Estimating density of terrestrial reptiles in forest habitats: The importance of considering availability in distance sampling protocols

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A B S T R A C T

Reptile populations are relevant components of biodiversity in both temperate and tropical forests. However, in forest habitats reptiles are secretive and the complex structure of the environment makes it difficult to assess with confidence their abundance and density. In general, capture-mark-recapture (CMR) or distance sampling (DS) are used to estimate demographic parameters of reptiles in these complex habitats. CMR may be expensive in terms of time, materials and sampling effort, while DS is strongly biased when animals lying on the transect line are overlooked. In this study, we applied a combination of CMR and hierarchical distance sampling (HDS) to estimate the density of the Common Wall Lizard (*Podarcis muralis*), a widespread Mediterranean terrestrial reptile. We randomly placed linear transects in a deciduous woodland (i.e. *Castanea sativa*), in a coniferous plantation forest (*Pinus nigra*) and in a dry prairie habitat, and we applied a hierarchical mark-recapture distance sampling (HMRDS) protocol. Density estimates were similar between the deciduous woodland (47 individuals/ha) and the dry prairie habitat (44 individuals/ha), while markedly lower in the coniferous plantation forest (13 individuals/ha). HMRDS data, analyzed in a Bayesian framework, showed the importance of correcting for the assumption of complete detection on the transect line, in all the three habitat types. Therefore, our approach should be useful when assessing the density of small and cryptic terrestrial animals, not only in forest but also in habitat with an apparently less complex vegetation structure.

1. Introduction

Forest ecosystems are being altered by both direct anthropogenic activities, such as deforestation, fragmentation and unregulated exploitation (*e.g.*, Carlson and Groot, 1997; Williams et al., 2007; Riffel et al., 2011), and indirect ones such as climate change and introduction of invasive species (*e.g.*, Simberloff et al., 2013; Wardle and Peltzer, 2017). Biological communities living in forests, if exposed to these alterations may experience variations in distribution, dynamics and composition of their constitutive populations, that sometimes undergo local collapse or even global extinction (Alroy, 2017). Therefore, adequate monitoring protocols, capable of identifying significant spatio-temporal changes in demography and dynamics are required (Lindenmayer and Likens, 2009). However, in the case of forest animals, not all individuals present in the environment can be detected or captured, due to both their peculiar biological features and to the structural complexity of the habitat. Indeed, in most cases detection or capture probability (p) may vary among species, among habitats and over time, even within the same population (Williams et al. 2002;

Schmidt, 2003). In these cases, incomplete detection (*i.e., $p < 1$*) yields biased estimates of occupancy, abundance and dynamic patterns, derived from uncorrected counts of the species of interest. Therefore, simple counts may hinder appropriate comparisons among different species and, within the same species, among populations sampled in different habitats, under different management policies, or over different time periods (*e.g.*, Beissinger et al., 2016; Basile et al., 2017; Costa et al., 2019; Costa et al., 2020). This is particularly the case for small terrestrial vertebrates, such as amphibians and reptiles, that are found on the forest floor or in the canopy of tropical and temperate forest ecosystems, all over the world. These animals, worldwide endangered (Gibbons et al., 2000; Stuart et al., 2004), are usually small and cryptic, characterized by secretive behaviors and low detection probabilities, and they remain inactive under shelters or burrows for long periods, even when microclimatic conditions are favorable (McDiarmid et al., 2012; Griffiths et al. 2015; Zipkin et al., 2020). Therefore, they are difficult to be monitored, especially in highly structured and complex ecosystems such as forests and woodlands (Rodda and Campbell, 2002; McDiarmid et al., 2012).

Lizards, in particular, are widely found in forest ecosystems all over the globe. In tropical and temperate forests, these reptiles are found on the floor, stumps, branches, in the foliage and within the canopy (Whiting and Fox, 2021). To estimate their abundance and to assess population trends, several methods that account for imperfect detection have been used, such as capture-mark-recapture (CMR), repeated counts (*i.e.* N-mixture modeling), and total removal and distance sampling (Erdelen, 1988; Rodda and Campbell, 2002; Zipkin et al., 2020). Repeated count data, usually analyzed by means of binomial N-mixture models (Royle, 2004), do not require capture, handling and marking, and are probably among the most cost-effective methods for estimating population size (Costa et al., 2016; Ficetola et al., 2018; Kéry and Royle, 2016; Romano et al., 2017). However, the reliability and effectiveness of binomial N-mixture models have been recently disputed when their parametric assumptions are not completely satisfied (Barker et al., 2018; Knape et al., 2018; Link et al., 2018). In any cases, one of the main downsides of binomial N-mixture modeling is the need for temporal replication, which implies several visits on many sampling sites within a season, in order to correctly estimate detection probability. Conversely, multinomial N-mixture models, relying on individual encounter histories, can be seen as a hierarchical variant of CMR models and may overcome the problem of temporal replication (Kéry and Royle, 2016). The reliability of multinomial N-mixture models has been evaluated for forest birds (Kéry, 2018; Botsch et al., 2020) and, also, for terrestrial salamanders in forest ecosystems through the application of multiple observer protocols (Costa et al., 2020; Romano et al., 2021).

Another cost-effective method widely employed for overcoming problems of imperfect detection is distance sampling (DS). This method consists in estimating density and abundance of animals through the measurement of their distance from a transect line or from the center of a circular plot (Buckland et al., 2001; 2004). In the first case, perpendicular distances of detected animals from the transect line are recorded, while in the second the radial distances from the observer point are measured. In this framework, a key underlying concept is that the probability of detecting an animal decreases as a function of distance from the observer (Buckland et al., 2001; 2004). Moreover, conventional distance sampling (CDS) relies on some critical assumptions, above all: i) all animals on the transect line, at zero distance, are detected ($p_{(0)} = 1$; Buckland et al., 2001; 2004); ii) animals are randomly and evenly distributed throughout the surveyed area, i.e. there is no significant variation in abundance or distribution of individuals within and between transects (Buckland et al., 2001; Williams et al. 2002; Rodda and Campbell, 2002). Violation of these assumption may imply severe bias in the estimation of abundance and density (Smolensky and Fitgerald, 2010; Burt et al., 2014).

In this study, we estimated the density of a terrestrial lizard species, taking into consideration and addressing all previous assumptions and illustrating their possible drawbacks on the reliability of estimates. In fact, lizard density was estimated along randomly spaced linear transects, by applying a Hierarchical Mark-Recapture Distance Sampling (HMRDS) modeling framework. In our sampling protocol, two observers independently detected the animals before measuring distances from the transect line. This HMRDS technique was applied in two structurally-different forests and also in an open prairie habitat, to obtain information on the applicability of this protocol in clearly different vegetation settings.

2. Materials and methods

2.1. Study species

The focal species is the lacertid Common Wall Lizard *Podarcis muralis* (Laurenti, 1768). This species is diurnal with a total length of about 15-20 cm and found all over Italy from sea level to about 2000 m (Biaggini et al., 2011). The Wall Lizard dorsal coloration is variable and highly mimetic, showing different shades of grey, brown and olive green,

usually reticulated with black spots. At the study sites, *P. muralis* is sympatric with only another lacertid lizard, the Western Green Lizard *Lacerta bilineata* Daudin, 1802, which is much larger (up to 40 cm) and characterized by an emerald-green dorsal coloration (Venchi et al., 2011). Juveniles of this latter species clearly differ from Wall Lizards by showing a homogeneous dorsal brownish coloration, usually with two or four longitudinal white lines along the flanks.

2.2. Study sites

Three differently structured habitats were sampled, all in NW Italy (Liguria, province of Genova). The first (Pa; 44.49°N, 8.81°E) is an open prairie classified as a European dry heath on siliceous soil (Mariotti, 2008), dominated by ericaceous species with scattered rocks, shrubs and trees. This site is situated at about 900 m a.s.l. and is regularly grazed by livestock such as sheep, cows, horses and donkeys. The second habitat (Wa; 44.53°N, 8.98°E), is a sub-Mediterranean coppice forest dominated by the deciduous Sweet Chestnut *Castanea sativa* (Mill., 1768) at about 700 m a.s.l. The forest structure is relatively uniform, with similar-sized coppices sprouting from the same plate, a dense semi-natural undergrowth and sparse canopy gaps (Fig. 1). The third habitat (Wb; 44.41°N, 9.44°E) is a sub-Mediterranean conifer plantation forest, dominated by pines of the *Pinus nigra* J.F. Arnold group. This forest stand is situated at about 950 m a.s.l. and is characterized by relatively large canopy gaps and a sparse undergrowth of *Pteridium* sp. ferns and *Rubus* sp. shrubs (Fig. 1). In Pa we surveyed 60 transects, while in Wa and Wb 30 transects for each site were surveyed.

2.3. Field sampling

Sampling was conducted following a double observer Distance Sampling framework (e.g., Burt et al., 2014; Conn et al., 2012; Oedekoven et al., 2014) in June-July 2021, during the advanced breeding season, when adults display the highest activity peak (Biaggini et al., 2011). Two observers slowly walked side-by-side along linear transects 50-m long. In the same habitat type, all transects were walked in the same day during the morning (9-11) or in the afternoon (15-17), in order to avoid the warmer hours of the day. Transect measurements were taken by means of a laser Bushnell Rangefinder. If an obstacle was present on the transect (e.g., bush, tree or stump), both observers walked around it, without recording animals, and then continued along the selected direction. Usually, two transects starting from a same random point and with randomly divergent directions were simultaneously sampled by two teams of observers. Lizard detections were partitioned following a double independent observer protocol, and noted as "1","2" or "3", depending on whether the animal was spotted by the first (1), the second (2) or both observers (3), respectively (Costa et al., 2020). The perpendicular distance from the transect line of each detected lizard was measured by means of a metallic measuring tape to the nearest 10 cm. During our surveys we only observed adult individual lizards and did not record any group. Non-identified animals were never recorded.

2.4. Data analysis

Distance sampling data of lizards, associated with detection histories of the double independent observer protocol, were analyzed by means of a four-part hierarchical distance sampling model (Kéry and Royle, 2015), independently for each sampling site. This model allows to relax the $p_{(0)} = 1$ assumption by combining mark-recapture and distance sampling data in a temporary emigration model, thus partitioning the detection probability in two components: availability, i.e. the probability that an individual of the population is available for sampling, and conditional on being available, detection probability. For this purpose, encounter histories of the double observer protocol (*i.e.* "1", "2", "3") and distance data (divided in 10 distance classes) were treated as categorical variables at the observation level. Kéry and Royle's (2015) four-
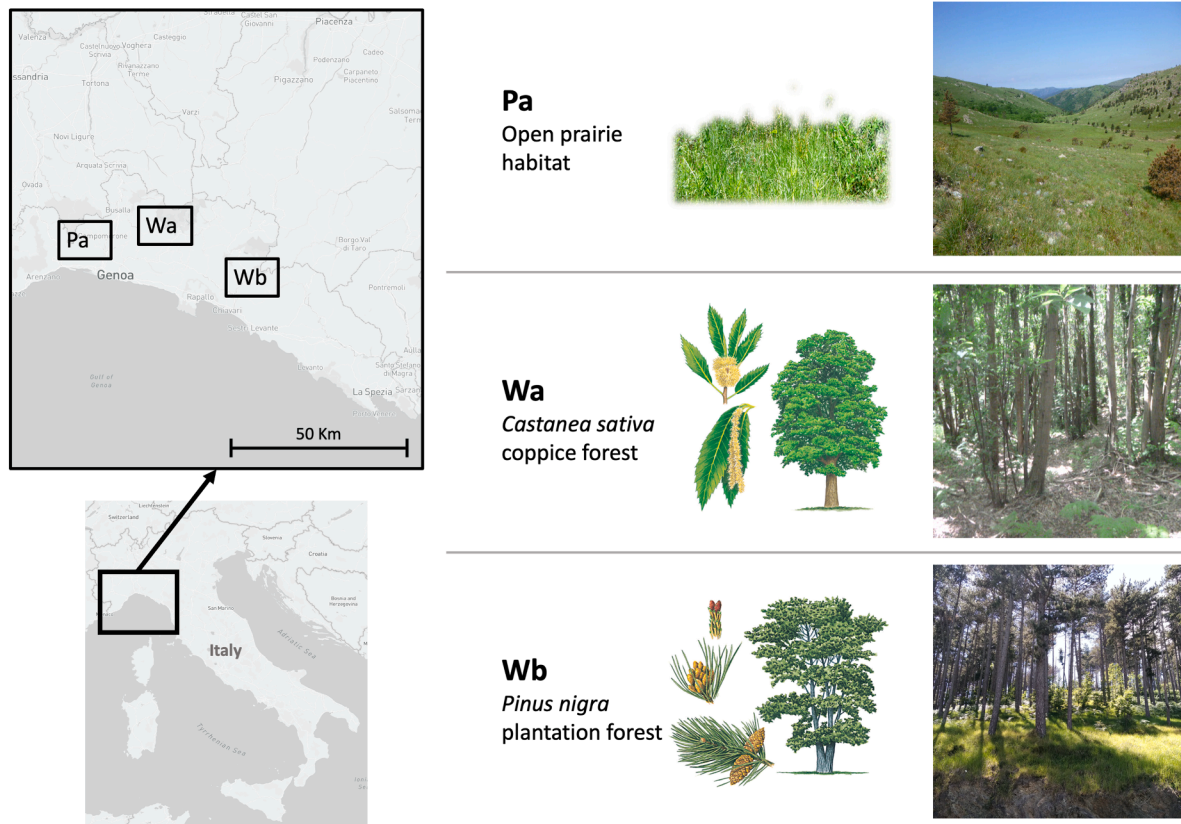
Fig. 1. Map with the location of the sampling sites in Northern Italy, and representative images of the study areas. Image partially adapted from Hammond et al. (2014).

part hierarchical distance sampling model (Supplementary Material 1) treat M_s, the population size at site s, as follows:

$$M_s \sim Poisson(\lambda_s)$$

with site specific mean abundance λ_s, and models availability using a random temporary emigration model with availability parameter ϕ, so that the number of available individuals on the transect is the outcome of a binomial process:

$$N_s \sim Binomial(M_s, \phi)$$

where N_s individuals are available to be detected by distance sampling and the availability parameter ϕ is the detection probability of the double observer sampling protocol. The observation process itself consists of:

i a binomial model for observed individuals n_s at site s, conditional on the number available to be detected, N_s:

$$n_s \sim Binomial(N_s, p_s)$$

where p_s is the probability of an individual being detected for site s;

i two component models for the distance classes and encounter histories, conditional on n_s, which are categorical variables with cell probabilities depending on a half-normal detection function and on the detection probability of the double observer protocol, respectively.

From the application of this model we obtained estimates of abundance for the available population (N_{tot}) exposed to distance sampling, when considering that $p_{(0)} = 1$, and for the whole population (M_{tot}) when considering that $p_{(0)} < 1$. We also obtained detection estimates of the double observer protocol (p_{avail}) and the distance sampling protocol (p_{det}). We estimated model parameters using a Bayesian approach with MCMC methods, using un-informative priors. We ran three chains, each one with 50,000 iterations, discarding the first 10,000 as a burn-in and thinning by 4. We considered that chains reached convergence when the Gelman-Rubin statistic (R-hat) was < 1.1 (Gelman and Rubin, 1992), and we considered that an effective sample size (ESS) of 400 was acceptable to obtain reliable estimates (Zitzmann and Hecht, 2019). Assessing model fit in hierarchical models is of primary importance in order to avoid assumption violations and severe bias in estimates (Duarte et al., 2018; Knape et al., 2018; Costa et al, 2021). For this purpose, we employed posterior predictive checks based on χ^2 statistics as a measure of the discrepancy between observed and simulated data, both for the availability and the detection models, and calculated a Bayesian p-value accordingly (Kéry and Schaub, 2011). Analyses were conducted calling program JAGS (V4.3.0; Plummer, 2003) from the R environment (R Core Team, 2020) with package "JagsUI" (V1.5.1; Kellner, 2015).

3. Results

During sampling we detected a total of 81 lizards: in particular, 40 were detected in Pa, 28 were detected in Wa, and 12 in Wb. The maximum perpendicular distance recorded from the transect line was 5.2 m in Pa, 4.5 m in Wa, and 6.1 m in Wb. Posterior predictive checks and Bayesian p-values, for both availability and detection sub-models, highlighted a very good fit for all sampling sites (Supplementary Material 2). Convergence, as revealed by the R-hat value, was successful for all parameters monitored. The complete list of monitored parameters considered in the present analysis, with 90% Credible Intervals (CRI), is

reported in Table 1 and summarized in Fig. 2. For what concerns the availability parameter, in Pa we estimated the lowest value of $p_{avail} = 0.64$ (0.46 – 0.79; 90% CRI), in Wa we estimated the intermediate value of $p_{avail} = 0.69$ (0.48 – 0.85; 90% CRI), while in Wb we estimated the highest availability parameter $p_{avail} = 0.83$ (0.59 – 0.97; 90% CRI). At the same time, detection probability of the DS protocol was lower in Pa ($p_{det} = 0.46$; 0.38 – 0.56; 90% CRI) when compared to Wa ($p_{det} = 0.76$; 0.49 – 0.98; 90% CRI) and Wb ($p_{det} = 0.74$; 0.40 – 0.99; 90% CRI). For what concerns abundance and density estimates, although CRI are partially overlapping, in Pa we obtained an estimate, for the available population, of 88 individuals (N_{tot}; 65 – 115; 90% CRI), while the total population estimate was $M_{tot} = 142$ individuals (92 – 212; 90% CRI), yielding a density estimate of 47 individuals/ha (30 – 68; 90% CRI). In Wa, the available population estimate was $N_{tot} = 39$ (28 – 60; 90% CRI), while the total population estimate was $M_{tot} = 60$ (34 – 99; 90% CRI), resulting in a density estimate of 44 individuals/ha (25 – 73; 90% CRI). Finally, in Wb we estimated an available population of 19 individuals (N_{tot}; 13 – 35; 90% CRI), and a total population of 24 individuals (M_{tot}; 13 – 45; 90% CRI), with a density of 13 individuals/ha (7 – 25; 90% CRI).

4. Discussion

By applying this protocol to lizard sampling, the main finding of our study highlights that, for small secretive vertebrates, the first assumption of DS (i.e. of certain detection on the transect line) is always violated, with the estimated availability parameter (p_{avail}) which is always < 1. Indeed, not only the inactive portion of the population gets missed by the observers, but also a fraction of the active one. Moreover, contrary to our expectations, in the apparently most simplified habitat, i. e. the open prairie (Pa), the availability bias was most severe than in forest habitats. However, in open prairies and in hedge habitats, given the reduced vegetation cover, reptiles are susceptible to a greater predation risk than in forested areas (Wilgers and Horne, 2007; Hansen et al., 2017) and tend to be more careful and discrete. Furthermore, they are more exposed to sunlight in open environments than in forest ones, which may affect their thermoregulatory activity in different ways, depending on the season on which sampling occurs, and in turn it may yield to a consequent reduction of lizards' activity, and thus to a lower availability, on open areas.

The violation of the first assumption of DS, $p_{(0)} = 1$, typically arises when individuals lying on the transect line are missed. This usually occurs when the habitat is structurally complex and individuals are small or cryptic, or they are temporary unavailable, e.g. animals are hiding underground or under some kind of shelter during the survey. The former situation is known as 'perception bias', while the latter is

known as 'availability bias' (Buckland et al., 2015), and both yield to a negative bias in abundance and density estimates. For what concerns reptile density estimation with DS methods, both De Infante Anton (2013), Couturier et al. (2013) and Ariefiandy et al. (2014) observed that DS estimates are usually lower and highly biased in comparison to other reference methods (e.g. CMR) in small or medium-sized Lizards, very large lizards such as Komodo dragons and tortoises, respectively, highlighting this behavior as a common trait of departure from the first assumption of DS. In particular, Couturier et al. (2013) directly observed, by means of radiotelemetry data, that availability of individual tortoises was responsible of the observed bias in DS density estimates.

Regardless of whether animals at distance zero are missed because of 'availability' or 'perception', sampling protocols and analytical methods have been developed to collect additional data in order to obtain robust abundance estimates while relaxing the $p_{(0)} = 1$ assumption. Typically, this is done by the implementation of mark-recapture protocols within a distance sampling survey, leading to the so-called mark-recapture distance sampling protocols (MRDS; Laake and Borchers 2004; Borchers et al. 2006). Mark-recapture sampling is implemented within DS in different ways, by the use of a double observer protocol (Burt et al., 2014), or by the use of a time removal sampling (e.g. Amundson et al., 2014). Including a mark-recapture sampling design in DS, allows to estimate the proportion of individuals undetected at zero distance (i.e. $p_{(0)}$), but active, and therefore to correct for both 'availability' and 'perception' bias (Amundson et al., 2014; Burt et al., 2014; Martin et al., 2015).

Concerning the second assumption of DS (i.e. of random and even distribution of individuals on the study area) it both ensures: i) that individual to transect distances are random and therefore allow the distance to the observed individual to be used to estimate detection probability; ii) that no local spatial variation in abundance and density occurs, thus allowing the estimated density for the sampled area to be representative of the whole study area (Buckland et al., 2001; Buckland et al., 2004; Buckland et al., 2015). Violations of this assumption usually arise when transects are not randomly placed, but instead are associated to topographic features such as trails or paths (Shirk et al. 2014; Chergui et al., 2019; De Andrade et al., 2019; Abrahão et al., 2021), ecotones or habitat patches (Rodriguez Caro et al., 2017), light gaps or clearings (Havery et al., 2018). Selecting these landscape features is a common practice in both ecological and conservation studies, because they are usually more cost effective to sample (Rodda and Cambell, 2002). However, microhabitat conditions near paths or trails often differ from those within the forest and may alter the distribution and behavior of reptiles (Rodda and Campbell, 2002; Lovich et al., 2012). For what concerns the assumption of random distribution and homogeneity of animals, this can be relaxed by implementing a model for local abundance: *i.e.* the case of hierarchical-distance-sampling (HDS, Royle et al. 2004; Royle and Dorazio, 2008). In this context, the reliability of our estimates is ensured by two factors: i) we randomly selected transects which were a real representation of the habitats, since we avoided topographic features, ii) we stratified data analysis per habitat, in order to account for different detection functions, since animal mobility and habitat structure might influence the accuracy of the detection processes and increase the arbitrary aspect of model adjustment (De Infante Anton et al., 2013). By applying this protocol, in our study, we observed that lizard density in coniferous plantation (Wb) is lower than in hardwood forests (Wa). It has been observed that coniferous plantations, in the Mediterranean region, show reduced abundances, diversity and species richness of the communities living therein, with respect to natural or hardwood plantations (Da Silva et al., 2019), and are also considered as low-quality habitats for reptiles (Ioannidis et al., 2008; Chergui et al. 2019). These formations are non-natural and constitute a structurally simplified forest habitat, with reduced soil moisture, less leaf litter and fewer dead wood structures, which could make this habitat less suitable for reptiles than a more natural deciduous woodland (Friend, 1980; Da

Table 1

Four-part hierarchical distance sampling model parameters' estimates for each sampling site. For model and parameter description see Materials and Methods section.

| Site	Parameter	Estimate	90% CRI	R-hat	ESS
Pa - Open prairie habitat	p_{avail}	0.64	0.46 – 0.79	1.000	12511
	p_{det}	0.46	0.38 – 0.56	1.001	2428
	M_{tot}	142	92 – 212	1.005	1072
	N_{tot}	88	65 – 115	1.002	1336
	Density	46	30 – 68	1.002	1072
Wa - *Castanea sativa* coppice forest	p_{avail}	0.69	0.48 – 0.85	1.000	26337
	p_{det}	0.76	0.49 – 0.98	1.005	427
	M_{tot}	60	34 – 99	1.002	1035
	N_{tot}	39	28 – 60	1.003	589
	Density	44	25 – 73	1.002	1035
Wb - *Pinus nigra* forest	p_{avail}	0.83	0.59 – 0.97	1.000	19332
	p_{det}	0.74	0.40 – 0.99	1.002	1316
	M_{tot}	24	13 – 45	1.001	30000
	N_{tot}	19	13 – 35	1.001	5582
	Density	13	7 – 25	1.001	30000
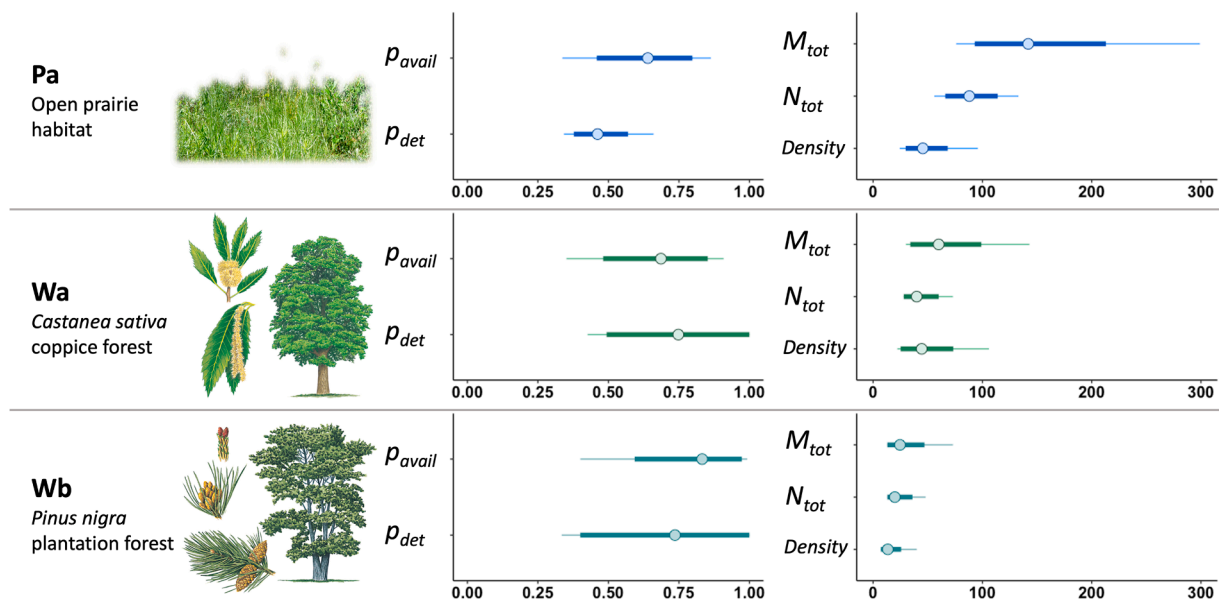
Fig. 2. Plot representing mean estimates (points), 90% CRI (thick lines) and posterior distribution (thin lines) of availability (p_{avail}), detection (p_{det}), total population abundance (M_{tot}), available population abundance (N_{tot}) and density, estimated with the four-part hierarchical distance sampling model for each study area. Image partially adapted from Hammond et al. (2014).

Silva et al., 2019).

5. Conclusions

Distance Sampling is an established method, applied in a multitude of environments, to obtain density estimates on a wide variety of applications, from small birds to large mammals populations, and even for deadwood and vascular plants in forest inventories (Buckland et al., 2001; Kissa and Sheil, 2012; Ritter and Saborowski, 2014). Despite its extensive use and acknowledged reliability, for some specific applications, *i.e.* the case of small vertebrates in complex habitats, density estimates obtained with DS can be severely biased if model assumptions are overlooked (Smolensky and Fitgerald, 2010; Burt et al., 2014). Assuming certain detection of individuals on the transect line may yield to biased estimates of abundance and density on terrestrial reptiles, as already observed in other studies (Smolensky and Fitzgerald, 2010; De Infante Anton et al., 2013; Couturier et al., 2013; Ariefiandy et al., 2014). However, this problem can be easily identified and addressed by applying a double observer Distance Sampling method, and analyzing data within a framework accounting for incomplete detection on the transect line. Therefore, despite several studies gave rise to concerns about the reliability of DS method, at least for secretive vertebrates in complex environments, we suggest that DS is a reliable tool for studying populations and communities of terrestrial reptiles inhabiting forest environments, provided that model assumptions get verified or relaxed by the application of specific sampling protocols.

CRediT: authorship contribution statement

Giacomo Rosa: Conceptualization, Fieldwork, Writing – Original Draft Preparation; **Sebastiano Salvidio:** Conceptualization, Fieldwork, Writing – Review and Editing; **Enea Trombini:** Fieldwork, Writing – Review and Editing; **Andrea Costa:** Conceptualization, Fieldwork, Data Analysis, Writing - Review and Editing.

Funding

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2021.100184.

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