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## Density regulation in the Mediterranean leaf-toed gecko *Euleptes europaea*

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**Abstract** Isolated populations are particularly prone to extinction, and understanding their temporal dynamics is relevant for conservation and management. In this study, the abundance of a population of the nocturnal leaf-toed gecko *Euleptes europaea* was estimated by mark-recapture over a 12-year period in northwest Italy. Simulation tests showed the presence of density-dependence, and autoregressive analyses indicated that direct density dependence was responsible for a large part of the variation in population growth rates. Density-dependent recruitment was suggested as the main demographic mechanism controlling population dynamics, which was also affected by solar radiation measured during the active gecko season. These results may contribute to implement conservation strategies in other small and isolated leaf-toed gecko populations.

**Keywords** Density dependence · Gekkonidae · Growth rates · Recruitment · Time series analysis

### Introduction

Recent research in population ecology has demonstrated that population growth rates are determined by a complex combination of endogenous and exogenous factors (e.g., Stenseth et al. 2002; Turchin 2003). Endogenous (i.e., density-dependent) factors act negatively on the reproduction and survival of individuals in response to increases in population densities, while stochastic (i.e., density-independent) factors are not correlated to densities, but may influence populations stability and persistence (Sibly and Hone 2003). Generally, direct density-dependence is the result of intraspecific competition for food, mates, or territories and is characterized by relatively small fluctuations in abundances, while delayed

density dependence is due to interspecific interactions with preys, predators or parasites and may produce large and cyclical fluctuations in population numbers (Royama 1992; Berryman 1999, 2001).

The analysis of time series (i.e., population abundances measured at regular intervals through time) has been successfully used to assess the relative importance of endogenous and exogenous variables in wild animal populations (e.g., Royama 1992; Bjørnstad and Grenfell 2001; Turchin 2003). Indeed, since autoregressive models correct for autocorrelation in the data sequence they seem particularly suited to analyze population growth rates and to provide information on the structure of the regulating mechanisms (Royama 1992; Bjørnstad and Grenfell 2001; Turchin 2003). However, time series analysis is seldom applied in the study of population dynamics of reptiles (e.g., Brook and Bradshaw 2006), probably because of the difficulties in obtaining reliable abundance estimates over long periods of time of these vertebrates, that are relatively small, cryptic and of little economic interest.

The aim of this study was to analyze the population dynamics of a threatened gecko through randomization tests and time series analysis to evaluate the relative importance of exogenous and endogenous factors controlling population dynamics. In particular we tried to elucidate if direct or delayed density-dependent regulation was present and if regional and or local climate affected the gecko population growth rates. Although the study population is found along the continental coast of Italy, it is isolated, and the results obtained from this study may be extrapolated to other populations inhabiting islands where historical extinctions have been reported (Salvidio and Delaugerre 2003).

### Materials and methods

Study species, site and climatic variables

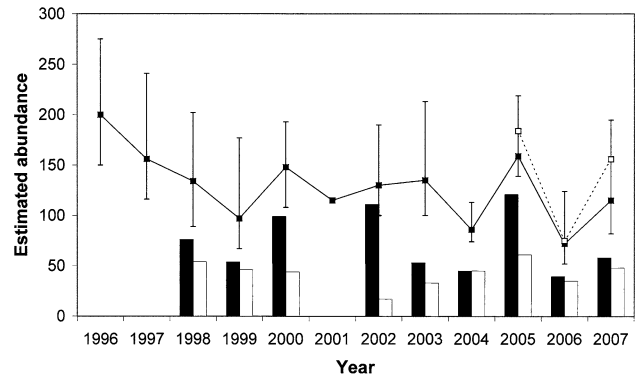
The leaf-toed gecko *Euleptes europaea* is a Mediterranean endemic with a geographical range composed by

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hundreds of isolated populations (Delaugerre 1997). The majority of leaf-toed gecko populations are insular, some of them living on islets less than 1,000 m<sup>2</sup> in surface, where this species is the only resident vertebrate (Delaugerre and Cheylan 1992). At the global scale, the species is considered “Near Threatened” by IUCN (Cox et al. 2006) and is listed in both Annexes II and IV of the “Habitats and Species” European Directive (92/43/EEC), thus deserving high conservation concern. The leaf-toed gecko is a small (adult weight <2.5 g, adult body length <50 mm) nocturnal insectivorous lizard. It is found in southern France, northwest and central Italy, Sardinia, Corsica, and satellite islands, as well as three islands off the coast of Tunisia (Delaugerre 1997). The study site was an isolated historical building outside the urban area of Genova (northwest Italy) at 320 m. The surrounding vegetation is composed mainly of pastured grasslands and abandoned olive yards, but sparse oaks (*Quercus pubescens*), chestnuts (*Castanea sativa*) and conifers (*Pinus pinaster*) are also present. The climate is typically submediterranean, and vegetation growth is limited by summer droughts. The nearest known population of *E. europaea* is about 4 km by air (Salvidio and Oneto, unpublished). Climate variables were selected in order to describe environmental conditions that could influence gecko mortality and reproduction. The North Atlantic Oscillation Index, measured from December to March (NAOI, [www.cru.uea.ac.uk/~timo/projpages/nao\\_update.htm](http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm)), was used as a large-scale climatic variable describing winter climate. NAOI is calculated from the normalized pressure difference between Azores and Iceland and its influence reaches the Mediterranean (Morri and Bianchi 2001; Stenseth et al. 2002). De Martonne’s index of aridity  $IA = [Rain/(Temp \times 10)]$ , where Rain is the annual rainfall and Temp the mean annual temperature, was used as proxy for vegetation productivity (Gavilán 2005). This index, correlated to the average April–October rainfall ( $P = 0.03$ ), was supposed to influence invertebrate prey abundance. Moreover, solar radiation in kJ/m<sup>2</sup> measured during the gecko active season (April–October) was used. This variable could influence thermoregulation efficiency of geckos (Hitchcock and McBrayer 2006) particularly of gravid females (Rock et al. 2002). Local climate data were obtained from Genova University weather station ([www.diam.unige.it](http://www.diam.unige.it)) about 2 km from the study site.

#### Abundance estimation and data analysis

The population was sampled in July from 1996 to 2007 with the exception of 2001. Geckos were captured by hand during three non-consecutive nights (four from 2005, see Fig. 1) within a timeframe of  $5.8 \text{ days} \pm 2.1 \text{ SD}$  (range 4–11). Geckos were measured in mm from snout to vent (SVL), batch-marked with different acrylic colors each night and released. Each year sample was decomposed by means of FiSAT software (Gayanilo et al. 1995) in three SVL groups: juveniles (mean SVL



**Fig. 1** Abundances ( $\pm 95\%$  confidence limits) of *Euleptes europaea* total population estimated by three captures. The 2001 value was extrapolated using a length-3 moving average. Open symbols are abundances estimated by four captures. Vertical bars are estimated abundances for adults (black) and juveniles (white)

=  $25.98 \pm 1.38 \text{ SD}$ ), subadults (SVL =  $33.14 \pm 2.15 \text{ SD}$ ) and adults (SVL =  $40.19 \pm 0.55 \text{ SD}$ ). In this study, subadults and adults were pooled and compared with juveniles; however, in 1996 and 1997, recaptured geckos were not measured and these years were excluded from comparisons.

CAPTURE software (White et al. 1982) was used to estimate population abundance. The Darroch  $M_t$  estimator, that allows for temporal variation in capture probabilities (CP) was selected, because mean CP decreased, although non-significantly, after the first capture: 0.22 in the first, 0.18 in the second and 0.19 in the third occasion (repeated measures ANOVA,  $F_2 = 2.09$ ,  $P = 0.149$ ), suggesting that animals could be disturbed by successive night captures. CP did not differ between adults ( $0.18 \pm 0.05 \text{ SE}$ ) and juveniles ( $0.26 \pm 0.12 \text{ SE}$ ) (repeated measures ANOVA,  $F_1 = 2.68$ ,  $P = 0.145$ ), and thus abundance was estimated by pooling all the captured animals. The 2001 missing value was obtained by a length-3 moving average. The presence of density dependence was assessed by parametric bootstrap likelihood ratio test (Dennis and Taper 1996) and randomization test (Pollard et al. 1987), with 10,000 replications in both cases. Moreover, gecko dynamics was analyzed by a linear combination of population autoregressive (AR) past values and random variation, fitting the general model (Royama 1992; Berryman 1999):

$$R = A + B_1 \ln(N_{t-1}) + \dots + B_p \ln(N_{t-p}) + Z_t,$$

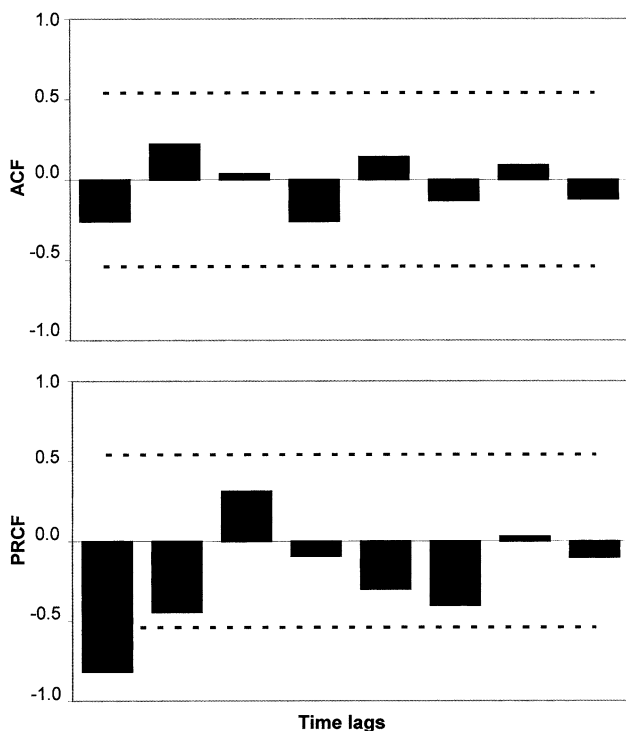
where  $R = \ln(N_{t-1}) - \ln(N_t)$  is the per capita growth rate,  $A$  is the maximum per capita growth rate,  $B$  is the autoregressive parameter,  $N$  is the population abundance,  $p$  is the order of the autoregressive parameters,  $t$  is the sampling interval, and  $Z$  is random variation. The dimension of the feedback structure was analyzed by autocorrelation (ACF) and partial rate correlation (PRCF) functions (Berryman and Turchin 2001), and the most parsimonious model was selected by

the Bayesian information criterion (BIC, Faraday and Chatfield 1998).

Regression of climatic variables on the residuals of the selected AR model was used to assess the role of climate in addition to endogenous feedback (Lima et al. 2002; Bommarco et al. 2007). Population growth rate CI were obtained using 2,000 bootstrappings. Poptools 2.6 software was used in simulation tests, all other statistical analyses were performed by means of Minitab 13.1 software.

## Results

The overall variability of the gecko time series was moderate (coefficient of variation = 0.28) and abundances estimated using four captures were similar to those obtained with three captures (Fig. 1). The variation in average CP (range 0.14–0.34) among years was significant (repeated measures ANOVA,  $F_{10} = 3.93$ ,  $P = 0.004$ ). The mean population growth rate was negative (−0.05), but since CI varied from −0.29 to 0.19 there was no evidence for a temporal trend in the data set. Both simulation tests showed the presence of density-dependent regulation in the gecko time series: Polard’s test  $P = 0.003$  and Dennis and Taper test  $P = 0.024$ . The ACF was not significant (Fig. 2) and showed a balanced saw-toothed pattern, typical of a stable first-order dynamics, while the PRCF confirmed



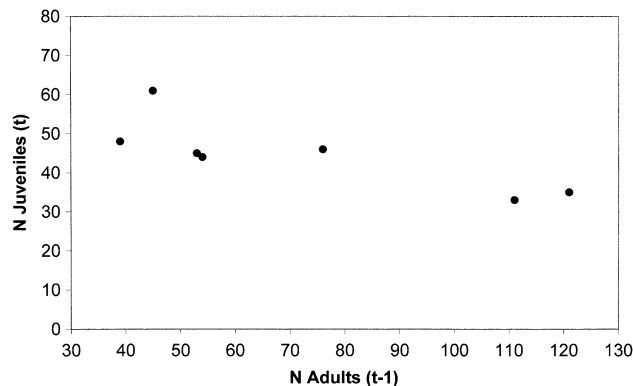
**Fig. 2** Autocorrelation function (ACF) and partial rate correlation function (PRCF) of log-transformed *Euleptes europaea* time series with 95% confidence limits (hatched lines)

that only direct density dependence influenced significantly population growth rate [PRCF(1) = −0.81, DF = 11,  $P = 0.02$ ,  $r^2 = 0.66$ ]. The AR(1) was the more parsimonious model (BIC = −24.95) in comparison to AR(2) (BIC = −23.15) and AR(3) (BIC = −19.05). There was a significant negative correlation between the number of juveniles recruited in 1 year and the adult abundance estimated in the previous one ( $r = -0.81$ , DF = 6, two-sided randomization test for regression slope  $P = 0.03$ ; Fig. 3). This result suggested that density-dependent recruitment was probably the main demographic mechanism controlling population growth rates.

The climatic variables were normally distributed (Anderson–Darling test,  $P > 0.05$ , in all cases), did not show any significant autocorrelation ( $P > 0.05$  in all cases). The results of the regression analysis, using the residuals from the AR(1) and climatic variables, are reported in Table 1. The most parsimonious model comprised solar radiation as a response variable and explained about 40% of the exogenous variability observed in the gecko time series ( $r = 0.41$ ,  $P = 0.03$ ).

## Discussion

This study clearly shows that both density-dependent and climatic factors were controlling the population dynamics of leaf-toed gecko *E. europaea*, but with different intensities. Direct density-dependence explained about 70% of the gecko time series variability, suggesting that the population had a robust regulation (Royama 1992). This is not an unexpected result, since the existence of endogenous regulatory mechanisms is well established in several wild populations of animals and plants (e.g., Sibly et al. 2005; Brook and Bradshaw 2006), and it should be especially expected in small populations living in relatively constant environments (Pimm 1991). The absence of delayed density-dependence in the study population suggests that its dynamics was not strongly influenced by interspecific interactions,



**Fig. 3** Relationship between juveniles at time  $t$  and adults at time  $t-1$  in the study population of *Euleptes europaea*:  $r = -0.81$ ,  $df = 6$ . Two-sided randomization test for slope  $P = 0.03$

**Table 1** Regression analysis of climatic variables on AR(1) residuals

Regression model	Parameters	BIC	$r^2$	$P$	A–D test	D–W test
IA	2	61.363	0.165	0.191	0.114 ns	2.07 ns
Rad	2	–66.009	0.416	0.022	0.982 ns	1.72 ns
NAOI	2	11.547	0.011	0.743	0.947 ns	2.17 ns
IA + Rad	3	–22.096	0.444	0.090	0.115 ns	2.02 ns
NAOI + Rad	3	–22.686	0.455	0.105	0.964 ns	2.37 ns
IA + NAOI + Rad	4	–19.906	0.485	0.133	0.365 ns	2.59 ns

*A–D test* Anderson–Darling test for normality of residuals; *BIC* Bayesian information criterion; *D–W test* Durbin–Watson test for autocorrelation of residuals; *IA* De Martonne’s index of aridity, *NAOI* North Atlantic Oscillation Index (December–March); *ns* not significant; *Rad* solar radiation measured in  $\text{kJ/m}^2$  during the gecko activity period (April–October)

such as those regulating prey–predator and host–parasite systems (Turchin 2003). As the leaf-toed gecko aggregates in large numbers inside retreat sites during the daytime (Cheylan and Delaugerre 1992) and does not show evidence of intraspecific aggressive behaviour when in captivity (Salvidio pers. obs.), food or retreat sites were probably involved in the regulation. However, as in Mediterranean ecosystems, De Martonne’s IA is a good proxy for vegetation growth (Gavilán 2005) and possibly arthropod abundance, the food-limiting hypothesis may not be the most reliable one. For this reason, intraspecific competition for nesting and/or hiding microhabitats may be more plausible, at least on the basis of the actual knowledge of the species ecology. As the population is isolated, immigration and emigration appear to have little role in regulation, while the observed density-dependent recruitment suggested a link between population density and female fecundity, possibly mediated through intraspecific competition for optimal nesting sites. Density-dependent recruitment is present, at least at high population densities, in other reptile species such as terrestrial tortoises (Gibson and Hamilton 1984), sea turtles (Girondot et al. 2002), and lizards (Hasegawa 1997). For example, in the case of an island population of the lizard *Eumeces okadae* a higher proportion of females reproduced successfully after the removal of conspecifics in comparison to females living at higher population densities (Hasegawa 1997).

Apart from endogenous regulation, about 30% of the overall variability in population growth rates was due to exogenous factors. There was no direct influence of the large-scale NAO index and the only weather variable that partially influenced gecko growth rate was the amount of solar radiation. This result indirectly confirms a previous study on the thermoregulation of *E. europaea* in Corsica (Delaugerre 1984). This study showed that leaf-toed geckos maintained relatively constant body temperatures over the entire day and that geckos active during the night had higher body temperatures in comparison to air (up to 7°C higher) and substrate (up to 4°C higher) (Delaugerre 1984). These data provided preliminary evidence that leaf-toed geckos achieved a regulated body temperature during the day, when hiding inside retreat sites. High body temperatures may be obtained by retreat-site selection or postural adjustments as demonstrated in the Australian gecko

*Christinus marmoratus* (Kearney and Predavec 2000) and in other temperate species such as *Eublepharis macularius* (Autumn and De Nardo 1995) and *Hemidactylus turcicus* (Hitchcock and McBrayer 2006).

Finally, the present results may have practical implications for implementing conservation strategies for *E. europaea* isolated population. The dynamics of this species appeared regulated by intraspecific interactions possibly related to the availability of egg laying, retreat and thermoregulation sites. Indeed, the complexity and the physical structure of available microhabitats seem to play a key ecological role in nocturnal geckos such as *Lepidodactylus lugubris*, *Gehyra variegata* and *Oedura lesueurii* in particular influencing both intra and interspecific interactions for food, territories and/or thermal benefits (Downes and Shine 1998; Petren and Case 1998). In the case of the leaf-toed gecko, the abundance of narrow and deep crevices well exposed to direct insulation may reduce predation risk and vulnerability to adverse weather conditions, while increasing the efficiency of thermoregulation and the number of egg-laying sites. Thus, artificially augmenting these microhabitats should be taken into consideration when implementing management actions. As a consequence, the increase in suitable nesting sites for females will increase recruitment, enhancing emigration towards new suitable environments enhancing connectivity between isolated sub-populations.

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