

# Intraspecific competition, not predation, drives lizard tail loss on islands

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## Summary

1. Tail autotomy is mainly considered an antipredator mechanism. Theory suggests that predation pressure relaxes on islands, subsequently reducing autotomy rates.
2. Intraspecific aggression, which may also cause tail loss, probably intensifies on islands due to the higher abundance.
3. We studied whether tail autotomy is mostly affected by predation pressure or by intraspecific competition. We further studied whether predator abundance or predator richness is more important in this context.
4. To test our predictions, we examined multiple populations of two gecko species: Kotschy's gecko (*Mediodactylus kotschy*; mainland and 41 islands) and the Mediterranean house gecko (*Hemidactylus turcicus*; mainland and 17 islands), and estimated their abundance together with five indices of predation.
5. In both species, autotomy rates are higher on islands and decline with most predation indices, in contrast with common wisdom, and increase with gecko abundance. In *M. kotschy*, tail-loss rates are higher on predator and viper-free islands, but increase with viper abundance.
6. We suggest that autotomy is not simply, or maybe even mainly, an antipredatory mechanism. Rather, such defence mechanisms are a response to complex direct and indirect biotic interactions and perhaps, in the case of tail autotomy in insular populations, chiefly to intraspecific aggression.

**Key-words:** autotomy, defence mechanisms, geckos, intraspecific aggression, islands, lizards, population abundance, predation pressure

## Introduction

Avoiding predation is crucially important for fitness. One of the most fascinating antipredatory adaptations is that of autotomy: the ability to voluntarily shed an organ if attacked by a predator. Autotomy has evolved independently in many animal groups (Fleming, Muller & Bateman 2007; Bateman & Fleming 2009). In lizards, caudal loss originated as an efficient form of last-line defence (Arnold 1988). The most common indices used for studying autotomy are the frequency of autotomized tails in sampled populations and the ease of tail loss under the simulated predation (sometimes called 'field autotomy' and 'laboratory autotomy', respectively, e.g. Brock *et al.* 2015). Accumulating evidence suggests a positive

correlation between predation levels and both field (Fox, Perea-Fox & Franco 1994; Pafilis, Pérez-Mellado & Valakos 2008) and laboratory autotomy rates (Fox, Perea-Fox & Franco 1994; Pérez-Mellado, Corti & Lo Cascio 1997; Brock *et al.* 2015). Some authors argued that field autotomy reflects predation intensity (i.e. the frequency of total predation attempts; Pianka 1970), whereas others demonstrated that it more closely reflects predation efficiency (i.e. the frequency of failed predation attempts; Schoener 1979; Medel *et al.* 1988; Bateman & Fleming 2011). Either way, tail shedding is considered an efficient antipredatory mechanism (Chapple & Swain 2002).

Theory predicts that under reduced predation, natural selection will eliminate evolutionarily expensive antipredator adaptations (Blumstein & Daniel 2005) such as autotomy. The low numbers of predator species on islands are perceived as diminishing predation pressure. Consequently, tail-loss frequencies are expected to be lower on

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islands (Pérez-Mellado, Corti & Lo Cascio 1997). However, ecological release from predation and interspecific competition is expected to drive the increased population densities in insular lizards and their predators (i.e. density compensation; Case 1975; Rodda & Dean-Bradley 2002; Buckley & Jetz 2007; Novosolov *et al.* 2016). Thus, declining species richness on islands may lead to increased tail-loss rates by driving predator populations to be denser (Luiselli *et al.* 2005). Thus, it is not clear *a priori* whether predation pressure will increase faster with increased predator richness or with increased predator abundance. Archipelagos, comprising islands varying in area and species richness, lend themselves to examining the effect of predation on tail loss. Studies of this question using diverse approaches and study systems have yielded the conflicting results. Some have identified the expected positive relationship between predation pressure and the rates of tail autotomy in the field (Pafilis, Pérez-Mellado & Valakos 2008; Pafilis *et al.* 2009b), whereas others have not (Schoener & Schoener 1980; Brock *et al.* 2015). Pafilis *et al.* (2009b) compared the autotomy rates across eight Mediterranean lizard species and pointed to the presence of vipers as the main determinant of autotomy, whereas Brock *et al.* (2015) failed to support these findings.

Tail autotomy is mainly considered an antipredator strategy, but may also be useful as defence against intraspecific aggression (Pafilis, Pérez-Mellado & Valakos 2008; Donihue *et al.* 2016), especially where cannibalism exists (e.g. Pafilis *et al.* 2009a). In dense populations, as often is the case on islands, strong intraspecific competition often triggers fierce aggression that frequently ends in tail loss (Pafilis *et al.* 2009b; Raia *et al.* 2010; Cooper, Dimopoulos & Pafilis 2015; Donihue *et al.* 2016; but see Stamps & Buechner 1985). However, the role of intraspecific aggression in the evolution of tail loss is little studied and remains unclear (Bateman & Fleming 2009). Some studies have revealed a positive relationship between insular lizard densities and field autotomy (Pafilis *et al.* 2009a; Donihue *et al.* 2016), while others have not (Brock *et al.* 2015). Bateman & Fleming (2009) suggested that biting off the tails of rivals might be adaptive for males of territorial species, although most studies have failed to detect the sexual differences in tail autotomy.

We examined the effect of predation pressure and intraspecific competition on tail-loss frequencies across multiple insular populations of two sympatric geckos, *Mediodactylus kotschy* (Steindachner, 1870) and *Hemidactylus turcicus* (Linnaeus, 1758), on numerous Aegean Sea islands, and compared them to mainland populations of both species. We predicted that:

- 1 If tail autotomy frequencies are driven by predation, then:
  - a. Autotomy will be lower on islands, compared with the mainland, due to the relaxed predation.

- b. Autotomy will be positively correlated with predation and will be lower on predator-free islands. Vipers (the main gecko predators in our study system; e.g. Cattaneo 2010) will be particularly important.

- 2 If tail autotomy frequencies are driven by intraspecific competition, then:

- a. Autotomy will be more frequent on islands, compared with the mainland, due to the increased intraspecific aggression.
- b. Autotomy will increase with gecko abundance.
- c. Males, which engage more in aggressive encounters with conspecifics, will lose tails more frequently than females.

## Materials and methods

### STUDY SITE AND SPECIES

The Aegean archipelago encompasses thousands of islands that vary tremendously in area (the islands in our study span four orders of magnitude in area: from the 0.034-km<sup>2</sup> Mikri Fteno to the 430.2-km<sup>2</sup> Naxos), distance from the mainland, habitat diversity, species richness, resource abundance and faunal composition (Valakos *et al.* 2008). We studied two gecko species that are common on many of these islands.

*Mediodactylus kotschy* (Fig. 1a) is a small [mean snout vent length (SVL) 42.2 ± 4.3 mm, mean mass 2.7 ± 0.9 g, Y. Itescu, unpublished data], mostly catemeral and saxicolous gecko. It ranges over the southern Balkans and eastern Mediterranean, including some of the smallest islets where it is often the only terrestrial vertebrate present (Valakos *et al.* 2008). It is insectivorous, highly territorial (Ajtić 2014) and varies greatly in morphology, life history and ecology across populations (e.g. Slavenko *et al.* 2015).

*Hemidactylus turcicus* (Fig. 1c) is a slightly larger (mean SVL 47.5 ± 4.5 mm, mean mass 3.1 ± 0.9 g, Y. Itescu, unpublished data), insectivorous, nocturnal species (Valakos *et al.* 2008), which mainly inhabits human dwellings. On the Aegean Sea islands, it is sympatric to *M. kotschy*, albeit being mostly absent from the smallest islands uninhabited by humans.

### DATA COLLECTION

We studied these lizards in the field yearly during May and June 2013–2016. We further examined the specimens in five museum collections [Zoologische Staatssammlung München, Zoologische Forschungsmuseum Alexander Koenig in Bonn, Natural History Museum of Crete (University of Crete), National Natural History Collections (Hebrew University of Jerusalem) and The Steinhardt Museum of Natural History (Tel Aviv University)]. We recorded sex, SVL and tail condition (intact/regenerated; see Fig. 1) for 1537 *M. kotschy* individuals from 108 islands and 159 individuals from mainland sites in Greece, Turkey and Israel. We also recorded the data for 282 *H. turcicus* individuals from 48 islands and for 70 individuals from mainland sites in Greece and Israel. Only adult individuals were examined. Population SVL means were calculated by averaging the means of males and females.



**Fig. 1.** The study species: (a) *Mediodactylus kotschy* with an intact tail from Mykonos; (b) *M. kotschy* with a regenerated tail from Mykonos; (c) *Hemidactylus turcicus* with an intact tail clinging to a house wall in Serifos; (d) *H. turcicus* with a regenerated tail from Kato Kufonisi. Photographs by: a and b – Simon Jami-son, c – Alex Slavenko, d – Yuval Itescu.

Population tail autotomy frequency was defined as the proportion of individuals with regenerated or lost tails. Museum specimens with cut tails were not examined since in many cases those tails were removed intentionally following the preservation (e.g. for genetic studies) and we cannot verify whether these tails were naturally autotomized. We compiled the island-specific lists of potential predators from the published studies and from our own observations in the field (see Appendix S1, Supporting Information).

We estimated the relative abundance across islands for both gecko species (41 islands for *M. kotschy* and 17 for *H. turcicus*) and for vipers (*Vipera ammodytes*, 10 islands). The abundance of *M. kotschy* was estimated by counting the number of geckos found per hour of search by one of us (YI), during peak hours of activity and clear sky conditions (Buckley & Roughgarden 2005). For *H. turcicus* and *V. ammodytes*, we estimated the relative abundance as the number of individuals found per day of search, per person searching.

## STATISTICAL ANALYSES

We first compared the tail-loss frequencies between the two species across islands on which we sampled both. We then examined the correlation between autotomy rates, predation and gecko abundance. Predation was evaluated in five ways: (i) mainland vs. islands (predation pressure is assumed to be lower on islands); (ii) predator richness (a common index of predation pressure, e.g. Cooper, Pérez-Mellado & Vitt 2004), which was estimated as the number of mammal, bird and reptile species that potentially prey on geckos (Appendix S1); (iii) presence vs. absence of predators on an island; (iv) presence vs. absence of vipers (*V. ammodytes*) on an island; and (v) viper abundance.

We compared the autotomy proportion on the mainland to that on islands, including all measured individuals (a total of 1696 *M. kotschy* and 352 *H. turcicus* individuals). Then, we tested the effects of predation (i.e. predator richness), gecko abundance and body size on autotomy frequencies across the insular populations. Since autotomy rates have a binomial error structure, we performed a binomial regression test and used

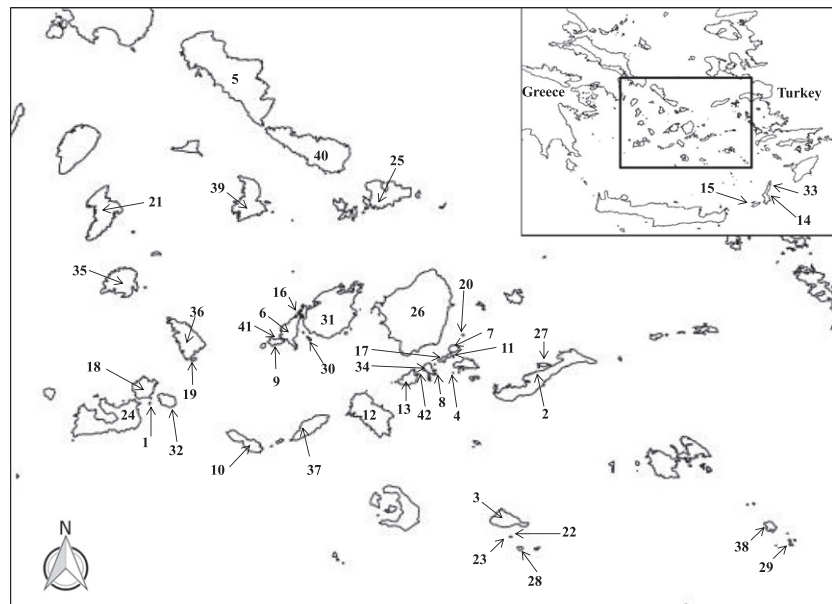
Akaike's information criteria (AIC) scores for model selection. Some studies have found autotomy frequency to be positively associated with body size (e.g. Pafilis *et al.* 2009b; cf. Fleming, Valentine & Bateman 2013). Thus, to account for the potential effects of body size, we included the mean SVL (log10-transformed, to meet the assumptions of parametric tests) of each population as an additional predictor. Island area is sometimes considered important in this context as well (e.g. Donihue *et al.* 2016). However, since island area was highly correlated with predator richness ( $R^2 = 0.78$ ,  $P < 0.01$ , variance inflation factor = 4.63), which was our main focus, we excluded it from our analyses (but see analysis results of the effect of island area on autotomy frequency in Appendix S2). Variance inflation factors did not exceed 2 in any other case (the results not shown), implying that multicollinearity in our analysed data set is low (O'Brien 2007). We analysed only populations with a minimum sample size of five individuals, for which we had data on all predictors. We also ran the sensitivity analyses for both species with minimum sample sizes of  $n \geq 10$  per island (and also  $n \geq 30$  per island for *M. kotschy*) to test whether our results are robust to the inclusion of small samples. This left us with 41 populations of *M. kotschy* (1237 individuals; Fig. 2, Table 1) and 17 populations of *H. turcicus* (229 individuals; Fig. 2, Table 1).

We also compared the autotomy frequencies between populations experiencing predation and predator-free populations of *M. kotschy* (we had no *H. turcicus* population from a predator-free island), as well as populations that coexist with *V. ammodytes*, and populations that do not – in both species. Then, we ran regression tests to examine the effect of viper abundance. Finally, we studied the sexual differences using paired *t*-test across populations with a minimum sample size of five individuals for each sex in *M. kotschy* (sample sizes were insufficient in *H. turcicus*).

## Results

Across all individuals, the autotomy frequency of *M. kotschy* was 75.5% (1281 of 1696 individuals), while that of *H. turcicus* was 66.5% (234 of 352 individuals).





**Fig. 2.** A map presenting the islands included in the interpopulation analyses of at least one species. Numbers correspond to those in Tables 1 and S1.

Autotomy frequencies did not differ between species across islands where both were examined (with a minimum of five individuals per population in each species; paired *t*-test: *M. kotschy* = 72.5%, *H. turcicus* = 66.1%,  $n = 17$  population pairs,  $t = 1.35$ ,  $P = 0.19$ ). However, they were not significantly correlated ( $r = 0.06$ ,  $P = 0.82$ ). Insular geckos of both species showed significantly higher caudal autotomy frequencies compared with mainland conspecifics (*M. kotschy*: 54% in the mainland, 77.7% on islands, total  $n = 159$  and 1537 individuals, respectively,  $\chi^2 = 67.9$ ,  $P < 0.01$ ; Fig. 3a; *H. turcicus*: 47.1% in the mainland and 71.3% on islands, total  $n = 70$  and 282, respectively,  $\chi^2 = 33.1$ ,  $P < 0.01$ ; Fig. 3b). Across insular populations, SVL was not associated with autotomy frequencies in either species ( $r = 0.04$ ,  $P = 0.78$ , in *M. kotschy* and  $r = 0.12$ ,  $P = 0.65$ , in *H. turcicus*).

#### TAIL AUTOTOMY IN MEDIODACTYLUS KOTSCHYI

The best model for *M. kotschy* showed that autotomy frequencies were positively correlated with gecko abundance and, surprisingly, negatively correlated with predator richness (Table 2, Fig. 4). These results remain qualitatively similar when analysing data sets with sample sizes of  $n > 10$  and  $n > 30$  per island (Appendix S2). Autotomy frequencies were higher on predator-free islands (predator-free = 85%,  $n$  populations = 13, vs. predator-inhabited = 73.4%,  $n = 28$ ,  $t = 2.79$ ,  $P = 0.01$ ) and on viper-free islands (80%,  $n = 29$ , vs. viper-inhabited = 69.9%,  $n = 12$ ,  $t = 2.60$ ,  $P = 0.02$ , Fig. 5a). Autotomy frequencies thus significantly increase where predators in general, and vipers specifically, are absent and where predator richness is low. Furthermore, on viper-free islands, tail autotomy frequencies were positively correlated with gecko abundance (Table 2). On the other hand, where vipers are present, their abundance was

positively correlated with tail-loss frequencies (Table 2). Males had higher autotomy frequencies than females (males = 81.2%, females = 72.9%, 31 populations,  $t = -2.46$ ,  $P = 0.02$ ).

#### TAIL AUTOTOMY IN HEMIDACTYLUS TURCICUS

Similar to *M. kotschy*, gecko abundance was positively correlated with autotomy frequencies in *H. turcicus* (Table 2, Fig. 4d); this result becomes non-significant when tested with sample sizes of  $n \geq 10$  individuals per island (see Appendix S2). This may be due to the loss of statistical power. Adding the only island with data on abundance and  $n = 9$ , Anafi Island, produces results that are qualitatively similar to the original results ( $P < 0.01$ ). However, predator richness was (negatively) correlated with tail loss only when avian predators were excluded from the predator richness counts. Viper presence had no impact on tail loss (viper-free = 70.9%, viper-inhabited = 59.8%, 7 and 10 islands, respectively,  $t = -1.49$ ,  $P = 0.16$ , Fig. 5b), and neither did their abundance ( $n = 10$ ,  $r = 0.31$ ,  $P = 0.38$ ).

#### Discussion

Tail autotomy is considered to be an antipredatory mechanism (e.g. Bateman & Fleming 2009). Nevertheless, we found a consistent evidence that population abundance (an index for intraspecific competition) is a more important driver of autotomy frequencies in both species. Surprisingly, tail-loss rates decline where the predation pressure is supposedly stronger according to most indices. The only predation index that positively correlated with autotomy frequencies was viper abundance (and only in *M. kotschy*), demonstrating the importance of this specific predator.

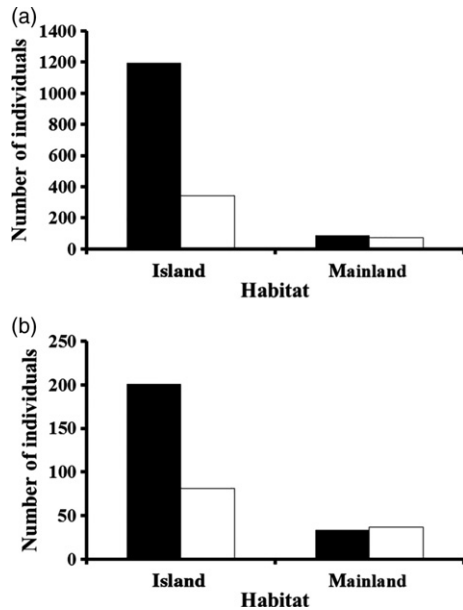
**Table 1.** Data of studied populations

#	Island	Latitude	Longitude	<i>Mediodactylus kotschy</i>			<i>Hemidactylus turcicus</i>			Predator richness	Viper presence (abundance)
				<i>n</i>	Autotomy frequency	Abundance	<i>n</i>	Autotomy frequency	Abundance		
1	Agios Eustathios	36-775	24-582	31	0-94	5-60	—	—	—	0 (0,0,0)	No
2	Amorgos	36-847	25-903	29	0-79	5-24	18	0-67	4-00	10 (3,4,3)	No
3	Anafi	36-367	25-782	30	0-70	2-22	10	1-00	8-00	5 (2,3,0)	No
4	Andreas	36-862	25-622	7	1-00	4-00	—	—	—	0 (0,0,0)	No
5	Andros	37-858	24-848	32	0-75	2-00	5	0-40	1-33	17 (4,7,6)	Yes (0-11)
6	Antiparos	37-000	25-054	51	0-71	4-00	8	1-00	—	10 (2,3,5)	Yes (0-296)
7	Apano Kufonisi	36-941	25-607	35	0-63	1-80	10	0-70	1-67	4 (1,1,2)	Yes (0-67)
8	Aspronisi	36-855	25-546	28	0-93	3-08	—	—	—	0 (0,0,0)	No
9	Despotiko	36-962	25-003	33	0-94	6-14	21	0-81	8-00	7 (1,1,5)	Yes (1-2)
10	Folegandros	36-615	24-930	—	—	—	7	0-71	1-17	9 (2,5,2)	No
11	Glaronisi	36-916	25-605	44	0-80	4-00	—	—	—	0 (0,0,0)	No
12	Ios	36-722	25-327	30	0-73	3-24	12	0-58	1-47	10 (2,5,3)	Yes (0-25)
13	Iraklia	36-840	25-454	38	0-71	2-99	11	0-55	0-92	6 (1,2,3)	Yes (0-253)
14	Karpathos	35-505	27-150	33	0-70	3-45	—	—	—	17 (3,10,4)	No
15	Kassos	35-391	26-921	69	0-87	4-80	—	—	—	6 (1,4,1)	No
16	Kato Fira	37-056	25-081	26	0-73	4-00	—	—	—	0 (0,0,0)	No
17	Kato Kufonisi	36-910	25-576	24	0-83	2-85	—	—	—	4 (1,2,1)	No
18	Kimolos	36-808	24-559	66	0-79	3-29	10	0-60	2-50	10 (2,3,5)	No
19	Kitriani	36-903	24-726	6	0-67	1-45	—	—	—	0 (0,0,0)	No
20	Kopria	36-987	25-638	5	1-00	4-00	—	—	—	0 (0,0,0)	No
21	Kythnos	37-406	24-424	13	0-77	4-00	6	0-50	3-50	12 (3,5,4)	No
22	Megali Fteno	36-311	25-800	37	0-78	2-00	—	—	—	0 (0,0,0)	No
23	Mikri Fteno	36-312	25-795	30	0-77	4-00	—	—	—	0 (0,0,0)	No
24	Milos	36-708	24-490	85	0-82	5-98	—	—	—	13 (2,5,6)	No
25	Mykonos	37-443	25-381	21	0-62	1-71	10	0-40	0-89	11 (2,4,5)	Yes (0-25)
26	Naxos	37-061	25-484	58	0-62	1-87	12	0-75	0-57	17 (3,8,6)	Yes (0-1)
27	Nikouria	36-882	25-917	5	0-80	2-00	—	—	—	1 (0,0,1)	No
28	Pachia	36-272	25-831	6	1-00	4-00	—	—	—	0 (0,0,0)	No
29	Plakida	36-286	26-745	10	0-90	4-27	—	—	—	0 (0,0,0)	No
30	Panteronisi	36-971	25-119	33	0-88	2-26	—	—	—	1 (0,0,1)	No
31	Paros	37-060	25-192	34	0-62	4-55	10	0-60	1-00	15 (3,5,7)	Yes (NA)
32	Polyaigos	36-767	24-637	13	0-69	2-41	—	—	—	7 (0,3,4)	No
33	Saria	35-864	27-220	11	0-73	0-74	—	—	—	3 (1,2,0)	No
34	Schinoussa	36-873	25-521	56	0-71	2-38	35	0-77	1-71	5 (1,2,2)	No
35	Serifos	37-161	24-481	31	0-64	1-49	7	0-71	1-50	11 (3,4,4)	No
36	Sifnos	36-972	24-702	36	0-81	2-67	—	—	—	10 (3,4,3)	No
37	Sikinos	36-680	25-121	25	0-68	2-86	10	0-70	1-57	7 (1,4,2)	Yes (0-143)
38	Syrna	36-345	26-676	5	0-60	2-29	—	—	—	0 (0,0,0)	No
39	Syros	37-433	24-914	14	0-86	2-26	10	0-50	1-00	12 (3,4,5)	Yes (0-5)
40	Tinos	37-585	25-184	19	0-53	2-67	—	—	—	19 (4,6,9)	Yes (NA)
41	Tsimintiri	36-976	25-018	24	0-62	4-00	—	—	—	1 (0,1,0)	No
42	Venetiko	36-855	25-485	35	0-94	3-11	—	—	—	0 (0,0,0)	No

*n* is the number of individual geckos examined. Abundance of *M. kotschy* is the number of geckos found per hour of search by YI. Abundance of *H. turcicus* and abundance of vipers are the numbers of animals found per day of search per person searching. Viper abundance is given in parentheses in the viper presence column. Predator richness includes all potential mammalian, avian and reptilian gecko predators, given in parentheses from left to right, respectively (see Appendix S1 for further details). Sex-specific autotomy rates and data for non-significant predictors (i.e. body size) are given in Table S1.

If tail loss is indeed an important antipredator mechanism, why do autotomy frequencies increase on predator-reduced, and especially predator-free, islands? Four of the five studied predation indices (i.e. mainland vs. islands, predator richness, predator presence vs. absence and *V. ammodytes* presence vs. absence) were negatively associated with autotomy rates (the last two only in *M. kotschy*). The reason for this discrepancy might stem from the compound nature of predation pressure and its two main components: intensity and efficiency.

On small islands, the numbers of predator and prey species decline, subsequently promoting 'density compensation' (Case 1975), in which the density of both predator and prey populations may increase (Rodda & Dean-Bradley 2002; Ajtíć *et al.* 2013). We found that viper abundance increases as islands become smaller (Appendix S2), possibly indicating a case of mesopredator release (Crooks & Soulé 1999). Abundance of *M. kotschy*, however, is independent of island area (Appendix S2). This, combined with the lower diversity of other potential prey, implies



**Fig. 3.** Autotomy frequency comparison of mainland and insular individuals of each species: black – autotomized tails, white – intact tails. (a) *Mediodactylus kotschy*; (b) *Hemidactylus turcicus*.

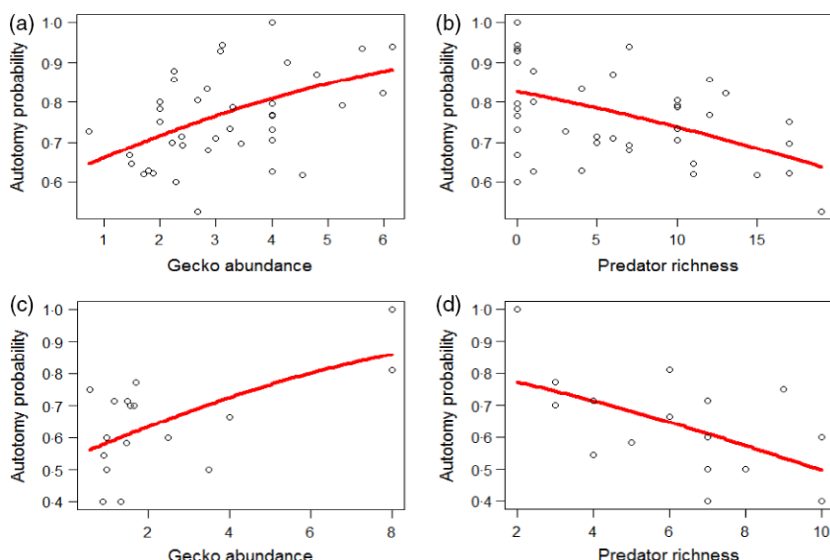
that vipers impose more intense predation pressure on geckos on the smallest, most species-poor islands.

Because vipers are dominant saurophagous predators (Pafilis *et al.* 2009b), we expected that they would strongly affect the tail autotomy frequencies. Interestingly, however, we found that autotomy rates were lower on islands with vipers. Predation efficiency varies across lizard predators (Medel *et al.* 1988), and vipers are considered highly efficient (Kreiner 2007; Pafilis *et al.* 2009b). *Vipera ammodytes* are ‘sit-and-wait’ venomous predators (Kreiner 2007). On the Aegean Sea islands, they exercise lizard-targeted luring behaviour, by moving the tip of their tail to resemble a maggot and attract their victims to approach,

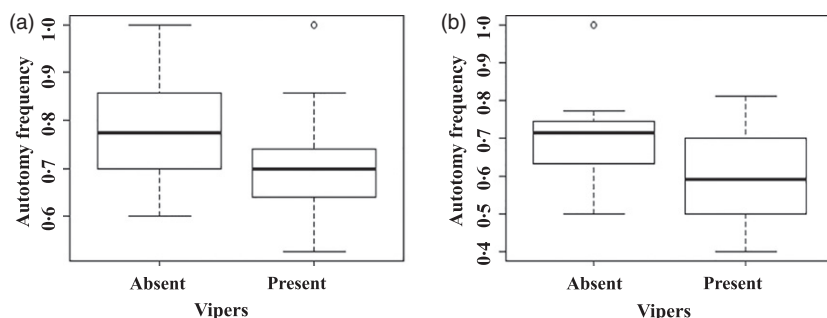
thus further increasing the chances of a successful strike (Cundall 2002; Kreiner 2007). Even if a lizard manages to disengage from the viper’s grasp following the strike, it will probably succumb shortly afterwards. Normally, a lizard can escape only if a viper attacks the tail, but not any other parts of the body. Autotomy is therefore a very effective antiviper mechanism only if the viper attacks the tail (and only if the tail was not already detached from its base before). *Vipera ammodytes* is known to specialize on hunting the most common available prey (Kreiner 2007), which on small Aegean Sea islands are lizards, and particularly *M. kotschy* (Valakos *et al.* 2008 and authors’ pers. obs.). The low frequencies of shed gecko tails on islands inhabited by vipers may thus reflect the fact that few geckos successfully survive viper attacks. The high efficiency of vipers can also explain the only predation-related positive correlation we found: increase in tail-loss rates with viper (and gecko) abundance on viper-inhabited islands. We suggest that viper abundance follows the high gecko abundance rather than regulates it (Nowak, Theimer & Schuett 2008), as the latter is a main food source for vipers in our study system (Cattaneo 2010). If predation efficiency does not change with viper abundance, the tail-loss rates should reflect mostly intraspecific aggression and are therefore positively correlated with gecko abundance. This means that the positive correlation of viper abundance with the tail-loss rates is a by-product of the correlation between gecko abundance and viper abundance. It should be noted, however, that the relationship we found between viper abundance, gecko abundance and tail-loss rates on viper-inhabited islands in *M. kotschy* is strongly determined by one influential point: Despotiko Island. Removing this island from the analysis eliminates the significance of the relationship between the autotomy rate and viper abundance ( $n = 9$ ,  $r = 0.14$ ,  $P = 0.71$ ). This island has the highest estimates of gecko abundance and viper abundance and a very high autotomy rate (94%).

**Table 2.** The best models for autotomy frequencies across different subsets of the data. For *Hemidactylus turcicus*, the predator richness excludes avian predators (as the model with the total predator species richness was not the best). None of the predictors was significant for *H. turcicus* in viper-inhabited islands

Species	Subset	Predictors	<i>n</i>	Slope	SE	Intercept	SE	<i>P</i>
<i>Mediodactylus kotschy</i>	All islands	Gecko abundance	41	0.212	0.052	0.827	0.209	<0.01
		Predator richness (total)		−0.045	0.012			<0.01
	Viper-inhabited islands	Gecko abundance	10	0.322	0.109	−0.004	0.320	<0.01
		Viper abundance	10	1.167	0.454	0.521	0.183	0.01
	Viper-free islands	Gecko abundance	29	0.020	0.067	0.910	0.247	<0.01
		Predator richness (total)		−0.040	0.017			<0.01
<i>Hemidactylus turcicus</i>	All islands	Gecko abundance	17	0.153	0.752	1.004	0.463	0.04
		Predator richness (mammals and reptiles)		−0.115	0.066			0.08
		Gecko abundance	17	0.173	0.075	0.304	0.227	0.02
	Viper-free islands	Predator richness (mammals and reptiles)	17	−0.125	0.065	1.495	0.406	0.05
		Predator richness (mammals and reptiles)	7	−0.271	0.130	2.279	0.692	0.04
		Predator richness (mammals and reptiles)						



**Fig. 4.** Logistic regression curves of autotomy frequencies against significant predictor variables (univariate analyses): (a) gecko abundance in *Mediodactylus kotschy*; (b) predator richness in *M. kotschy*; (c) gecko abundance in *Hemidactylus turcicus*; (d) predator richness (non-avian) in *H. turcicus*.



**Fig. 5.** Autotomy frequencies of *Mediodactylus kotschy* on viper-free islands compared with the frequencies on viper-inhabited islands: (a) *M. kotschy*; (b) *Hemidactylus turcicus*.

Although we have no reason to doubt these estimates, we urge caution in interpreting the trend. The reason *H. turcicus* is not affected by vipers is probable that *V. ammodytes* mostly avoids entering human habitations (authors' pers. obs.), the favourite dwelling of the house gecko. *Hemidactylus turcicus* usually clings to building walls (authors' pers. obs.) – too high for the ground-dwelling vipers to reach.

Predator richness is regularly used as an index of predation pressure (e.g. Pérez-Mellado, Corti & Lo Cascio 1997; Cooper, Pérez-Mellado & Vitt 2004; Pafilis *et al.* 2009b). The association between predator richness and predation intensity (i.e. the rate of predation attempts), however, has been questioned (Jaksic & Busack 1984; Wright, Kimsey & Campbell 1984). Predation intensity has been shown to positively correlate with the autotomy rates in some lizard species (e.g. Fox, Perea-Fox & Franco 1994). The negative association we found here between the tail-loss rates and predator richness supports Jaksic & Busack's (1984) questioning of the relationship between predator richness and predation intensity. We suggest that the autotomy rates reflect a trade-off between predation intensity and efficiency: tail loss increases with intensity (Pianka 1970 cf. Jaksic & Busack 1984; Fox, Perea-Fox & Franco 1994) and declines where predators

are more efficient (Schoener 1979; Medel *et al.* 1988; Bateman & Fleming 2011).

Our findings suggest that intraspecific competition is the most important selection agent affecting the tail loss. Autotomy frequencies of both gecko species are higher in dense populations and in *M. kotschy* on predator-free islands as well. On small, densely populated islands, intraspecific aggressive encounters are frequent and strong (Raia *et al.* 2010), and hence, the autotomy rates increase (Pafilis *et al.* 2009b; Cooper, Dimopoulos & Pafilis 2015; Donihue *et al.* 2016). *Mediodactylus kotschy* is highly territorial (Ajtić 2014), and individuals fight fiercely with conspecifics. In such encounters, geckos bite off their rivals' tails, yet rarely fight to the death (Bauer 2013). Aggressive encounters over basking positions, which we have witnessed on predator-free islets, corroborate our findings. Predator–prey encounters, however, may be lethal, and only some leave autotomized lizards alive. Moreover, the ability of a lizard that has already autotomized its tail to successfully reuse this defence mechanism is lower than that of a lizard that had never used it (Naya *et al.* 2007). This increases the likelihood of succumbing to another predation attempt (Congdon, Vitt & King 1974; Downes & Shine 2001). Thus, many more individuals who previously used autotomy survive (and



can be detected) in predator-free dense populations, and higher proportions of lizards with regenerated tails therefore accumulate. Where predation is rife, lizard population densities may be kept low (Case 1975), and thus, predators in effect reduce the frequency of the aggressive intraspecific interactions that result in autotomy. However, our data do not demonstrate such associations between gecko abundance and predation indices (e.g. predator richness and viper abundance; Appendix S2) and therefore do not support this mechanism.

Sexual differences in autotomy are uncommon in lizards (e.g. Chapple & Swain 2004; Brock *et al.* 2015; but see Bateman & Fleming 2011). Male lizards are much more aggressive towards male conspecifics than they are towards females, and they are also more aggressive than females are (e.g. Cooper, Dimopoulos & Pafilis 2015 and references therein). Autotomy frequencies in males are therefore expected to be higher than in females (Bateman & Fleming 2009). Males in our study system had significantly higher tail-loss rates than females, further suggesting that intraspecific aggression drives the tail loss.

We conclude that although predation is commonly considered as the main force driving autotomy, intraspecific aggression constitutes an even stronger driver than predation, at least in some species and ecosystems, such as those we studied. Defence mechanisms such as autotomy do not merely reflect the predation pressure and are the fruit of a complex ensemble of selection pressures. Our results contrast those of previous studies (Cooper, Pérez-Mellado & Vitt 2004; Pafilis, Pérez-Mellado & Valakos 2008) and demonstrate that different species of lizards do not respond uniformly to the same environmental conditions. Additional detailed data on predation efficiency and intensity (in general and for specific predators), as well as on the prevalence and fierceness of intraspecific encounters, and their impact on caudal autotomy frequencies, could contribute to further elucidating the patterns and drivers of tail-loss evolution.

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## Data accessibility

All data are included in the paper and supporting information and also archived from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.2qd2g> (Itescu *et al.* 2016).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Data for non-significant predictors and sex-specific autotomy frequencies.

**Appendix S1.** Reference list of predator-data sources.

**Appendix S2.** Results of supporting regression tests mentioned in the main text.