# Measuring bird abundance - A comparison of methodologies between capture/recapture and audio-visual surveys

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Abstract – Research on species-habitat relationship implies that a specific parameter related to the species, such as abundance, has to be measured and compared to environmental features. Different methods have been implemented in the collection of abundance data on birds and different statistical techniques have been developed to deal with the great diversity of data collection. The aim of this study is to compare different sampling methods and statistical techniques currently used to estimate abundance, employing them in a dense forest environment: capture-mark-recapture vs. point counts. Short-toed treecreepers *Certhia brachydactyla* were captured through mist-netting and surveyed through song count. Capture data were analysed using a classical approach and a spatially-explicit approach (SECR), while count data were analysed with N-mixture models. Results show that classical capture analyses yield a lower abundance, while SECR and N-mixture models give similar and higher estimates. An optimization of the sampling design for studies regarding birds' abundance and species-habitat relationship should consider the use of point counts for song/visual detection of individual birds while fitting N-mixture models for abundance estimation.

Key-words: ringing, treecreeper, point counts, deciduous woodland, forest-dwelling passerine.

### INTRODUCTION

The conservation and management of ecosystems require the knowledge of animal population size and their relationships with the surrounding environment. How animals respond to habitat changes is an important issue to address in order to face eventual habitat alteration or disturbance. However, not all animal species' responses are easily assessed, due to differences in their life history and ecological traits. Birds have been often proved to be a reliable *taxon* to explore species-habitat relationship, due to their high susceptibility to ecosystem changes and alterations (Schwenk *et al.* 2012, Zhang & Wang 2012), their short-time response to disturbance (Baker & Lacki 1997, Schmiegelow *et al.* 1997) and their ease to be counted (Bibby *et al.* 2000). When the target is the population or the community, individuals need to be counted and eventually the population abundance estimated, except for presence/absence surveys.

Different methods have been implemented to collect data on birds' abundance and distribution (Bibby *et al.* 2000, Sutherland 2006) and different statistical techniques have been developed to deal with the great diversity of data collection (e.g., Otis *et al.* 1978, Dorazio & Royle 2003, Efford 2004, Royle 2004a). If the dependent variable of interest is abundance, birds should be correctly counted and every potential source of bias avoided (e.g. double counts). There are two main kinds of methods to sample birds, based on whether individuals are captured or not. Capture-mark-recapture (CMR) methods are largely used by ornithologists, even if mostly for the study of migration or for estimating demographic change in survival rates than for abundance estimation (Nichols *et al.* 1981, Bibby *et al.* 2000, Spina & Volponi 2008). CMR methods rely mostly on netting to capture and individually mark birds which are unlikely to be distinguished otherwise (i.e. cryptic species or identical phenotype in both sexes) (Sutherland 2006). Although researchers have often used abundance indexes (e.g. hourly capture rate) (Machtans *et al.* 1996, Dunn & Ralph 2002, Ellis & Betts 2011) instead of abundance estimates, statistical techniques to estimate abundance are well-known (Nichols *et al.* 1981) though the effective trapping area is usually unknown and need to be estimated as well (White *et al.* 1982, Jett & Nichols 1987). Progress on this issue has been made in recent years with the development of a spatially-explicit capturerecapture (SECR) method for density estimation (Efford 2004).

On the other side there are methods that do not require capture but rely on acoustic/visual counts. Among these, the point count technique is one of the most used (Blondel *et al.* 1981). However, the possibility to obtain population estimates by means of point counts was developed (Buckland *et al.* 2001, Royle & Nichols 2003), as the previous studies were based mostly on abundance indexes that could eventually overestimate rare species and underestimate common species (Bibby *et al.* 2000). In particular, the development of N-mixture models to estimate the abundance and the detectability from counts has been proved useful and easily applicable (Royle 2004b).

The aim of the present study is to compare different sampling methods currently used to obtain abundance estimates: CMR vs point counts. We aim at assessing which method returns the best trade-off between ease of application in the field and precision of the estimates, as well as the ability to detect species-habitat relationship. Considering that the CMR approach is more expensive in both time and energy invested in, we investigate if CMR can add any value to normal observer-based survey techniques.

# MATERIALS AND METHODS

#### Study area

The 32 ha study area is located within the Bosco Pennataro Regional Forest (Molise Region, Italy, 41°44'N, 14°11'E), the elevation of the studied patch is around 1,000 m a.s.l. Mean annual temperature is 8.6 °C and rainfall averages 1,100 mm/year. Woodland consisted mainly of a continuous and high-growth Turkey Oak (*Quercus cerris*) mature stand, mixed with other deciduous species (mainly *Acer* sp., *Fagus sylvatica*, *Sorbus* sp. and *Carpinus betulus*). Average basal area was 41 m<sup>2</sup> ha<sup>-1</sup>, and mean diameter at breast height (dbh) was 16.5 cm, while mean dbh of the dominant tree layer was 43 cm (Di Salvatore *et al.* 2016).

#### Target species

The Short-toed Treecreeper *Certhia brachydactyla* Brehm, 1820 (hereafter treecreeper) was selected as target species due to its close link with forest characteristics and small home range size (ranging from 0.4 ha in Germany to 26 ha in Maritime Alps, but on average 4-5 ha), fitting the extent of the study area (Cramp 1988, Fornasari *et al.* 2010, Brichetti & Fracasso 2011). The treecreeper is a monotypic species that does not show sexual dimorphism and males sing constantly during the breeding season (spring-summer), especially early in the morning (Brichetti & Fracasso 2011). Adult males are recognizable in the hand during the breeding season due to cloacal protrusion (Svensson 1992).

#### Sampling

We located 24 capture sites following a systematic design (Fig. 1). Distance between netting sites ranged from 92 to 127 m (mean = 111.8). Each trap consisted of three mist nets (length = 6 m; height = 2.4 m; mesh = 60 mm) arranged to form a net triangle around a tree, at the base of which a playback device was placed as an acoustic lure to attract and capture treecreepers (Fig. 2). The playback was activated at sunrise and was switched off after four hours. Nets were patrolled constantly. Activation consisted on the opening of the mist-nets while turning on the playback. The playback was inaudible to humans farther than 60-70 m and only the bird (rarely more than one) that had its own territory near the trap was quickly attracted by the playback, as tested in a pilot sampling session (Basile et al. 2015). We captured treecreepers from April to May 2013 during 6 capture sessions. Each session consisted of three days, during which only 8 randomly selected traps per day were activated, to avoid adjacent traps operating at the same time. Indeed, every trap was sampled within three consecutive days/sessions, so that the whole area was sampled in a short period. Every captured individual was marked with a standard metal ring with a unique alphanumeric code, provided by the National Institute for the Environmental Research and Protection (ISPRA). Ringing operations were conducted by an authorized bird ringer (RB).

Acoustic surveys (unlimited radius) were conducted at 27 points, of which 24 overlapped with the trapping sites. Each point was surveyed 3–6 times (mean = 4.5; total = 123) in 2013, from May to late-June, later than the capture field work. Surveys lasted 5'/point and were carried out from sunrise to 11 a.m. Only males were taken into consideration during the two sampling methods (i.e. capture and point counts).

Forest structure was sampled for each of the 27 sites within 3 circular plots (572 m<sup>2</sup>/plot, clustered sampling de-



Figure 1. Bosco Pennataro Regional Forest satellite view with sampling location. Black triangle = netting site; white circle = point count site.



Figure 2. Mist-net disposal; at the base of the tree an acoustic playback is placed and the tree is surrounded by three nets. A close-up of the panel warning hikers of ongoing activity.

sign) placed at the vertices of a triangle whose centre overlapped with the treecreeper's sampling point; for the sampling methods we followed the National Forest Inventory approach (Tabacchi *et al.* 2006). We measured and classified (diameter at breast height, tree height, species and development stage) trees with diameter  $\geq 2.5$  cm. We derived nine variables, commonly used in forest-wildlife studies: tree density (Dha) and its standard deviation (Dds), basal area/ha (Gha), mean basal area diameter (dg), maximum diameter (dmax), mean height (Hm) and its standard deviation (HmDS), stem volume/ha (Vha) and tree species diversity (Shannon's H') (Tabacchi *et al.* 2011). Similarity among sites has been estimated by Morisita indexed analyses of similarity (Morisita 1962, Clarke 1993).

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#### Statistical analyses

The capture history was first tested for closure using two tests (Otis *et al.* 1978, Stanley & Burnham 1999). Consequently, abundance was estimated by means of two statistical techniques. A model for closed population with heterogeneity in capture probability among occasions was implemented using the software CARE-2 V. I.5 (Otis *et al.* 1978, Chao & Yang 2003). Then, SECR models were built taking into consideration the individual's capture history as a Poisson point process and the captures as a multi-catch system. The full likelihood and an iterative procedure for model selection were employed (Borchers & Efford 2008). Simple models were first tested to select the best distribution of capture probability, between half-normal (eq. 1) and exponential (eq. 2):

1) 
$$g(d) = g_0 \exp\left(\frac{-d^2}{2\sigma^2}\right)$$

2) 
$$g(d) = g_0 \exp\left(\frac{-d}{\sigma}\right)$$

where g is the capture probability,  $\sigma$  is the spatial process (*i.e.* how the probability change in space) of the captures and d is the distance of the trap from the home range centre. Then, different types of response in capture probability, *i.e.* behavioural (individuals can learn to avoid the trap) or temporal (individual's response change among occasions), were assessed. Finally, one forest covariate per time was added to the best model, as response variable of the abundance, and the model run. Model selection by means of AIC score (Akaike 1973) was applied at each step, taking into account that  $\Delta$ AIC  $\leq$  2 could mean that models may have the same empirical support and that small sample need to be selected through AICc (Burnham & Anderson 2002). SECR analysis was carried out using the R package secr v. 2.9.3 (Efford 2015).

Point counts were analysed by means of N-mixture models (Royle 2004b). Average counts per site were first tested for spatial correlation through a Moran test (Moran 1950). Three distributions were tested to model the latent abundance N at site i: Poisson, zero-inflated Poisson and negative binomial. Counts y at site i during the occasion j were assumed as binomials, as follows:

# $y_{ii} \sim Binomial(Ni; p_{ii})$

A Pearson  $\chi^2$  goodness of fit test (1000 bootstrap resampling) was used to select among the three models. Then, an eventual temporal response in the detectability was assessed. Finally, forest covariates were added to the models. Model selection was applied at each step using the AIC score, following the same rule of thumb as for SECR

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modelling (Burnham & Anderson 2002). The R packages unmarked v. 0.10-4 and AICmodavg v. 2.0-3 have been used for these analyses (Fiske & Chandler 2011, Mazerolle 2015).

#### RESULTS

During the trapping occasions, fifteen adult males were captured. Three of them were recaptured once and two were recaptured twice, for a total of 22 captures, with an average capture rate per occasion of 1.2 captures (range: 0-7). Fourteen out of the 24 mist-netting sites attracted and captured the treecreeper. Most of the recaptured treecreepers were re-caught in the same mist-netting site they were captured the first time, except 2 birds, caught 172 m and 117 m away, respectively.

Point counts yielded 61 records in 24 out of the 27 points, ranging from 0 to 2 detections per point (average = 0.5). Considering all surveys, instead, there were an average of 2.3 records/point (range = 0.6).

Forest structure was quite homogeneous among sites, with a mean Morisita value of  $0.93 (\pm 0.09 \text{ SD})$ .

The assumption of closed population has been confirmed by the two tests (z = -0.05, p = 0.48;  $\chi^2$  = 6.88, df = 8, p = 0.55). The population size of males was 23.7 (± 10.99 SE) individuals, according to the model M<sub>t</sub> (Tab. 1). SECR model selection resulted in one empirically supported model ( $\Delta$ AICc < 2) (Tab. 2), which estimated a population of 31.5 (± 10.5 SE) males and a density of 0.72 (± 0.27 SE) males/ha (Tab. 1). Forest variables had no significant effect on the abundance. Capture probability (g<sub>0</sub>) estimate was 0.66 (± 0.23 SE).

Average counts showed low spatial correlation (Moran I = 0.23; p = 0.02). The distribution that best fitted point count data was the Poisson, even if data appeared underdispersed (c-hat < 1) (Tab. 3). Model selection showed that detectability did not change among sampling occasions. The best model returned the abundance constrained to any forest variable. The population size of males was estimated at 41.6 (CI<sub>95%</sub> = 25 - 89), and the abundance per site (N<sub>i</sub>) was 1.54 ( $\pm$  0.52 SE) (Tab. 1). Detectability was 0.34 ( $\pm$  0.11 SE).

#### DISCUSSION

The need of unbiased data for conservation and management is an issue that most researchers are worried about (e.g. Romesburg *et al.* 1981, Eberhardt & Thomas 1991, Anderson 2001). However, determining which survey and

**Table 1**. Estimates from capture-recapture ( $M_t$  and SECR) and point counts (N-mixture model) data. Standard error and 95% confidence interval in brackets.  $M_t$  = close population model with heterogeneity in capture probability;  $\beta$  = linear predictor of the true abundance or untransformed estimate of abundance; D = individual/ha;  $N_t$  = local abundance.

Model	β	D	N <sub>i</sub>	Population size
Mt	-	-	-	23.7 (16.27 – 70.07)
SECR	-0.34 (0.37)	0.72 (0.27)	-	31.5 (20.2 - 66.7)
N-mixture model	0.43 (0.34)	-	1.54 (0.52)	41.6 (25 - 89)

**Table 2**. SECR model selection. Best model is in bold. Models with covariate variability in abundance did not have empirical support and were not included in table. g = capture probability; (.) = null covariate; (T) = time response; (B) = behavioural response.

Model	Distribution	AICc	ΔAICc
g(.)	half-normal	168.2	8.8
g(.)	exponential	164.9	5.4
g(T)	exponential	159.4	0
g(B)	exponential	168.4	8.9

**Table 3**. Results of the goodness of fit test on the three N-mixture models built with different distribution. P = Poisson; ZIP = zero-inflated Poisson; NB = negative binomial; <sup>2</sup> = Pearson's test statistic; c-hat = over-dispersion parameter.

Distribution	χ <sup>2</sup>	p value	c-hat	AIC
P	64.3	0.997	0.687	171.7
ZIP	64.4	0.995	0.679	173.7
NB	64.4	0.996	0.306	173.7

analysis method is best is challenging under field conditions, when the true number of animals in a population is unknown. One of the main sources of bias in abundance estimates concerns the unclear boundaries of the study area (Efford & Fewster 2013). Especially if sampling is carried out in a limited area, the surroundings can affect the estimated parameters. The use of spatially explicit capturerecapture methods reduce this source of bias (Chandler et al. 2011, Efford & Fewster 2013). SECR method was tested mostly on reptiles and mammals, when it is feasible to capture many individuals in a relatively small area or it is possible to use more efficient detectors, like hair traps (Obbard et al. 2010, Marsot et al. 2013, Ruiz de Infante Anton et al. 2013, Efford & Fewster 2013, du Preez et al. 2014). In this research, instead, an ad hoc sampling design was necessary to circumvent the logistical difficulties, increasing for capturing in a wide area. Our results are similar to those published, in which the classic approach (e.g. Otis et al. 1978) may return biased estimates, depending on the area considered (Efford & Fewster 2013). But in our case, estimates lack in precision, and confidence intervals are largely overlapped. However, it has to be said that the small captures dataset add some uncertainty to the estimates. The Short-toed Treecreeper, like many other forest dwelling passerines, inhabits places where traps are difficult to manage. Hence, obtaining robust estimates is problematic. Our results highlight these difficulties, as 18 capture occasions returned only 15 individuals. However, our aim was to compare methods, not population size estimates, and, in these circumstances, both methods gave similar results, while the point counts needed much less effort.

Density estimate of 0.72 males per hectare is higher than previous density estimates for the Italian peninsula (Brichetti & Fracasso 2011). This discrepancy can be caused by: (i) published densities concerning studies carried out over very wide areas (usually from 10 ha to 1 km<sup>2</sup>), where sampling points are consequently very sparse, where the Short-toed Treecreeper, being a territorial species (Cramp 1988, Brichetti & Fracasso 2011), can be actually underestimated, considering that one sampling point can intercept more than one territory; (ii) previous estimates do not consider the problem of incorrect detection and false negatives, that usually lead to underesti-

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mates (Kéry et al. 2005). Indeed, our estimate can be more conceivable, due to the territoriality and the limited movements of the Short-toed Treecreeper, mainly during the breeding season, as well as, considering that a treecreeper territory can be even smaller than 1 hectare (Smith & Shugart 1987, Cramp 1988, Pasinelli 2000, Brambilla & Ficetola 2012). Since counts did not show strong spatial correlation, N-mixture models were not implemented in a spatially explicit way. Nonetheless, estimates resulted similar to those of SECR. Previous comparisons of N-mixture with capture-recapture statistical techniques are scattered. In Couturier et al. (2013) the N-mixture models underestimated the population compared to the classical M<sub>o</sub> of Otis et al. (1978). However, their study on Hermann's Tortoise Testudo hermanni was peculiar due to the use of 5 ha areas instead of points and the limited number of replicas, that can alter the estimates (Kéry et al. 2005). On the contrary, in other studies researchers obtained a good performance although they used open population N-mixture models (Dail & Madsen 2010, Zipkin et al. 2014).

Species-habitat relationship did not emerge, probably due to the homogeneity of the forest structure across the study site, suggesting a lack of explanatory power at least for the accounted variables at the scale of our study area. N-mixture model indicated that forest structure may have a role in influencing abundance, considering that model selection included models with abundance covariates, but this variation was not considered significant.

Most resource managers are seeking the 'perfect' manner in which to estimate animal abundance. Our results may indicate that in specific habitat type, like dense forest, captures can be avoided if the aim is to estimate population size. We used a typical forest species and also highlight the fact that our results may be applicable to many other species, such as the Eurasian Treecreeper C. familiaris, Nuthatch Sitta europaea or Lesser-spotted Woodpecker Dendrocopos minor, which heavily depend upon forest resources and mature forests as the Short-toed Treecreeper. However, depending on the information that researchers or professionists are seeking, the trade-off can be balanced towards a more onerous sampling to gain more precise estimates or not. We also remarked that these results are relevant for specialist and territorial birds, whose ecology and behaviour can account for little if any concern about spatial auto-correlation over small areas.

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## REFERENCES

- Akaike H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov B. N. & Cazakil F. (eds), Second Int Symp Inf Theory. Akademiai Kidao, Budapest, Hungary, pp 267–281.
- Anderson D.R., 2001. The need to get the basics right in wildlife field studies. Wildl. Soc. Bull. 29: 1294–1297.
- Baker M.D. & Lacki M.J., 1997. Short-term changes in bird communities in response to silvicultural prescriptions. For. Ecol. Manage. 96: 27–36.
- Basile M., Balestrieri R., Buoninconti F., Capobianco G., Altea T., Matteucci G. & Posillico M., 2015. Studio preliminare sulla catturabilità del rampichino comune *Certhia brachydactyla*. In: Pedrini P., Rossi F., Bogliani G., Serra L. & Susteric A. (eds), XVII Conv. Ital. Ornitol., Trento, Italy, pp 93–94.
- Bibby C.J., Burgess N.B., Hill D.A. & Mustoe S., 2000. Bird census techniques, 2nd edn. Academic Press, London.
- Blondel J., Ferry C. & Frochot B., 1981. Point counts with unlimited distance. In: Ralph J. C. & Scott J. M. (eds) Estimating Numbers of Terrestrial Birds. Studies in Avian Biology, Asilomar, California, USA, pp 414–420.
- Borchers D.L. & Efford M.G., 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64: 377–385.
- Brambilla M. & Ficetola G.F., 2012. Species distribution models as a tool to estimate reproductive parameters: a case study with a passerine bird species. J. Anim. Ecol. 81: 781–7.
- Brichetti P. & Fracasso G., 2011. Ornitologia Italiana vol. 7 Paridae-Corvidae. Oasi A. Perdisa Ed., Bologna.
- Buckland S.T., Anderson D.R., Burnham K.P., Laacke J.L., Borchers D.L. & Thomas L., 2001. Introduction to distance sampling: estimating abundance of biological population. Oxford University Press, Oxford, UK.
- Burnham K.P. & Anderson D.R., 2002. Model selection and multimodal inference, 2nd edn. Springer-Verlag, New York.
- Chandler R.B., Royle J.A. & King D.I., 2011. Inference about density and temporary emigration in unmarked population. Ecology 92: 1429–1435.
- Chao A. & Yang H.-C., 2003. Program CARE-2 (for Capture-Recapture Part. 2). Program and user's guide.
- Clarke K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Austr. J. Ecol. 18: 117–143.
- Couturier T., Cheylan M., Bertolero A., Astruc G. & Besnard A., 2013. Estimating abundance and population trends when detection is low and highly variable: a comparison of three methods for the Hermann's tortoise. J. Wildl. Manage. 77: 454–462.
- Cramp S., 1988. The Birds of the Western Paleartic. Oxford University Press, Oxford, UK.
- Dail D. & Madsen L., 2010. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67: 577–587.
- Dorazio R.M. & Royle J.A., 2003. Mixture models for estimating the size of a closed population when capture rates vary among individuals. Biometrics 59: 351–364.
- Di Salvatore U., Tonti D., Chiavetta U., Cantiani P., Fabbio G., Becagli C., Bertini G., Sansone D., Skudnik M., Kobal M., Kutnar L., Ferreira A., Kobler A., Kovač M. & Ferretti F., 2016. ManFor C.BD sites and the drivers of forest functions. In: De Cinti B., Bombi P., Ferretti F., Cantiani P., Di Salvatore U., Simončič P., Kutnar L., Čater M., Garfi V., Mason F. & Matteucci G. (eds), From the experience of LIFE+ ManFor

C.BD to the Manual of Best Practices in Sustainable Forest Management. Ital. J. Agronomy 11(s1): 64-95.

- du Preez B.D., Loveridge A.J. & Macdonald D.W., 2014. To bait or not to bait: a comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. Biol. Conserv. 176: 153–161.
- Dunn E.H. & Ralph J.C., 2002. Use of mist nets as a tool for bird population monitoring. Stud. Avian. Biol. 29: 1–6.
- Eberhardt L.L. & Thomas J.M., 1991. Designing environmental field studies. Ecol. Monogr. 61: 53–73.
- Efford M., 2004. Density estimation in live-trapping studies. Oikos 106: 598–610.
- Efford M. G., 2015. Package 'secr'.
- Efford M.G. & Fewster R.M. 2013. Estimating population size by spatially explicit capture-recapture. Oikos 122: 918–928.
- Ellis T.M. & Betts M.G., 2011. Bird abundance and diversity across a hardwood gradient within early seral plantation forest. For. Ecol. Manage. 261: 1372–1381.
- Fiske I.J. & Chandler R.B., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43: 1–23.
- Fornasari L., Londi G., Buvoli L., Tellini Florenzano G., La Gioia G., Pedrini P., Brichetti P. & de Carli E., 2010. Distribuzione geografica e ambientale degli uccelli comuni nidificanti in Italia, 2000-2004 (dati del progetto MITO2000). Avocetta 34: 5–224.
- Jett D. & Nichols J.D., 1987. A field comparison of nested grid and trapping web density estimators. J. Mammal. 68: 888– 892.
- Kéry M., Royle J.A., Schmid H., 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecol. Appl. 15: 1450–1461.
- Machtans C.S., Villard M.-A., Hannon S.J., 1996. Use of riparian buffer strips as movement corridors by forest birds. Conserv. Biol. 10: 1366–1379.
- Marsot M., Chapuis J.-L., Gasqui P., Dozières A., Masséglia S., Pisanu B., Ferquel E. & Vourc'h G., 2013. Introduced Siberian chipmunks (*Tamias sibiricus barberi*) contribute more to Lyme borreliosis risk than native reservoir rodents. PLoS One 8: e55377. doi: 10.1371/journal.pone.0055377.

Mazerolle M.J., 2015. Package 'AICcmodavg'.

- Moran P.A.P., 1950. Notes on continuous stochastic phenomena. Biometrika 37: 17–23.
- Morisita M., 1962. Iô-Index, A Measure of Dispersion of Individuals. Res. Popul. Ecol., Kyoto 4: 1–7.
- Nichols J.D., Noon B.R., Lynne Stokes S. & Hines J.E., 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. In: Ralph J.C. & Scott J.M. (eds), Studies in Avian Biology. Asilomar, USA, pp 121–136.
- Obbard M.E., Howe E.J. & Kyle C.J., 2010. Empirical comparison of density estimators for large carnivores. J. Appl. Ecol. 47: 76–84.
- Otis D.L., Burnham K.P., White G.C. & Anderson D.R., 1978. Statistical inference from capture data on closed animal population. Wildl. Monogr. 62: 3–135.

- Pasinelli G., 2000. Oaks (*Quercus* spp.) and only oaks? Relations between habitat structure and home range size of the middle spotted woodpecker (*Dendrocopos medius*). Biol. Conserv. 93: 227–235.
- Romesburg H.C., 1981. Wildlife science : gaining reliable knowledge. J. Wildl. Manage. 45: 293–313.
- Royle J.A., 2004a. Generalized estimators of avian abundance from count survey data. Anim. Biodivers. Conserv. 27: 375– 386.
- Royle J.A., 2004b. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60: 108–15.
- Royle J.A. & Nichols J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84: 777–790.
- Ruiz de Infante Anton J., Rotger A., Igual J.M. & Tavecchia G., 2013. Estimating lizard population density: an empirical comparison between line-transect and capture–recapture methods. Wildl. Res. 40: 552.
- Schmiegelow F.K.A., Machtans C.S., Hannon S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78: 1914– 1932.
- Schwenk W.S., Donovan T.M., Keeton W.S., Nunery J.S., 2012. Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. Ecol. Appl. 22: 1612–1627.
- Smith T.M. & Shugart H.H., 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology 68: 695–704.
- Spina F. & Volponi S., 2008. Atlante della Migrazione degli Uccelli in Italia. 2. Passeriformi. Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Istituto Superiore per la Protezione e la Ricerca Ambientale. Tipografia SCR, Roma.
- Stanley T.R. & Burnham K.P., 1999. A closure test for time-specific capture-recapture data. Environ. Ecol. Stat. 6: 197–209.
- Sutherland W.J., 2006. Ecological Census Techniques. Cambridge Univ. Press, Cambridge, UK.
- Svensson L., 1992. Identification guide to European Passerines. Stockholm, Sweden.
- Tabacchi G., Di Cosmo L., Gasparini P. & Morelli S., 2011. Stima del volume e della fitomassa delle principali specie forestali italiane. Equazioni di previsione, tavole del volume e tavole della fitomassa arborea epigea. Consiglio per la Ricerca e la sperimentazione in Agricoltura, Unità di Ricerca per il Monitoraggio e la Pianificazione Forestale, Trento.
- White G.C., Anderson D.R., Burnham K.P. & Otis D.L., 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Lab, Los Alamos, New Mexico, USA.
- Zhang J. & Wang C., 2012. Biodiversity and ecosystem functioning: exploring large-scale patterns in mainland China. iForest - Biogeosciences For. 5: 230–234.
- Zipkin E.F., Thorson J.T., See K., Lunch H.J., Campbell Grant E.H., Kanno Y., Chandler R.B., Letcher B.H. & Royle A.J., 2014. Modeling structured population dynamics using data from unmarked individuals. Ecology 95: 22–9.

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