NORTH-WESTERN JOURNAL OF ZOOLOGY 15 (1): 55-61 ©NWJZ, Oradea, Romania, 2019
Article No.: e171511 *http://biozoojournals.ro/nwjz/index.html*

# Sexual maturation and reproduction of the Balkan green lizard *Lacerta trilineata* specimens in mainland and island populations from Greece

Kostas SAGONAS[1]*, Panayiotis PAFILIS[2], Petros LYMBERAKIS[3] and Efstratios D. VALAKOS[1]

1. Department of Human and Animal Physiology, Faculty of Biology, University of Athens, Panepistimioupoli Zografou, 15784 Athens, Greece.
2. Department of Zoology and Marine Biology, Faculty of Biology, University of Athens, Panepistimioupoli Zografou, 15784 Athens, Greece.
3. Natural History Museum of Crete, University of Crete, Knossos Ave, P.O. Box 2208, 71409 Irakleio, Crete, Greece.
*Corresponding author, K. Sagonas, E-mail: ksagonas@biol.uoa.gr

Received: 13. February 2017 / Accepted: 11. November 2017 / Available online: 29. November 2017 / Printed: June 2019

**Abstract.** Studies on life history characters are of pivotal importance to understand population dynamics and demography and, if required, to propose effective conservation measures. The Balkan green lizard (*Lacerta trilineata*) is the most widespread lizard species in the Balkans but, interestingly, there are no studies on its reproductive biology. Herein, we focused on life history traits of *L. trilineata*, examining 369 museum specimens deriving from 12 island and 5 mainland populations from Greece. We measured the testicle size and the length of the epididymis in males, and the presence, number and size of oviductal eggs and vitellogenic follicles in females during activity seasons (from March to September). Our results suggest that the annual reproductive cycle in both sexes starts in mid-April and ends in July, though insular lizards seem to slightly prolong their reproductive season. Both sexes reached sexual maturity at a minimum body size of approximately 80 mm. Clutch size varied greatly depending on maternal body size. Clutch size and mean egg volume differed between mainland and island populations: in a striking deviation from the island syndrome, insular females carried more (13) but smaller eggs compared to their mainland conspecifics (nine but larger eggs). Mean egg volume was negatively correlated with clutch size.

**Key words:** reproduction, Lacertidae, clutch size, islands, Greece.

## Introduction

Life history represents a constellation of traits that ultimately determine the success of a given species (or population) to colonize a given habitat (James 1991). Among the numerous traits engaged, subjected to trade-offs, age and size at sexual maturity, clutch size and volume, and mean offspring size stand out in shaping an organism's reproductive biology (Dunham et al. 1988, Meiri et al. 2012). Reproductive biology may vary considerably in temporal and spatial scale in response to different ecological and environmental conditions (Castilla & Bauwens 2000, Lukanov & Tzankov 2016). Such variations are well known from insular populations, where differences from mainland norms are magnified (MacArthur & Wilson 1967, Pafilis et al. 2011, Novosolov et al. 2013).

Insular populations often deviate from the mainland ones in many aspects of their overall biology (e.g. demography, physiology, morphology, behaviour, body size and feeding ecology), in response to the different ecological and physical features prevailing on the islands (Van Damme 1999, Buckley & Jetz 2007, Pafilis et al. 2011, Brock et al. 2014, Li et al. 2014, Sagonas et al. 2014). Life history also follows a distinct pattern on islands (Meiri et al. 2012, Novosolov et al. 2013). Animals may adopt *K* or *r* reproductive strategies that differ in the number and size of eggs/offsprings (Martín & López 2011). While *r*-strategists display early maturity, and produce large clutches of small eggs/offsprings, *K*-strategists mature later, increase the parental investment and produce less but larger eggs/offsprings (MacArthur & Wilson 1967). The strategy a population/species adopts depends mainly (but not exclusively) on the physical conditions of the habitat (Adamopoulou & Valakos 2000, Pafilis et al. 2011, Meiri et al. 2012, Polović et al. 2013). Unstable environments harbouring low population densities usually favor the *r*-strategy, while stable environments with dense populations favour *K*-strategists (Martín & López 2011). Islands have a rather stable and benign climate thanks to the buffering effect of the sea (Schwaner 1989, Whittaker & Fernández-Palacios 2007, Sagonas et al. 2013). Insular populations do not experience strong predation pressure and/or high interspecific competition thanks to the depauperate island communities (MacArthur & Wilson 1967, Whittaker & Fernández-Palacios 2007). Nonetheless, the lack of predators and competitors very often leads to high densities and, consequently, to high intraspecific competition (Cooper et al. 2014, Donihue et al. 2015). Ergo, island populations chose to invest more in somatic growth to survive intraspecific competition (Melton 1982, Pafilis et al. 2009) and less in reproduction, laying smaller clutches of larger eggs (*K*-strategy), one of the most typical parameters of the so-called 'island syndrome' (Adler & Levins 1994).

The genus *Lacerta* sensu stricto (green lizards; Nettman 2001) comprises nine species that occur in Europe and western Asia (Arnold et al. 2007). *Lacerta trilineata* is the largest green lizard [snout to vent length (SVL) up to 16 cm] and the most widespread lizard in the Balkan Peninsula (Arnold & Ovenden 2002). However, though the reproductive biology of other *Lacerta* species has been adequately studied (Marco et al. 1994, in den Bosch & Bout 1998, Amat et al. 2000, Saveliev et al. 2006), the life history of the very common *L. trilineata* remains largely understudied, with only few available data on reproductive output and egg incubation period (Nettmann & Rykena 1984).

In this study, we provide the first thorough life history data for *L. trilineata*. To that end, we dissected museum specimens from 12 island and five mainland populations from Greece, and measured several reproductive traits (oviductal egg number, size and volume; number and volume of vitellogenic follicles; testicle size and volume and the length of epididymis). We aimed to define the mean clutch size and volume, the duration of the reproductive cycle and the body size at sexual maturity. We also intended to detect whether island and mainland populations differ in their reproductive biology. Recent studies on this species highlighted the effect of insularity on trophic ecology, thermal physiology and morphology of the feeding apparatus (Sagonas et al. 2013, Sagonas et al. 2014, Sagonas et al. 2015a, Sagonas et al. 2015b). As *Lacerta trilineata* is distributed both on islands and the mainland Greece, it is possible to examine the potential effect of insularity on the reproductive biology within a single species, eliminating any phylogenetic effects. We postulated that insular lizards would differ from mainland populations and would shift towards *K* strategy (smaller clutches of larger eggs), in response to island life particularities (Novosolov & Meiri 2013).

## Materials and Methods

### Specimens and measurements

*Lacerta trilineata* is a diurnal, heliothermic lizard that feeds on a great variety of invertebrates in continental habitats, whereas insular populations may enhance their diet with plant material (Valakos et al. 2008, Sagonas et al. 2014, Sagonas et al. 2015a). In Greece, the species occurs in the majority of mainland and island biotopes (Schmidtler 1997) and is the most frequently observed lizard (Valakos et al. 2008).

We examined 369 specimens (137 males, 170 females and 62 juveniles/subadults) belonging to the Herpetological Collection of the Zoological Research Institute and Museum Alexander Koening in Bonn (*N*= 129) and the Natural History Museum of Crete (*N* = 240). 192 of the specimens corresponded to insular populations (12 from Lesvos, 13 from Milos, 12 from Naxos, 10 from Andros, 9 from Rhodes, 16 from Skiathos, 7 from Skopelos, 8 from Kythira, 18 from Skyros, 7 from Serifos, 4 from Corfu and 76 from Crete) and 177 from the mainland (51 from Thessaly, 26 from Epirus, 29 from Peloponnese, 24 from Macedonia and 47 from Sterea Ellada, Fig. 1). We measured the body size (SVL) and recorded the sex and month of capture for all specimens. In male individuals, we recorded the size of the right testicle by measuring the longest and shortest axes and calculated its volume and also measured the length of epididymis. In females, we recorded (if present) the number and diameter of vitellogenic follicles, the length and width of oviductal eggs, clutch size (the number of oviductal eggs), clutch volume (the sum of all eggs' volume) and mean egg volume. Female sexual maturity was assessed by the presence of vitellogenic follicles larger than 3 mm in diameter or enlarged oviductal eggs (Vitt 1983, Adamopoulou & Valakos 2000). Male sexual maturity was defined by the size of testicles and the length of epididymis (Tinkle 1967a, Sexton & Turner 1971, Marco et al. 1994, Galán 1996, Adamopoulou & Valakos 2000, Saveliev et al. 2006, Rezende-Pinto et al. 2009). Additionally, female specimens were searched for signs of reproductive activity such as bites in the abdomen (i.e. copulation marks). Small-sized lizards without vitellogenic follicles and oviductal eggs were classified as non-reproductive, non-adult females.

All measurements were recorded using a digital caliper (Silverline 380244, accurate to 0.01mm). Eggs and testicles volume was calculated by approximating the volume of an ellipsoid: $V = (4/3)\ \pi ab2$, where a is half the longest axis and b is half the shortest axis (Mayhew 1963).

### Statistical analyses

Data were examined for heteroscedasticity and normality and were transformed if parametric assumptions were not met. If transformations were unsuccessful, non-parametric tests were performed, otherwise we used parametric tests. We conducted *t*-test to compare SVL between sites (mainland vs. islands) and sexes. To determine male body size at sexual maturity, we performed Pearson correlation analysis between testicles volume and testicles length and SVL. We used Kruskal-Wallis analysis of variance (ANOVA) to estimate the monthly gonadal activity in males, taking into account testicle volume (as dependent variable) and month (as independent variable).

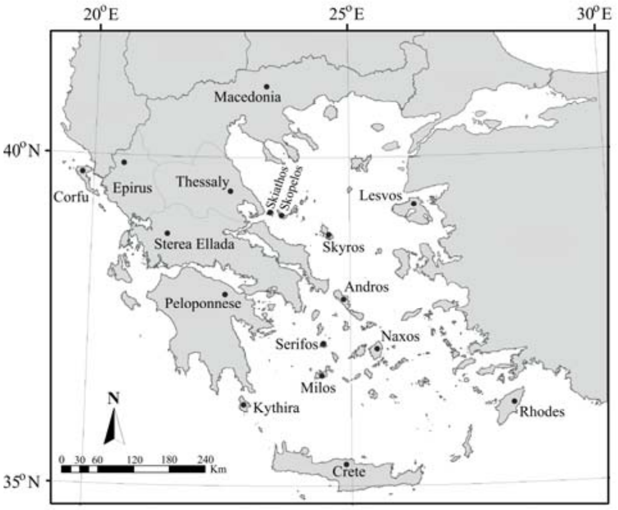

Figure 1. Map of Greece at East Mediterranean Sea, denoting the sampling localities.

In females, we used Pearson correlation to search for relations between clutch size and SVL, mean egg volume and SVL, and clutch size with mean egg volume. The reproductive cycle of female lizards was determined based on the presence of oviductal eggs and/or vitellogenic follicles. Furthermore, we conducted Mann-Whitney U test between mainland and island females to search for possible geographical differences in clutch size (i.e. the number of oviductal eggs), the number of vitellogenic follicles, mean oviductal egg volume and clutch volume. To remove any SVL effect on clutch size (intercept = 66.22 ± 2.28, slope = 4.09 ± 0.10, $P < 0.001$, $N = 61$) between habitats, we did *t*-test analysis using the residuals of the number of eggs against SVL. All statistical analyses were carried out in R v.3.2.3 (R Development Core Team 2015).

## Results

### Body size at sexual maturity

Pearson correlation analysis between SVL and testicle volume, and between SVL and testicle length revealed two distinct groups in males (Fig. 2). The first group comprised individuals with SVL above 80 mm, whereas lizards with SVL below 75 mm were included in the second group. The minimum body size of males having large, round and inflated testicles and distended epididymis (~11-13 mm length) was 78.3 mm (Fig. 2 and Table 1). It is worth noting that only two out of the 191 examined specimens were reproductively mature (~1%) and had SVL above 80 mm. Male lizards with SVL less than 75 mm were clearly immature, having small, flat testicles and tenuous epididymis (~6-9 mm length).

Likewise, in females we found that lizards larger than 79.4 mm had signs of copulation marks, whilst specimens larger than 82.1 mm bore oviductal eggs or vitellogenic follicles (Table 1).

### Female reproductive traits

The percentage of sexually mature females with or without vitellogenic follicles and/or oviductal eggs between March and September is plotted in Fig. 3. The first vitellogenic follicles appeared in mid-April for both mainland and island populations, with a peak occurring from mid-April to mid-May (Fig. 3). Larger females (SVL = 125.06 ± 14.18) were able

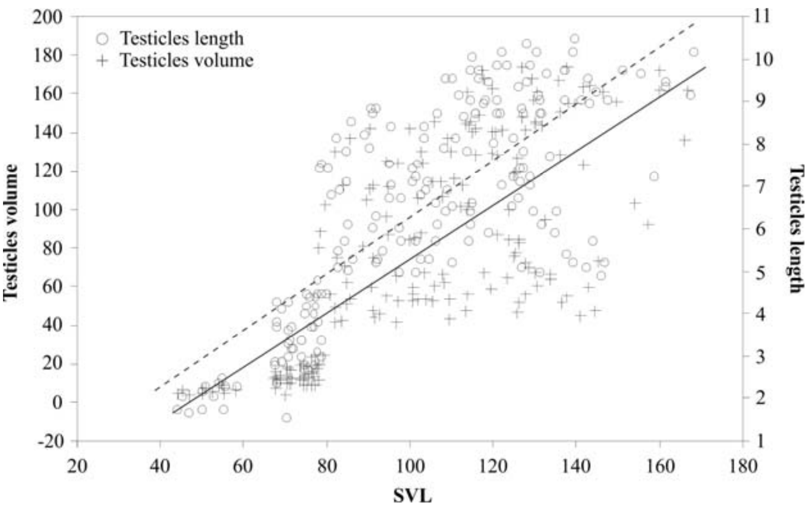

Figure 2. Pearson correlation analysis between body size and testicles volume as well as body size and testicles length for all male specimens and populations examined. Open circles refer to testicles volume, while crosses to testicles length.

Table 1. Descriptive statistics for measurements of the number of vitellogenic follicles, clutch size (number of oviductal eggs), clutch volume (total eggs volume), mean egg volume, size at sexual maturity for examined male and female *Lacerta trilineata* specimens for both mainland and island populations. The mean ± standard deviation (SE) and sample size (*N*) are given for each parameter.

| Variable | Islands | Mainland |
|---|---|---|
| Number of vitellogenic follicles | 15.91 ± 2.97 (*22*) | 9.53 ± 6.83 (*17*) |
| Clutch size | 12.77 ± 2.92 (*31*) | 9.42 ± 1.87 (*33*) |
| Clutch volume (mm$^3$) | 6597.92 ± 1665.49 (*31*) | 5966.73 ± 1972.37 (*33*) |
| Mean oviductal volume (mm$^3$) | 530.32 ± 122.24 (*31*) | 656.37 ± 250.99 (*33*) |
| Mean SVL reproductive female | 108.66 ± 20.75 (*88*) | 108.87 ± 14.79 (*76*) |
| Minimum SVL reproductive female | 79.4 mm (*94*) | 81.3 mm (*84*) |
| Mean SVL reproductive male | 115.31 ± 20.82 (*62*) | 114.49 ± 20.72 (*75*) |
| Minimum SVL reproductive male | 78.3 mm (*95*) | 80.6 mm (*96*) |

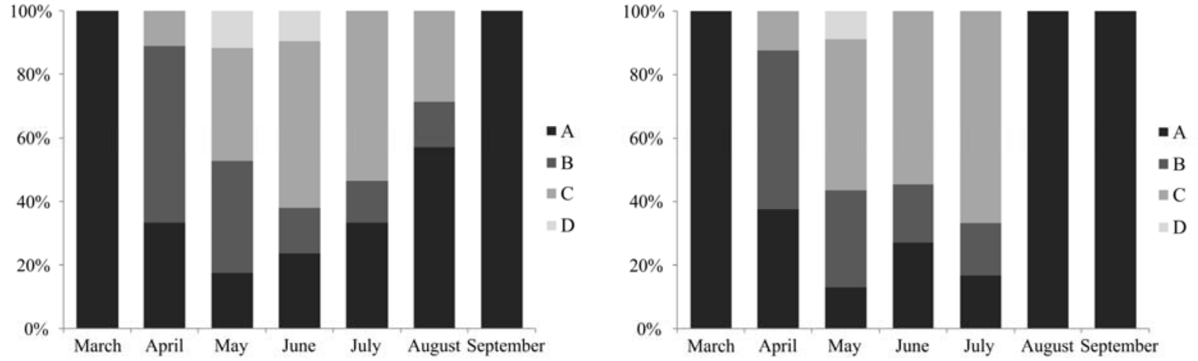

Figure 3. Monthly variations from March to September in the percentage of sexually mature females of insular and mainland populations of *Lacerta trilineata* (N = 163). Females with (A) refer to no reproductive activity, (B) vitellogenic follicles, (C) oviductal eggs, (D) oviductal eggs and vitellogenic follicles.

to produce more than one clutch per year compared to the smaller ones (105.19 ± 20.05; Mann-Whitney test; *Z* = 2.31, *P* = 0.02), as indicated by the simultaneous occurrence of oviductal eggs and vitellogenic follicles (Fig. 3). Mainland and island females did not differ in their SVL (t-test; *t* = -0.09, *df* = 162, *P* = 0.93).

Clutch size (12.77 ± 2.92 eggs vs. 9.42 ± 1.87 eggs; Mann-Whitney test; *Z* = 4.45, *P* < 0.001) and the number of vitellogenic follicles (15.91 ± 2.97 vs. 9.53 ± 6.83; Mann-Whitney test; *Z* = 4.91, *P* < 0.001) showed significant differences, with island females laying more eggs than their mainland conspecifics (Table 1). On the other hand, average egg volume from insular females was significantly smaller than that from mainland females (530.32 ± 122.24 mm$^3$ vs. 656.37 ± 250.99 mm$^3$ respectively; Mann-Whitney test; *Z* = -1.98, *P* = 0.04; Table 1). However, average clutch volume was similar for both island and mainland females (Mann-Whitney test; *Z* = 0.91, *P* = 0.36; Table 1). Pearson correlation analysis revealed that the number of oviductal eggs (islands: *r* = 0.82, *P* < 0.001, *N* = 31; mainland: *r* = 0.52, *P* = 0.002, *N* = 33) and vitellogenic follicles (islands: *r* = 0.67, *P* < 0.001, *N* = 22; mainland: *r* = 0.53, *P* = 0.03, *N* = 17) were positively corre-

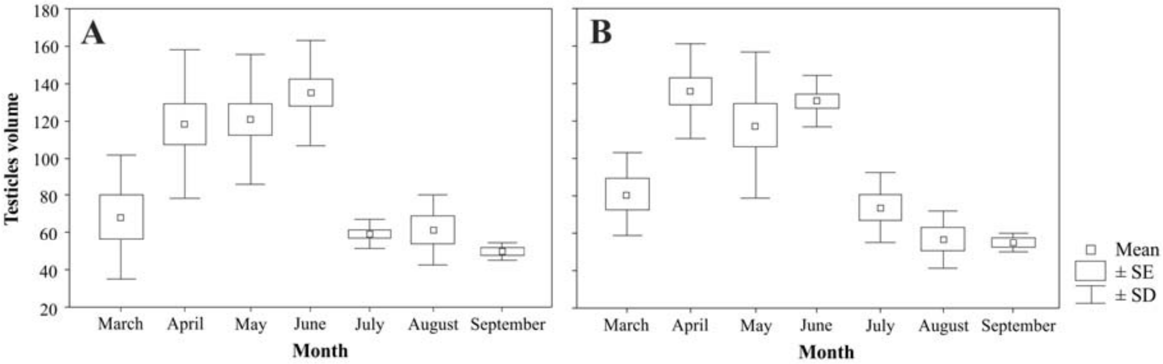

Figure 4. Monthly variations of testicular volume from March to September for A) mainland and B) island adult males.

lated to maternal body size. Whereas, mean oviductal egg volume and clutch size were negatively correlated to each other (islands: $r$ = -0.51, $P$ = 0.003; mainland: $r$ = -0.48, $P$ = 0.005). We found no relation between maternal body size and the mean volume of oviductal eggs (islands: $r$ = 0.25, $P$ = 0.17, $N$ = 31; mainland: $r$ = 0.01, $P$ = 0.94, $N$ = 33).

### Male reproductive traits

As expected, testicular volume was positively correlated to SVL (islands: $r$ = 0.52, $P$ = 0.001, $N$ = 37; mainland: $r$ = 0.33, $P$ = 0.03, $N$ = 44) during the reproductive period (April to June). Spermatogenesis in males occurred from mid-April until mid-June, when testicular volume is maximal (Kruskal-Wallis ANOVA; islands: $H_{6,62}$ = 39.68, $P$ < 0.001; mainland: $H_{6,75}$ = 43.96, $P$ < 0.001; Fig. 4). Reduction of testicle volume occurred rapidly at the end of the reproductive period in June (Fig. 4).

## Discussion

Here we report the first detailed information on the reproductive biology of *L. trilineata*, one of the most common lacertids in the Balkans, whose life-history remained largely unknown to date (Nettmann & Rykena 1984, Valakos et al. 2008). Like many lacertid species, *L. trilineata* demonstrates a narrow reproductive cycle, produces more than one clutch per year and displays the classic trade-off between egg size and clutch size. However, our study yielded some unexpected results regarding the clutch size and egg volume, namely that insular populations laid more but smaller eggs than the mainland populations, which deviate from what the islands syndrome predicts.

### Body size at sexual maturity

To our knowledge, these are the first empirical data on the relation between body size and reproduction to define sexual maturity in *L. trilineata*. SVL and copulation marks are often used to define adulthood in lizards (Ruby & Dunham 1985, Galán 1996, in den Bosch & Bout 1998, Vitt & Caldwell 2014). In green lizards, in particular, SVL is considered an important proxy for age (Arnold 1987, Angelici et al. 1997, Amat et al. 2000, Pafilis & Valakos 2008). Reptiles, however, grow continuously and show asymptotic growth curves (Kratochvíl & Frynta 2002, Vitt & Caldwell 2014). Thereby, estimations of sexual maturity on the basis of SVL can, sometimes, provide erroneous conclusions (Daan 1967).

Our results revealed that both sexes initiate reproductive activities and become sexually mature at approximately 80 mm SVL, a body size threshold that was observed for both mainland and island lizards (Table 1). This is in agreement with the 70-80 mm SVL threshold that has been introduced by Arnold (1987) and Pafilis & Valakos (2008) to distinguish between adult and juvenile *L. trilineata*. In other words, our findings suggest that sexual maturity in *L. trilineata* is strongly associated with a minimum body size rather than a certain age, and that distinguishing immature from mature lacertid lizards on the basis of body length is plausible (Tinkle 1967b, Galán 1996, Castilla & Bauwens 2000). Nevertheless, to fully unravel this issue further data on the growth rate of both sexes are required.

### Reproductive cycle of *L. trilineata* and geographical differences

Like many other lacertids (Maragou et al. 1999, Amat et al. 2000, Galan 2004), *L. trilineata* demonstrated a well-defined reproductive period (copulation activities and egg-laying), which starts by late March and lasts till August (Valakos et al. 2008). However, small differences in the reproductive cycle of mainland and island populations were revealed.

The simultaneous occurrence of oviductal eggs and vitellogenic follicles (Fig. 3) in six female specimens (four from the islands and two from the mainland) indicates that *L. trilineata* may produce more than one clutch per year (Vitt 1982, Polović et al. 2013) as *L. agilis* (Jensen 1981) and *L. viridis* do (Rehák 2015). Females that were able to produce a second clutch were larger than females with a single clutch. This finding conforms to the typical trend predicting that the number of clutches per year depends on female SVL, since large females usually reproduce earlier in the breeding season and are able to produce multiple clutches (Galán 1996, Castilla & Bauwens 2000).

The comparison between island and mainland females yielded an interesting result: oviductal eggs or vitellogenic follicles were absent from mainland females after July but were present in insular females that displayed a slightly prolonged reproductive cycle extending till the end of August (Fig. 3). We believe that this divergence could be attributed to the more benign island climate, which is more stable and has fewer annual fluctuations compared to the mainland

(Schwaner 1989, Whittaker & Fernández-Palacios 2007, Sagonas et al. 2013). These favourable conditions allow insular lizards to start reproducing earlier and also lay their eggs later within the year. Similar spatial or temporal interpopulation differences in the reproductive output of a single species in response to environmental conditions are rather common in reptiles (e.g. Marco et al. 1994, Amat et al. 2000, Castilla & Bauwens 2000, Pizzatto & Marques 2006). Males exhibited a synchronized, but shorter, reproductive cycle (Amat et al. 2000) with females. As such, testicular volume follows a pattern of seasonal variation (Fig. 4). In contrast to females, males' gonadal activity did not differ between insular and mainland populations and the period of spermatogenesis occurred during spring, from April to June, a period that also coincides with the copulation marks observed on sexual females.

### Reproductive output and variation between island and mainland populations

The clutch size of the Greek *L. trilineata* populations showed a high variation (7-18 eggs) in accordance with the only other report we are aware of (4-30; for a review see Nettmann & Rykena 1984), falling within the range reported for other *Lacerta* members (in den Bosch & Bout 1998, Amat et al. 2000, Valakos et al. 2008, Rehák 2015). However, significant geographical differences in the reproductive output arose. A rather surprising finding was related to the number and size of eggs: females from the islands laid more and smaller eggs than their mainland conspecifics, contradicting our initial hypothesis.

Irrespective of maternal origin (island or mainland) our results showed that the number of oviductal eggs and vitellogenic follicles were positively correlated to maternal body size. The increase in the reproductive output with female SVL is widespread, though not universal, in lacertid lizards and is linked to the space available in the body cavity (Roff 1992, Maragou et al. 1999, Castilla & Bauwens 2000, Pafilis et al. 2011). This increase in clutch size, however, led to a reduction in the mean egg size, and smaller females from both habitats were able to produce large eggs. This finding complies with previous studies reporting that larger clutches comprise smaller eggs regardless of dam body size due to physical limitations (Vitt & Congdon 1978, Castilla & Bauwens 1989, 2000, Winck & Rocha 2012).

The comparison between island and mainland populations showed that insular females demonstrated a pronounced increase in clutch size and the number of vitellogenic follicles compared to their mainland conspecifics. Variation in the clutch size among different populations of a single species has been reported previously (Chondropoulos & Lykakis 1983, Pafilis et al. 2011) and has been attributed mainly to differences in body size of females. Interestingly, in the case of *L. trilineata*, the increase in the reproductive output was not followed by an increase in female body length, and females from both mainland and islands had similar SVLs. Nevertheless, clutch size has been reported to relate to several biotic and abiotic conditions. As such, the observed differences could be the result of any of the following factors: climate, latitude, food resources, predation pressure and/or interspecific competition that deviate between mainland and island habitats (Ballinger 1977, Vitt 1983, Taylor et al. 1992, Maragou et al. 1999, Pafilis et al. 2011). In order to fully understand the underlying reasons for this variation, further research is required.

Oviductal egg volume, but not clutch volume, was also significantly reduced in island populations (Table 1). In reptiles, trades-off between egg size and clutch size are common and usually related either to space constraints or energy allocation and nutrient limitations (Castilla & Bauwens 2000, Uller et al. 2009). In that way, lizards maintain an optimum balance between egg number and the energy expenditure per egg/offspring. Together with the fact that clutch volume was similar for both island and mainland females, which in turns suggests that *L. trilineata* has reached an evolutionary optimum in clutch volume (Adamopoulou & Valakos 2000, Pafilis et al. 2011), we assumed that the increased egg number of island *L. trilineata* resulted in a decrease in the average egg volume.

An alternative explanation for the smaller size of eggs in insular populations could be the different climatic conditions on islands. Spatial and temporal temperature fluctuation is less severe on islands compared to the mainland (Schwaner 1989, Whittaker & Fernández-Palacios 2007, Sagonas et al. 2013), allowing insular *L. trilineata* populations to prolong their reproductive period for more than a month (Fig. 3). In that way, smaller eggs that require shorter incubation period at a given temperature (Chondropoulos & Lykakis 1983, Sinervo 1990) are preferred as they result in hatchlings that emerge earlier in autumn when food availability is higher (Sagonas et al. 2015a).

However, these findings contradict the island syndrome, according to which insular populations reduce the number but increase the size of offspring in respect to the particular conditions prevailing on islands (Adler & Levins 1994). Island communities are depauperate in predators and competitors supporting high lizard densities (MacArthur & Wilson 1967, Rodda et al. 2001). These dense populations suffer from high intraspecific competition that may include cannibalism (Blondel 2000, Cooper et al. 2014, Novosolov et al. 2016). As a result, island populations adopt the *K* selection strategy to survive in such crowded niches, investing in fewer, but larger, offspring that have a higher probability of surviving to adulthood (Melton 1982, Adler & Levins 1994). In contrast to the aforementioned, our results suggest that *L. trilineata* islanders are *r*-strategists that increased their energy allocation towards reproduction, laying more but smaller eggs. The generality of the island syndrome has been questioned by recent studies that reported alternatives. Insularity is considered a major promoter of species diversification and island populations usually deviate from their mainland ones in several ways (Vicente 1999). Surprisingly, however, our results did not corroborate the typical assumptions of the island syndrome. Our study offers support to previous research that challenged the generality of the island syndrome and brought out alternative reproductive strategies (Raia et al. 2010, Pafilis et al. 2011, Monti et al. 2013, Novosolov & Meiri 2013).

**Acknowledgements**. We would like to thank Prof. Dr. W. Boehme, who kindly allowed us to examine the *L. trilineata* specimens of the Zoological Research Museum Alexander Koenig in Bonn.

## References

Adamopoulou, C., Valakos, E. (2000): Small clutch size in a Mediterranean endemic lacertid (*Podarcis milensis*). Copeia 2000: 610-614.

Adler, G.H., Levins, R. (1994): The island syndrome in rodent populations. Quarterly Review of Biology 69: 473-490.

Amat, F.O., Llorente, G.A., Carretero, M.A. (2000): Reproductive cycle of the sand lizard (*Lacerta agilis*) in its southwestern range. Amphibia-Reptilia 21: 463-476.

Angelici, F.M., Luiselli, L., Rugiero, L. (1997): Food habits of the green lizard, *Lacerta bilineata*, in central Italy and a reliability test of faecal pellet analysis. Italian Journal of Zoology 64: 267-272.

Arnold, E.N. (1987): Resource partition among lacertid lizards in southern Europe. Journal of Zoology 1: 739-782.

Arnold, E.N., Arribas, O., Carranza, S. (2007): Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa 1430: 3-86.

Arnold, E.N., Ovenden, D.W. (2002): Reptiles and Amphibians of Europe. Princeton University Press, Princeton.

Ballinger, R.E. (1977): Reproductive strategies: food availability as a source of proximal variation in a lizard. Ecology 58: 628-635.

Blondel, J. (2000): Evolution and ecology of birds on islands: Trends and prospects. Vie et Milieu 50: 205-220.

Brock, K.M., Donihue, C.M., Pafilis , P. (2014): Novel records of frugivory and ovophagy in *Podarcis* lizards from East Mediterranean Islands. North-Western Journal of Zoology 10: 223-225.

Buckley, L.B., Jetz, W. (2007): Insularity and the determinants of lizard population density. Ecology Letters 10: 481-489.

Castilla, A.M., Bauwens, D. (1989): Reproductive characteristics of the lacertid lizard *Lacerta lepida*. Amphibia-Reptilia 10: 445-452.

Castilla, A.M., Bauwens, D. (2000): Reproductive characteristics of the lacertid lizard *Podarcis atrata*. Copeia 2000: 748-756.

Chondropoulos, B.P., Lykakis, J.J. (1983): Ecology of the Balkan wall lizard, *Podarcis taurica ionica* (Sauria: Lacertidae) from Greece. Copeia 4: 991-1001.

Cooper, J.W.E., Dimopoulos, I., Pafilis, P. (2014): Sex, age and population density affect aggressive behaviors in island lizards promoting cannibalism. Ethology 121: 260-269.

Daan, S. (1967): Variation and taxonomy of the hardun, *Agama stellio* (Linnaeus, 1758) (Reptilia, Agamidae). Beaufortia 14: 109-134.

Donihue, C.M., Brock, K.M., Foufopoulos, J., Herrel, A. (2015): Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. Functional Ecology: 30(4).: 566-575.

Dunham, A.E., Miles, D.B., Reznick, D.N. (1988): Patterns in squamate reptiles. pp.441-522. In: Gans, C., Huey, R.B. (eds.), Biology of the Reptilia. Alan R. Liss, New York.

Galan, P. (2004): Structure of a population of the lizard Podarcis bocagei in northwest Spain: variations in age distribution, size distribution and sex ratio. Animal Biology 54: 57-75.

Galán, P. (1996): Sexual maturity in a population of the lacertid lizard *Podacis bocagei*. Herpetological Journal 6: 87-93.

in den Bosch, H.A.J., Bout, R.G. (1998): Relationships between maternal size, egg size, clutch size, and hatchling size in European lacertid lizards. Journal of Herpetology 32: 410-417.

James, C.D. (1991): Population dynamics, demography, and life history of sympatric scincid lizards (*Ctenotus*) in central Australia. Herpetologica 47: 194-210.

Jensen, J.K. (1981): Sand lizard (*Lacerta agilis* L.) with a second clutch in Denmark. Amphibia-Reptilia 2: 267-267.

Kratochvíl, L., Frynta, D. (2002): Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). Biological Journal of the Linnean Society 76: 303-314.

Li, B., Belasen, A., Pafilis, P., Bednekoff, P., Foufopoulos, J. (2014): Effects of feral cats on the evolution of anti-predator behaviours in Island reptiles: Insights from an ancient introduction. Proceedings of the Royal Society B: Biological Sciences 281.

Lukanov, S., Tzankov, N. (2016): Life history, age and normal development of the Balkan-Anatolian crested newt (*Triturus ivanbureschi* Arntzen and Wielstra, 2013) from Sofia district. North-Western Journal of Zoology 12: 22-32.

MacArthur, R.H., Wilson, E.O. (1967): The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Maragou, P., Chondropoulos, B., Valakos, E. D. (1999): Comparative data on reproduction in *Podarcis erhardii*, *Podarcis peloponnesiaca*, and *Podarcis taurica* (Reptilia, Sauria, Lacertidae). Israel Journal of Zoology 454: 487-496.

Marco, A., Pérez-Mellado, V., Gil-Costa, M.J. (1994): Reproductive strategy in a montane population of the lizard *Lacerta schreiberi* (Sauna: Lacertidae). Herpetological Journal 4: 49-55.

Martín, J., López, P. (2011): Pheromones and Reproduction in Reptiles. pp. 141-167. In: David, O.N., Kristin, H.L. (eds.), Hormones and Reproduction of Vertebrates. Academic Press, London.

Mayhew, W.W. (1963): Reproduction in the granite spiny lizard, *Sceloporus orcutti*. Copeia 1963: 144-152.

Meiri, S., Brown, J.H., Sibly, R.M. (2012): The ecology of lizard reproductive output. Global Ecology and Biogeography 21: 592-602.

Melton, R.H. (1982): Body size and island *Peromyscus*: a pattern and a hypothesis. Evolutionary Theory & Review 6: 113-126.

Monti, D.M., Raia, P., Vroonen, J., Maselli, V., Van Damme, R., Fulgione, D. (2013): Physiological change in an insular lizard population confirms the reversed island syndrome. Biological Journal of the Linnean Society 108: 144-150.

Nettman, H.K. (2001): Die Smaragdeidechsen (*Lacerta* s. str.) – Eine Übersicht über Verwandtschaft und Formenvielfalt. Mertensiella 13: 11-32.

Nettmann, H.K., Rykena, S. (1984): *Lacerta trilineata* (Bedriaga, 1886) - Riesensmaragdeidechse [Balkan green lizard]. pp. 100-128. In: Böhme, W. (ed.), Handbuch der Reptilien und Amphibien Europas, Echsen (Sauria) II. Wiesbaden: AULA-Verlag, German.

Novosolov, M., Meiri, S. (2013): The effect of island type on lizard reproductive traits. Journal of Biogeography 40: 2385-2395.

Novosolov, M., Raia, P., Meiri, S. (2013): The island syndrome in lizards. Global Ecology and Biogeography 22: 184-191.

Novosolov, M., Rodda, G.H., Feldman, A., Kadison, A.E., Dor, R., Meiri, S. (2016): Power in numbers. Drivers of high population density in insular lizards. Global Ecology and Biogeography 25: 87-95.

Pafilis, P., Foufopoulos, J., Sagonas, K., Runemark, A., Svensson, E., Valakos, E. D. (2011): Reproductive biology of insular reptiles: Marine subsidies modulate expression of the "Island Syndrome". Copeia 2011: 545-552.

Pafilis, P., Meiri, S., Foufopoulos, J., Valakos, E. (2009): Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften 96: 1107-1113.

Pafilis, P., Valakos, E.D. (2008): Loss of caudal autotomy during ontogeny of Balkan green lizard, *Lacerta trilineata*. Journal of Natural History 42: 409-419.

Pizzatto, L., Marques, O.A.V. (2006): Interpopulational variation in reproductive cycles and activity of the water snake *Liophis miliaris* (Colubridae) in Brazil. Herpetological Journal 16: 353-362.

Polović, L., Pešić, V., Ljubisavljević, K., Čađenović, N. (2013): Preliminary data on the reproductive characteristics and diet in an insular population of the lacertid lizard *Algyroides nigropunctatus*. North-Western Journal of Zoology 9: 201-205.

R Development Core Team (2015): R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raia, P., Guarino, F., Turano, M., Polese, G., Rippa, D., Carotenuto, F., Monti, D., Cardi, M., Fulgione, D. (2010): The blue lizard spandrel and the island syndrome. BMC Evolutionary Biology 10: 289.

Rehák, I. (2015): Protecting and managing a local population of the European Green lizard *Lacerta viridis* at the Prague Zoo, Czech Republic. International Zoo Yearbook 49: 56-66.

Rezende-Pinto, F.M., Verrastro, L., Zanotelli, J.C., Barata, P.C.R. (2009): Reproductive biology and sexual dimorphism in *Cnemidophorus vacariensis* (Sauria, Teiidae) in the grasslands of the Araucaria Plateau, southern Brazil. Iheringia. Série Zoologia 99: 82-91.

Rodda, G.H., Perry, G., Rondeau, R., Lazell, J. (2001): The densest terrestrial vertebrate. Journal of Tropical Ecology 17: 331-338.

Roff, D.A. (1992): The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Ruby, D.E., Dunham, A.E. (1985): A population analysis of the ovoviviparous lizard *Sceloporus jarrovi* in the Pifialeño mountains of southeastern Arizona. Herpetologica 40: 425-436.

Sagonas, K., Pafilis, P., Lymberakis, P., Donihue, C. M., Herrel, A., Valakos, E. D. (2014): Insularity affects head morphology, bite force and diet in a Mediterranean lizard. Biological Journal of the Linnean Society 112: 469-484.

Sagonas, K., Pafilis, P., Lymberakis, P., Valakos, E.D. (2015a): Trends and patterns in the feeding ecology of the widespread Balkan lizard *Lacerta trilineata* (Squamata: Lacertidae) in insular and continental Greece. North-Western Journal of Zoology 11: 117-126.

Sagonas, K., Pafilis, P., Valakos, E.D. (2015b): Effects of insularity on digestive performance: living in islands induces shifts in physiological and morphological traits in a Mediterranean lizard? The Science of Nature 102: 55-62.

Sagonas, K., Valakos, E.D., Pafilis, P. (2013): The impact of insularity on the thermoregulation of a Mediterranean lizard. Journal of Thermal Biology 38: 480-486.

Schmidtler, J.F. (1997): *Lacerta trilineata* Bedriaga, 1886. pp. 264-265. In: Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martinez Rica, J.P., Maurin, H., Oliveira, M.E., Sofianidou, T.S., Veith, M., Zuiderwijk, A. (eds.), Atlas of amphibians and reptiles in Europe. Societas Europaea Herpetologica & Museum National d'Histoire Naturelle, Paris.

Schwaner, T.D. (1989): A field study of thermoregulation in black tiger snakes (*Notechis ater niger*: Elapidae) on the Franklin Islands, South Australia. Herpetologica 45: 393-401.

Sexton, O.J., Turner, O. (1971): The reproductive cycle of a neotropical lizard. Ecology 52: 159-164.

Sinervo, B. (1990): The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. Evolution 44: 279-294.

Taylor, H.L., Cooley, C.R., Aguilar, R.A., Obana, C.J. (1992): Factors affecting clutch size in the teiid lizards *Cnemidophorus tigris gracilis* and *C. t. septentrionalis*. Journal of Herpetology 26: 443-447.

Tinkle, D.W. (1967a): The life and demography of the side blotched lizard, *Uta stansburiana*. Museum of Zoology, University of Michigan, Ann Arbor, USA.

Tinkle, D.W. (1967b): The life and demography of the side blotched lizard, *Uta stansburiana*. Museum of Zoology, University of Michigan, Ann Arbor.

Uller, T., While, G.M., Wapstra, E., Warner, D.A., Goodman, B.A., Schwarzkopf, L., Langkilde, T., Doughty, P., Radder, R.S., Rohr, D.H., Bull, C.M., Shine, R., Olsson, M. (2009): Evaluation of offspring size–number invariants in 12 species of lizard. Journal of Evolutionary Biology 22: 143-151.

Valakos, E.D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., Foufopoulos, J. (2008): The Amphibians and Reptiles of Greece. Chimaira, Frankfurt am Main, Germany.

Van Damme, R. (1999): Evolution of herbivory in lacertid lizards: effects of insularity and body size. Journal of Herpetology 33: 663-674.

Vicente, L. (1999): Evolutionary strategies in insular environments. Natura Croatica 8: 301-323.

Vitt, L.J. (1982): Sexual dimorphism and reproduction in the microteid lizard *Gymnophalmus microscolatus*. Journal of Herpetology 16: 325-329.

Vitt, L.J. (1983): Reproduction and sexual dimorphism in the tropical teiid lizard *Cnemidophorus ocellifer*. Copeia 1983: 359-366.

Vitt, L.J., Caldwell, J.P. (2014): Herpetology: An Introductory biology of Amphibians and Reptiles. Fourth edition. Academic Press, London, UK.

Vitt, L.J., Congdon, J.D. (1978): Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. The American Naturalist 112: 595-608.

Whittaker, R.J., Fernández-Palacios, J.M. (2007): Island Biogeography: Ecology, Evolution and Conservation. Second edition. Oxford University Press, Oxford.

Winck, G.R., Rocha, C.F.D. (2012): Reproductive trends of brazilian lizards (Reptilia, Squamata): the relationship between clutch size and body size in females. North-Western Journal of Zoology 8: 57-62.