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Temporal trends in *Podarcis muralis* and *Lacerta bilineata* populations in a fragmented landscape in western France: Results from a 14 year time series

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Identifying population changes is a prerequisite for any conservation efforts, but to evaluate trends requires long-term data sets. In this paper, changes in population numbers in two species of European lizards, *Lacerta bilineata* and *Podarcis muralis*, are described. The results are based on counts of mortalities and live lizard presence on roads collected over a 14 year period, which indicated wide annual fluctuations in numbers in both species, with inter-specific annual trends strongly correlated. Snout to vent lengths (SVL) in *L. bilineata* were generally longer when annual numbers were higher but not in *P. muralis*. Regression analysis of the logarithmic transforms of annual lizard numbers as dependent variables and year as the independent variable indicated that despite population fluctuations, numbers of both species were stable or increased during the period of observation. Jackknife analysis identified unusually high numbers of *L. bilineata* in 2012 and *P. muralis* in 2010, but data from these years had minimal influence on the general trends with the peudo-regression coefficients generated from the Jackknife analysis in agreement with the true regressions. The results were therefore congruent, indicating annual fluctuations in both species were underpinned by long-term population stability.

Keywords: lizards, *Lacerta bilineata*, *Podarcis muralis*, population changes, road ecology

INTRODUCTION

Habitat fragmentation and potential impact of climate change are just two of the frequently cited threats that potentially impact on reptiles and amphibians (e.g. Alford & Richards, 1999; Gibbons et al., 2000; Chamaille – Jamme et al., 2006; Araujo et al., 2006; Luiselli et al., 2018). Perhaps due to their perceived role as indicators of environmental health, studies of amphibians appear more frequently in the scientific literature (e.g. Alford & Richards, 1999; Beebee & Griffiths 2005). However, reptiles may also be particularly sensitive to climatic effects and documenting major changes in populations, especially in the face of potential climatic effects, is central for any conservation effort. This requires long-term data sets that will enable sufficient statistical power to evaluate trends (Gibbons et al., 2000). Within the European/Mediterranean reptilia, long-term studies have mostly concerned snakes (e.g. Lourdais et al., 2002; Reading et al., 2010; Capula et al., 2014; Rugiero et al., 2014; Luiselli et al., 2018; Graitson et al., 2018; Bauwens & Claus, 2018). Fewer studies have examined the more numerous lizards (e.g. Barbault & Mou, 1988; Saint Girons et al., 1989; Capula et al., 1993; Roitberg & Smirna, 2006; Leão et al., 2018), which is perhaps surprising given that lizards are now considered as model organisms in studies of life-history and demography (Pianka & Vitt, 2003). For example, in a recent overview on density dependence, a 10-year minimum time series criteria for inclusion resulted in only four species of lizard in the analysis (<6 % of the reptile total: Leão et al., 2018).

The aim of the present study is to examine long-term population changes in two species of European lizards, *Podarcis muralis* and *Lacerta bilineata*, both of which are common over large parts of western Europe. In the study locality they occupy a fragmented landscape where *L. bilineata* typically operates as a sentinel predator and is associated mostly with hedgerows and light urban areas. The smaller *P. muralis* operates mainly as an active forager and is more commonly found in human-dominated environments and along woodland edge (Meek, 2014). The results are based on a 14-year time series derived from two sources; road mortalities and sighting frequencies of live lizards that have entered roads. Lizards may utilise roads for several reasons including thermal opportunities, predator and prey detection, and as ecological pathways (e.g. Koenig et al., 2002; Delgado Garcia et al., 2007; Lebboroni & Corti, 2006; Meek, 2009, 2014).

METHODS

The study area (46°27`N;1°53`W) was established in 2005 and composed of a fragmented landscape dominated by

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agriculture but with wooded areas, small villages, and isolated houses and gardens. Apart from some new housing construction, mostly in the villages, the area had otherwise experienced little or no major changes in land use other than agricultural activities in the same fields during the 14-year study period. The locality is approximately 10 km from the Bay of Biscay with a mild oceanic climate; June, July and August monthly mean air temperature is 26 ˚C, and November through to February monthly mean is 10.2 ˚C. Highest precipitation is usually between October and January (monthly mean = 85.7 mm) with June, July, and August the lowest rainfall, with the monthly mean of 51.3 mm.

The use of road mortalities to estimate animal numbers assumes that carcasses on roads represent approximations of animal numbers in adjacent habitat (Fitch, 1987). This approach has been usefully employed as a proxy to estimate population changes in amphibians (e.g. Meyer et al., 1998; Meek, 2018) and snakes (e.g. Capula et al., 2014; Rugiero et al., 2018) and while representing only an index of abundance, if carcasses are removed after detection, they are independent of double counting and autocorrelation. The presence of live lizards on roads provides an additional data source since the absence of visual barriers facilitates ease of detection and species identification (Meek, 2014). VEF (visual encounter frequency) is less robust to double counts but if made over a long time period and large geographical area, risk of double counts should be low.

Data on road mortalities and live counts were collected over a total distance ≈16 km between a wetland area close to the village of St Denis du Payre and the wetland on the edge of the village of Chasnais from 2005 to 2018. The distance between the two villages is approximately 6 km (see Meek, 2012 for a schematic view). Surveying for road mortalities began in January 2005 and was undertaken between four and six times every month throughout each year until December 31, 2018. A single observer on a bicycle travelling at 5–10 km/hour carried out surveys. This method enables good detection of lizards especially in the more brightly coloured *L. bilineata*, and hence observer error is believed to be low in this species. Possible observer error in *P. muralis* is a little higher due to its smaller size and less vivid colouring (see Meek, 2012). Road traffic volume increased slightly during surveying – see Meek (2012). Data are derived from lizards that were either present on roads or found as road-kill. When a road-killed lizard was found, snout to vent length (SVL) in mm, its location, proximate roadside habitat and distance from the road edge were recorded. Measurements of road–killed lizard SVL had a maximum estimated error of <5 mm depending on body condition. Measurements of live lizards were approximate (±10 mm) and based on photographic records, which were then compared with some object in the immediate vicinity. A number of live lizards were caught, including five injured individuals on roads, but in total this was less than 10 (see text).

Statistical analysis.

Before analysis, tests for normality were evaluated using the Anderson-Darling a^2 test. Differences in mean SVL were determined by ANOVA with a post hoc Tukey HSD test for unequal sample sizes (Tukey, 1949; Kramer, 1956). This evaluates all possible pair-wise comparisons of means at α = 0.05, with the null hypothesis that means are in statistical agreement. Comparison of inter-specific differences in the extent of population fluctuations were made using F-tests for equality of variances. The null hypothesis is that variances do not differ (i.e., H_0: $s^2_1 / s^2_2 = 1$). Tests for departures for equality of annual lizard counts were done using *G*-test Goodness-of-Fit at n-1 d.f. with the expected annual counts; 1/n, where n is the year count; that is the combined road mortalities and live counts across all years, 23.7 for *L. bilineata* and 25.1 for *P. muralis*.

Long-term population trends were evaluated using regression analysis of the logarithmic transforms of road mortalities and live counts as dependent variables, with corresponding years as the independent variables. This gave an equation of the form:

$$\log_e N = b + m\text{year}$$

where $\log_e N$, represents either road mortalities, live counts or the pooled data sets, *m* the regression coefficient, and *b* the y-intercept. The null hypothesis is that $\log_e N$ is stable when $m = 0$; significant departures from 0 are indicative of population change, which was evaluated using a *t*-test at n-2 d.f. (Bailey, 1995).

Since unusually high or low year counts may have an inordinate effect on *m*, a test for influence function (Gotelli & Ellison, 2004) to estimate the sampling errors of the regression coefficients was made using jackknifing (Sahinler & Topuz, 2007). Jackknifing has the advantage of giving exact repeatable results by systematically removing one-year data sets from the sample and then re-calculating regression coefficients for these restricted samples. The true regression coefficients were then compared to the distribution of the pseudo-*m* values. Long term climatic data, rainfall and temperatures, were sourced from the nearest weather station at La Rochelle-Le Bout Blanc (around 25 km from the study locality).

RESULTS

A total of 332 *L. bilineata* (265 road mortalities + 67 live individuals) and 354 *P. muralis* (282 road mortalities + 72 live individuals) were recorded on roads. Figure 1 shows SVL distributions of mortalities and SVL estimates of live lizards between 2005 and 2018. In both species, all distributions were negatively skewed toward larger individuals; *L. bilineata* live = -1.15 & mortalities = -1.23; *P. muralis* live = -1.26 with mortalities only moderately skewed = -0.27.

Lacerta bilineata were found as road mortalities between maximum dates of April 8 and October 25 and live individuals between maximum dates of April 9 and September 22. Peak mortalities were in August and peak live sightings in April. Mortalities of *P. muralis* were found between March 24 and November 12 with live sightings between April 4 and October 18 of each year. Live counts

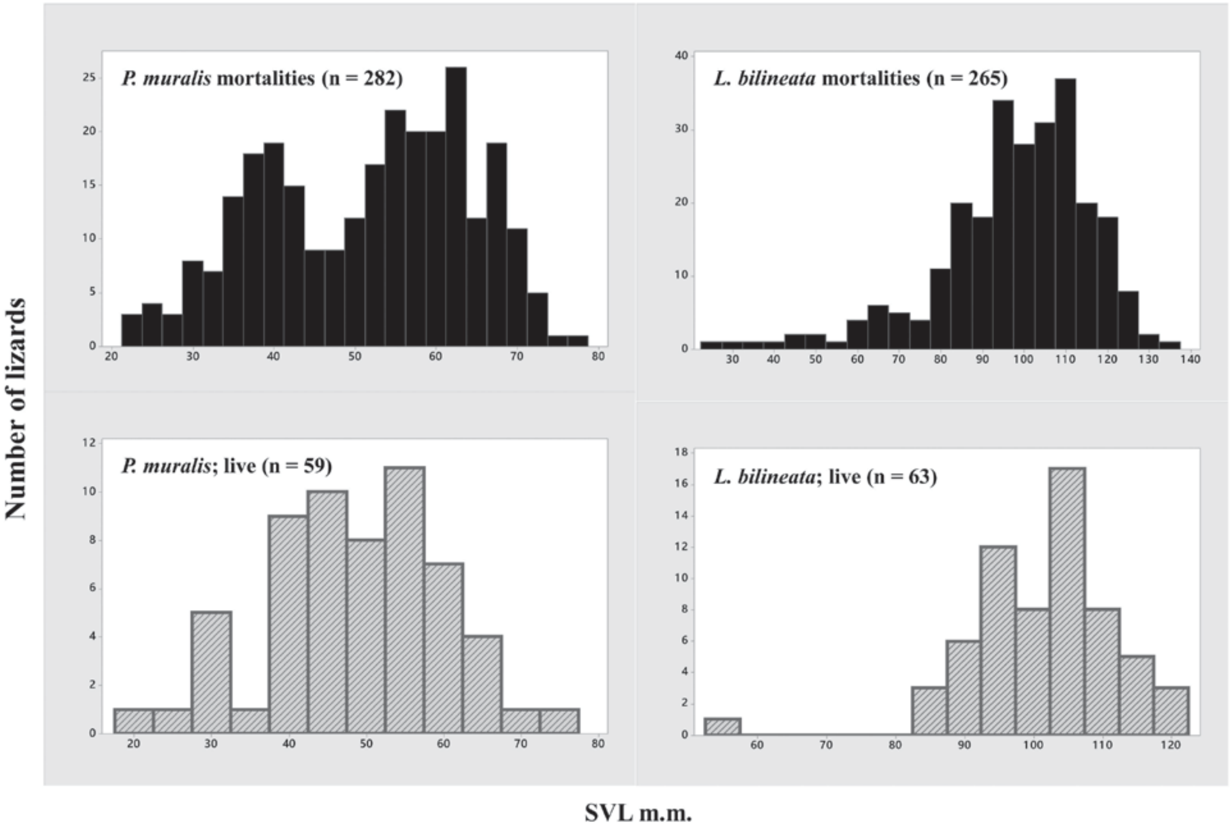

Figure 1. SVL's of lizards measured from 2005–2018. Live SVL's are approximate values derived from lizards that were sighted on roads and estimates considered possible. Note scale differences on the x-axis.

Table 1. Basic statistics of annual numbers of lizards found as mortalities or as live counts on roads over the 14 year period. See text for statistical comparisons.

	Mortalities *Mean* all years	**Std Dev**	**Max**	**Min**	**Live *Mean* all years**	**Std Dev**	**Max**	**Min**
P. muralis	20.1	14.7	46	3	5.1	4.5	16	1
L. bilineata	18.9	8.6	33	8	4.8	4.8	17	1

and mortalities peaked during September. These data are partly derived from Meek (2014) based on data collected between 2005 and 2013, with additional data from 2013 to 2018. Table 1 shows the basic statistics of the pooled annual data.

Long term trends.

Both species showed wide fluctuations in annual mortalities and live road presence. The *G*-tests for equality of annual counts indicated fluctuations were significant both in *L. bilineata*; mortalities, G = 49.48; live, G = 51.95; pooled, G = 65.49, all P <0.0001 and *P. muralis*; mortalities, G = 145.6; live, G = 43. 8; pooled, G = 154.8 all P <0.0001. Anderson Darling tests on annual numbers of lizards (mortalities + live) indicated normal distributions for both species (*L. bilineata* a^2 = 0.48, P = 0.2; *P. muralis* a^2 = 0.46, P = 0.22) with the *F*-test indicating that the variances of the annual counts for both species were in good agreement (F = 1.54, P = 0.44) as were the long term trends in annual fluctuations of both species (Pearson correlation, r = 0.68, P = 0.008). Figure 2 shows the trends along with the overall means across all years.

The regressions of annual road mortalities + live counts against year produced coefficients (Table 2) indicating either population stability or a significant increase in numbers during the study period (Fig 1). In *L. bilineata*, jackknifing identified 2012 with unusually high numbers and a potential influence function. However, re-analysis with the 2012 data jackknifed gave a pseudo-regression coefficient in agreement with the true coefficient (jackknifed 2012 m = 0.07±0.02, true m = 0.07±0.01). Jackknifing indicated unusually high numbers of *P. muralis* in 2010 but removal and re-analysis gave a pseudo-regression coefficient (0.15±0.04) in close agreement with the true coefficient (0.14±0.04). In neither species did Jackknife analysis support long-term population decline (Table 2).

Comparison of annual SVL was applied only to mortalities due to potentially greater error in the measurement of live lizards. There was no significant difference in annual mean SVL of road mortalities in *P. muralis* ($F_{(13,\ 266)}$ = 1.12, P = 0.35). However, significant

Table 2. Regression analysis of temporal changes in annual road mortalities and live counts of *L. bilineata* and *P. muralis*. The regression coefficients *m* are shown with standard errors along with values of *b* the y-intercepts. The *t*-tests and P-values represent the results of tests of the estimated regression coefficients against a hypothetical regression of 0, indicative of long-term population stability. The tests of M (mortalities) versus L (live counts) are intra-specific variance comparisons between annual counts. See text for further details.

L. bilineata	***m***	**Std error**	***b***	***t***	**p**	**tests M v L**
mortalities	0.07	0.02	-142	2.89	0.01	
live	0.08	0.06	-167	1.37	0.19	L=3.0, P=0.09
pooled	0.07	0.02	-147	3.03	0.01	
P. muralis						
mortalities	0.17	0.04	-350	3.87	0.002	
live	0.05	0.06	-109	0.98	0.35	L=14.1, P=0.001
pooled	0.14	0.04	-288	3.61	0.004	

differences were identified in *L. bilineata* ($F_{(13, 249)}$ = 3.94, P = 0.0001). Post hoc tests showed SVL's in 2012 were significantly longer and during 2005 and 2009 significantly smaller. *Lacerta bilineata* SVL's were generally longer when annual numbers were higher (Pearson correlation *r* = 0.56, P = 0.04) but not in *P. muralis* (Pearson correlation *r* = 0.31, P = 0.29). Figure 3 shows the general trends.

Data from the La Rochelle-Le Bout Blanc weather station indicated higher than average annual rainfall from 2009 – 2011 (mean increase 11.1 cm), the period preceding several years of high lizard numbers, but no longer-term correlation between lizard numbers and rainfall patterns could be found in either species (P = 0.43 & 0.10). Annual temperature changes are an additional possibility, but were moderately correlated only in *L. bilineata* (Pearson *r* = 0.57, P = 0.04).

DISCUSSION

The results indicate that in a fragmented landscape, despite wide annual fluctuations, numbers of both species were relatively stable over the 14 year time period, with no indications of population decline. A potential to recover from very low numbers is fast generation times (Barbault & Mou, 1988; Bauwens & Díaz-Uriarte, 1997) which must be a key factor in enabling long term population stability. Support for this notion is the capacity of introduced populations of *P. muralis* and *L. bilineata* to rapidly attain high numbers from small founding introductions (e.g. Hedeen 1984; Allan et al., 2006; Mole, 2010; Heym et al., 2013). This capability is apparently due to rapid growth and short time to maturity, which have been cited as key contributory factors in Canada where introduced *P. muralis* reached maturity in their second full summer. Where both species have been monitored as invasive species, rates of population increase were similar (Mole, 2010). This agrees well with populations in their native range (e.g. Bauwens & Díaz-Uriarte, 1997; Allan et al., 2006). In the present locality female *P. muralis* produce two clutches of eggs annually, that must also contribute to enabling rapid population increases. The high numbers in both species between 2010 and 2014 included a significant increase in SVL's in *L. bilineata* (Fig. 2). This could reflect a longer life span. For example, in western France potential maximums of 8 – 9 years have been observed (Saint Girons, et al., 1989). In general, larger lacertids live longer adult lives with higher annual fecundity than smaller species (e.g. Strijbosch, & Creemers, 1988; Bauwens & Díaz-Uriarte, 1997), but age at maturity is apparently similar in *L. bilineata* and *P. muralis* (Bauwens & Díaz- Uriarte, 1997) and may explain comparable inter-specific population trends over the 14-year time period.

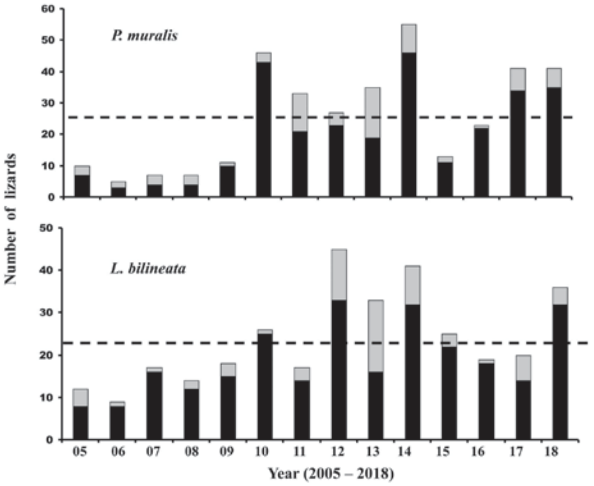

Figure 2. Histograms showing annual numbers of *P. muralis* and *L. bilineata* mortalities or live count presence on roads. Black bars represent road mortalities and grey bars live counts. The broken line indicates the overall mean of year counts for the pooled data of live lizards and road mortalities and represents the expected number under a null hypothesis of equality of annual counts. See text for further details.

Life spans and growth in lacertids are strongly influenced by climate (e.g. Roitberg & Smirna, 2006) and hence climate is probably the first area to examine for population drivers but little correlation was found in this study. However, rainfall has been shown to influence lizard populations in other regions (e.g. Tinkle, 1993; Spiller & Schoener, 1995; Gibbons et al., 2000) but weather effects on lizards are likely complex and must also involve additional variables such as food availability. It is clearly no simple task to identify climatic effects on

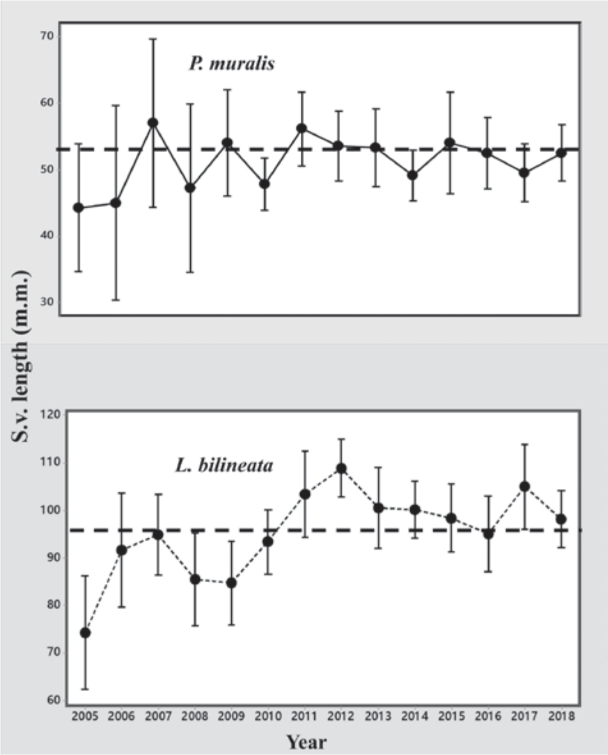

Figure 3. Annual changes in mean SVL (in mm) of *P. muralis* and *L. bilineata* road mortalities. Circles represent mean values and vertical bars 95 % confidence intervals. The broken lines show the degrees of departure of the annual means from the long-term means (mean of means). See text for further details.

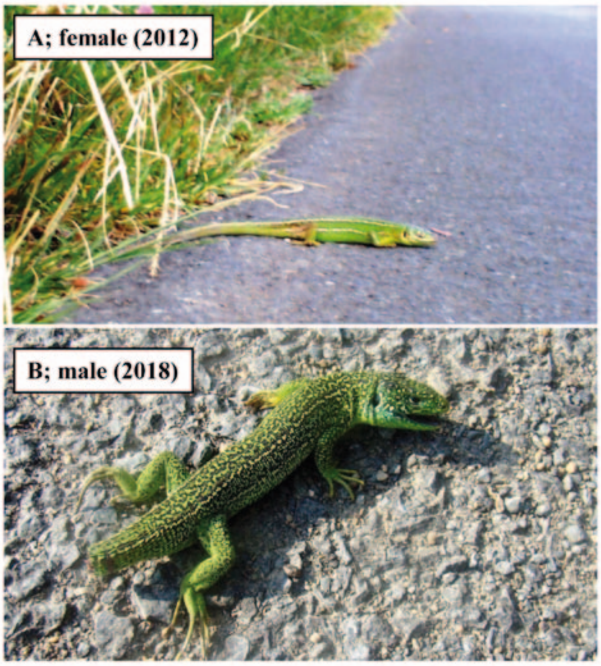

Figure 4. Examples of road-injured *L. bilineata* that appear unrelated to road traffic collisions. **A)** female 2012, SVL 97, **B)** male SVL 106. See text for details.

population fluctuation, especially from simple time series (Krebs & Berteaux, 2006; Knape & de Valpine, 2012; Flesch et.al., 2017). Of interest is that increases in lizard numbers commencing 2010 mirrored similar increases in sympatric amphibians (Meek, 2018 and unpublished data) suggesting that a more informative approach would be to simultaneously examine the ecology of several sympatric species.

In non-lacertid lizards, population fluctuations have been linked to population density by influencing growth rates and survivorship in yearling lizards (Dunham, 1981; Tinkle et al., 1993). Population density impacts on the lacertid *Z. vivipara* numbers due to male aggression towards adult females reducing survivorship and fecundity, leading to population decline (Le Galliard et al., 2005). In the present study, potential examples of intra-specific aggression in *L. bilineata* were found during years of high numbers in four males and one female. These lizards were found (April - May) on roads in an apparent state of semi-consciousness displaying no flight behaviour when approached with no apparent injuries (2), recent tail loss (2) and one example of head injuries (Meek, 2011). Except for one lizard, all recovered after treatment. Examples are shown in Fig. 4. *Podarcis muralis* and *L. bilineata* are known for intense territorial behaviour and intra-sexual conflict (Arnold, 2002) and density dependence aggressive encounters may serve to operate as a regulatory mechanism. Aggressive encounters that spilled onto roads resulting in mortalities from road vehicles have been observed in male *L. agilis* (Bird, personal communication).

Density dependence is now recognised as a common mechanism of population regulation (e.g. Brook & Bradshaw, 2006; Knape & de Valpine, 2012) but detection is problematic (Solow & Steele, 1990). Although analytic methods for detecting density dependence have improved in recent years, the required long-term time series studies are limited but crucial (Leão et al., 2018). In part this is due to various mathematical approaches giving conflicting results, and the quality of long-term time series (e.g. Knape, 2008; Knape & de Valpine, 2012), especially in lizards. Discussing amphibians Pechmann et al. (1991) cautioned that if population fluctuations are large relative to the length of the data set, certain trends could be misinterpreted as declines – this can be expected on other groups including lizards where fluctuations are a normal dynamic. The long-term studies that are required may have funding issues in addition to the logistic difficulties involved, however if used in conjunction with other approaches (e.g. skeletochronology; Smirina et al., 1984) may provide essential insight into lacertid population dynamics and are a fundamental requirement for our understanding of effects of habitat loss and climate change on animal populations (Araújo et al., 2006).

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