

Evolution of antipredator defenses in an island lizard,

Podarcis erhardii

by

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ABSTRACT

Over evolutionary time, many organisms have developed an array of antipredator defenses to avoid and escape predation. Evolutionary theory predicts that ‘costly’ antipredator behaviors are to be selected against in the event a prey becomes isolated from predators. Predator naïveté, the ignorance of prey to threats imposed by predator species, is a phenomenon often observed on islands where limited space and resources lead to the extinction of predator species. Here, we took advantage of a Pleistocene land-bridge island system with varying degrees of predator diversity and period of isolation to explore the maintenance of antipredator behaviors in a widely distributed prey species. We report on the evolution of antipredator defenses of a model island prey species (*Podarcis erhardii*; Squamata, Lacertidae), and identify the factors responsible for the expression or loss of antipredator defenses in island populations. We focus on two antipredator behaviors (flight initiation distance and caudal autotomy), which were quantified for 37 different islands and one mainland location that vary in predator diversity, isolation period, and area. The results suggest that as predator diversity is lost, both flight initiation distance and laboratory caudal autotomy defenses decrease steadily with loss of predators. Contrary to previous studies of herpetofaunal autotomy in this system, we found that field autotomy rates were significantly higher on predator-free islands, and laboratory-induced autotomy was not explained solely by the presence of vipers as reported in an earlier study. While we found that behaviors could erode relatively quickly after isolation from some predators (4 years), in general, behaviors eroded progressively with a duration of isolation with the longest isolated populations having the least expressed antipredator behaviors.

KEY WORDS: Antipredator behavior, flight initiation distance, caudal autotomy, islands, evolution

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DEDICATION

This work is dedicated to the memory of two great women. My grandmother, Mary Margaret Gruppi, who passed away while I was completing the fieldwork required this project. My grandmother was patient, kind, and a relentless supporter of my adventures.

To Courtney Wilson, a fellow SNREd whose smile lit up a room. Courtney embodied hard work and dedication, and her untimely passing inspired me every day to work harder and give myself wholly to my passion.

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Introduction:

Predation exerts powerful selective pressure on the behavior and physiology of prey species (Edmunds 1974; Blumstein and Daniel 2005; Blumstein 2006; Losos et al. 2006; Shepard 2007). Antipredator defenses are a prey's response to the threats imposed on an individual by an approaching predator (Bulova 1994). It is assumed that all else being equal, the persistence of antipredator behaviors should only occur if the benefits outweigh the costs incurred, and that costly behaviors will be eliminated by selection if they serve no benefit (Magurran 1999; Blumstein 2002; Blumstein and Daniel 2005; Pafilis et al. 2009_a). Costs vary by prevailing environmental pressures and behavior type. Therefore, we would expect the degree of expression of antipredator behavior to be related to the prevailing predation environment.

Many native island species have few predators, and little in the way of behavioral or physiological defenses (Blumstein and Daniel 2005; Cooper and Pérez-Mellado 2012). This phenomenon, termed predator naïveté, likely occurs where costly antipredator behaviors and physiological adaptations have been naturally selected against in reduced predation environments (Blumstein and Daniel 2005). Predator naïveté can be particularly pronounced on islets where large-bodied top predators are absent due to limited space and resources (Darwin 1839; MacArthur and Wilson 1967; Curio 1976; Arnold 1984; Pérez-Mellado et al. 1997; Blumstein 2002; Cooper et al. 2004). As a result, island endemic species have been disproportionately affected by the introduction of novel predators into previously predator-free environments (Baillie et al. 2004; Beauchamp 2003; Losos et al. 2006; Bonnaud et al. 2010). This is a major concern for conservation, and has prompted further investigation into the selective mechanisms responsible for the retention of antipredator behavior.

The Multipredator Hypothesis (MPH) attempts to explain the persistence of antipredator behavior when a species becomes isolated from some, but not all, of its predators (Blumstein 2006). One main prediction of the MPH is that the 'presence of any predators may be sufficient

to maintain antipredator behavior for missing predators', presumably via pleiotropy and linkage of genes influencing antipredator behavior (see Blumstein 2006). Systemic loss of antipredator behavior was found during a study on macropodid marsupials from populations isolated on islands with no predation (Blumstein and Daniel 2005), and in a study of group-size effects on vigilance of tammar wallabies (*Macropus eugenii*) (Blumstein et al. 2004). While previous studies provide insights into patterns of antipredator behavior loss on islands with reduced predation (Beauchamp 2004; Blumstein and Daniel 2005; Pafilis et al. 2009_a, Cooper and Pérez-Mellado 2012), most of these studies only focus on one behavior in a few islands where predation pressure is generalized as 'none, low, and high.' The MPH can best be tested in a system where one continuous population of a prey species with multiple predators has become geographically separated and isolated with varying subsets of the original predation regime, eliminating potential complicating factors such as founder effects (Blumstein and Daniel 2005; Blumstein 2006). Here, we take advantage of such a system, the Cyclades, a group of land-bridge islands located in the central Aegean Sea. We compare the expression of the two main antipredator behaviors of island populations of a common lacertid lizard, *Podarcis erhardii*, a habitat generalist that is known to be a poor over-water disperser (Foufopoulos and Ives 1999). Thus, in this region lizards were originally exposed to a diverse predator community which slowly dwindled, or in some cases disappeared, as hilltops in a continuous coastal landscape were fragmented into islands by rising sea levels. (Hurston et al. 2009).

Animals have evolved an array of antipredatory responses, with a common frontline defense being flight to a refuge (Greene 1988; Cooper 1997; Blumstein and Daniel 2005; Cromie and Chapple 2013). When an animal detects an advancing predator it must determine when and how it will escape because fleeing is energetically costly (Ydenberg and Dill 1986; Martín and López 2003; Pérez-Cembranos et al. 2013), and may decrease opportunities for fitness-enhancing activities such as foraging and mating (Ydenberg and Dill 1986; Cooper and Frederick 2007). Assessing the cost of remaining in place or fleeing is largely an experience-

dependent antipredator defense (Magurran 1990; Blumstein et al. 2004; Stankowich and Blumstein 2005; Cooper 2011), meaning that animals exposed to regular predation pressure have a refined sense of when to remain or when to flee. The flight initiation distance (FID) of a prey species is considered to be a quantifiable measure of perceived predation risk (Bonenfant and Kramer 1996; Blumstein and Daniel 2005; Amo et al. 2006; Cooper 2011). Thus, it is expected that the prevailing predation environment should affect the flightiness of a prey species (Cooper and Pérez-Mellado 2012).

Beyond relatively widespread antipredator defenses like fleeing, several organisms have additional, specialized physical adaptations to avoid predation. Caudal autotomy, or the self-severing and regrowth of the tail, is a common antipredator defense among lizards (Arnold 1984; Bateman and Fleming 2009; Pafilis et al. 2009_a). Autotomy occurs along specialized breakage planes located within vertebrae throughout the tail (Bateman and Fleming 2009; Chapple and Swain 2002_a; Lin and Ji 2005). The shed tail writhes about for a period of time (ranging anywhere from 4-9 min in *P. erhardii*), a process thought to increase handling time and distract the predator from the escaping lizard (Arnold 1984; Arnold 1988; Pafilis et al. 2009_a). While tail shedding is a highly effective escape strategy (Daniels 1985; Arnold 1988), it is also a very costly defense that is usually only deployed after frontline defenses such as crypsis, hiding, or fleeing have failed (Arnold 1984; Cromie and Chapple 2013). The tail contains a significant portion of fat deposits, and losing those energy stores is costly (Ballinger and Tinkle 1979; Bateman and Fleming 2009; Pafilis et al. 2009_a). Regrowth of the tail, which occurs at various rates among species, also requires a considerable amount of energy (Vitt and Cooper 1986; Pafilis et al. 2008; Pafilis et al. 2009¹). Lizards with autotomized tails have impaired locomotive capabilities (Chapple and Swain 2002_b; Lin and Ji 2005). Lowered social status (Fox and Rostker 1982; Schall et al. 1989; Salvador et al. 1995) and decreased reproductive output are additional transient, negative effects incurred by recently autotomized individuals (Pafilis et al. 2009_a; Ballinger and Tinkle 1979; Vitt and Cooper 1986; Cromie and Chapple 2013). Because

autotomy can occur accidentally and without survival benefit during non-aggressive interactions (Vitt et al. 1977), and agonistic intra-specific interactions (Bateman and Fleming 2009; KB *personal observation*), ease of autotomy in a population should reflect associated costs and benefits.

Previous studies regarding antipredator behavior in island populations suggest behavioral decay was due to a complete absence of predators (Beauchamp 2004; Blumstein and Daniel 2005, Blumstein 2006; Pafilis et al. 2009_a). Other studies of predator isolation effects have largely focused on explaining the loss of one type of defense behavior (Beauchamp 2004; Pafilis et al. 2009_a; Garcia et al. 2012), or the removal of one predator species (reviewed in Blumstein 2006). This is problematic when attempting to identify the major factors influencing the maintenance antipredator defenses of a species with multiple predators that has developed an arsenal of specialized defenses to respond to specific predator encounters. While predators demonstratively exert selective pressures on antipredator behavior (Edmunds 1974; Blumstein and Daniel 2005; Losos et. al 2006; Shepard 2007; Pafilis et al. 2009_a), it remains unclear whether predators are the sole selective agent whose absence results in the erosion of defense behavior, or if this relationship is exacerbated by prevailing environmental factors. Because lizards on Aegean islands have been isolated with varying subsets of the original predation regime, they provide an excellent opportunity to study evolutionary mechanisms responsible for the retention of antipredator behavior. Thus, we ask the following questions: (1) Does the expression of antipredator behavior vary across island lizard populations living in the Greek archipelago?, (2) Is antipredator behavior maintained similarly on islands with any predators, per the second prediction of the Multipredator Hypothesis (Blumstein 2006)?, (3) Is antipredator behavior maintained specifically by the presence of certain predators?, and (4) How does duration of isolation from more diverse predator regimes affect the retention of antipredator behavior?

The present study is focused on the evolution of antipredator behaviors in distinct populations of a model island lizard species. In particular, it aims to elucidate mechanisms that influence the maintenance of antipredator behavior throughout evolutionary time following years of isolation from some historic predators (see Blumstein 2006). We model the degree of expression of the two main antipredator behaviors (flight initiation distance and caudal autotomy) in lizards from Mediterranean islands that contain varying subsets of predators from original Pleistocene conditions. Based on our ecological knowledge of the Aegean Sea region and previously documented patterns of behavior (Pafilis et al. 2009_{a,b}), we predict the following: (1) flight behavior varies across the Greek Archipelago and decays with loss of predator diversity, (2) ability for autotomy is influenced by the presence of vipers specifically (see Pafilis 2009_a), and (3) erosion of both FID and autotomy behavior are related to the period of isolation from more diverse predator regimes. To test our predictions, we assumed that all lizards pre-Pleistocene sea-level rise experienced identical predation conditions and exhibited similar flight behavior, and innate predisposition for autotomy. Cycladic populations of *P. erhardii* provide the perfect system for studying the evolution of antipredator behavior on islands due to the poor over-water dispersal abilities of the taxon (eliminating founder effects), shared climatic conditions among islands, and varying degrees of predator isolation.

Methods:

Study Area and Species

The Cyclades are a group of land-bridge islands situated in the central Aegean Sea (Fig. 1), that were formed since the last glacial maximum when rising sea levels flooded parts of a large Pleistocene large island mass termed 'Cycladia' (Foufopoulos and Ives 1999; Broodbank 2002; Poulos et al. 2009). The current climate is typical of the Mediterranean region with a pronounced warm, dry summer season and cool, rainy winters. The islands experience more temperate conditions relative to the mainland due to their proximity to the sea and the very

strong winds that prevail much of the year (Valakos et al. 2008). Vegetation cover is largely shaped by anthropogenic disturbance over thousands of years (Rackham and Grove 2001). It consists of a patchwork of agricultural areas, sclerophyllous evergreen maquis, and an endemic, summer-deciduous dwarf scrub formation termed 'phrygana' (Fielding and Turland 2008).

The Aegean Wall Lizard (*Podarcis erhardii*) is a small, ground-dwelling lacertid, with an adult snout-vent length (SVL) of 49-78 mm, and a tail twice as long as the body (Gruber 1987). This species is endemic to the southern Balkans and many Aegean islands, and occurs in a variety of habitats. It preferentially inhabits areas with dry stone walls and spiny vegetation, which serve as refugia from terrestrial and aerial predators. This species is insectivorous (Arnold, 1987), feeding mainly on Coleoptera (Adamopoulou et al. 1999), but has been observed foraging opportunistically on fruits (Brock et al. 2013 *in press*). A once continuous *P. erhardii* population on Cycladia was fragmented and isolated by rising sea levels into >60 small island populations. Reflecting the diversity of present day island conditions, these populations differ greatly in regard to their morphology and life history. Predator diversity decreases with island size, and small islets (<.05 km²) tend to be completely predator free. We divided predators into six categories based on taxonomic affiliation, hunting strategy, and occurrence on the islands. Predator categories (listed in order of occurrence from smallest to largest islands) are: 1. rats (*Rattus rattus*) 2. sand boas (*Eryx jaculus*), 3. avian predators (*Falco tinnunculus* and *Buteo buteo*) 4. Colubrid snakes (*Dolichophis caspius*, *Elaphe quatuorlineata muenteri*, *Natrix natrix persa*), 5. mammals (feral cats [*Felis catus*], stone martens, [*Martes foina*]), and 6. vipers (*Vipera ammodytes*). We divided snake predators into three different categories because of pronounced differences in hunting strategy. Thus, vipers are sit-and-wait predators that ambush and envenomate their prey (Nowak et al. 2008, Pafilis et al. 2009_a), while Colubrid snakes hunt down their prey following active searching. The sand boa *E. jaculus* preys sometimes on adult lizards though more often engages in fossorial lizard egg predation (JF *personal observation*; Cattaneo 2010). We also distinguish rats from the 'mammalian predator'

category because rats in the Cyclades are small-bodied opportunistic predators that lack the capacity of cats and stone martens to prey efficiently on lizards. We determined the predator community on each island by combining published information with field surveys conducted over the course of several visits.

Environmental island characteristics were determined remotely using spatial analysis tools. Information on island area (km²) was either readily available from published or government sources for inhabited islands (Foufopoulos and Ives 1999; Poulos et al. 2009). For uninhabited islets without published spatial data we used ArcGIS ArcMap 10 Field Calculator to calculate polygon area (km²) (spatial data courtesy of the Natural History Museum of Crete). We used fine-scaled bathymetric data derived from navigation charts and targeted sonar measurements collected by one of us (JF) in the field, in conjunction with geomorphological reconstructions of past sea levels from global and local sea level change graphs in order to determine the time of separation of islands from each other (USDMA 1991; Foufopoulos and Ives 1999; Hurston 2009; Poulos et al. 2009). Anthropogenic modification of the abiotic landscape through the construction of dry stone walls provide lizards refuge space from predators. We therefore recorded the presence or absence of dry stone walls on islands to test for relationships with FID.

In addition to predator regime, other biotic parameters were measured at the island-level. Vegetation cover (%) was determined using a combination of Google Earth image data and measurements on the ground. Non-predatory seabirds preferentially nest on a small subset of uninhabited islets in the Cyclades during the summer (Pafilis et al. 2009_b; Foufopoulos, *unpublished data*). While there are no records of seabirds preying on *P. erhardii*, or lizards in general (Cooper et al. 2004; Pafilis et al. 2009_b), co-habitation on small islets may maintain flight behavior through historic avian predator recognition (Curio 1993; Blumstein 2006). We measured nesting seabird densities by counting the number of nests per island, and assumed each nest belonged to two birds (Foufopoulos and Mayer 2007). We measured the relative

abundance of lizards on all island study sites. On Aegean islands with few predators, population densities of lizards are high, which could intensify intra-specific competition, potentially having an effect on the maintenance of the ability to autotomy (Pafilis et al. 2009_{a,b}). Lizard densities were determined by slowly walking a 1-2 100 m (4 m width) transects of suitable habitat (most islands were too small for multiple transects, see Pafilis et al. 2009_b and Jaeger 1994) and recording any *P. erhardii* seen or heard (lizards per 100 m). To evaluate effects of detection distance (distance at which lizard detects surrogate predator presence) on FID, we measured detection distance by measuring the distance at which an observer became first visible to lizards and correlated that to actual FID. Finally, to investigate possible effects of body size on FIDs, we also collected SVL data for a subset of our study sites where it was possible to capture >15 individuals to produce reliable size estimates.

Behavioral Data Collection

Flight Initiation Distance

We measured the flight initiation distance (FID) of *P. erhardii* (N=913) from 37 Cycladic islands and one mainland Greece site (Fig. 1, Table 1). FID measurements took place during the species' main activity period (May-early July) on warm (22-26°C), sunny days with little to no wind (wind speed < 10 km/h). Exposed, resting lizards were located by walking across an island in one direction until an individual was detected through binoculars, usually from a distance of 5-10 m. Because island scrub habitat was very similar on all study sites, being comprised of open rocky ground interspersed by low (< 80 cm), sclerophyllous evergreen bushes (*Juniperus phoenicea*, *Pistacea lentiscus*), visibility of lizards was similar between sites. To simulate a predation event, the same observer approached every focal animal by walking directly toward it at a practiced pace of approximately 80 m/min (Pérez-Cembranos et al. 2013). Cooper et al. (2009) found that at this speed, the detection distance did not have an effect on FID in a similar species, *Podarcis lilfordi*. The same individual performed every approach in the same attire to

avoid confounding effects (Amo et al. 2006; Pérez-Cembranos et al. 2013), and never returned to previously visited areas to avoid encountering the same lizard twice. Since direction and angle of approach may have an effect on a lizard's response to predation (Burger and Gochfeld 1990), we only performed head-on approaches. Flight initiation distance (FID) was recorded as the distance between the observer and the focal animal when escape was initiated. Both the published literature (Dill and Houtman 1989; Bonenfant and Kramer 1996; Amo et al. 2006) and our own data indicated that FID is positively correlated to the distance a lizard has to cover to reach the nearest refuge (DR); we therefore record this measure for every observation of FID (Dill and Houtman 1989; Bulova 1994; Kramer and Bonenfant 1996; Amo et al. 2006; Cooper and Pérez-Mellado 2012). Other variables found to have an effect on FID (e.g. body size – Cooper 2011, and distance when first detected – Cooper et al. 2009) were also recorded and tested for covariance. We measured detection distance (distance between the focal animal and surrogate predator when focal animal detects the presence of the surrogate predator) and as well as body size (SVL in cm) at several sites to check for potential relationships with FID.

Field Autotomy

We measured the ability of lizards to shed their tail across the study islands by quantifying two aspects of it: field autotomy and lab autotomy (Pafilis et al. 2009). Lizards were located using the same methods described for FID. Once an animal was detected in the field, we observed the tail condition through binoculars and noted whether it was intact or previously autotomized. Previously autotomized tails are readily distinguishable from intact tails by size, shape, color, and scale morphology (Simou et al. 2008). Field autotomy rates were calculated for each island population as the percent of the lizards encountered that had previously autotomized tails. Scientists have argued that aggressive intra-specific interactions, predator efficacy, microhabitat use, and age of individuals within a population can confound the relationship between predation pressure and field autotomy rate, necessitating a closer

examination of predator type and finer measurement of autotomy (Turner et al. 1982; Medel et al. 1988; Bateman and Fleming 2009; Pafilis et al. 2009_a). We therefore use a standardized measure of autotomy induced under controlled laboratory conditions to distinguish between the innate predisposition of a population to shed its tail and the environmentally determined opportunity for this to occur (Pafilis et al. 2009_a, Hare and Miller 2010, Bateman and Fleming 2011).

Laboratory Autotomy

Laboratory autotomy rates (LAR) were obtained from 28 of our study sites (Fig.1, Table 1) Previous research has shown that the ability to autotomize a tail is affected both by age (Pafilis et al. 2008; Bateman and Fleming 2009), sex (Vitt 1981; Bateman and Fleming 2009) and prior condition of the tail (Arnold 1984; Bateman and Fleming 2009). We therefore limited all autotomy observations in laboratory experiments to adult male lizards with intact tails to avoid potential confounding effects from differences in age, sex, or physiological condition of the tail (Bellairs and Bryant 1985; Simou et al. 2008; Bateman and Fleming 2009; Pafilis et al. 2009_a). Lizards were located in the field using the same methods described for flight initiation distance and field autotomy. Specimens were captured in the wild using a noose to minimize chance of tail autotomy that often occurs during hand-catching. We immediately removed the lizard from the noose, and transferred the individual to a tube sock for transportation back to our laboratory on Naxos.

Lizards were housed in shoebox terraria (32 cm × 16 cm × 12 cm) for 48 h before conducting the caudal autotomy measurements. Because autotomy in reptiles is potentially affected by an animal's body temperature (Pafilis et al. 2009_a; Daniels 1984), animals were exposed to a regulated photoperiod (12 h of light, 12 h of darkness) and allowed to thermoregulate freely along a thermal gradient until the time of procedure. Lizards were extracted from the thermal gradient and individually placed on a rough cork substrate placed at

a 45° angle where they could firmly hold on. To standardize pressure across all trials, a pair of calipers was placed approximately 20 mm behind the cloacal vent and then closed to half the diameter of the tail for a period of 15 sec (Pafilis et al. 2009_a). At the end of the 15 sec trial, we recorded whether the lizard autotomized or not. Laboratory autotomy rates [LAR] are reported as the proportion of tails that were autotomized for each population.

Effects of Isolation on Antipredator Behavior

Land-bridge islands provide an excellent opportunity to explicitly test the effects of duration of isolation on the extent of the erosion of anti-predator behaviors. We estimated ancestral predator diversity by assuming all present-day islands shared the same predator communities when they were joined as Cycladia prior to Pleistocene sea-level rise. Thus, we can evaluate the change in antipredator behavior in lizards over time by subtracting the expression of flight initiation distance or autotomy rate of the older island from the newer islet. We restricted our work to those islets that split directly off from Cycladia as opposed to being derived from a post-Cycladia intermediate-sized island.

Statistical Analyses and Model Selection

We used a mixed modeling approach to study the erosion of flight behavior at varying degrees of predation (Table 2). Analysis of FID was completed fitting the following model:

$$y = X\beta + Zu + \epsilon.$$

The fixed effects (β) are the categorical predation variables. Random effects (u), are given by a vector with mean $E(u) = 0$, and a covariance matrix $var(u) = G$. We used random effects for intercept and distance to the refuge (DR), with the subject category being island. Detection distance, lizard body size, and the relative abundance of intra-specific lizards did not correlate with FID, and were not included as covariates in our models (Appendix 1.). We formulated seven *a priori* hypotheses based on our ecological knowledge of the study area and published

literature on predator-lizard interactions (Nowak et al. 2008; Pafilis et al. 2009_a), in order to identify predators most important for the maintenance of specific defenses.

To test the effect of total predation on FID, and take advantage of the widely varying diversity of predators on the islands, we combined for each island all presence/absence data into an aggregate measure of 'Total Predation' (Σ Predation) by totaling the number of predator categories present for each island (Cooper et al. 2004; Pafilis et al. 2009_{a,b}; Cooper and Pérez-Mellado 2012). Conversely, we also test a model that considers all predator categories simultaneously and individually ('V+OS+M+E+AP+R' Table 2). Other models were formulated to test hypotheses about the effects of specific predators thought to have the greatest impact on FID, with all remaining predators being pooled into an aggregate 'other predators' (OP) category (Table 2). Based on previous work on antipredator behavior in this system and our knowledge of hunting strategies in general, we formulated five models that tested the role of mammals (M), avian predators (AP), and vipers (V) in determining FID. As a result the composition of the OP_i category varied slightly from model to model and this was denoted with differing subscripts. Our model selection process was to compare model AICc scores and their corresponding Akaike weights (w_i) (Burnham and Anderson 1998; Turkheimer et al. 2003). Models were compared using AICc values and their associated Akaike model weights were calculated as $w_i = \exp(-\Delta_i/2) / \sum_{r=1}^M \exp(-\Delta_r/2)$. (Turkheimer et al. 2003). We use AICc instead of AIC to correct for finite sample size and decrease the probability of overfitting data with too many parameters (Burnham and Anderson 2002; Burnham and Anderson 2004).

Field and laboratory autotomy rates were studied using general linear models (GLMs). We formed three competing hypotheses prior to data analysis to explain variation in autotomy at the island level, which we compared against each other, using AICc and the corresponding Akaike weights. Predictors implemented in the model building process include 'Total Predation' (the summation of all predator categories present on an island), '0 Predation' (a categorical 'yes/no' variable indicating there are no predators versus any amount of predators on an island),

and 'Vipers' (a categorical 'yes/no' variable noting the presence or absence of vipers on an island). Intercept was a fixed effect in all autotomy GLMs, and dependent variables were either field autotomy or laboratory autotomy. Given the relatively small sample sizes ($N < 50$ islands) of field and laboratory autotomy data, we constructed the simplest models possible that use just one predictor variable to avoid overfitting.

To examine effects of isolation time on the erosion of flight initiation distance and autotomic capacity, we calculated the change in FID and laboratory autotomy rate from a baseline predator-rich Cycladia population to the present day islet populations [$\Delta\text{Behavior} = \text{Behavior}_{\text{islet}} - \text{Behavior}_{\text{large island}}$]. The Cycladia baseline population was conservatively assumed to be similar to Naxos, the largest island with the most diverse present day predator population. We ran simple linear regressions of change in behavior against period of isolation (Ln-transformed) to gain insights on the erosion of antipredator behavior over time (Fig. 3a). Additionally, we regress the change in antipredator behavior from large island to islet against the change in number of predator types (Figs. 4a,b). All correlations are given using Pearson's r unless otherwise noted.

Results:

Flight Initiation Distance

Flight initiation distance (FID), varied widely between individual lizards (10-855 cm: $\bar{x} = 180.2$ cm, $N = 913$). Because FID was positively correlated with distance to the refuge (DR) ($r = .0358$, $p = < 0.001$, $N = 913$), we included DR as a covariate in our mixed model analysis (Table 2). Predator category measurements were correlated with each other (Cohen's Kappa $p < 0.05$, $N = 38$) due to the partially nested nature of where species occur on islands, however, mixed modeling accounts for multiple correlated variables. Greater predator diversity on an island was associated with longer FIDs ($r = 0.618$, $p < 0.01$, $N = 38$) (Fig. 2.). The candidate model that simply summed the number of predator categories present (' Σ Predation'), under the

assumption that they are interchangeable, had the least predictive power of FID, whereas the model that considers all predator categories separately had a much higher relative likelihood and associated AIC model weight, even when penalized for the inclusion of six explanatory variables (Table 2). This suggests that all predator categories are not interchangeable and that each is important in a distinct manner in determining the expression of flight behavior (Table 2). An analysis of the marginal means from the final model shows that avian predators and mammals exerted the strongest effect on FID, whereas the effect of vipers, *Eryx*, rats and other snakes was negligible (Fig. 3). The model that accounted for each predator class individually, nonetheless, greatly outperformed that accounting for avian predators and mammals and lumping all other predators together (Table 2).

In single variable analyses of abiotic factors, island area correlated with FIDs while island age and presence of dry stone walls did not show any significant patterns (see Appendix 1). We regressed our final model residuals separately against all other measured island traits (see Appendix 1), and found no significant unexplained variation in flight behavior.

Field Autotomy

We obtained *P. erhardii* field autotomy rates for 32 of our 38 study sites (mean = 0.7, range: 0.5 – 1.0, N = 32; Table 1). Of our competing general linear models, '0 Predation' had the highest likelihood and associated AIC weight (Table 3). Thus, field autotomy rates were significantly higher on islands without any predators, than on all islands with even one predator category (mean FAR of 0 predator and predator islands were .85 [N=4] and .67 [N=28], respectively). Field autotomy rates from islands containing any number of predator categories ('Total Predation' score 1-6) did not statistically differ from each other (Kruskal-Wallis, $p = 0.143$, $H = 8.241$, $df = 5$). In contrast to other studies on Mediterranean herpetofauna (Diego-Rasilla 2003; Cooper et al. 2004; Pafilis et al. 2009_a), we found that field autotomy rates did not reflect predation levels (in terms of predator diversity), nor were they correlated with induced laboratory

autotomy rates (Spearman's $\rho = 0.088$, $p > 0.05$, $N = 28$). Given this, we tested for an association between relative abundance of lizards and field autotomy rate with the idea that increased population density would drive aggressiveness towards conspecifics, but found no relationship in an analysis of all islands (Spearman's $\rho = -.017$, $p = .925$, $N = 32$), and islands without predators (Spearman's $\rho = -.316$, $p = .684$, $N = 4$).

Laboratory Autotomy

We observed a wide range of laboratory autotomy rates across our different island populations ($\bar{x} = 0.34$, range: 0 – 0.58, $N = 28$). Laboratory autotomy rates (LAR) increased linearly with increased predator category diversity (Fig. 5b). Of the three general linear models (GLMs) tested, 'Total Predation' (Σ Predation model, Table 3) explained most of the variation in laboratory autotomy. In contrast, the 'Viper model', which emphasized the importance of vipers by separating islands with vipers from islands without, and the '0 Predation' model that separated islands without predators and islands with any amount of predation, had a much lower model weights (Table 3). This was unexpected given earlier work on autotomy in a related system had emphasized the importance of vipers as a driving factor underlying the retention of LAR on low predation island environments (Pafilis et al. 2009_b). Given that vipers had a non-random distribution only on the largest and most predator rich-islands and as such may create the false appearance of an overall predator diversity effect, we repeated this analyses only on those islands that were without vipers to investigate whether the relationship between laboratory autotomy and predator diversity would still hold for viper-free islands ($N = 22$). Including viper islands, laboratory autotomy rates were highly correlated with predator diversity ($r = .825$, $p < 0.001$, $N = 28$) like our best model suggests (Table 3). When we exclude viper islands, we see that the overall pattern still holds ($r = .672$, $p < 0.001$, $N = 22$), suggesting that autotomy rates are strongly shaped by predation pressure, independent of the presence of vipers.

Effects of Isolation on Antipredator Behavior

Lizards from islets that became directly separated from larger, more predator diverse islands experienced an average decrease in flight initiation distance of 79.5 cm. Erosion of FID on islets increased with period of isolation ($r = -.621$, $p < 0.01$, $N = 16$, Fig. 4a). We investigated whether the decrease in the number of predators from baseline was relevant to the magnitude of these decreases in flight behavior, and found no relationship ($r = .307$, $p = .248$, $N = 16$).

Lizard populations occurring on islets that became separated from predator-rich islands experienced, similar to FID, a decay in their propensity for autotomy, with a 19% average decrease in laboratory autotomy rate ($N = 12$). However, there was no relationship between the change in lab autotomy rate and period of isolation ($r = -.361$, $p = .249$, $N = 12$), though this result may be due to a limited sample size. Change in laboratory autotomy from island to islets was, however, strongly correlated with change in predator diversity ($r = -.942$, $p < 0.01$, $N = 12$) (Fig. 4b), which, when considered with results from our model selection process, suggest tail-shedding ability is largely influenced by the prevailing predation environment.

Discussion:

In this study we aimed to determine the causal factors underlying the retention of ancestral antipredator behavior in isolated populations living in island environments with relaxed predation. In particular, we tested for differences in the expression of antipredator behavior between islands, if behaviors are retained similarly in populations experiencing any amount of predation (per the MPH), and if behavior varies with a specific predation regime. Using a model lizard species that lives on a broad range of land-bridge island populations, each with different predator suites that are subsets of the ancestral regime, we looked at the extent of loss of antipredator defenses in relaxed predation environments over time. Results from our mixed and general linear model selection suggests that two antipredator defenses, flight response and autotomy, not only vary between islands, but that this variation is strongly correlated with the

prevailing predation regime. For FID, different types of predators had different effects, with mammals and aerial predators having the largest effects. For autotomy, total number of predators predicted ease of autotomy with no special effect of vipers apparent. Neither antipredator behaviors studied followed the second prediction of the Multipredator Hypothesis, as both decayed steadily with decreasing predator diversity, and thus, were not maintained the continued presence of any of the species' historic predators. The MPH would predict a similar expression of antipredator behavior on islands with any kind of predator and a significant decrease in expression where animals are living predator-free. Finally, *P. erhardii* from islets that have been isolated for longer periods of time and lost predator diversity experienced decreased expression of both flight behavior and autotomy.

While predator diversity was positively correlated with longer FIDs, we found it was the presence of mammalian and aerial predators in particular, that had the strongest effect on the retention of flight behavior (Figs. 2-4). Thus, presence of either mammalian or avian predation increased lizard FID on average by 60cm and 40cm respectively (Fig. 3 Estimated Marginal Means). This is probably best explained by the particular hunting strategies employed by these predator guilds, and the ability of lizards to recognize these particular predators prior or attack. Feral cats (*Felis catus*), and stone martens (*Martes foina*) the main mammalian predators on the islands, hunt by using speed to close the gap between themselves and the prey (Peck et al. 2008). Similarly, predatory birds fly in from a distance, often casting a recognizable shadow (Curio 1976). These approaches differ dramatically from snake predators present in this island system, which usually employ a sit-and-wait hunting strategy (Valakos et al. 2008; Pafilis et al. 2009_a). Hence, the reliance on speed to approach a prey item from afar means that lizards that escape early reap the largest benefits. Further, mammals and birds tend to focus attacks on the head of prey items, allowing the prey animal some opportunity for visual contact (Curio 1976; Smith 1976; Langkilde et al. 2004; Shepard 2007).

Populations of *P. erhardii* showed progressive declines in flight behavior with increasing duration of isolation in low-predation environments (Fig. 4). Thus this evidence for gradual loss expands on past work that showed that island populations have attenuated antipredator responses (Blumstein 2002; Blumstein and Daniel 2005; Cooper and Pérez-Mellado 2012). While these studies have shown that isolated populations have lost antipredator defenses, they provide little insight into the rate at which behaviors erode. Failure to recognize potentially threatening predators was particularly evident during visits to very old islands (KB *personal observation*, and see Figs. 4a. and b.). For example lizards from some of the oldest islands (450,000 years), were tame enough to approach within arm's reach, and would sit in one's hand after capture without attempting to flee. Again, because flight behavior is largely recognized as an experience-dependent antipredator behavior, tameness on islands with limited predation is probably due to an inability to adequately identify predators and correctly respond (Blumstein 2002). However, where previous work has suggested that behavioral loss can occur rapidly (Blumstein 2002), we found that short-term isolation (4-1,000 years) of populations experienced minimal loss (8 – 61cm), and a greater behavioral loss occurring over thousands of years (15 – 176cm). Further, the inability for insular populations to mount an adequate endocrine stress response could also be related to the predator naïveté we observed (see Rödl et al. 2007). Clearly, flight behavior is not maintained as predicted by the Multipredator Hypothesis (Blumstein 2006), and erosion of FID is probably the result of a combination of decreased predator diversity (especially hawks and mammals), subsequent loss of predator experience and recognition, and increases with period of isolation.

Previous work has suggested the highest incidences of field autotomy should occur in areas with inefficient predators (because failed attacks are likely to result in autotomy and escape), or a greater diversity of predators (Cooper et al. 2004; Pafilis et al. 2009_a; Bateman and Fleming 2011). The five study sites with the full gamut of predators present (Naxos, Andros, Ios, Irakleia, and Parnitha on mainland Greece) did not exhibit higher rates of field autotomy

than sites with fewer or no predators (Fig. 5a.). Instead, we found that the highest rates of autotomy actually occur on islets completely isolated from predators. Further, rates of autotomy in the field were not correlated with laboratory autotomy trials, which is inconsistent with similar investigations in the Mediterranean region on several species of lizard, including *P. erhardii* (Diego-Rasilla 2003; Cooper et al. 2004; Pafilis et al. 2009_{a,b}), and elsewhere (Bateman and Fleming 2011). While accidental shedding may account for some tail autotomy on predator-free islands (Arnold 1984; Hare and Miller 2010), our field observations suggest that the elevated rates of tail shedding are the result from aggressive intra-specific encounters (Vitt and Zani 1997, Bateman and Fleming 2009). Increased intra-specific aggressiveness on islets without predators is likely a product of intensified competition for food, territory, and mates (Pafilis et al. 2009_b; Raia et al. 2010). Small islet populations in particular are extremely territorial, and males defend their territory with behavioral displays such as tail wagging, aggressive chasing, and biting (Valakos et al. 2008; Font et al. 2012; KB *unpublished data*). Other authors have noted that older populations of lizards tend to have slightly higher rates of autotomy, because older individuals are more likely to have autotomized (Bateman and Fleming 2009; Pafilis 2009_a). Given this, it is possible that small islet populations also exhibit higher rates of autotomy because lizards are not being killed by predators, and therefore contain, on average, older individuals. Further investigation is required into intra-specific dynamics, food availability, and population structure on predator-free islands to explain why these wild populations have such high autotomy rates.

Laboratory autotomy rates were positively correlated with the total number of different predator categories found on an island. Unlike field autotomy, LARs declined linearly with the loss of any predator category (Fig. 5b). Of our three competing hypotheses, the 'Total Predation' GLM captured the most variation in laboratory autotomy rates (Table 3). A post-hoc investigation of the influence of vipers supports the claim that overall predator diversity has a strong relationship with retained autotomic abilities. After the removal of islands where vipers

were present from our analysis, a correlation comparison revealed that the linear pattern still holds, and is contained within the 95% confidence interval. That does not mean that vipers do not shape evolutionary ability to autotomy, but rather that predators beyond vipers are important in shaping caudal autotomy. Viperid predators generally occur only on the larger islands in the Cyclades, which usually also harbor at least four other predator categories (Valakos et al. 2008; Table 1). Therefore, it is difficult to untangle the effects of vipers and island size, which are both also highly correlated with overall predator diversity. Mammalian and avian predators, which usually focus attacks on the head and eyes of prey, will still induce autotomy when handling of prey involves the tail appendage. Additionally, rats inhabiting the Cyclades are known to attack lizards (McCallum 1986; Hare and Miller 2010, JF *personal observation*), and several studies identified rats as being responsible for population declines (Bateman and Fleming 2009; Hare and Miller 2010). Thus, it seems that all predator categories exert selective pressure on the maintenance of caudal autotomy.

A reduction of ability to respond to predation seems to be related to period of isolation from diverse predator regimes. In general, islets that were isolated for longer periods of time lost more predator types, specifically vipers, mammals, other saurophagous Colubrid snakes, and hawks. Lizards from islets that that experienced a decrease in the amount of predator types from original pre-Pleistocene conditions had shorter FIDs than their large island counterparts that today still live with a diverse array of predators. For experience-dependent behavior, such as FID (Blumstein 2002; Blumstein and Daniel 2005; Rödl et al. 2007), it follows that lizards living in predator-free environments, or with greatly reduced predator diversity, for longer periods of time would exhibit less refined behavioral responses to predation threats. However, the degree to which differences observed were heritable or phenotypically plastic remains unknown, and awaits further investigation.

Laboratory autotomy rates also decreased with longer period of isolation and reduced predator regimes. This is not surprising, given the lifetime fitness costs of autotomy. Testing for

the retention of hard-wired traits such as caudal autotomy gives us confidence that differences observed between lizards from younger, predator-diverse islands and older islets with only a subset of predators reflect the high costs of autotomy, which has been selected against in predator-poor environments. While reduced ability to autotomy may be advantageous to a lizard's fitness in a less diverse predation environment, individuals may not have the capacity to adapt if a novel predator were suddenly introduced.

The lizard population of Kato Fira island is unusual in a number of aspects. The animals on this island, located in the Paros cluster, and separated from neighboring Antiparos approx. 1,000 years ago, exhibit extreme shyness, long FIDs (210.952 cm, on average), and very low laboratory autotomy rates. Hawks, feral cats, sand boas, and rats are the predator species present on the islet. The laboratory autotomy rate of Kato Fira (11%) was the lowest of any island harboring four predator types, and was an outlier in our autotomy analyses (see Fig. 5B). A recent study (Hurston et al. 2009) identified lizards from this island as having a highly divergent haplotype from other island populations in the region. More importantly, the Kato Fira population also had the lowest level of allelic diversity, of any islands in the region, which may have resulted from a past population bottleneck and subsequent genetic drift (Hurston et al. 2009). We hypothesize that ability for caudal autotomy may have been lost due to genetic drift, and that lizards on this island compensate for this by augmenting their FIDs. Further investigation into tradeoffs between different antipredator behavior is required to validate this claim, but it is an interesting strategy to consider moving forward in the study of animal behavior in the context of conservation.

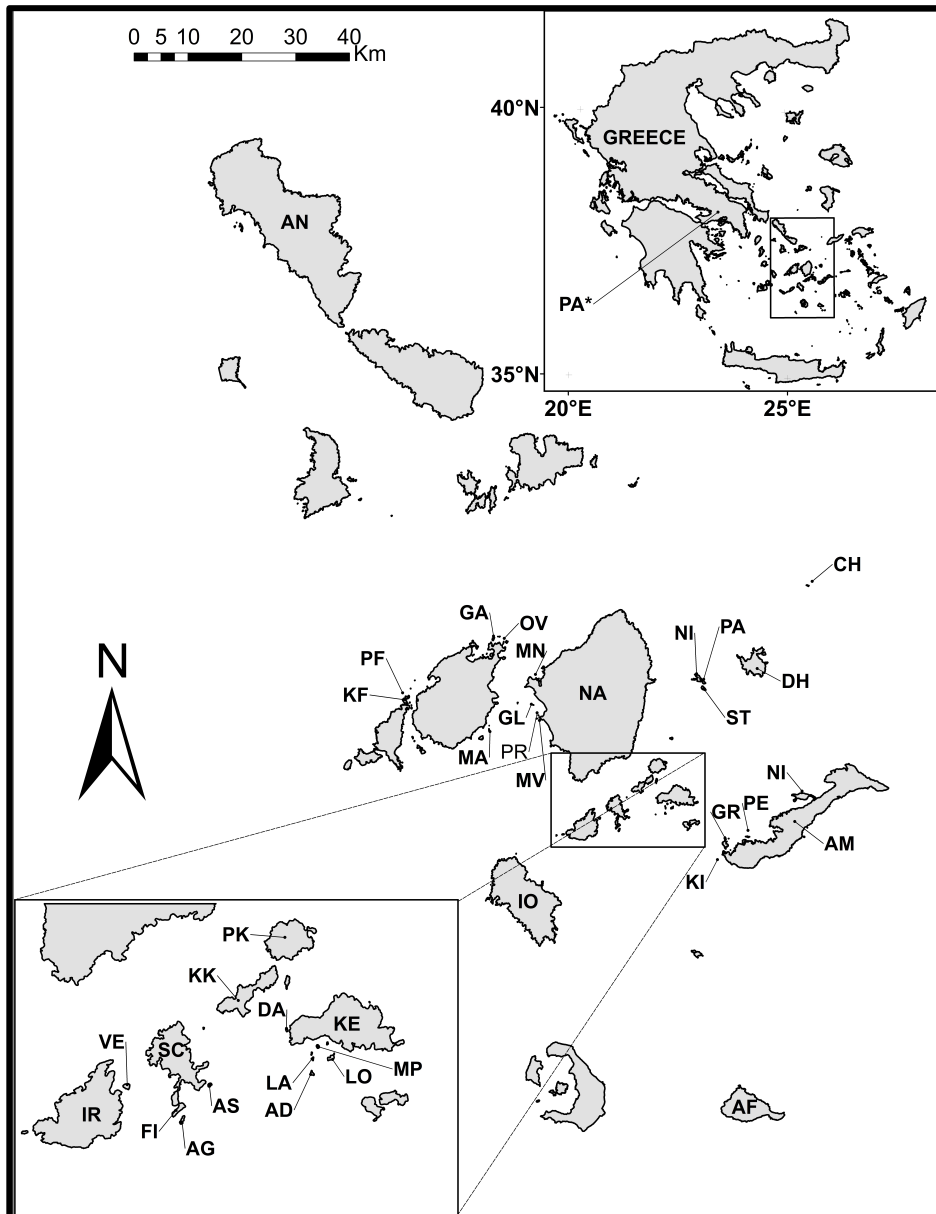
Using mixed and general linear models, we show that a species' arsenal of antipredator defenses is predominately shaped by the prevailing predation environment, in this case predator diversity. The results of this study are interesting for several reasons: (1) we demonstrate that expression of antipredator behaviors in animals with multiple predators varies sensitively according the number of predator species the prey is exposed to, and that certain predator

types are more important for the preservation of experience-dependent behaviors; (2) whereas previous studies have claimed that field autotomy can be used as an indicator of predation pressure (Bateman and Fleming 2011), we found the opposite – at least in an island environment setting, rates of field autotomy are significantly higher in predator-free environments; and (3) controlled autotomy trials revealed that the presence of vipers (or any one predator type) is not the sole predictor for the retention of this defense behavior as previously thought (Pafilis et al. 2009_a), rather, there is a strong linear relationship between autotomy and predator diversity that suggests the removal of any one predator category will eventually result in decreased ability to autotomize, and (4) Decay in the expression of antipredator increases with duration of isolation and the diversity of predators lost.

Our results indicate the retention of lizard antipredator behaviors are largely determined by local predation regime diversity. Island populations of *P. erhardii* are sensitive to both increases and decreases in predator diversity, and thus at risk of local extinction via predator naïveté if a predator introduction should occur. Antipredator behaviors, especially defenses such as flight behavior that are ‘experience-dependent’ (Blumstein et al. 2004; Blumstein and Daniel 2005), seem to fade away quickly in the absence of selective pressure. The potential synergistic effects of introduced novel predators and continued fragmentation of islands from rising sea levels may threaten small-bodied prey species in the future. Conservation managers looking to reintroduce, or relocate a species several generations out of the wild into a novel environment need to have a good understanding of the entire suite of predators a species faces in order to successfully establish a healthy population. However, often times species-specific behavioral data are unavailable and expensive to acquire, leaving conservation managers to guess at how to fill gaps in empirical research that pertains to their situation. Insights from our study can be applied in a broader context than just this species of island reptile on one particular island chain. Conservation managers looking to reintroduce, or relocate a prey

species bred *ex-situ* should expose captive animals to historical predator simulations to preserve and refine experiential antipredator behaviors such as flight initiation.

Figure 1. Map of Greece and Aegean study sites. Agios Nikolaos (NI), Agia Paraskevi (PA), Agriloussa (AG), Amorgos (AM), Anafi (AF), Andreas (AD), Andros (AN), Aspronissi (AS), Chtenia CH), Daskalio (DA), Dhonoussa (DH), Fidussa (FI), Gaiduronissi (GA), Glaronissi (GL), Gramvoussa (GR), Ios (IO), Irakleia (IR), Kato Fira (KF), Kato Kufonissi (KK), Keros (KE), Kisiri (KI), Lazaros (LA), Loumboudiaris (LO), Makronissi (MA), Mando (MN), Megali Plaka (MP), Mikri Vigla (MV), Naxos (NA), Nikouria (NI), Ovriokastro (OV), Pano Fira (PF), Pano Kufonissi (PK), Parnitha* (PA), Parthenos (PR), Petalidi (PE), Schoinoussa (SC), Strongylo (ST), Venetiko (VE). An asterisk signifies the mainland location.



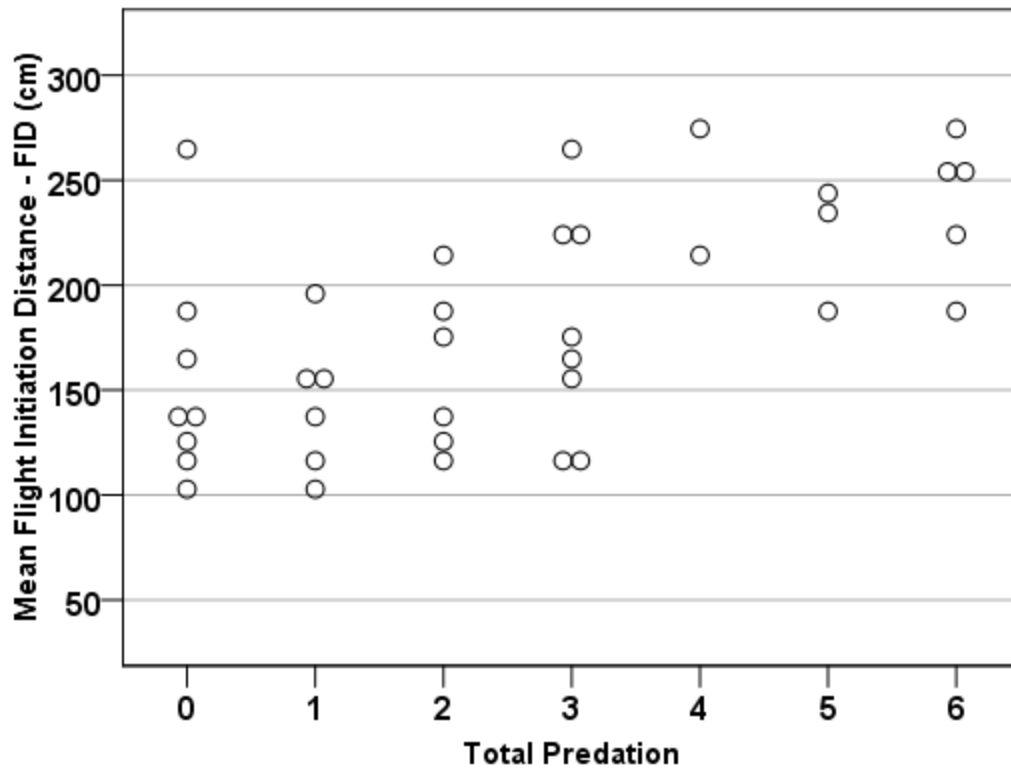


Figure 2. Scatterplot of mean flight initiation distance by total predation score per island. Each circle represents an island. Mean FID increases as predation regime intensifies ($R^2=.382$, $p<0.001$, $N=38$).

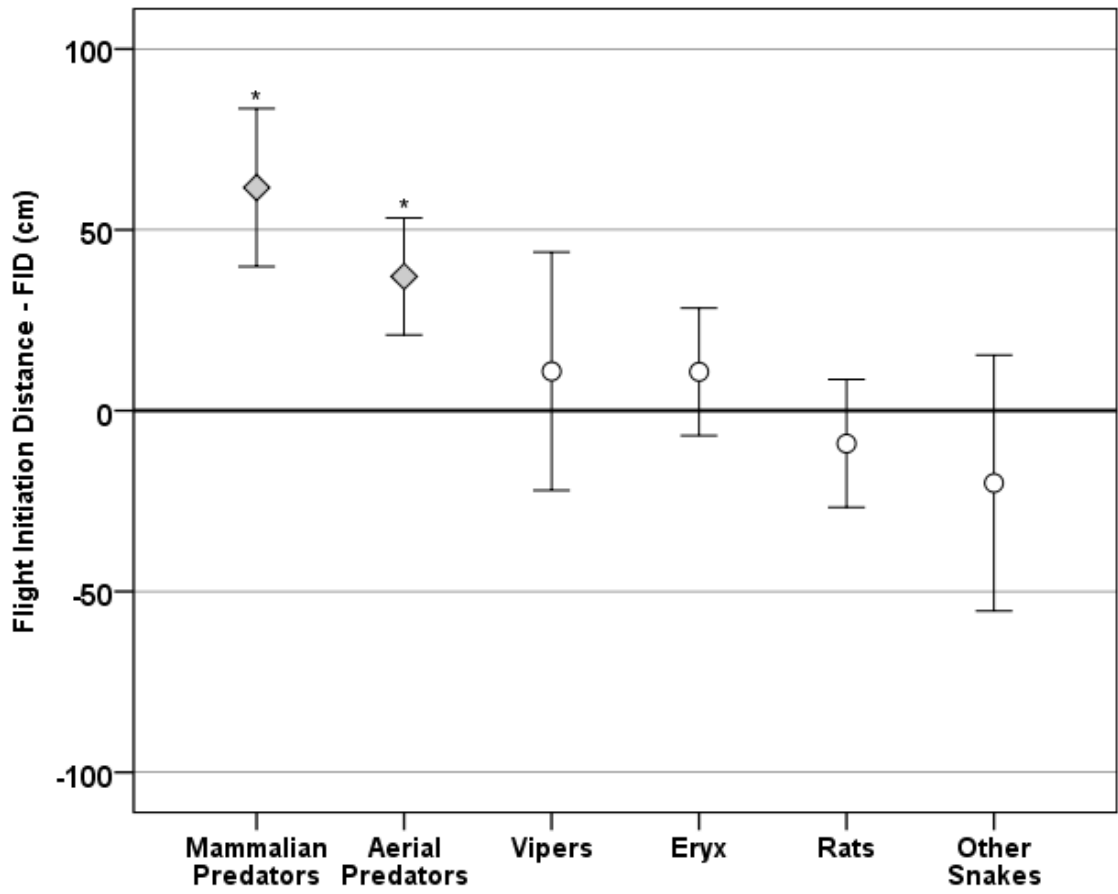


Figure 3. Marginal means of flight initiation distances by predator presence from final model [FID~DR+V+OS+M+E+AP+R]. Means notated by diamonds were statistically significant ($p < 0.05$). Means and error bars are representative of the average change in FID given the presence of that predator. Large lizard FIDs are most strongly associated with the presence of mammalian and aerial predators.

Figure 4a. (Top). Change in average flight initiation distance (cm) on islets relative to their pre-fragmentation baseline, against duration of isolation from the main island landmass. **5b. (Bottom).** Change in lab autotomy rate on islets relative to their baseline. This represents the erosion of antipredator defenses with increasing period of isolation and reduced predator regime. Change in FID and LAR were calculated as $[\Delta\text{Behavior} = \text{Behavior}_{\text{islet}} - \text{Behavior}_{\text{large island}}]$. Overlapping points were jittered for clarity.

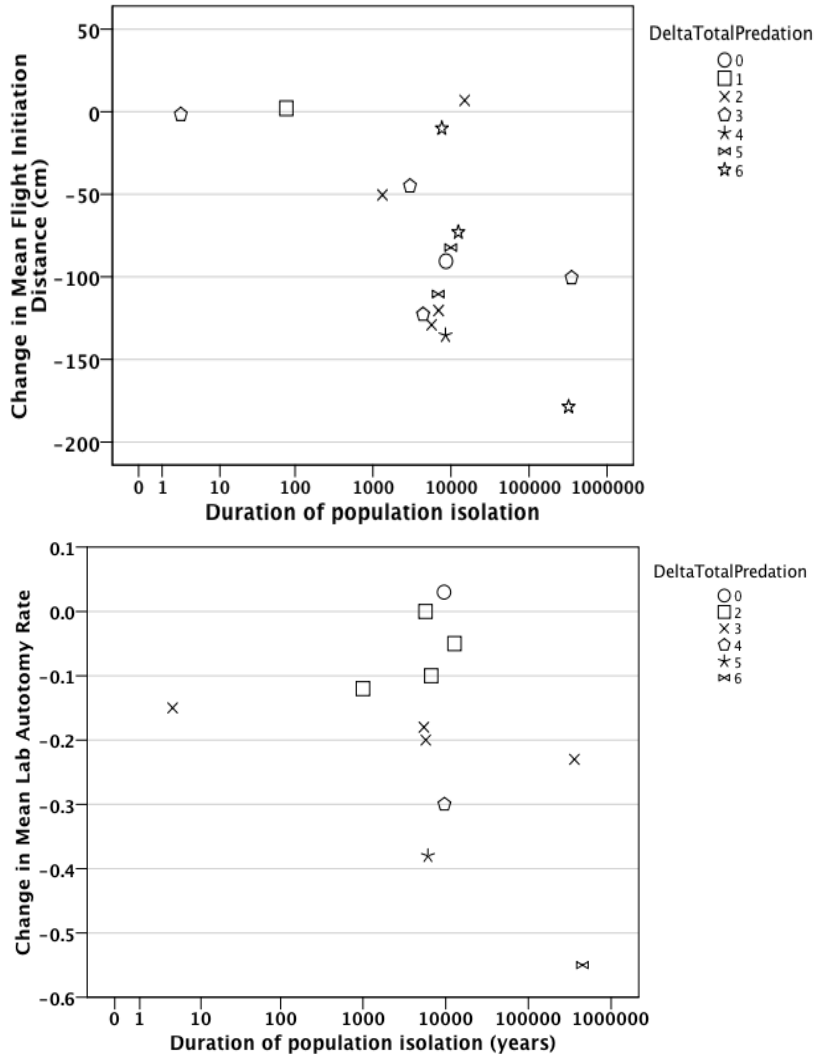
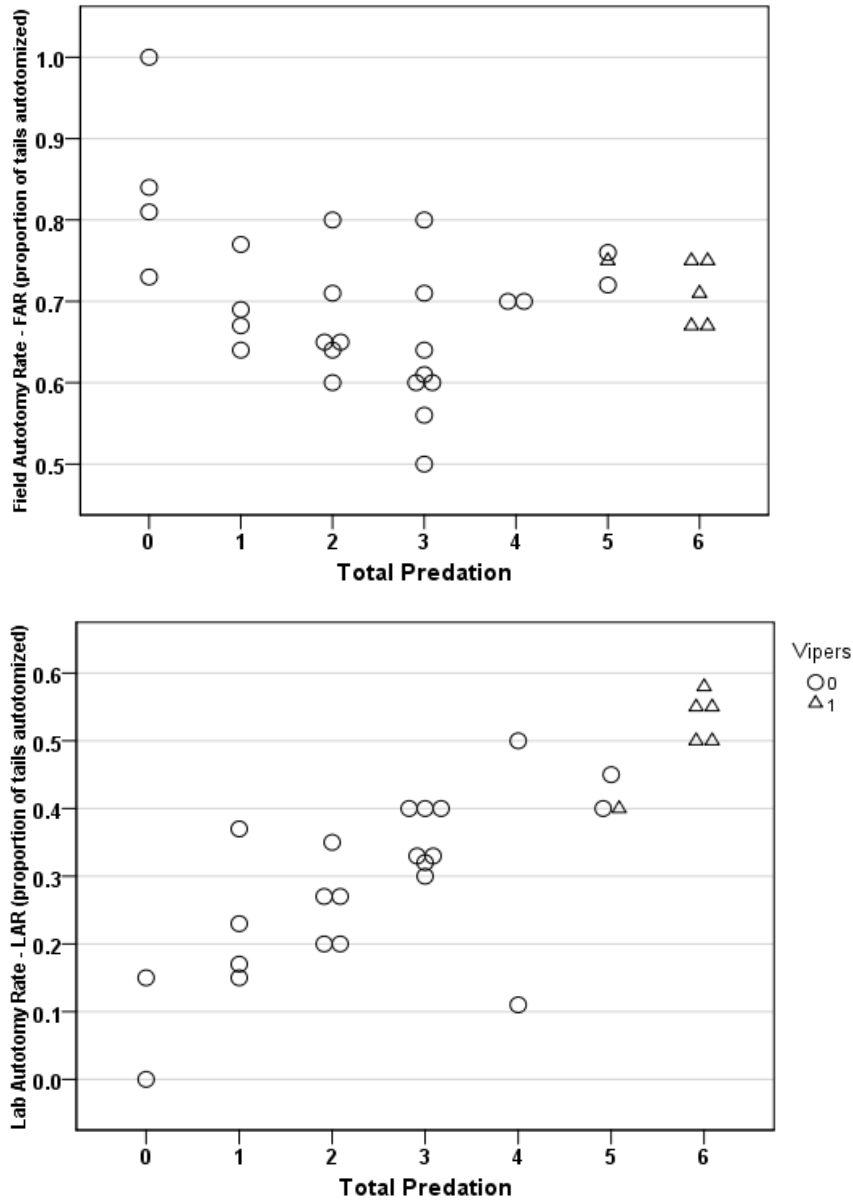


Figure 5a. (Top). Field autotomy rate (FAR) versus total number of predator categories per island. Field autotomy rates did not increase with rising predator diversity, although predator-free islands had significantly higher FARs, than islands with any amount of predation (Mann-Whitney U, $p=0.005$). Because past work (Pafilis et al. 2009) suggested a special effect of viperids on autotomy rates, islands inhabited by vipers are marked with triangles. **5b. (Bottom).** Laboratory autotomy rate (LAR) versus total amount of predator categories per island. Triangles represent islands with vipers, and circles islands without vipers. Laboratory autotomy rates increased steadily with increased number of predator categories present.



| Island | Isolation Period | MeanFID (cm) | Mean FAR | Mean LAR | Predators | Total Predation |
|---------------------|------------------|--------------|----------|----------|-------------|-----------------|
| Agios Nikolaos (NI) | 11,900 | 137 | .60 | .20 | a,b | 2 |
| Agia Paraskevi (PA) | 11,900 | 117 | .65 | .27 | a,b | 2 |
| Agriloussa (AG) | 9,650 | 151.9 | .67 | .15 | a | 1 |
| Amorgos (AM) | 200,000 | 243.8 | .72 | .40 | a,b,c,e,f | 5 |
| Anafi (AF) | 36,000 | 168.9 | .61 | .32 | a,c,f | 3 |
| Andreas (AD) | 9,100 | 137.1 | .84 | .15 | none | 0 |
| Andros (AN) | 5,800 | 252.8 | .67 | .50 | a,b,c,d,e,f | 6 |
| Aspronissi (AS) | 5,450 | 191.7 | .65 | .27 | c | 1 |
| Chtenia CH) | 450,000 | 100 | 1 | 0 | none | 0 |
| Daskalio (DA) | 2,000 | 217.5 | .71 | ... | a,c | 2 |
| Dhonooussa (DH) | 12,800 | 272.2 | .70 | .50 | a,b,c,f | 4 |
| Fidussa (FI) | 1,000 | 172.5 | .64 | .33 | a,b,c | 3 |
| Gaiduronissi (GA) | 7,100 | 139.1 | .69 | .23 | a | 1 |
| Glaronissi (GL) | 6,100 | 194.4 | .77 | .17 | c | 1 |
| Gramvoussa (GR) | 6,700 | 113.9 | .56 | .30 | a,b,c | 3 |
| Ios (IO) | 11,750 | 255.3 | .75 | .50 | a,b,c,d,e,f | 6 |
| Irakleia (IR) | 9,800 | 191.2 | .75 | .58 | a,b,c,d,e,f | 6 |
| Kato Fira (KF) | 1,000 | 210.9 | .70 | .11 | a,b,c,f | 4 |
| Kato Kufonissi (KK) | 5,000 | 158 | .50 | .33 | a,b,c | 3 |
| Keros (KE) | 9,150 | 222.9 | .60 | .40 | a,b,c | 3 |
| Kisiri (KI) | 5,700 | 127.7 | .64 | .20 | a,c | 2 |
| Lazaros (LA) | 9,100 | 160.7 | ... | ... | none | 0 |
| Loumboudiaris (LO) | 8,100 | 117.1 | ... | ... | none | 0 |
| Makronissi (MA) | 6,700 | 183.5 | .73 | ... | none | 0 |
| Mando (MN) | 4 | 267.9 | .80 | .40 | a,b,c | 3 |
| Megali Plaka (MP) | 8,100 | 135.5 | .81 | ... | none | 0 |

| | | | | | | |
|---------------------|--------|-------|-----|-----|-------------|---|
| Mikri Vigla (MV) | 6,100 | 261.4 | ... | ... | none | 0 |
| Naxos (NA) | 0 | 276.7 | .71 | .55 | a,b,c,d,e,f | 6 |
| Nikouria (NI) | 5,700 | 116.5 | .71 | .40 | a,b,c | 3 |
| Ovriokastro (OV) | 5,600 | 178.1 | .80 | .35 | a,b | 2 |
| Pano Fira (PF) | 100 | 221.5 | .50 | --- | a,c,f | 3 |
| Pano Kufonissi (PK) | 9,000 | 186.7 | .75 | .40 | a,b,c,d,e | 5 |
| Parnitha* (PA) | 0 | 226.5 | .67 | .55 | a,b,c,d,e,f | 6 |
| Parthenos (PR) | 5,650 | 158.9 | --- | --- | c | 1 |
| Petalidi (PE) | 6,700 | 105.7 | --- | --- | a | 1 |
| Schoinoussa (SC) | 9,550 | 234.4 | .76 | .45 | a,b,c,e,f | 5 |
| Strongyllo (ST) | 11,900 | 118.7 | .64 | .37 | a | 1 |
| Venetiko (VE) | 9,550 | 123.3 | --- | --- | none | 0 |

Table 1. Island trait data for all 38 of our study sites. Islands are listed alphabetically. Isolation Period is given in years and is the inferred age of the island as calculated from bathymetric data and regionally calibrated sea level change graphs. The average flight initiation distance (FID) is reported in centimeters. Average field autotomy rates (FAR) and average laboratory autotomy rates (LAR) are reported as the fraction of tails autotomized per island. Predator categories are listed for each island (a=rats, b=sand boas (*Eryx*), c=avian predators, d=vipers, e=other saurophagus snakes, and f=mammals). The 'Total Predation' score is given in the last column and is the summation of predator categories present on an island. Parnitha (marked by an asterisk), is a Greek mainland location (located 15 km north of Athens, 38.1734°N, 23.7174°E)

| Model | AICc | ΔAIC_c | Akaike Weight |
|-------------------------|-------------------|----------------------------------|-------------------------|
| V+OS+M+E+AP+R | 10,435.906 | - | .99999813 |
| M+AP+OP _{M,AP} | 10,462.648 | 26.742 | 1.559×10 ⁻⁶ |
| M+V+OP _{M,V} | 10,465.908 | 30.002 | 3.056×10 ⁻⁷ |
| M+OP _M | 10,474.875 | 38.969 | 3.451×10 ⁻⁹ |
| AP+OP _{AP} | 10,476.109 | 40.203 | 1.862×10 ⁻⁹ |
| V+OP _V | 10,478.728 | 42.822 | 5.027×10 ⁻¹⁰ |
| Σ Predation | 10,487.734 | 51.828 | 5.568×10 ⁻¹² |

Table 2. Selection criteria data for the seven mixed models constructed to explain variation in FID of Cycladic populations of *P. erhardii*. All models include flight initiation distance as the dependent variable, and distance to the refuge (DR) as a covariate. The output of our final model is boldfaced. Predator predictors in this study include: V=vipers; OS=other Colubrid snakes; M=mammalian predators; E=*Eryx jaculus* boas; AP=avian predators; R=rats; OP=other predators, calculated as the sum of all other predators present besides the categorical predator predictor entered separately in the model; Σ Predation = summary of all predator categories on an island. Models were formulated *a priori* (Burnham and Anderson 1998) and were compared using AIC_c values and their associated Akaike model weights, calculated as $w_i = \exp(-\Delta_i/2) / \sum_{r=1}^M \exp(-\Delta_r/2)$ (Turkheimer et al. 2003).

| | Model | AICc | Δ AICc | Akaike Weight |
|----------------------------|--------------------------------------|-------------|---------------------------------|-----------------------|
| Field Autotomy | 0 Predation | - 61.568 | - | .998183 |
| | Vipers | - 48.595 | 12.973 | 1.52×10^{-3} |
| | Σ Predation | - 46.389 | 15.179 | 5.05×10^{-4} |
| Laboratory Autotomy | Σ Predation | - 44.376 | - | .998203 |
| | Vipers | - 31.694 | 12.682 | 1.76×10^{-3} |
| | 0 Predation | - 26.136 | 18.240 | 1.09×10^{-4} |

Table 3. Model selection criteria for caudal autotomy rates in the field and laboratory. The '0 Predation' model fit a line through autotomy data separated into islands without predators and with any amount of predators, the 'Vipers' model separated islands with and without vipers, and the ' Σ Predation' model that accounted for predator diversity of an island. General linear models were formulated *a priori* and evaluated using AICc values and corresponding Akaike weights. Best models are boldfaced.

Appendix 1

Mean FID vs. Mean Body Size (SVL), (Pearson $r = -.257$, $p = 0.397$, $N = 13$). Pg. 16.

FID and Detection Distance, (Spearman's $\rho = -0.35$, $p = 0.11$, $N = 21$). Pg. 16.

Mean FID and Vegetation Cover (%), (Pearson $r = .245$, $p = 0.201$, $N = 29$). Pg. 16.

Mean FID and Seabird Densities (Pearson $r = .007$, $p = 0.966$, $N = 35$). Pg. 16.

Mean FID and Walls (yes/no), (Independent Samples T-Test $p = .452$, $F = .578$, $N = 37$, $df = 36$) Pg. 16.

Mean FID and LnIslandAge, (Pearson $r = -.316$, $p = .061$, $N = 36$)

Mean FID and Island Age, (Pearson $r = -.150$, $p = .374$, $N = 37$)

Mean FID and LnIslandArea, (Pearson $r = .456^{**}$, $p = .004^{**}$, $N = 38$)

Mean FID and Island Area, (Pearson $r = .370$, $p = .022^*$, $N = 38$)

Mean FID and LAR, (Pearson $r = .644^{**}$, $p < .0001$, $N = 28$)

Mean FID and FAR, (Pearson $r = -.024$, $P = .898$, $N = 32$)

Δ Mean FID and Δ LAR, (Pearson $r = .440$, $p = .175$, $N = 11$)

Δ Mean FID and Δ Total Predation, (Pearson $r = -.235$, $p = .381$, $N = 16$)

Δ Mean FID and LnIsletArea, (Pearson $r = .086$, $p = .752$, $N = 16$)

FAR and Predator Categories, (mean ranks of 0 predator versus predator islands were 28.75 and 14.75, respectively**, $U = 7.000$, $Z = -2.798$, $p = 0.005$, $N = 32$, Mann-Whitney U test).

* Indicates statistical significance at 0.05 level

** Indicates statistical significance at 0.01 level

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