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Insights into how predator diversity, population density and habitat type may affect defensive behaviour in a Mediterranean lizard

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Various factors may alter anti-predatory responses among conspecifics. Here we assess some of these factors using three populations of a Mediterranean lizard (*Acanthodactylus schreiberi*) in Cyprus that differ in their habitat type, predator diversity and population density. We expected that predation would affect flight initiation distance (FID; the approach distance allowed to an observer before the lizard flees), escape distance (ED; the distance covered by the lizard from the point an escape attempt starts to the first place the lizard stops) and tail autotomy (autotomy rates, economy of autotomy, post-autotomy tail movement). We also predicted that juveniles, being more exposed to predators, would be more effective in their defensive responses. Our findings suggest that predation and population density appear to be associated with most autotomy traits but were not associated with FID and ED, which are better explained by refuge availability. The only ontogenetic difference was detected in the economy of autotomy: juveniles are more prone to autotomise, possibly because they do not experience such high costs as tailless adult individuals. Our results suggest that anti-predatory responses are influenced by a variety of factors. Unravelling the compound effects of all the factors involved should be the focus of future research.

KEY WORDS: *Acanthodactylus*, lizard, anti-predatory behaviour, FID, tail autotomy, ontogeny.

INTRODUCTION

Predation is a major driver that shapes numerous aspects of animal biology (Lima & Dill 1990; Shepard 2007; Lagos & Herberstein 2017). The most direct impact of predation is related to anti-predatory mechanisms (Blumstein & Daniel 2005; Losos et al. 2006), the extent of which may vary depending on the identity and effectiveness of

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predators (Langridge et al. 2007; Rundus et al. 2007; Rodríguez-Prieto et al. 2010). The most decisive factor defining the nature of anti-predatory responses is the balance between costs and benefits of escaping or remaining in place when threatened (Lima 1992; Taraborelli et al. 2003; Pafilis et al. 2009a). Escape theory predicts that when the cost of staying may be lethal, flight is the most profitable decision (Ydenberg & Dill 1986; Stankowich & Blumstein 2005). Escaping predation may comprise just running away from the predator or hiding in a shelter, but also may include more sophisticated mechanisms such as shoaling in fish (Hoare et al. 2000) and autotomy (the voluntary shedding of body parts) in rodents (McKee & Adler 2002), crustaceans (Smith 1990) and lizards (Arnold 1984).

Most lizards have the ability to voluntarily shed their tail when seized by a predator (Arnold 1988). After caudal autotomy, the discarded tail thrashes vigorously, distracting the predator from the escaping lizard (Dial & Fitzpatrick 1981, 1983). The extra time required for handling the thrashing tail offers the lizard better opportunity for escape (Congdon et al. 1974; Dial & Fitzpatrick 1984). Although caudal autotomy is considered highly effective, it comes with serious costs (Arnold 1984, 1988). Many lizards use their tails for lipid storage, so shedding part of the tail entails the direct loss of energy reserves (Vitt et al. 1977; Cooper et al. 2004). Moreover, individuals with autotomised tails may experience reduced social status and exclusion from reproduction (Martin & Salvador 1993; Salvador et al. 1995). Also, since the tail serves as an auxiliary limb in locomotion, caudal loss may result in impaired locomotor capacities (Cromie & Chapple 2013; McElroy & Bergmann 2013; Savvides et al. 2017). According to the traditional theory, tail shedding is mainly affected by predation pressure (Pianka 1970; Turner et al. 1982; Cooper et al. 2004). However, the importance of intraspecific competition as a cause of autotomy has been recently acknowledged (Corti et al. 2008; Pafilis et al. 2009b; Donihue et al. 2016; Itescu et al. 2017a, 2017b).

Although autotomy is quite common among lizards, flight remains the more common and "cheap" anti-predatory response (Cooper et al. 2006; de Barros et al. 2010; Cooper & Martín 2016). The majority of studies use flight initiation distance (FID; the approach distance allowed to an observer before the lizard flees) and escape distance (ED; the distance covered by the lizard from the point an escape attempt starts to the first place the lizard stops) to assess escape parameters (Amo et al. 2006; Cooper & Wilson 2007; Cooper 2011). Escape theory predicts that the higher the assumed danger of an approaching predator, the more vigilant the prospective prey would be, and that it would flee for a longer distance (Ydenberg & Dill 1986; Martin & López 2003; Ventura et al. 2016). Escape by running is more advantageous compared to tail loss, but still costly (Martin & López 2003; Pérez-Cembranos et al. 2013).

Since both flight and caudal autotomy impose certain costs, predation pressure remains an important factor determining the use of these anti-predatory mechanisms, aside from the influence of intraspecific competition, the importance of which has been recently highlighted. According to evolutionary theory, in low predation regimes (e.g. on isolated islands) decreased risk causes relaxation of defensive mechanisms and individuals become bolder (Magurran 1999; Blumstein & Daniel 2005; Pafilis et al. 2009b). This means that lizards from predator-free islands have in general lower tail autotomy rates (Pérez-Mellado et al. 1997; Pafilis et al. 2008, 2009b; but see cases of high intraspecific competition, Dappen 2011; Cooper et al. 2015) and demonstrate shorter FIDs (Cooper et al. 2014; Brock et al. 2015). In contrast, conspecific mainland populations experiencing higher predation pressure show high frequency of tail autotomy rates and longer FIDs that strongly depend on anti-predator mechanisms (Maloney

& McLean 1995; Cooper et al. 2014). Also, in some cases, maturity may reduce predation risk: juveniles are more exposed to predators, whereas adults may lose autotomy ability since they have fewer predators due to their larger body size (Pafilis & Valakos 2008; Hawlena 2009).

In this study, we investigated the evolution of certain behavioural defensive mechanisms (FID, ED and tail autotomy) in Schreiber's spiny-footed lizard (*Acanthodactylus schreiberi*, Boulenger 1878). We focused on three Cypriot populations that differ in their habitat type, population density and predation regime. Moreover, we tested the effect of age on these anti-predator mechanisms. We formulated three hypotheses: first, we expected that FIDs, EDs, autotomy performance, ease of autotomy and post-autotomy tail movement would be higher in populations experiencing higher predation diversity. Second, we predicted that lizards from dense populations (that could experience high or low predation diversity) would shed their tails more often, as high population density induces intense intraspecific competition that may lead to more incidences of caudal autotomy (Knell 2009; Pafilis et al. 2009a). Third, we anticipated that juveniles would exhibit longer FIDs and EDs, coupled with higher ease of autotomy and longer post-autotomy tail movement, as they are more exposed to predators due to their highly active lifestyle (Nagy 2000; Hawlena et al. 2006; Herczeg et al. 2007).

MATERIALS AND METHODS

Study species

Schreiber's spiny footed lizard is a medium-sized lacertid with a snout-to-vent length (SVL) varying between 73–93 mm for males and 55–76 mm for females. The tail is long and can be almost two-thirds of the total body length. The abdominal tail colour in males and females is white and yellow, respectively, and red in juveniles (Baier et al. 2009). The species is distributed on Cyprus (in a vast variety of habitats, from sea level up to 1300 m) and in a limited coastal area of southeastern Turkey (Baier et al. 2009; Tamar et al. 2014).

We captured individuals from three populations (Geri: 35°05′50″N, 33°26′21″E, elevation 183 m a.s.l. (above sea level); Agros: 34°56′27″N, 33°00′14″E, elevation 1348 m a.s.l.; Akrotiri: 34° 36′33″N, 32°55′45″E, elevation 1 m a.s.l.) that differ considerably in terms of habitat. The Geri habitat is a sub-urban shrubland with many medium-sized rocks and low stone piles on fine-grained soil (Fig. 1a). The habitat in Agros comprises meadows with shrubs, grasses, herbs and rocks in a Turkish pine forest (*Pinus brutia*) (Fig. 1b). Akrotiri is located in a coastal sand dune system with sparse low shrubs (Fig. 1c).

Fig. 1. — The three sampling habitats: (a) Geri, (b) Agros, (c) Akrotiri.

Besides their habitat, the focal populations differ in predation regime. Predation pressure is hard to evaluate, though in some cases direct (mark and recapture of predators) or indirect (use of clay models) methods have provided valuable results (Wilson 1991; Husack et al. 2006; Watson et al. 2012). However, such methods encompass innate biases and the assessment of predation has been a problem in similar studies (Turner et al. 1982; Hill & Dunbar 1998; Vervust et al. 2007). Future research should focus on this issue and try to unravel its compound nature. In our study, we followed the common practice of compiling lists of predators (Chapple & Swain 2004; Losos et al. 2004; Pafilis et al. 2009a, 2009b; Raia et al. 2010; Cooper & Pérez-Mellado 2012; Bateman & Fleming 2014; Brock et al. 2015; Itescu et al. 2017a). A mere catalogue of predators is not, of course, an extensive and complete measurement of predation pressure, but it still provides a helpful and easy to compile index of predation (Table 1). Based on the numbers (and, to a certain extent, the identity) of predator species (predator diversity) found in each habitat, we assumed that predator diversity in Geri is the highest of the three populations and that of Akrotiri the lowest. At this point, however, we have to admit that we did not measure directly the effectiveness of each predator.

Field measurements (population density, field autotomy rates, FID, ED)

In early August 2016, we estimated the population density in each population using the line transect method (Lovich et al. 2012). The same observer (P. Savvides) walked five line transects of 100 m in length and recorded all lizards seen within a 4-m wide belt, 2 m on either side of the survey line (total area covered per trail = 400 m²). Recordings were obtained during morning hours, from 8:00 to 11:00 am, when lizard activity peaks (P. Savvides pers. obs.). This method

Table 1.

Comparative data for the three focal populations. Predator categories (species codes at the end of the table), total predation (summation of all predators), population density (individuals per hectare), flying initiation distance and escape distance with and without refuge (in meters, mean ± SD; sample size), laboratory autotomy rates (LARs, percentage; sample size), field autotomy rates (FARs, percentage; sample size) and duration of post-autotomy movement (in sec, meamean ± SD; sample size).

	Geri	Agros	Akrotiri
Predators	Snakes: 1, 3, 4, 5	Snakes: 1, 2, 3, 4, 5	Snakes: 1, 4, 5
	Birds: 1, 2, 5	Birds: 3, 4	Birds: 1, 2, 5
	Mammals: 1, 2, 3	Mammals: 2, 3	Mammals: –
Total predation	10	9	6
Population density	2108	1243	845
FID without refuge	3 ± 0.52; 16	3.39 ± 0.71; 9	3.16 ± 0.67; 10
ED without refuge	2.53 ± 0.95; 16	3.14 ± 1.84; 9	3.63 ± 2.1; 10
FID with refuge	2.4 ± 0.61; 21	2.9 ± 0.79; 13	2.99 ± 0.75; 27
ED with refuge	1.66 ± 0.88; 21	1.51 ± 0.54; 13	3.46 ± 1.96; 27
LAR	70.27; 37	65.51; 29	29.1; 24
FAR	15.8; 76	25.9; 58	22; 59
Duration	193.5 ± 81.17; 26	212.3 ± 127.8; 19	187.7 ± 111.8; 7

Snakes: (1) *Dolichophis jugularis*; (2) *Hierophis cypriensis*; (3) *Malpolon insignitus*; (4) *Hemorrhois nummifer*; (5) *Macrovipera lebetina*. Birds: (1) *Falco naumanni*; (2) *F. tinnunculus*; (3) *Upupa epops*; (4) *Corvus corax*; (5) *C. corone*. Mammals: (1) *Felis catus*; (2) *Rattus rattus*; (3) *Vulpes vulpes*.

provides reliable data on the relative population abundance and is widely used in lacertid lizard studies (Martín & Lopez 2002; Díaz et al. 2006; Pafilis et al. 2013).

In addition, we performed field observations for 2 days in each population and recorded the number of individuals with autotomised or regenerated tails (field autotomy rates, FAR), as well as their age group (adults or juveniles). Overall, we recorded 193 individuals, 50 of which had autotomised or regenerated tails.

We recorded FIDs and EDs using the methodology proposed by Cooper and Wilson (2007) and Cooper et al. (2009a). First, we ensured that all individuals participating in the experiment were aware of the researcher's presence. The approaches were performed by the same researcher (P. Savvides) from a distance of 6 m at a previously practised speed of ca 96 m/min. In all approaches lizards had continuous visual contact with the researcher (always the same person with the same clothing). In each trial, we recorded the lizard's age group (adult or juvenile), the distance the researcher was allowed to approach to before the lizard fled (FID), the distance covered by the lizard until its first stop (ED) (with the use of a measure tape), whether the lizard ran into a refuge (e.g. bush, burrow, rock), and the condition of the tail. We recorded data for 96 individuals.

Lab measurements (lab autotomy rates – LAR)

For the tail autotomy experiment we used exclusively individuals with intact tails. First, we let all individuals thermoregulate for 1 hr in a specifically designed terrarium with ice bags on one end and a heating bulb (150 w) on the other, providing a thermal gradient ranging from 10 to 50 °C (Van Damme et al. 1986). This was done because body temperature may affect autotomy performance (Daniels 1984; Pafilis et al. 2005). To measure laboratory autotomy rates (LAR), we adopted the methodology used by Pérez-Mellado et al. (1997). Each individual was placed in a terrarium with a cork substrate that provided grip. We then simulated a predator's grasp with a digital caliper and applied pressure on the tail at 20 mm from the cloaca for 15 sec. If the lizard did not shed its tail, we repeated the procedure at a distance of 40 and 60 mm distal to the cloaca. The applied pressure was equal to half of the diameter of the tail at each point (Pérez-Mellado et al. 1997). Though this method has been widely used (e.g. Cooper et al. 2004; Pafilis et al. 2005, 2017; Pafilis & Valakos 2008; Li et al. 2014; Brock et al. 2015) and hence offers the chance for direct comparison with other studies, it has certain flaws. The main problem is a bias towards observing more autotomy incidents in the position closer to the cloaca (at 20 mm) just because this position is tested first, even when autotomy could be induced with an equal likelihood at the other positions (40 and 60 mm). This fact should be taken into account in future research.

Prior to the experiment we recorded SVL, weight and body temperature (using a cloacal thermometer, T-4000, Miller & Weber, Inc., Queens, NY, accurate to 0.1 °C) of each individual. If autotomy occurred we also recorded the duration of post-autotomic tail movement.

Statistical analysis

We used a chi-square test to check for differences in the frequencies of autotomised tails in the field, the frequencies of refuge use during an escape attempt and the autotomy rates among populations. Analysis of variance (ANOVA) was used to check for differences in FIDs, EDs and the duration of post-autotomy tail movements between age groups and among populations. Log-transformed data were used in the analysis in order to meet the criteria for parametric tests. Differences in autotomy performance between males and females were tested using a Mann-Whitney test, because of the small sample size of females from Akrotiri.

RESULTS

The estimated population densities were quite high, exceeding 800 individuals per hectare (Table 1). In fact, the populations from Geri (2108 ind./ha) and Agros (1243 ind./ha) had the highest densities ever reported from an eastern Mediterranean island (Lymberakis et al. 2016).

No statistically significant differences were found in FIDs and EDs between adults and juveniles in any population (ANOVA: Geri, FID, $F_{(1,35)}$ = 0.155, P = 0.696; ED, $F_{(1,35)}$ = 0.840, P = 0.366. Agros, FID, $F_{(1,20)}$ = 2.731, P = 0.114; ED, $F_{(1,20)}$ = 1.016, P = 0.325. Akrotiri, FID, $F_{(1,35)}$ = 1.100, P = 0.301; ED, $F_{(1,35)}$ = 0.470, P = 0.498), so the data were pooled. FIDs in Geri (mean = 2.66 m) were significantly different from those in Agros (mean = 3.1 m) and Akrotiri (mean = 3.04 m) (Table S1). Also, EDs from Akrotiri (mean = 3.51 m) differed significantly from both Geri (mean = 2.04 m) and Agros (mean = 2.18 m) (Table S1).

Individuals from Geri that ran into a refuge after their escape performed significantly shorter FIDs (mean = 2.4 m) and EDs (mean = 1.66 m), than those that did not use refuges (mean FID = 3 m, mean ED = 2.56 m), (ANOVA: FID, $F_{(1,35)}$ = 11.111, P = 0.002; ED, $F_{(1,35)}$ = 9.929, P = 0.003). Agros FIDs did not statistically differ regardless of whether lizards used a refuge (mean = 2.9 m) or not (mean FID = 3.39 m). Nonetheless, EDs were significantly shorter when lizards resorted to a refuge (mean = 1.51 m) than when they did not (mean ED = 3.14 m). In Akrotiri neither FIDs nor EDs had statistically significant differences between individuals that used (mean FID = 2.99 m, mean ED = 3.46 m) or did not use (mean FID = 3.16 m, mean ED = 3.63 m) a refuge. When we compared the three populations, we found that lizards that did not use a refuge showed no significant differences in FIDs and EDs (Tables 1 and S2). On the contrary, individuals that used refuges showed statistically significant differences among populations in both FID and ED values (Tables 1 and S2). All populations tended to use refuges at the same frequency after an escape attempt.

We found no age-related differences in FAR (Fig. 2), so the data for juveniles and adults in all populations were pooled. We failed to detect any differences in the frequencies of FAR among populations.

Males and females did not differ in LAR, economy of autotomy (chi-square test) and the duration of post-autotomy tail movement (Mann-Whitney test) so the data were pooled. Adults (N = 24 for Geri, N = 16 for Agros, N = 14 for Akrotiri) and juveniles (N = 13 for Geri, N = 13 for Agros, N = 10 for Akrotiri) had similar LARs in all three populations (chi-square test) (Fig. 3). When we compared the economy of autotomy (autotomy position at 20 mm, 40 mm, and 60 mm from the cloaca) between adults and juveniles, we found that only individuals from Geri (χ^2 = 11.985, P = 0.007) and Agros (χ^2 = 8.318, P = 0.04) showed significant differences. In these sites juveniles shed their tails more easily in the first position than adults did (Fig. 3). LAR and economy of autotomy of Akrotiri adults differed significantly from both Geri and Agros (Table 2). In juveniles, the only significant difference was that between Geri and Akrotiri regarding the economy of autotomy (Table 2).

The duration of post-autotomy tail movement did not differ between adults and juveniles (ANOVA) in any population, so the data were pooled. Comparing the three populations, we found significant differences between Akrotiri and the other two populations (ANOVA: $F_{(2,86)}$ = 6.521, P = 0.002; post hoc Tukey HSD test: Geri-Agros, P = 0.860; Geri-Akrotiri, P = 0.002; Agros-Akrotiri, P = 0.016). Tails from Akrotiri performed the shortest post-autotomy movements (mean duration: Geri = 193.5 sec, Agros = 212.3 sec, Akrotiri = 187.7 sec).
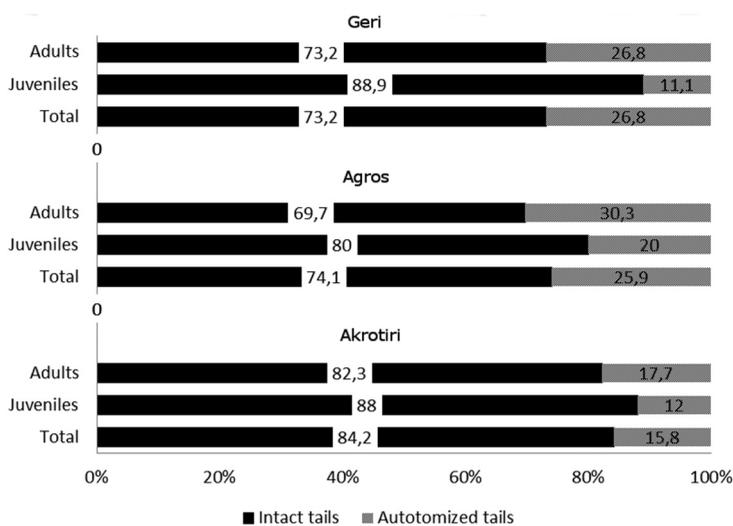
Fig. 2. — Field autotomy rates for adults and juveniles.

DISCUSSION

In this study, we aimed to address the impact of certain parameters on the variation of lizard defensive mechanisms. Our results confirmed some of our predictions and refuted others. Predator diversity and population density seemed to affect some parameters of tail autotomy while having no effect on others. However, the effect of predation on FIDs and EDs was not the expected one. Also, we failed to detect any impact of age on anti-predator mechanisms, with the single exception of the economy of autotomy.

Predator diversity did not have a consistent effect on all tail autotomy features. LARs were higher, the economy of autotomy in adults (but not in juveniles) was lower and the duration of post-autotomy movement was more prolonged in populations with higher total predation (Table 1 and Fig. 3). However, FAR did not differ considerably among the three populations (Table 1 and Fig. 2). The observed difference between FARs and LARs is a rather common finding, attributed to the nature of these metrics (Pafilis et al. 2009b; Brock et al. 2015). LARs possibly reflect the innate ability for autotomy, whereas FARs stem from a combination of intrinsic predisposition and external stimuli (predation and/or intraspecific competition) (Pafilis et al. 2009b). The focal populations seem to maintain high propensities for tail shedding. A greater diversity of predators can increase autotomy performance (Cooper et al. 2004; Bateman & Fleming 2011). That could be the reason why lizards from the population subject to a more diverse predator fauna (Geri) achieved the highest LARs (70.27%), whereas individuals from the predator poor site (Akrotiri) achieved the lowest (29.1%). Males and females did not differ in autotomy performance, a finding that seems to be the rule in lacertid lizards (Pafilis et al. 2017). Nevertheless, we have to stress that different costs are related to tail autotomy, particularly as it concerns reproductive output. In gravid females, the costs of tail shedding are higher and more direct: previous research showed that the investment of energy into tail regeneration may lead to
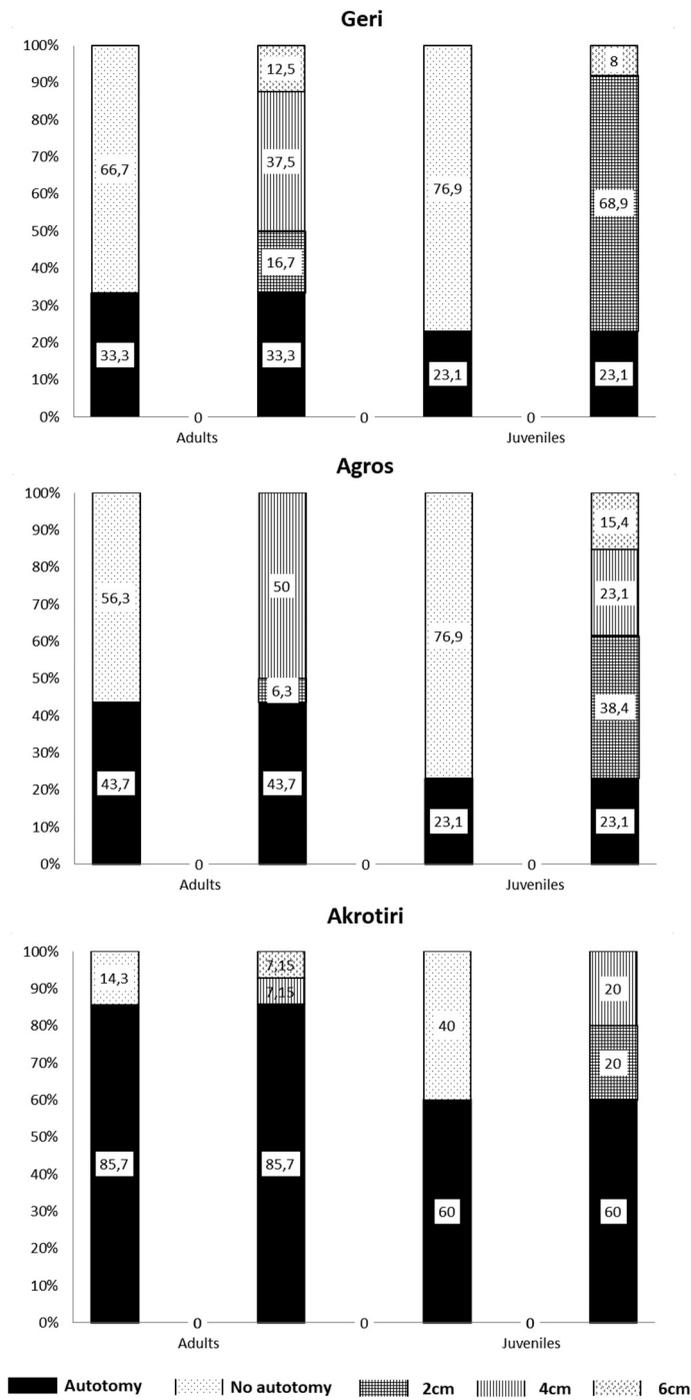
Fig. 3. — Left bar: laboratory autotomy rates for adults and juveniles; Right bar: economy of autotomy.

Table 2.

Comparison of frequencies of autotomy performance for adults and juveniles between populations. Significant results are given in bold.

	LAR		Autotomy economy	
	χ^2	*P*	χ^2	*P*
Adults				
Geri-Agros	0.444	0.505	3.464	0.325
Geri-Akrotiri	**7.238**	**0.002**	**7.566**	**0.016**
Agros-Akrotiri	**3.772**	**0.017**	**7.232**	**0.034**
Juveniles				
Geri-Agros	0	1	4.476	0.214
Geri-Akrotiri	3.235	0.072	**8.203**	**0.042**
Agros-Akrotiri	3.235	0.072	4.165	0.244

smaller clutch sizes, smaller individuals or even to the subsequent death of the juveniles (Dial & Fitzpatrick 1981; Niewiarowski et al. 1997; Chapple et al. 2002; Bateman & Fleming 2009).

Economy of autotomy, the position at which lizards shed their tails, indicates a possible influence of predation diversity (based on the list of the number of predator species). Both adults and juveniles were prone to autotomise in the most "expensive" first position (20 mm from the cloaca) at Geri, where predator diversity was higher, while they were more reluctant to autotomise at Akrotiti where predation was relaxed (Fig. 3). Our results agree with previous studies that described a direct relationship between predation regime and tail loss economy: stronger predation induces lower economy (more shedding incidents at the first position, Pérez-Mellado et al. 1997) and a greater latency to autotomy (Cooper et al. 2004). The position of autotomy is quite important due to the numerous problems autotomy causes (see Introduction). The closer to the cloaca that lizards shed their tails, the more severe would be the autotomy aftermath. Thus, tails are more likely to break towards the tip than close to the cloaca (Cooper et al. 2004; Lovely et al. 2010) unless predation pressure dictates otherwise. Costly anti-predator mechanisms can evolve because of predation, but they can also be subject to negative selection in populations with relaxed predation (Vervust et al. 2007). The impressive deviation in the economy of autotomy between the two high predation sites (Geri and Agros) might be explained by the presence of cats at Geri. Cats are very capable predators that considerably increase predation pressure on lizards (Medina & Nogales 2009; Li et al. 2014).

The analysis of shed-tail thrashing duration revealed a clear grouping. The two populations experiencing high predator diversity and/or intraspecific competition did not differ and showed more prolonged movement durations, while the low predator diversity, sparse population (Akrotiri) had the shortest movement durations (Table 1). The duration of post-autotomy movement plays an important role in lizard escape as it increases the handling time required by an attacker (Arnold 1984; Pafilis et al. 2005). In intense predation regimes, tail movement is significantly longer compared to habitats with relaxed predation (Pérez-Mellado et al. 1997; Cooper et al. 2004; Pafilis et al. 2008,

2009b). A longer post-autotomy movement is particularly favourable when predators lack forelimbs (snakes or birds) and thus the handling of the thrashing tail becomes challenging (Dial & Fitzpatrick 1983; Downes & Shine 2001). Geri and Agros host more avian and reptilian predators than Akrotiri (Table 1), and this possibly explains the longer durations. The highest values were recorded in Agros where only two saurophagous birds were recorded. However, one of them is the hoopoe (*Upupa epops*), a skilful predator that regularly includes lizards in its diet (Fournier & Arlettaz 2001; El-Bakary 2011).

Against our initial hypothesis, escape behaviour was not affected by predation, at least not according to our expectation. FID and ED values did not differ among the three populations, despite the divergences in predation diversity (Tables 1–2). Nevertheless, a clear difference arose when the use of a refuge after fleeing was taken into account: FIDs and EDs were shorter in the high predation sites, but longer in the more relaxed predation regime at Akrotiri (Tables 1 and S2). Escape theory predicts that FID would increase as predation pressure increases (Ydenberg & Dill 1986; Cooper & Pérez-Mellado 2012). However, our results seem to suggest the exact opposite. This apparent contradiction can potentially be explained by the crucial role of refuges. FID is largely affected by the distance to the nearest refuge (Bulova 1994; Bonenfant & Kramer 1996; Cooper 1998). Previous studies reported that fleeing distances increased as the distance to a refuge increased (Dill & Houtman 1989; Kramer & Bonenfant 1997; Stankowich & Blumstein 2005). The availability and accessibility of refuges may also affect lizard FIDs (Martin & Lopez 1995; Cooper & Whiting 2007; Cooper & Wilson 2007; Corti et al. 2008; Biaggini et al. 2010). Akrotiri is a typical dunal habitat with few shrubs and no rocks. Lizards that dwell there have to deal with a scarcity of refuges and so cover long distances (being exposed to predators) when they shuttle between them. This is probably the reason why ED values in Akrotiri were more than double compared to the other two populations (Table 1). The absence of differences between the two latter populations is maybe due to the similar predation regime coupled with high refuge availability in both localities (Table 1). FID quantifies risk-taking and reflects adaptive decision-making (Samia et al. 2015). It seems that in our study system, refuge availability plays a primary role in escape behaviour.

In line with our second hypothesis, population density seems to affect autotomy performance: the higher LARs were observed in the more abundant populations (Fig. 3). High population density is known to intensify intraspecific competition (Mougeot et al. 2003; Knell 2009; Calsbeek & Cox 2010). In lizards, intraspecific aggressive interactions very often lead to tail amputation (Jennings & Thompson 1999; Pafilis et al. 2008; Cooper et al. 2009b; Itescu et al. 2017a). Population densities in the focal Cypriot populations were very high (Table 1), actually the highest reported so far from the eastern Mediterranean (Lymberakis et al. 2016). It seems that within these dense populations, lizards skirmish quite often and this results in tail autotomy.

We have to stress here an obvious flaw regarding the interpretation of tail loss results. In our analysis, we took into account both the main drivers of caudal autotomy, predation and intraspecific competition. The role of the latter enhances the long debate between the importance of predation pressure per se (high predation results in high levels of autotomy; Pianka 1970; Turner et al. 1982; Cooper et al. 2004) and that of predator efficiency (efficient predation results in low levels of autotomy, as most lizards are consumed entirely; Schoener 1979; Medel et al. 1988; Bateman & Fleming 2011). Recent studies acknowledge intraspecific competition as an important factor in caudal autotomy performance (Pafilis et al. 2008; Hare & Miller 2010; Donihue et al. 2016) or even recognise it as the primary cause (Pafilis et al. 2009a; Itescu et al. 2017a, 2017b). In

our study system, it is not easy to define which factor interferes more and to what extent. However, based on the literature, our findings regarding the high LARs and possibly the high cost of autotomy together with the long durations of tail movement, seen in the two densely populated habitats (Geri and Agros), may have resulted from intense intraspecific interactions.

Contrary to our predictions, age did not have an important effect on defensive mechanisms. Ontogenetic differences were restricted only to the economy of autotomy. Adults were considerably more reluctant to shed their tails at the first "expensive" position compared to juveniles (Fig. 3). Given the numerous roles of the tail in the overall biology of an adult lizard (energy storage allocated for vitellogenesis and offspring production, social status for mate choice, intra-male competition) (Dial & Fitzpatrick 1981; Maginnis 2006; Bateman & Fleming 2009), the negative effects of tail shedding might be greater for adults than for juveniles. Thus, adults may autotomise at similar rates as juveniles but, at the same time, tend to retain their tails and shed them only at the second position (Fig. 3). Juveniles are more susceptible to predation due to their smaller size (Daniels et al. 1986; Whiting et al. 1991; Bateman & Fleming 2009) and their higher exposure to predators (Nagy 2000; Hawlena et al. 2006; Herczeg et al. 2007). This higher predation pressure may account for the observed ontogenetic differences in the ease of autotomy. Additionally, juveniles of *A. schreiberi* tend to expose themselves to predators to a larger extent compared to adults (Hawlena 2009). We believe that juveniles autotomise more easily to compensate for the higher risk, particularly as they do not directly experience the severe consequences that adults experience.

Our findings shed light on the compound effect of predation regime, population density and habitat structure on the anti-predatory responses of a single lizard species. The three focal populations differed in the above-mentioned parameters and these deviations yielded considerable variation in defensive traits. Whether this variation among populations is indicative of plasticity or evolutionary divergence under different selective regimes has to be further explored. Lizards can adjust their anti-predatory responses according to several factors (Martin & López 2003). The distinct influence of each of the numerous factors involved is hard to define, and this remains a challenging task for future research.

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