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| Keywords: | hierarchical models, monitoring, population dynamics, population size, species decline, trend |
| Abstract: | Population size is a fundamental state variable in ecology, and the analysis of temporal variation in abundance, i.e. the detection of trends, is a prime objective in wildlife monitoring. However, population abundance cannot be directly observed because part of the population remains undetected and methods that account for imperfect detection should be employed. These approaches give reliable estimates of abundance, but are time- and effort-consuming, while in the last decade the application of hierarchical, or N-mixture, models that use repeated counts of unmarked animals seem to give great advantages in the estimation of population size. Hierarchical models require repeated surveys at multiple sites, while sometimes only data obtained for a single site in successive years are available. In this note we applied the time-for-space substitution approach of Yamaura et al. (2011), implemented within the N-mixture modelling framework, to estimate population size and evaluate the dynamics of an endangered gecko surveyed over twenty years. These results were compared with capture-mark-recapture estimates obtained from the same population and over the same time period. Estimates and trends were comparable and, therefore, the application of the time-for-space substitution in hierarchical modelling seems valuable and may be useful in species monitoring and conservation. |
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RH: Costa et al. · *N*-Mixture Long Term

**Time-for-Space Substitution in *N*-Mixture Modeling and Population Monitoring**

ANDREA COSTA,[1] *Dipartimento di Scienze della Terra dell'Ambiente e della Vita (DISTAV), Università degli Studi di Genova, Genova, Italy*

FABRIZIO ONETO, *Dipartimento di Scienze della Terra dell'Ambiente e della Vita (DISTAV), Università degli Studi di Genova, Genova, Italy*

SEBASTIANO SALVIDIO, *Dipartimento di Scienze della Terra dell'Ambiente e della Vita (DISTAV), Università degli Studi di Genova, Genova, Italy*

**ABSTRACT** Population size is a fundamental state variable in ecology, and the analysis of temporal variation in abundance (i.e., detection of trends) is a prime objective in wildlife monitoring. However, population abundance cannot be directly observed because part of the population remains undetected and methods that account for imperfect detection are often not used. Capture-Mark-Recapture approaches give reliable estimates of abundance, but are time- and effort-consuming. In the last decade, the application of hierarchical, or *N*-mixture, models that use repeated counts of unmarked animals seem to give great advantages in the estimation of population size. Hierarchical models require repeated surveys at multiple sites, but sometimes only data obtained for a single site in successive years are available. We applied the time-for-space substitution implemented within the *N*-mixture modeling framework, to estimate population size and evaluate the dynamics of the endangered European leaf-toed gecko (*Euleptes europaea*) surveyed >20 years. We compared these results with capture-mark-recapture estimates obtained from the same population and over the same time period. Estimates and trends were comparable and both methods indicated similar population declines, moreover N-mixture modeling indicated temperature affected detection. Therefore, the application of the time-for-space substitution in hierarchical modeling seems valuable and may be useful in species monitoring and conservation.

[1] *Email:* andrea-costa-@hotmail.it

**KEY WORDS** hierarchical models, monitoring, population dynamics, population size, species decline, trend.

Population size is one of the fundamental state variables in ecology and the analysis of its temporal variation in abundance (i.e., detection of trends) is a major objective in wildlife monitoring and species conservation (Yoccoz et al. 2001, Williams et al. 2002). However, population abundance usually cannot be directly observed because part of the population of interest may remain undetected (Schmidt 2002, Williams et al. 2002). Therefore, methods that account for imperfect detection, such as capture-mark-recapture (CMR) or removal methods, should be employed to obtain robust population estimates (Williams et al. 2002). These approaches give reliable estimates of abundance and other demographic parameters but are time- and effort-consuming. In the last decade, the application of *N*-mixture models (Royle 2004), which use repeated count data without the need of individual capture and identification, seem to give great advantages for estimating population size with reduced field effort. *N*-mixture models received a great interest in the last few years and their reliability has been evaluated by simulation studies, casting doubts on the usefulness of these models because of parameter identifiability problems; in particular in presence of assumptions violation and unmodeled heterogeneity in the abundance or the detection parameter (Barker et al. 2017, Link et al. 2018). However, Kéry (2018) showed how binomial N-mixture model estimates are in agreement with those obtained with a hierarchical variant of a capture-recapture model. Finally, several studies compared N-mixture models with other techniques for abundance estimation such as CMR or removal methods, obtaining comparable results (Priol et al. 2014, Ficetola et al. 2018). *N*-mixture models are typically used for repeated surveys at multiple sites (Kéry and Royle 2016), but sometimes only monitoring data for single sites or populations obtained in successive years are available.

Time-for-space substitution in *N*-mixture models, where multiple counts are conducted each year at the same site, consists of substituting space replicates (i.e., sites) by time replicates (i.e., years), and within-year repeated counts (i.e., surveys) are employed as temporal replications (i.e., the population is considered demographically closed within each year). This framework has been employed by Yamaura et al. (2011) for a multi-species system with detection–non-detection data of bird species during 9 consecutive years at a single site in Japan. This application is also described and evaluated against simulation scenarios by Kéry and Royle (2016), but further applications with real field data and, in particular, a validation of the method with another one based on CMR techniques are lacking.

We applied the time-for-space substitution approach proposed by Yamaura et al. (2011) within the *N*-mixture modeling framework to estimate the abundance and trend from 20 years of repeated sampling data of a single population of European leaf-toed geckos (*Euleptes europaea*; Gené, 1839) monitored since 1996, in northwest Italy (Salvidio and Oneto 2008). We also compared the population estimates obtained by *N*-mixture modelling with time-for-space substitution with population estimates obtained from the same population and the same 20-year time frame, estimated by the CMR approach in order to evaluate the performance of N-mixture models in this particular context.

## STUDY AREA

We monitored European leaf-toed geckos annually since 1996 on an abandoned historical building in the outskirts of the town of Genova, Liguria, northwest Italy, at an elevation of 320 m above sea level and about 4 km from the sea coast. Results of this monitoring have already published and described the study area (Salvidio and Delaugerre 2003, Salvidio and Oneto 2008, Salvidio et al. 2011). The study site is relatively isolated and surrounded by pastured grasslands, interspersed with houses and sparse trees. The climate of this area is submediterranean, with a mean annual rainfall of 1,303 mm and a relatively dry and hot period in July, when <40 mm of mean monthly rainfall are recorded (Genova – meteorological station of Ponte Carrega, Agenzia Regionale per la Protezione dell'Ambiente Ligure [ARPAL] 2013).

## METHODS

The European leaf-toed gecko is a diminutive (max. snout-cloaca length = 48 mm; mass < 2 g) nocturnal lizard endemic to the northwest Mediterranean area. It is found on the coastal mainland of northwest Italy and southern France on large (i.e., Sardinia and Corsica) and small offshore islands and on some islets off the coasts of northern Tunisia (Delaugerre et al. 2011, Salvidio et al. 2011). This gecko is a narrow crevices specialist, living on rock cliffs and stony habitats, but it is also able to colonize artificial habitats, such as abandoned buildings and dry stone walls (Salvidio et al. 2011). The species' altitudinal distribution ranges from sea level to about 1,500 m in Corsica but never goes beyond 900 m on the mainland (Salvidio et al. 2011). The European leaf-toed gecko is a species of conservation concern, has been evaluated as Near Threatened by the International Union for Conservation of Nature (Corti et al. 2009), and is listed in Annex II and IV of the European Habitats Directive (92/43/EEC), therefore deserving protection in the entire European Union.

**Capture-Mark-Recapture Analysis**

We sampled the gecko population each year in July from 1996 to 2016, during 3 or 4 non-consecutive nights, with the exception of 2001. We spotted geckos with flashlights, captured them on building walls, sexed and measured them, and temporarily marked them with acrylic paint (Salvidio and Delaugerre 2004, Salvidio and Oneto 2008). At the end of each nocturnal survey, we released all the geckos on the building and did not observe mortality related to capture. The number of operators varied among nights and years, but in all cases captures terminated after 2 completely unsuccessful searches on the building walls. From 1996 to 2009, we batch-marked geckos by painting a single dorsal spot with a different color each night, whereas from 2010 to 2016 we individually marked all animals with a progressive acrylic number painted on their back. In all years captures were executed with permits of the Italian Ministry of Environment ( capture permits: SCN/2D/98/8670, SCN/99/2D/12326, SCN/2D/2000/2431, DCN/2D/2002/3026/, DCN/2D/10985/2003/, DPN/IID/2005/6708, DPN/2D/2006/7547, DPN/2007/001058, DPN/2009/0010376, DPN/2010/0010807, 0042466/PNM/2013, 0013862/PNM/2016 ).

We estimated population abundance by means of Program CAPTURE, a software suited for closed populations (White et al. 1982) that performs a population closure test and a model selection procedure for all available models but only when the complete CMR matrix is available (i.e., full individual capture histories). In the present study, the closure test was non-significant ($P > 0.05$) in all years in which it was applicable, indicating that the population can be considered demographically closed, and in these cases the model selection procedure could be successfully employed. In a previous study in which geckos were batch-marked, Salvidio and Oneto (2008) used the time-dependent estimator, $M_{(t)}$, which allows for variation in capture probabilities among occasions (White et al. 1982). Concerning the data obtained from 2010, the model assuming constant capture probabilities, $M_{(0)}$, was supported in 6 out of 8 years, whereas models $M_{(t)}$ and $M_{(h)}$, the latter allowing individual variation in capture probabilities (White et al. 1982), were selected once each.

### *N*-Mixture Model Analysis

We conducted *N*-mixture model analyses with the number of geckos captures per night. To minimize stochastic heterogeneity in detection probability (Kéry and Royle 2016) we evaluated several covariates capable of explaining the detection process: temperature (temp), wind speed, relative humidity of the survey night, and the number of surveyors. We built 5 different models, with Poisson error distributions, each including a different covariate for detection probability (plus a model assuming constant detection probability). In each model we added a year numeric variable on the abundance side of the formula to model population trend (Kéry and Royle 2016). We standardized all covariates prior to analysis and assessed collinearity between covariates with Pearson product-momentum correlation (MacNally 2002).

We evaluated goodness of fit of the global model (i.e., the model with all the covariates and in which other candidate models are nested) using a Pearson chi-square test (MacKenzie and Bailey 2004), using a parametric bootstrap procedure (5,000 re-sampling). Moreover, we also evaluated model fit by computing a quasi-coefficient of variation (QCV) following Duarte et al. (2018) and inspecting residuals following Knape et al. (2018). We ranked all candidate models with Akaike's Information Criterion corrected for small samples ($AIC_c$). We conducted model selection and considered models with $\Delta AIC_c > 2$ as having less support than the top-ranked model (Burnham and Anderson 2002). We obtained abundance estimates for each year, with 95% confidence intervals, from the posterior distribution of the latent abundance (function ranef() in package unmarked). We conducted *N*-mixture model analyses in the R environment with package unmarked (Fiske and Chandler 2011) and package AICcmodavg (Mazerolle 2017).

## RESULTS

The MacKenzie and Bailey (2004) goodness-of-fit assessment resulted in a good fit ($P = 0.26$) and estimated a low overdispersion ($\hat{c} = 1.08$). Likewise, residuals and QVC highlighted a good fit of the model (QCV = 0.11). The most parsimonious *N*-mixture model included night temperature as a covariate on the detection parameter with the probability of detecting the geckos active on the building walls increasing with air temperature. This model estimated a mean detection probability of 0.22 (95% CI = 0.14–0.34; estimates at mean value of temp). The effect of year numeric variable ($\beta year = -0.35$; 95% CI = −0.42 to −0.27) highlighted a negative trend in population abundance. Population abundance estimates, obtained from the selected model, were largely in agreement with those obtained by CMR (Fig. 1). In addition, the 95% confidence interval of the annual estimates from CMR and *N*-mixture methods overlapped in all years except 2005, and the mean relative bias ($B$) between CMR estimates ($\mathrm{CMR}\hat{n}$) and *N*-mixture estimates ($\mathrm{Nmix}\hat{n}$), calculated as $B = (\mathrm{CMR}\hat{n} - \mathrm{Nmix}\hat{n})/\mathrm{CMR}\hat{n}$, was $B = 0.27 \pm 0.05$ (SE). Finally, the temporal trends obtained by both methods were similar, suggesting that the *N*-mixture model with time-for-space substitution was able to capture the long-term dynamics of the gecko population.

## DISCUSSION

Our results showed how *N*-mixture population estimates were comparable to the values obtained by CMR, and both methods were able to detect long-term population dynamics, specifically highlighting a similar declining trend. Moreover, the values of relative bias observed in our dataset were in line with the expected ones for low detection probability (<0.3) simulation scenarios (Ficetola et al. 2017, Duarte et al. 2018). In general, Duarte et al. (2018) report that *N*-mixture models, in cases of low detection probability and unmodeled heterogeneity in detection, tend to overestimate the real population abundance, whereas Veech et al. (2016) reported that Poisson *N*-mixture models typically underestimate abundance in the presence of intrinsic heterogeneity (i.e., detection probability varies among individuals). In our application, the *N*-mixture model appeared to systematically underestimate population abundance in comparison to CMR; we obtained lower values in comparison with CMR in about 75% of years. Therefore, these findings seem to be more in line with the simulations of Veech et al. (2016). The overall agreement between N-mixture and CMR estimates let us assume that identifiability problems and other major sources of bias, recently raised against these models (Barker et al. 2017, Link et al. 2018), are not of concern, at least in this study. In the future it would be important to assess the reliability of our *N*-mixture approach in systems with even lower values of detection probability values (i.e., <0.15) that are found when monitoring animals in tropical areas (Ferraz et al. 2011), or snakes (Durso et al. 2011, Steen et al. 2012).

## MANAGEMENT IMPLICATIONS

Many species, of high management and conservation value, have very narrow geographic ranges, few presence locations are known or few populations can be studied. In these situations, the application of CMR protocols to monitor species long-term seems impossible or unsustainable over a prolong period. The conservation and management of these species may benefit from the application of a more cost-effective monitoring method based on repeated counts of unmarked individuals, instead of a CMR approach. We suggest that wildlife managers interested in long-term population surveys could reduce monitoring costs by using time-for-space substitution, after a period of validation by other independent methods, such as CMR.

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Figure captions

Figure 1. Population trends of the European leaf-toed gecko in Genova, Liguria, northwest Italy, estimated with capture-mark-recapture (black) and *N*-mixture models with time-for-space substitution (red). Vertical error bars represent 95% confidence intervals.

Table 1. Results of model selection of *N*-mixture models with time-for-space substitution for abundance (λ) and detection (*p*) of European leaf-toed geckos in Genova, Liguria, northwest Italy, 1996–2016, based on Akaike's Information Criterion ($AIC_c$) and model weights ($w_i$).

| Model[a] | Parameters | $AIC_c$ | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| λ(yr)*p*(temp) | 4 | 589.33 | 0.00 | 0.62 |
| λ(yr)*p*(surv) | 4 | 592.07 | 2.73 | 0.16 |
| λ(yr)*p*(.) | 3 | 592.20 | 2.87 | 0.15 |
| λ(yr)*p*(rh) | 4 | 595.01 | 5.68 | 0.04 |
| λ(yr)*p*(wind) | 4 | 595.36 | 6.03 | 0.03 |

[a] Detection covariates include temperature (temp), the number of surveyors (surv), no covariates (.), relative humidity (rh), and wind speed (wind).

**Article Summary**

*N*-mixture models usually require repeated surveys at multiple sites, but time-for-space substitution in the *N*-mixture modeling framework allows estimates of abundance on a single population. Estimates and trends using this method are comparable with those from capture-mark-recapture methods for European leaf-toed geckos; therefore, this approach seems valuable and may be useful in species monitoring and conservation.

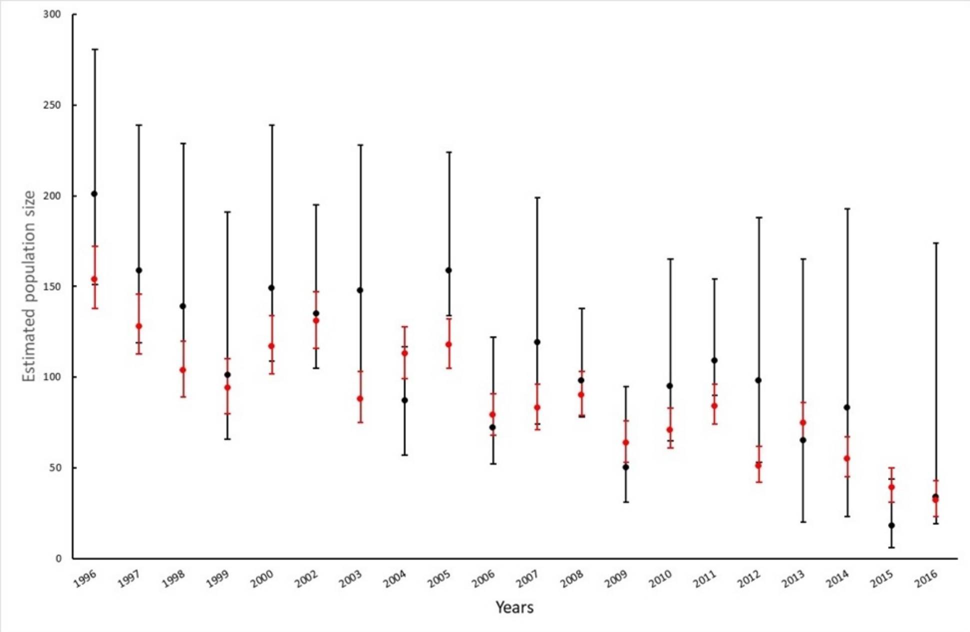


Figure 1. Population trends of the European leaf-toed gecko in Genova, Liguria, northwest Italy, estimated with capture-mark-recapture (black) and N-mixture models with time-for-space substitution (red). Vertical error bars represent 95% confidence intervals.

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