Crithmum maritimum*), the third, 'C', comprised sand, rocks and few plants of halophytic species, such as *Salicornia ramosissima*, and the fourth, named 'D', comprised exclusively rocks and pools of salted water (Table 1). These last two categories are suboptimal habitats for lizards and marked the region between the vegetated area and the sea. Nevertheless, we do not know the importance of these habitats that lizards use for shelter and in search of food.

Line transect

In October 2012, each islet was visited during three consecutive days, with the exception of MO that was visited two additional days to evaluate the effect of a longer sampling period on density estimates. According with island surface, we considered three line transects per day at CA, five line transects per day at GU and seven line transects per day at MO, making a total of 59 line transects (Table 1). In the largest islet (MO), we were able to survey each habitat separately but this was not possible in the other two islets where transect lines would have been too short (except Habitat C in GU). Following Buckland *et al.* (2001), an observer travelled along a line of variable and known length and recorded the perpendicular distance of each observed lizard to the transect in 10-cm classes. Transects were performed daily by the same observer. We first ran a global analysis merging the data from all islets and contrasting a model assuming a constant density value with one with an islet effect. Subsequently, we repeated this analysis for each island by stratifying the data per habitat type (in MO), or a combination of them (in CA and GU), and occasion. Finally, we considered together those habitats encompassed by the trap array to facilitate comparisons with estimates derived from capture–recapture data (see below). Data truncation was applied when probability of detection was less than 0.15; otherwise, extra parameters were needed to fit the long tail function. The cut-point for right truncation is arbitrary but it is advised to cut at <0.15 of the detection probability or 5% of the observation (Buckland *et al.* 2001; Thomas *et al.* 2010). Transects in Habitat C and in Habitat D at GU were discarded when stratified for occasion. For each island, observations were analysed with DISTANCE 6.0 Release 2 (Thomas *et al.* 2010). Following Buckland *et al.* (2001), graphical fit was used to group observations into distance classes and the best model for each island was selected on the basis of the AIC value.

Capture–mark–recapture

Capture–mark–recapture data were collected in each island with an array of pit-fall traps ($n = 26$ in CA, $n = 25$ in GU, and $n = 31$ in MO). Traps were unevenly spaced and positioned ~4 m apart along shrub edges and within the vegetation. In each islet, the array encompassed two types of habitat. In CA, it included Habitats B and D (Habitat A and Habitat C were absent). In GU, it included Habitats A–C, and in MO Habitats A and C (Habitat D was absent). Individuals were recognised by photo-identification, according to the method proposed in Sacchi *et al.* (2010), with the aid of a customised computer procedure (O. Moya, P.-L. Mansilla, S. Madrazo, J.-M. Igual, A. Rotger, G. Tavecchia, unpubl. data). Observations were coded as capture–recapture histories, a series of '1' and '0' coding at each occasion for presence and absence, respectively. We assessed whether all individuals had an equal probability of recapture in CA and GU, by using the Cormack's test designed for three-occasion studies (Cormack 1966 cited in Krebs and Houston 1989). In MO, where data were collected over five occasions, the homogeneity across individuals in the probability of recapture was also assessed through contingency tables and directional Z-tests, using software U_CARE (Choquet *et al.* 2005; appendix I in Tavecchia *et al.* 2008). After examining for trap homogeneity, we obtained a direct estimate of lizard density in each islet by using spatially explicit models with package 'SECR' (Efford 2012) in software R (R Core Team

2012). SECR models use the location of each encounter to fit a spatial model of the detection process, which is assumed to follow a distribution with a given mean and a variance, referred to as $g0$ and s, hereafter (Efford 2004). The parameters $g0$ and s are estimated by maximum likelihood. We assumed s to be constant and we fit models with constant and time-dependent $g0$, namely '$g0(.)$' and '$g0(t)$', respectively. Detector type was set to 'multiple' because several animals might be captured by the same trap during the same session. We considered the model with the lowest AIC as the best compromise between model residual deviance and model complexity (Burnham and Anderson 2001). We first selected the type of function for $g0$ by contrasting a model assuming a negative exponential function with one assuming a half-normal function. We then assumed a temporal variation in $g0$ and retained the model with the lowest AIC value. After modelling density in each islet separately, we merged the data into a single analysis and compared a model assuming an islet effect with one assuming the same density across islets as a general test for an islet effect. Finally, we obtained a third measure of population density without considering a spatial component. For this, we first estimated the population size, N, using the Schnabel's index (Seber 2002). We then divided this estimate by the minimum convex polygon (MCP) encompassing the traps, with the addition of an external strip 0.5 nTD metres wide, where nTD is the average nearest-neighbour distance in metres between traps calculated by the SECR package (Efford 2012). Seber (2002, p. 51) used as a strip width, W, the mean diameter of the home range of lizards during the trapping period. However, we wanted an estimate of a strip width independent from the spatial information on individuals. In this case, lizards do not need to be individually marked. This final density measure was referred to as 'CMR'.

Results

Line transect

We had a total of 2050 contacts with an average of 35 lizards per transect per day on each island (Table 1). When all data were merged, the AIC of a model assuming that density changes across island was 23.44 points lower than that of a model assuming a constant value, suggesting an overall difference in density across the three populations. When the data for each islet were analysed separately, we found that the half-normal function for detection probability was the more appropriate to describe the detection probability, except for MO, in which a cosine expansion was necessary (Table 2). Density estimates across islets changed from 1306 to 2093 individuals ha^{-1}; this range was likely to be the consequence of the difference in habitat composition rather than islet area *per se* (Fig. 1). Indeed, within an islet, estimates had a similar range of values when stratified by habitat type (Table 2). Also, densities in Habitat C in GU and MO were lower than in other habitats, but nearly two times higher in MO than in GU. Density tended to be higher in habitat or combination of habitats with low vegetation (Habitat B; Fig. 2). However, we were not able to statistically test for a difference among habitats because habitat-type combinations differed across islets. On top of these differences, estimates varied among occasions. At GU islet, for example, density was estimated to be 1534 individuals ha^{-1} at the second occasion and 2651 individuals ha^{-1} the day after. Similarly, at MO, densities ranged from 1990 individuals ha^{-1} to 3708 individuals ha^{-1} over the 5 days of the survey (results not shown). This variability, caused in part by the lizard response to weather changes, reflects also a higher sampling error of the detection process in vegetated habitats (Fig. 2). In MO, where three habitat types were surveyed simultaneously and during five occasions, the coefficient of variation (CV) per habitat was 0.38, 0.19 and 0.16 in high vegetation, low vegetation and coastal habitat, respectively (Fig. 2). Indeed, in vegetated habitats, the detection function had a more difficult adjustment because of a lower than expected number of observations at a short distance (Fig. 3). LT estimates obtained by analysing sequentially the 5-day data at MO were variable, with no particular relation with the number of occasions (CV: 0.11; Fig. 4). Note that the confidence intervals of the daily estimates are independent and relate to the amount and sparseness of the data collected that day.

Capture–recapture

The goodness of fit test supported the assumption of equal recapture probability across individuals in all 3-day datasets (CA: Z = 0.162, P = 0.106; GU: Z = 0.654, P = 0.32; MO:

Table 2. Density estimates ($\hat{D}$) per habitat type in the three islets by line-transect method, using distance-sampling technique

Surveys were conducted during 3 days in CA and GU and 5 days in MO. A = high vegetation, B = low vegetation, C = shore and scattered plants, D = rocks, TL = total daily transect length, CL = confidence limits, F = distribution function to describe the distribution of detection probability (HN = half-normal, HNC = half-normal and cosine), and CV = coefficient of variation. Models selected for comparison with capture–recapture spatially explicit models (SECR) are in bold

Islet	Habitat	TL (m)	$\hat{D}$ (ind. ha^{-1})	95% CL	F	CV (%)
Es Caragol (CA)	**B+D**	**147**	**1799**	**1505–2151**	**HN**	**8.9**
Na Guardia (GU)	A+B+C+D	617	1306	1139–1498	HN	7
	A+B+C	**439**	**1784**	**1551–2051**	**HN**	**7.1**
	A+B	301	2622	2256–3048	HN	7.7
	C	138	649	443–949	HN	19.1
	D	178	–	–	–	–
Na Moltona (MO)	A+B+C+D	1227	2003	1806–2222	HNC	4.9
	A+C	**942**	**2093**	**1732–2529**	**HNC**	**7.6**
	A	661	1884	1499–2368	HNC	9.1
	B	285	3351	2528–4442	HNC	11
	C	281	1463	1080–1981	HNC	13.4

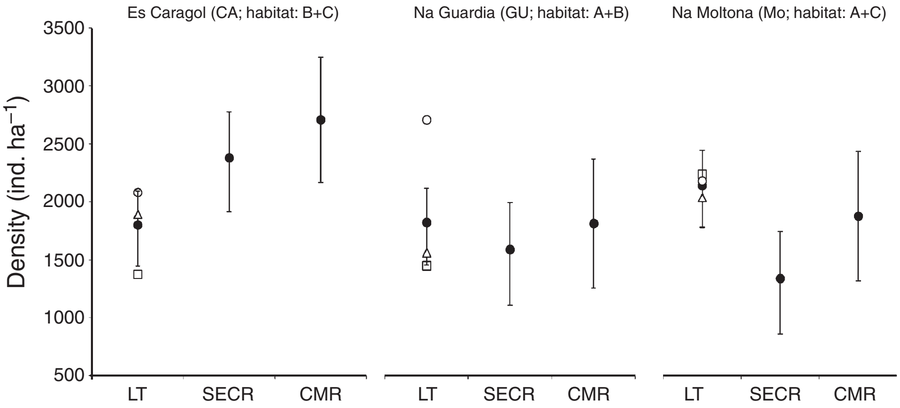

Fig. 1. Autumn population density of Balearic lizard estimated by line-transect (LT) and capture–recapture spatially explicit (SECR) models and Schnabel index (CMR) in three islets, with average value estimated over three occasions (●), at Occasion 1 (□), at Occasion 2 (△) and at Occasion 3 (○). Islet surface is increasing from left to right. Vertical bars indicate 95% confidence intervals for the average estimates. Habitats: A = high vegetation, B = low vegetation, C = shore and scattered plants, and D = rocks only.

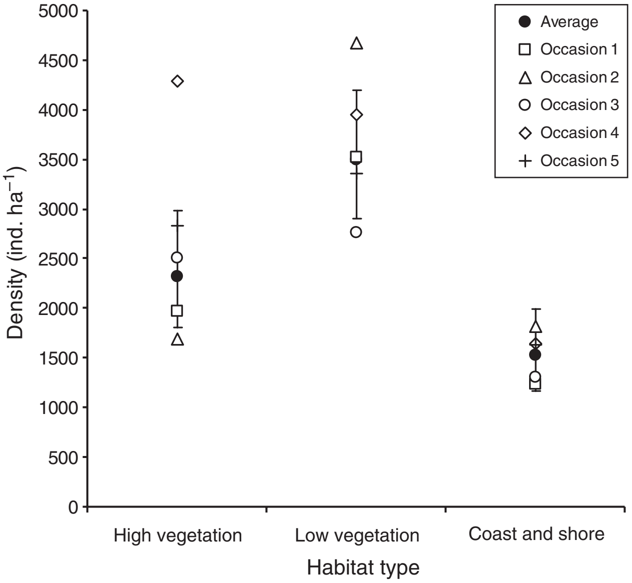

Fig. 2. Autumn density (individuals ha^{-1}) at Na Moltona (MO) islet according to habitat type and occasions, estimated by line transect. The coefficient of variation per habitat was 0.38, 0.19 and 0.16 in high vegetation, low vegetation and in coastal-shore habitat, respectively.

Z = 1.309, P = 0.169). Similarly, in all three islets, a negative exponential function for g*0* was preferred to the half-normal distribution (Table 3), indicating that recapture probability abates rapidly with the distance from the trap. The model, g*0*(t), assuming a different recapture probability in each occasion was preferred in all populations, reflecting a change in the recapture process. The goodness of fit of the 5-day survey at MO supported the hypothesis of a homogeneous capture probability across individuals ($\chi^2_2 = 1.854$, $P = 0.396$) and the absence of a trap response (Z = 0.53, P = 0.596). Estimates from the retained models indicated that the highest density of lizards was in CA (2381 individuals ha^{-1}; 95% CL: 1989–2851), followed by GU (1560 individuals ha^{-1}; 95% CL: 1141–2132) and MO (1316 individuals ha^{-1}; 95%CL: 963–1798). As the structure of g*0* was the same in all islets, we merged the datasets and contrasted a model assuming a different density across islets with one including a constant value. The AICc of the model assuming an islet-dependent density was 4.451 points lower, suggesting an overall statistically significant difference in density across islets. CMR estimates, without spatial information, were systematically higher but comparable with those obtained by SECR models (Figs 2, 4). However, point estimates at MO using the CMR method decreased with the number of occasions (from 2591 individuals ha^{-1} to 1637 individuals ha^{-1} when two or five occasions were considered, respectively; CV: 0.22). The highest drop, however, was between two and three occasions (Fig. 4). Interestingly, this was not the case for the SECR-derived estimates (CV: 0.02). As expected, the standard error of the estimates decreased with the number of occasions considered for SECR as well as conventional CMR methods (Fig. 4). Note that CMR results of Fig. 4 islet would be 22% higher when W is used instead of nTD (Table 1). This difference increases to nearly 30% in the other two islands and can be calculated as 1 – A/A (nTD).

Discussion

We empirically compared the density estimates of three island populations of lizards derived by two common, but seldom contrasted, sampling designs, namely, LT surveys and capture–recapture sampling. In addition, capture–recapture data were analysed using models including the capture locations (SECR) or those without the locations (CMR), to assess the influence of accounting for animal home range in parameter estimates. The performance of a given method should be assessed using simulated data in which the real parameters are known (Rodda and Campbell 2002; Tenan *et al.* 2013). However, simulated data do not typically include the many constraints and variance components that one might experience in empirical data and, despite their limitation, a 'soft' validation (*sensu* Rodda and Campbell 2002; Rodda

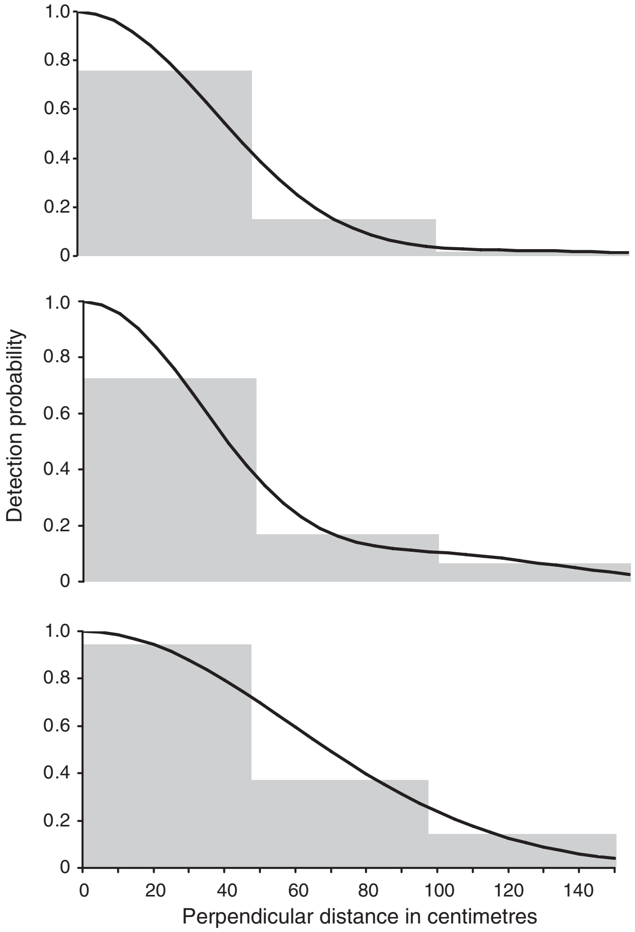

Fig. 3. Detection functions of lizards observed from line transects at Na Moltona islet according to habitat from 5-day survey. Columns = observed, line = expected from the selected model; see text for details. Top = high vegetation (half-normal cosine detection function), centre = low vegetation (half-normal cosine detection function), and bottom = coast and shore (half-normal).

2012) of density estimates can be informative. A first limitation of our study was that real densities were unknown, preventing the assessment of the accuracy for a given method. Nevertheless, important empirical indications on method performance arose from the comparisons across the approaches used (see below). Results suggested that differences across islands found by LT and SECR models were mediated by the different proportion of vegetated habitat in each population (Tables 1, 2). In particular, results from LT surveys indicated that greater density of lizards was found in low vegetation, possibly owing to food availability, habitat conditions and thermoregulatory behaviour. Also, estimates in high vegetation had a larger CV, suggesting that the use of this habitat changed during the 5 days of sampling. We used a qualitative characterisation of habitat type based on macro-similarities such as plant species and shrub height. It is possible that a more quantitative measure based on, for example, habitat fragmentation or plant cover would provide a better description of density variability. LT methods assumed that all animals are detected previous to their movement, that all individuals on the transect line are detected with certainty and that detection abates with the distance from the line. We have found evidence of possible departures from model assumptions, depending on the habitat considered. Indeed, LT models predicted more lizards close to the transect in vegetated habitats than was actually observed and the half-normal distribution function for detection probability has to be extended to account for a larger number of lizards observed distant from the line than what was expected (Fig. 3). This is probably due to the fact that lizards perceived the approaching observer as a danger and were detected only after the movement occurred, in contrast with what is assumed by the model in that animals are recorded before they move either toward or away from the observer. This phenomenon seems less pronounced in open habitats, where lizards are likely to be seen sooner. A possible departure from model assumptions might also explain why LT densities were higher than CMR and SECR estimates in islets with high vegetation, but not in CA where vegetation is mainly low or absent (Fig. 1). Note that LT densities might be biased upward as well as downward, depending on animal and observer speed, on the graphical adjustment and the cut-off point of the detection curve (Buckland *et al.* 2001). Anderson *et al.* (2001) and Smolensky and Fitzgerald (2010) found that the violation of complete detection of individuals on the transect line led to underestimates of population density. These studies concluded that densities are generally underestimated because of

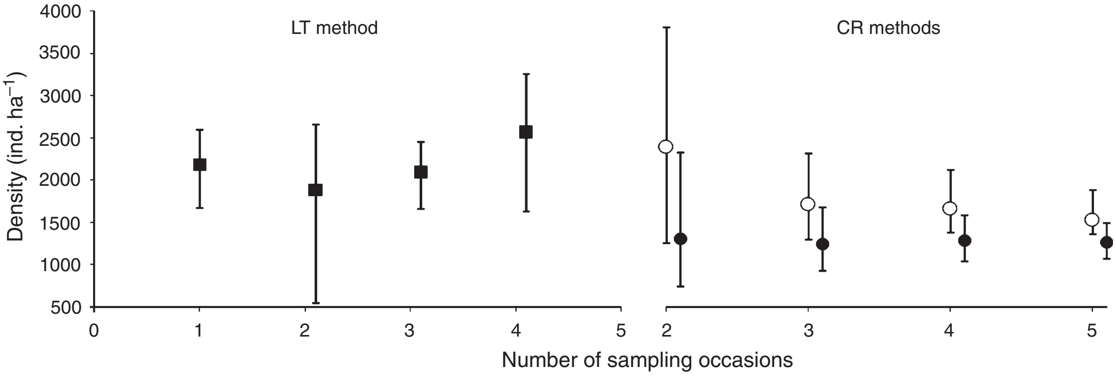

Fig. 4. Density estimates at Na Moltona islet according to the number of sampling occasions obtained by different methods. Left = LT method, right = CR methods. SECR models are indicated by solid symbols, and CMR models by open symbols; see text for details.

Table 3. Modelling recapture function with capture–recapture spatially explicit (SECR) models at three islets

For a given islet, the trap grid encompassed two types of habitat, except on Na Guardia that had three habitat types. A = high vegetation, B = low vegetation, C = shore and scattered plants, D = rocks (see text), . = constant, t = time, distribution = function to describe the distribution of detection probability, half-normal or negative exponential (Neg. Exp.), AIC = Akaike's information criterion, *np* = number of parameters, and MLE-D = maximum-likelihood density estimates and 95% confidence interval (in parentheses). Models retained are in bold

Model and notation	Distribution	AIC	*np*	MLE-D
Es Caragol (CA; habitat type in trap array: B + D)				
1 g0(.)	Half-normal	966.45	3	2213 (1853–2644)
2 g0(.)	Neg. Exp.	915.65	3	2398 (2002–2873)
3 *g*0(t)	**Neg. Exp.**	**913.5**	**5**	**2381 (1989–2851)**
Na Guardia (GU; habitat type in trap array: A + B + C)				
1 g0(.)	Half-normal	637.62	3	1384 (1028–1863)
2 g0(.)	Neg. Exp.	617.83	3	1603 (1171–2196)
3 *g*0(t)	**Neg. Exp.**	**606.51**	**5**	**1560 (1141–2132)**
Na Moltona (MO; habitat type in trap array: A + C)				
1 g0(.)	Half-normal	793.731	3	1082 (788–1485)
2 g0(.)	Neg. Exp.	773.556	3	1339 (979–1830)
3 *g*0(t)	**Neg. Exp.**	**766.623**	**5**	**1316 (963–1798)**

inactive lizards. In our case, because the real density was unknown, we could not test this hypothesis and inactive lizards are likely to be absent from both LT and CMR datasets, allowing a relative comparison of the methods.

CMR density estimates are based on recapture processes estimated from the encounter histories of marked animals. Recently developed SECR models (Efford 2004, 2010) incorporate a model for animal movements built on capture locations. These models gave estimates that were always lower than those obtained without the spatial information on captures (CMR; Fig. 1). A similar result was found by Noss *et al.* (2012) when comparing estimates from capture–recapture data of mammals with and without spatial information (see also Efford *et al.* 2005). Krebs *et al.* (2011) also found that at high-density SECR estimates were systematically smaller, whereas the opposite was true at low density. The lower SECR than CMR estimates were probably a consequence of boundary-strip measures being expected to be underestimates of the effective trapping area (Efford 2009; Krebs *et al.* 2011). CMR estimates are sensitive to the way the boundary strip around the array area is calculated. In our case, for example, using the average maximum distance between detections pooled over individuals (*W*), instead of the nearest-neighbour distance between traps (nTD), would have led to an increase of 20–30% in the population density (Table 1). Finally, MacLulich (1951, in Seber 2002, p. 51) suggested a method for the simultaneous estimation of population density and animal home range, providing the trap arrays are large enough to catch most of the animals whose ranges overlap the trapping area. Boundary strip is then assumed to be half the mean diameter of the home range (Seber 2002, p. 51).

In a simulated study, Rees *et al.* (2011) found that CMR estimates depend on the number of occasions. Our results provided empirical support for these findings, although, in our study, the real density values were unknown; however, the most important change was between two and three occasions. Interestingly, SECR estimates, which consider spatial information of recapture, did not vary with the number of occasions and appeared to have a higher precision (Fig. 4). In agreement with Noss *et al.* (2012), we advise to include, when possible, the spatial information to avoid the potential biases resulting from the way the sampled area is measured. With the exception of the smallest islet, CMR estimates are generally lower than those provided by LT. It is possible that some animals, e.g. small animals, do not visit the traps and CMR methods result in a partial sampling of the population. At the moment, we are not able to verify this hypothesis; however, future research might focus in comparing estimates with removal sampling or in manipulating trap density, to further explore this point.

Buckley and Jetz (2007) reported that lizards on islands occur on average at a density of 1920 (±574) individuals ha^{-1}, with these values being over an order of magnitude higher than those on mainland. Pérez-Mellado *et al.* (2008) reported a great variation of LT densities of the Balearic lizard in 43 islets of the Balearic archipelago. These authors found that estimates ranged from 35 to 8000 individuals ha^{-1} (average density: 1500 lizards ha^{-1}, median density 700 individuals ha^{-1}), with no apparent relationship with islet characteristics. We found between 1500 and 2500 individuals ha^{-1}, which is within the same range of the estimates as previously reported (Pérez-Mellado *et al.* 2008) and in agreement with the average value found by Buckley and Jetz (2007).

Implications for sampling design

LT and capture–recapture methods have both pitfalls and payoffs that mostly depend on the realism of the assumptions made (for assumptions, see Introduction). LT methods provide a simple and economic way to estimate wild-population density. The fundamental implication for survey design is that density estimate can be obtained with only one session and animals do not need to be individually marked nor physically captured. However, we have shown that animal mobility and habitat structure might influence the accuracy of the detection processes and increase the arbitrary aspect of model adjustment (Figs 3, 4). Hence, it is recommended to stratify data per habitat to account for different detection functions. On top of a spatial variability, LT estimates appeared variable over time when compared with those from other methods. CMR methods need more sampling effort than does LT, but have the advantage of collecting individual-based information, to investigate, for example, movement patterns. Overall, CMR methods appeared to better satisfy model assumptions when sampling a small camouflaged, elusive animal in medium to high vegetation. LT estimates from the 5-day survey showed variations within habitat (Fig. 3) and among occasions (Fig. 4), but with no particular association with the number of sampling occasions. Density estimates with conventional CMR models were affected by the number of occasions (see also Rees *et al.* 2011), whereas those derived by spatially explicit models (SECR; Efford 2004) were not.

Acknowledgements

We are grateful to Camilla Aviaaja Enoksen for her help during the field campaign and to Murray Efford for his help in fitting SECR models. We also thank two anonymous referees for the constructive criticism to the first draft of this manuscript. We thank IB-port, Excursion Boat and Lucia Bonnet for the logistic support. JRdI was supported by a 'J. Benedí' fellowship (IMEDEA – CSIC/UIB). The project was founded by the Spanish Minister for Science and Innovation (BFU2009-09359). Permission to handle the animals was agreed by the Conselleria d Agricultura, Medi Ambient i Territori of the Government of Balearic Islands, n.5906-06/2012. Funds were partially provided by the Regional Government of Balearic Islands and FEDER funding.

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