

Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears?

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Received April 11, 2014

Accepted October 1, 2014

Organisms generally have many defenses against predation, yet may lack effective defenses if from populations without predators. Evolutionary theory predicts that “costly” antipredator behaviors will be selected against when predation risk diminishes. We examined antipredator behaviors in Aegean wall lizards, *Podarcis erhardii*, across an archipelago of land-bridge islands that vary in predator diversity and period of isolation. We examined two defenses, flight initiation distance and tail autotomy. Flight initiation distance generally decreased with declining predator diversity. All predator types had distinctive effects on flight initiation distance with mammals and birds having the largest estimated effects. Rates of autotomy observed in the field were highest on predator-free islands, yet laboratory-induced autotomy increased linearly with overall predator diversity. Against expectation from previous work, tail autotomy was not explained solely by the presence of vipers. Analyses of populations directly isolated from rich predator communities revealed that flight initiation distance decreased with increased duration of isolation in addition to the effects of current predator diversity, whereas tail autotomy could be explained simply by current predator diversity. Although selection against costly defenses should depend on time with reduced threats, different defenses may diminish along different trajectories even within the same predator–prey system.

KEY WORDS: Antipredator behavior, autotomy, flight initiation distance, islands, predation, selection-natural.

Predation selects on the behavior and physiology of prey species (Edmunds 1974; Blumstein and Daniel 2005; Blumstein 2006; Losos et al. 2006; Shepard 2007), and potential prey use many antipredator behaviors to reduce the possibility of becoming actual prey (Bulova 1994). While being eaten has obvious costs, antipredator defenses also have costs (Ydenberg and Dill 1986; Salvador et al. 1995; Pérez-Cembranos et al. 2013), which vary with environmental pressures and type of defense. All else being equal, the persistence of antipredator behaviors should only occur if the benefits outweigh the costs incurred, and costly behaviors should be eliminated by selection if they serve no benefit

(Magurran 1999; Blumstein 2002; Blumstein and Daniel 2005; Pafilis et al. 2009a). Therefore, the degree of expression of antipredator behavior seems to be related to the prevailing predation environment (Darwin 1839; Reynolds and Bruno 2013).

Islands generally host fewer predators than the mainland, and prey species may show little in the way of behavioral or physiological defenses (Darwin 1839; MacArthur and Wilson 1967; Pérez-Mellado et al. 1997; Blumstein and Daniel 2005; Cooper and Pérez-Mellado 2012). This phenomenon, termed island tameness, likely occurs where costly antipredator behaviors and physiological adaptations have been selected against in



reduced predation environments (Blumstein and Daniel 2005), for instance in Galápagos marine iguanas (*Amblyrhynchus cristatus*) (Berger et al. 2007), and tamar wallabies (*Macropus eugenii*) on Australian islands (Blumstein and Daniel 2005). As such, naïve island species, perhaps most infamously the dodo (*Raphus cucullatus*), have been disproportionately affected by the introduction of novel predators into previously predator-free environments (Beauchamp 2003; Baillie et al. 2004; Blackburn et al. 2004; Losos et al. 2006; Bonnaud et al. 2010).

When approached by a potential predator, animals commonly flee to a refuge (Greene 1988; Cooper 1997; Blumstein and Daniel 2005; Cromie and Chapple 2013). 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), animals balance the costs of fleeing against the costs of remaining in place (Magurran 1990; Stankowich and Blumstein 2005). The flight initiation distance (FID) (distance between predator and prey the moment before the prey flees) of prey is a quantifiable measure of perceived predation risk (Bonenfant and Kramer 1996; Blumstein and Daniel 2005; Amo et al. 2006; Cooper 2011), and is predicted to reflect the prevailing predation regime for prey populations (Cooper and Pérez-Mellado 2012).

Tail autotomy, or the self-severing of the tail, is a common antipredator defense among lacertid lizards (Arnold 1984; Bateman and Fleming 2009; Pafilis et al. 2009a). Autotomy in lacertids occurs along specialized breakage planes located within vertebrae throughout the tail (Chapple and Swain 2002a; Lin and Ji 2005). The shed tail writhes about for a period of time, a process thought to distract the predator from the escaping lizard (Dial and Fitzpatrick 1983; Arnold 1984, 1988). Although tail shedding is a highly effective escape strategy (Dial and Fitzpatrick 1984; Daniels 1985), it is also a very costly defense that is usually only deployed after frontline defenses such as hiding or fleeing have failed (Arnold 1984; Cromie and Chapple 2013). In many species the tail contains a significant portion of fat deposits, and losing those stores is energetically expensive (Ballinger and Tinkle 1979; Bateman and Fleming 2009; Pafilis et al. 2009a). Regeneration of the tail, which occurs at various rates among species, also requires a considerable amount of energy (Vitt and Cooper 1986; Pafilis et al. 2009a; Tsasi et al. 2009). Costs related to tail loss in various lizard species include impaired locomotive capabilities, making quick and efficient escape difficult (Chapple and Swain 2002b; 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 (Ballinger and Tinkle 1979; Vitt and Cooper 1986; Pafilis et al. 2009a; Cromie and Chapple 2013). Because autotomy can occur accidentally and without

survival benefit during intraspecific interactions (Vitt et al. 1977, Jennings and Thompson 1999; Pafilis et al. 2008; Vervust et al. 2009), ease of autotomy in a population should reflect associated costs and benefits.

Although predators demonstratively exert selective pressures on behavior (Edmunds 1974; Blumstein and Daniel 2005; Losos et al. 2006; Shepard 2007), the mechanistic factors underlying island tameness and the rate at which it occurs are unclear. Previous behavioral studies on islands have largely focused on comparing island behavior to mainland behavior (Blumstein and Daniel 2005), often across many species (Beauchamp 2004; Cooper et al. 2014), with vague predation variables (e.g., low, medium, high). We aim to provide unprecedented resolution in the study of island tameness by comparing many populations of one species in a system where predator presence and history of isolation are known in detail.

The present study focuses on the evolution of antipredator behaviors in distinct populations of the Aegean wall lizard (*Podarcis erhardii*), a habitat generalist that is found in southeast Europe and islands in the Aegean Sea (Greece) (Hurston et al. 2009). This species is known to be a poor overwater disperser (Foufopoulos and Ives 1999) and because lizards on Cyclades islands have been isolated with varying subsets of the original pre-Pleistocene predation regime, they provide an excellent opportunity to study evolutionary mechanisms responsible for the retention of antipredator behaviors. We focus on two defenses: FID and tail autotomy, which are considered here together in a combined frame to enhance our understanding of antipredator behavior evolution. Further, we develop a novel approach to assess the rate of island tameness by combining geomorphological seafloor and historic sea-level data to identify island ages and assess the relationship between duration of isolation from predators and behavior. Based on the ecological knowledge of the Aegean Sea region and previously documented patterns of behavior (Pafilis et al. 2009a,b; Li et al. 2014), we predicted that (1) flight behavior would vary across the Cyclades Archipelago with current predator diversity, (2) ability for autotomy would be mostly influenced by the presence of vipers (see Pafilis et al. 2009a), and (3) FID and tail autotomy rates would decrease with longer isolation in reduced predation environments.

Methods

STUDY SYSTEM

The Cyclades are a group of land-bridge islands located in the central Aegean Sea (Fig. 1), which were formed when rising sea levels since the last glacial maximum flooded parts of a large Pleistocene island mass termed “Cycladia” (Foufopoulos and Ives 1999; Broodbank 2002; Poulos et al. 2009). The current climate is typical of the Mediterranean region with warm, dry summers

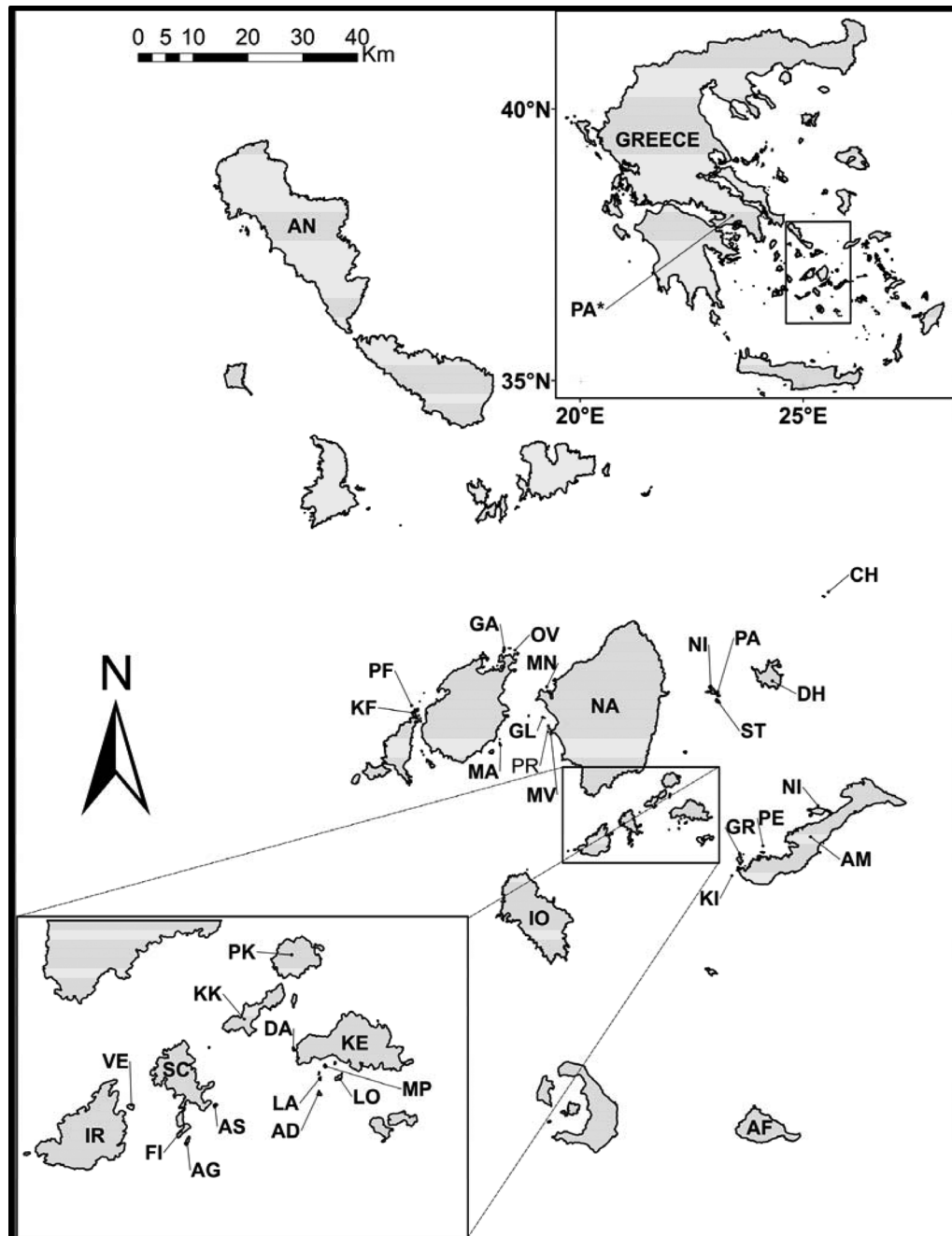


Figure 1. Map of Greece and Cycladic island sites in the Aegean. Agios Nikolaos (NI), Agia Paraskevi (PA), Agriloussa (AG), Amorgos (AM), Anafi (AF), Andreas (AD), Andros (AN), Aspronissi (AS), Chtenia (CH), Daskalio (DA), Dhonoussa (DH), Fidussa (FI), Gaiduronissi (GA), Glaronissi (GL), Gramvoussa (GR), 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), Strongyllo (ST), Venetiko (VE). An asterisk signifies the mainland location.

and cool, rainy winters. The islands experience more temperate conditions than 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 has been shaped by anthropogenic disturbance over thousands of years (Rackham and Grove 2001).

It consists of a patchwork of agricultural areas, sclerophyllous evergreen maquis, and a diverse, summer-deciduous dwarf scrub community termed “phrygana” (Fielding and Turland 2008).

The Aegean wall lizard (*P. erhardii*) is a small, ground-dwelling lacertid, with an adult snout-vent length 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 eats mainly arthropods (Arnold 1987), especially Coleoptera (Adamopoulou et al. 1999), but has been observed foraging opportunistically on fruits and plant matter (Brock et al. 2014). A once continuous *P. erhardii* distribution across Cycladia was fragmented and isolated by rising sea levels into >60 small island populations experiencing different subsets of the pre-Pleistocene predation regime (Foufopoulos and Ives 1999; Hurston et al. 2009; Poulos et al. 2009).

QUANTIFICATION OF ISLAND CHARACTERISTICS

We measured the relative abundance of lizards on all island study sites and one mainland location ($N = 38$). On Aegean islands with no predators, population densities of lizards are high, which could intensify intraspecific competition, potentially having an effect on the maintenance of the ability to autotomy (Pafilis et al. 2009a,b). Lizard densities were determined by walking one or two transects (100 m length and 4 m width) of suitable habitat (most islands were too small for multiple transects, see Jaeger 1994; Pafilis et al. 2013) and recording any *P. erhardii* detected within this area. All transects were conducted during the months of May–early June under favorable weather conditions (sunny, nearly windless 22–26°C) and during the peak activity hours of the species (0900–1100 and 1500–1700).

Due to the restricted time window we had for each island, we assessed the predator community on 37 islands and one mainland location by combining published information (Valakos et al. 2008; Pafilis et al. 2009a, and references within) with field surveys conducted over the course of several visits. Surveys of uninhabited islets consisted of walking an entire island searching for signs of known, regional predators (e.g., skins, fecal material, burrows, or live individuals). Our predator species were elusive in several different ways (nocturnal, semifossorial, and aerial hunters), and thus it was not possible to obtain predator population densities during our visits to the scattered, often uninhabited islands. We therefore use an index of predation pressure applied in other behavioral studies of similar taxa (Pérez-Mellado et al. 1997; Cooper et al. 2004; Pafilis et al. 2009a) wherein predator categories are determined by life-history, taxonomic affiliation, and hunting strategy. We calculated this index by noting the presence or absence of predator types and summing all present categories for a measure of “Total Predation.” We divided predators on the islands into six categories: (1) rats (*Rattus rattus*), (2) sand boas (*Eryx jaculus*), (3) birds (*Falco tinnunculus* and *Buteo buteo*), (4) Colubrid snakes (*Dolichophis caspius*, *Elaphe quatuorlineata muenteri*, *Natrix natrix persa*, referred to

as “other snakes”), (5) mammals (feral cats [*Felis catus*], stone martens [*Martes foina*]), and (6) vipers (*Vipera ammodytes*). The three different categories of snake predators differ markedly in hunting strategy. Vipers are sit-and-wait predators that ambush and envenomate their prey (Nowak et al. 2008, Pafilis et al. 2009a), whereas 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 (J. Foufopoulos, pers. obs.; Cattaneo 2010). We also distinguish rats from the “mammals” 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. Cats (*F. catus*) and rats (*R. rattus*) were introduced to the Greek islands thousands of years ago (Klippel and Snyder 1991; Serpell 2000). Because both species are now well-established parts of local ecosystems and both have been implicated in the extinctions of island endemic reptiles (Iverson 1978; Pérez-Mellado et al. 2008; Nogales and Medina 2009), we treat them the same as our other predator categories.

Environmental characteristics of islands were determined remotely using spatial analysis tools combined with field surveys. Information on island area (km²) for inhabited islands was available either from published or from government sources (Foufopoulos and Ives 1999; Poulos et al. 2009). For uninhabited islets without published spatial data we used the ArcGIS ArcMap 10 Field Calculator to calculate polygon area (km²) (spatial data courtesy of the Natural History Museum of Crete). To determine the time of separation of islands, we used fine-scaled bathymetric data derived from navigation charts and targeted sonar measurements collected by one of us (J. Foufopoulos) in the field, in conjunction with geomorphological reconstructions of past sea levels from global and local sea-level change graphs (Pirazzoli 1991, 1996; USDMA 1991; Foufopoulos and Ives 1999; Hurston 2009; Poulos et al. 2009). Evergreen bush vegetation cover was calculated using a combination of Google Earth image data and measurements on the ground ($N = 29$ islands). We walked 100-m-long random transects and estimated the percent of the landscape covered by woody evergreens, and representativeness of these results were then confirmed by investigating large-scale aerial photographs. Dry stone walls provide lizards refuge space from predators. We therefore recorded the presence or absence of dry stone walls on all islands to test for relationships with FID. We also checked for a relationship between FID and human presence on islands (humans inhabited 11 of 37 islands). Nonpredatory seabirds preferentially nest on a small subset of uninhabited islets in the Cyclades during the summer (Pafilis et al. 2009b; Foufopoulos, unpubl. data). Although there are no records of seabirds preying on *P. erhardii*, or lizards in general (Cooper et al. 2004; Pafilis et al. 2009b), cohabitation on small islets may maintain flight behavior through historic avian predator recognition (Curio 1993;

Blumstein 2006). We measured nesting seabird densities ($N = 35$ islands) by counting the number of nests per island, and assumed each nest belonged to two birds (Foufopoulos and Mayer 2007).

ANTIPREDATOR BEHAVIOR

Flight initiation distance

We measured the FID of adult *P. erhardii* ($N = 913$) from 37 Cycladic islands and one site on mainland Greece (Fig. 1, Table 1). FID was recorded as the distance between the observer and the focal animal when escape was initiated (Ydenberg and Dill 1986; Blumstein et al. 2003; Amo et al. 2006; Pérez-Cembranos et al. 2013; Cooper et al. 2014). This method presumes that the focal animal responds primarily to visual stimuli (the approaching predator). FID was measured in the morning hours during the species' main activity period (May to early July) on warm (22–26°C), sunny days with little 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). We avoided measuring the flight response of gravid female lizards due to their predilection for remaining close to refugia and differing physiological requirements during the reproductive period (Braña 1993). Cooper et al. (2009) found that at this speed detection distance did not have an effect on FID in a similar species, *P. lilfordi*. All approaches in this study were performed by the same individual (K. M. Brock), wearing the same attire to avoid confounding effects (Amo et al. 2006; Pérez-Cembranos et al. 2013). Further, the observer never returned to previously sampled areas to avoid encountering the same lizard twice. Because direction and angle of approach, as well as observer shadow may have an effect on a lizard's response to predation (Burger and Gochfeld 1990), we only performed head-on approaches where no shadow was apparent. Both the published literature (Dill and Houtman 1989; Bonenfant and Kramer 1996; Amo et al. 2006; Li et al. 2014) and our own data suggest that FID is positively correlated to the distance a lizard has to cover to reach the nearest refuge; we therefore recorded this measure (henceforth referred to as distance to the refuge, DR) for every observation of FID (Dill and Houtman 1989; Bulova 1994; Kramer and Bonenfant 1997; Amo et al. 2006; Cooper and Pérez-Mellado 2012). As suggested by previous studies of other lizards (see Cooper et al. 2009; Cooper 2011), we measured detection distance (distance between the focal animal and surrogate predator when focal animal detects the presence of the surrogate predator), as well as

body size (snout-vent length in cm) for a subset of the observed lizards at several island sites to test for potential relationships with FID (see Appendix S1).

Field autotomy

Field autotomy rates were calculated for each lizard population as the proportion of individuals encountered that had previously autotomized tails. We observed how often lizards lost their tails in the field using well-established methodologies (see Pafilis et al. 2009a). Lizards were located using the same methods described for FID. Once an animal was detected in the field, through binoculars we observed the sex of the individual and whether its tail 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). We considered adult males and females in analyses of field autotomy.

Laboratory autotomy

Beyond predation pressure, field autotomy depends on additional factors such as aggressive intraspecific interactions, predator efficacy, microhabitat use, and average age of individuals within a population (Turner et al. 1982; Medel et al. 1988; Bateman and Fleming 2009; Pafilis et al. 2009a). We therefore used a standardized measure of autotomy induced under controlled laboratory conditions to distinguish between the innate predisposition of members of a population to shed their tails and the environmentally determined opportunity for this to occur (Pafilis et al. 2009a; Hare and Miller 2010; Bateman and Fleming 2011). Laboratory autotomy rates (LARs) were obtained for lizards from 28 of our study sites (Fig. 1, Table 1). Individual lizards were wild-caught using a noose to minimize chance of tail autotomy that often occurs during capture by hand. Because ability to autotomize a tail is affected by age (Bellairs and Bryant 1985; Pafilis and Valakos 2008), sex (Vitt 1981; Simou et al. 2008), and prior condition of the tail (Arnold 1984; Bateman and Fleming 2009), as well as to remain consistent with the methodologies used by Pafilis et al. (2009a), we limited laboratory autotomy analyses to adult male lizards with intact tails. Although it is possible that inclusion of females may produce slightly different results, a prior study on this genus failed to reveal any intersexual differences (Pafilis 2003).

Lizards were housed in individual terraria (32 cm × 16 cm × 12 cm) for 48 h before conducting the tail autotomy measurements. Because autotomy in reptiles is potentially affected by an animal's body temperature (Daniels 1984; Pafilis et al. 2005), animals were allowed to thermoregulate freely along a thermal gradient until the time of procedure. Lizards were then individually placed on a rough cork substrate placed at a 45° angle where they could firmly hold on. To standardize pressure across all trials, the same observer placed a pair of calipers approximately 20 mm behind the cloacal vent and then closed to half the diameter of

Table 1. Island trait data for all 38 of our study sites.

Island	Isolation period	Island area	Mean FID (cm)	FAR	LAR	Predators	Total predation	Vegetation cover (%)	Lizard density
Naxos (NA) a	0	448	276.7 (107)	0.71 (21)	0.55 (18)	r, sb, b, v, os, m	6	...	6
Parnitha* (PA)	0	1000	226.5 (13)	0.67 (24)	0.55 (47)	r, sb, b, v, os, m	6	...	5
Mando (MN) aa	4	0.025	267.9 (75)	0.80 (30)	0.40 (10)	r, sb, b	3	51	6
Pano Fira (PF) dd	100	0.35	221.5 (13)	0.50 (12)	...	r, b, m	3	50	3
Fidussa (FI) cc	1000	0.632	172.5 (8)	0.64 (14)	0.33 (12)	r, sb, b	3	25	2.5
Kato Fira (KF) d	1000	0.728	210.9 (21)	0.70 (30)	0.11 (18)	r, sb, b, m	4	51	5
Daskalio (DA)	2000	0.018	217.5 (4)	0.71 (21)	...	r, b	2	80	8
Kato Kufonissi (KK)	5000	4.3	158 (10)	0.50 (20)	0.33 (18)	r, sb, b	3	...	1.5
Aspronissi (AS) cc	5450	0.038	191.7 (24)	0.65 (20)	0.27 (22)	b	1	80	12
Ovriokastro (OV)	5600	0.22	178.1 (21)	0.80 (25)	0.35 (20)	r, sb	2	22	5.5
Petalidi (PE) bb	5600	0.05	105.7 (23)	r	1	10	2
Parthenos (PR) aa	5650	0.004	158.9 (19)	b	1	100	11
Nikouria (NI) bb	5700	2.75	116.5 (20)	0.71 (21)	0.40 (10)	r, sb, b	3	90	6.75
Kisiri (KI) bb	5750	0.012	127.7 (13)	0.64 (11)	0.20 (10)	r, b	2	22	3.5
Andros (AN)	5800	384	252.8 (16)	0.67 (24)	0.50 (48)	r, sb, b, v, os, m	6	...	4
Glaronissi (GL) aa	6100	0.0102	194.4 (25)	0.77 (35)	0.17 (17)	b	1	100	19
Mikri Vigla (MV)	6100	0.002	261.4 (7)	None	0	40	7
Gramvousa (GR) bb	6700	0.759	113.9 (33)	0.56 (18)	0.30 (10)	r, sb, b	3	51	3.67
Makronissi (MA)	6700	0.039	183.5 (69)	0.73 (22)	...	None	0	80	14
Gaiduronissi (GA)	7100	0.133	139.1 (74)	0.69 (42)	0.23 (13)	r	1	13	8
Loumboudiaris (LO)	8100	0.096	117.1 (14)	None	0	38	8
Megali Plaka (MP)	8100	0.031	135.5 (11)	0.81 (16)	...	None	0	35	1.5
Pano Kufonissi (PK)	9000	13	186.7 (3)	0.75 (16)	0.40 (10)	r, sb, b, v, os	5	...	0.5
Andreas (AD)	9100	0.045	137.1 (14)	0.84 (13)	0.15 (13)	None	0	5	1.5
Lazaros (LA)	9100	0.0137	160.7 (14)	None	0	19	3
Keros (KE)	9150	15.05	222.9 (7)	0.60 (10)	0.40 (5)	r, sb, b	3	70	4

(Continued)

Table 1. Continued.

Island	Isolation period	Island area	Mean FID (cm)	FAR	LAR	Predators	Total predation	Vegetation cover (%)	Lizard density
Schoinoussa (SC) c	9550	8.83	234.4 (9)	0.76 (13)	0.45 (11)	r, sb, b, os, m	5	...	1
Venetiko (VE) ee	9550	0.11	123.3 (21)	None	0	39	7
Agrioussa (AG) cc	9650	0.084	151.9 (21)	0.67 (24)	0.15 (20)	r	1	54	8
Irakleia (IR) aa, e	9800	18.078	191.2 (17)	0.75 (28)	0.58 (12)	r, sb, b, v, os, m	6	...	3
Ios (IO)	11,750	109.02	255.3 (47)	0.75 (56)	0.50 (12)	r, sb, b, v, os, m	6	...	5
Agios Nikolaos (NI)	11,900	0.89	137 (22)	0.60 (20)	0.20 (15)	r, sb	2	40	10
Agia Paraskevi (PA)	11,900	0.27	117 (27)	0.65 (20)	0.27 (18)	r, sb	2	50	14
Strongyllo (ST)	11,900	0.36	118.7 (31)	0.64 (44)	0.37 (16)	a	1	30	13
Dhonoussa (DH) aa	12,800	15	272.2 (18)	0.70 (20)	0.50 (10)	r, sb, b, m	4	35	3.5
Amorgos (AM) b	200,000	123	243.8 (8)	0.72 (22)	0.40 (10)	r, sb, b, os, m	5	80	2
Chtenia (CH) aa	450,000	0.004	100 (15)	1 (18)	0 (6)	None	0	70	12
Anafi (AF) aa	3,600,000	49	168.9 (19)	0.61 (21)	0.32 (25)	r, b, m	3	...	4

Islands and their corresponding abbreviations (Fig. 1) are listed by increasing period of isolation. 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. Parnitha is marked with an asterisk (also in Fig. 1) to indicate it is a mainland location. Island area is in square kilometers. The average flight initiation distance (FID) is reported in centimeters, and sample sizes are given in parentheses. Field autotomy rates (FAR) and laboratory autotomy rates (LARs) are reported as the fraction of tails autotomized per island with sample sizes in parentheses. Predator categories are listed for each island (r = rats, sb = sand boas [*Eryx jaculus*], b = birds, v = vipers [*Vipera ammodytes*], os = other saurophagous Colubrid snakes, and m = 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). Islands used in our isolation analyses are notated with matching symbols: predator-rich baseline islands (a, b, c, d, e) and corresponding islets that had a direct split (aa, bb, cc, dd, ee) ($N = 16$ for FID, and $N = 12$ FAR and LAR). Fields for which we could not obtain data are marked with ellipses.

the tail for a period of 15 s (Pérez-Mellado et al. 1997). At the end of the 15 s trial, we recorded whether the lizard autotomized or not. Each lizard was tested only once and was not included in other experiments. LARs are reported as the proportion of tails that were autotomized for each island population.

Effects of isolation on antipredator behavior

Land-bridge islands provide an excellent system to systematically test the effects of duration of isolation on loss of antipredator 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. All previously mentioned predator types were included in analyses of isolation. We restricted our isolation analyses to those islets that split directly off from large, predator diverse post-Cycladia

islands (FID $N = 17$, field and laboratory autotomy $N = 12$, see Table 1 and Appendix S1), for which we have confidence of the ancestral predator community, as opposed to being derived secondarily from an intermediate-sized island that had itself split off from a large island.

STATISTICAL ANALYSES AND MODEL SELECTION

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

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

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, with the subject

Table 2. Selection criteria data for the seven mixed models constructed to explain variation in FID of Cycladic populations of *P. erhardii*.

Model	AIC _c	Δ AIC _c	Akaike weight
V + OS + M + SB + B + R	10,435.906	-	0.99999813
M + B + OP _{M,B}	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
B + OP _B	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

All models include flight initiation distance as the dependent variable, and distance to the refuge (DR) as a covariate (FID and DR Pearson corr = 0.0358, $P < 0.001$, $N = 913$). The output of our final model (boldfaced), which considers all predator categories separately, suggests not all predator categories are interchangeable and each is distinctly important. Predator predictors in this study include: V = vipers; OS = other saurophagus Colubrid snakes; M = mammalian predators; SB = sand boas (*Eryx jaculus*); B = predatory birds; 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).

category being island. Detection distance, lizard body size (snout-vent length), and the relative abundance of intraspecific lizards were also tested for relationships with FID to implement as potential covariates in our models. We tested for correlation between predator categories, and addressed this potential situation with mixed modeling techniques followed by model selection.

To identify predators most important for the maintenance of specific defenses, we compared seven models developed from our a priori knowledge of the study area and published literature on predator–lizard interactions (Nowak et al. 2008; Pafilis et al. 2009a; Reynolds and Bruno 2013). One model (“Total Predation” Σ Predation) simply summed the number of categories of predators present for each island (Cooper et al. 2004; Pafilis et al. 2009a,b; Cooper and Pérez-Mellado 2012). This model assumes that each predator category adds a similar amount to predation pressure. At the other extreme, we tested a model that considers all predator categories simultaneously and individually (“V + OS + M + SB + B + R” Table 2). Other models followed an intermediate logic in individually testing 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 prior research in this system and our knowledge of hunting strategies in general, we formulated five models that highlighted the role of mammals (M), avian predators (AP), and vipers (V) in determining FID. As a result the composition of the “OP” category varied from model to model and this was denoted with differing subscripts (Table 2).

Models were compared using AIC_c values and their associated Akaike model weights

$$w_i = \exp(-\Delta_i/2) / \sum_{r=1}^M \exp(-\Delta_r/2)$$

(see Burnham and Anderson 1998; Turkheimer et al. 2003). We used AIC_c instead of AIC scores to correct for finite sample size

and decrease the probability of overfitting data with excessive parameters (Burnham and Anderson 2002, 2004).

Field and LARs were studied using generalized linear models. We formed three competing hypotheses prior to data analysis to explain variation in autotomy at the island level, which we again compared using AIC_c 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 noting the presence or absence of any predators on an island), and “Vipers” (a categorical “yes/no” variable noting the presence or absence of vipers on an island). An earlier study of 15 Mediterranean lizard species found that ease of autotomy was largely explained by the presence of vipers (Pafilis et al. 2009a), therefore, we specifically analyzed the effects of vipers on the retention of antipredator behavior. Intercept was a fixed effect in all autotomy models. Given the relatively small sample sizes ($N < 30$ islands) of field and laboratory autotomy data, we constructed simple models with just one predictor variable to avoid overfitting. To avoid potential confounding effects of excluding sex from the models, we compared male and female field autotomy rates with Pearson’s Chi-square analysis.

To examine effects of isolation time on FID and autotomic capacity, we modeled behaviors from islets directly separated from larger post-Cycladia populations (Table 1 and Appendix S1). Large, post-Cycladia islands similar to Naxos (with diverse present-day predator regimes) were used as a baseline to compare younger, smaller islets that were directly separated by rising sea levels. Of our 38 study locations, 17 islets fit our selection criteria and were directly separated from much larger, predator-diverse islands. Autotomy data (both field and laboratory measurements) only existed for 12 of this subset of 17 islands. We compared two mixed models of each antipredator strategy, one using the same

variables from the best predation model, and the other adding period of isolation (Ln-transformed) as a predictor variable to see if time of isolation improves predictive power of antipredator behaviors on islands. All correlations are given using Pearson's r unless otherwise noted. Where hypotheses had a clear direction, we report one-tailed P values.

Results

FLIGHT INITIATION DISTANCE

FID varied widely between individual lizards (10–855 cm: $\bar{X} = 180.2$ cm, $N = 913$). As expected, FID was positively correlated with distance to refuge ($r = 0.358$, one-tailed $P < 0.001$, $N = 913$). A preliminary analysis of a large subset of our data revealed similar FIDs for males and nongravid females ($F_{1,309} = 0.308$, $P = 0.579$, $N = 142$ females, 169 males), thus we included all nongravid individuals in our analyses. Predator category measurements were correlated with each other (Cohen's Kappa, K range: 0.194–0.857, $P < 0.038$, $N = 38$) due to the partially nested nature of where species occur on islands. Detection distance, lizard body size, relative abundance of intraspecific lizards, nesting non-predatory seabird density, vegetation cover, presence of humans, and presence of walls had no relationship with FID, hence they were not included as covariates in our models (see Appendix S1).

FID was best described by the diversity of predator types of an island (Table 2). Lizards from islands with greater predator diversity fled at greater distances ($r = 0.618$, one-tailed $P < 0.001$, $N = 38$) (Fig. 2). Predator diversity decreases with island size ($r = 0.676$, $P < 0.01$, $N = 38$), and small islets (< 0.05 km²) tend to be completely predator-free (Table 1). An analysis of the marginal means from the final model shows that predatory birds and mammals exerted the strongest effect on FID, whereas the effects of vipers, sand boas, rats, and other snakes were small (Fig. 3). These small effects are apparently distinct, however, as the model that accounted for each predator class individually greatly outperformed the model that separated birds and mammals and lumped all other predators together (Table 2).

FIELD AUTOTOMY

We obtained field autotomy rates for *P. erhardii* at 32 of our 38 study sites (mean = 0.7, range: 0.5–1.0, $N = 32$; Table 1). Of 301 females 209 (approximately 69%) had autotomized tails, and of 430 males 306 had previously autotomized (approximately 71%). Autotomy rates were similar for males and females pooled across islands ($\chi^2 = 0.254$, $P = 0.614$, $N = 731$), so we combined data from both sexes in further analyses. Of our competing generalized linear models, "0 Predation" had the highest likelihood and associated AIC weight (Table 3). Field autotomy rates were higher on islands without any predators ($\bar{X} = 0.85$, $N = 4$) than on

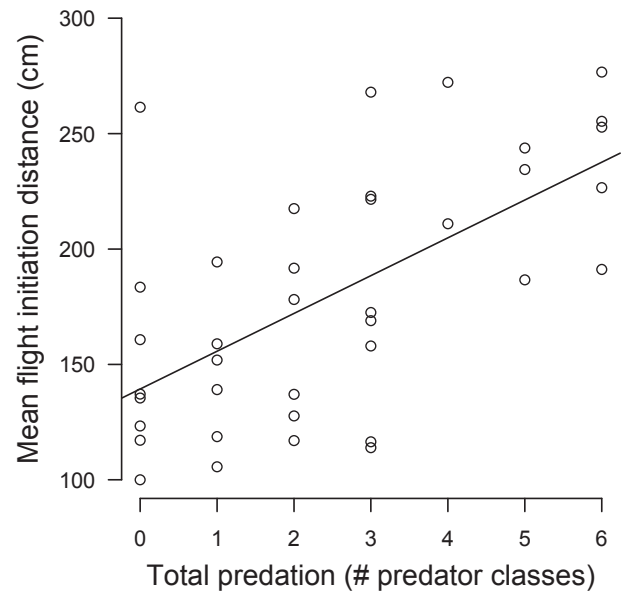


Figure 2. Scatterplot of mean flight initiation distance by total number of predator types per island. Each circle represents an island. Mean FID increases as predation regime intensifies ($R^2 = 0.382$, $r = 0.618$, $P < 0.001$, $N = 38$).

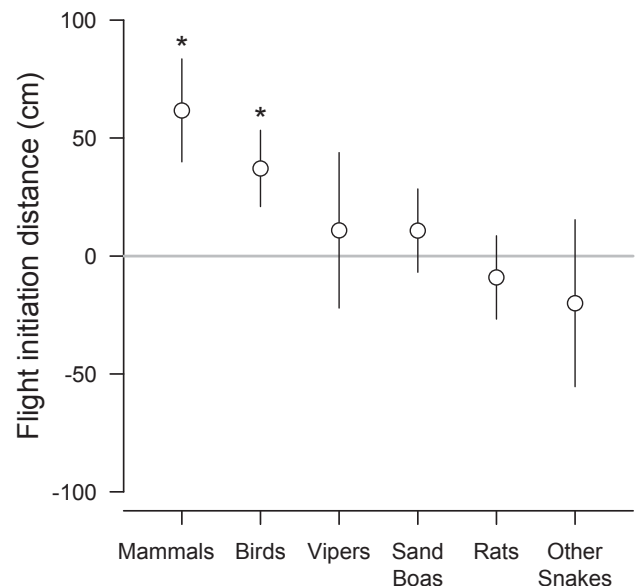


Figure 3. Effects for how each class of predators affected flight initiation distances estimated by the marginal means from the best model [FID ~ DR + V + OS + M + SB + B + R]. Means and error bars represent the average change in FID given the presence of that predator. Means notated by asterisks have 95% confidence intervals that do not overlap the overall average, which is notated as 0 ($N = 913$). Large lizard FIDs are most strongly associated with the presence of mammalian and aerial predators, although all predators have an effect on the expression of this behavior.

Table 3. Model selection criteria for tail autotomy rates in the field ($N = 32$) and laboratory ($N = 28$).

Measure	Model	AIC _c	ΔAIC _c	Akaike weight
Field autotomy	0 Predation	-61.568	-	0.998183
	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	-	0.998203
	Vipers	-31.694	12.682	1.76×10^{-3}
	0 Predation	-26.136	18.240	1.09×10^{-4}

The “0 Predation” model fit a line through autotomy data separated into predator-free islands and islands with any amount of predators, the “Vipers” model separated islands with and without vipers, and the “Σ Predation” model accounted for predator diversity of an island. Generalized linear models were formulated a priori and evaluated using AIC_c values and corresponding Akaike weights. Best models for each measure of autotomy are boldfaced. Field autotomy rates were best explained by the “0 Predation” model, which grouped islands into two groups: predator-free islands and islands with any amount of predator types. Laboratory autotomy rates follow a pattern that is best explained by the total number of predator types on an island (Σ Predation). Neither measure of autotomy was especially influenced by the presence of vipers as predicted.

all islands with even one predator category ($\bar{X} = 0.67$, $N = 28$) (Mann–Whitney $U = 7.000$, $P = 0.005$, $N = 32$). Additionally, field autotomy rates did not differ with predator diversity among islands having one to six predator types (Kruskal–Wallis, $P = 0.143$, $H = 8.241$, $df = 5$, and see Fig. 4A). Interestingly, field autotomy rates were significantly higher for males than females only on predator-free islands ($\chi^2 = 19.324$, $P < 0.001$, $N = 69$). We found no association between relative abundance of lizards and field autotomy in an analysis of all islands (Spearman’s rho = -0.017 , $N = 32$), and islands without predators (Spearman’s rho = -0.316 , $N = 4$).

LABORATORY AUTOTOMY

LARs varied substantially across the different island populations ($\bar{X} = 0.34$, range: 0–0.58, $N = 28$), and increased linearly with increased predator category diversity (Pearson $r = 0.825$, one-tailed $P < 0.001$, $N = 28$, Fig. 4B), similar to FID (Pearson correlation of mean FID and LAR: $r = 0.644$, one-tailed $P < 0.001$, $N = 28$). Of our competing models, summing the number of predator types (“Total Predation”) explained most of the variation in laboratory autotomy (Table 3). In contrast, models separating islands with and without vipers, or separating islands with and without any predators, had much lower model weights (Table 3). Earlier work in a related system had emphasized the importance of vipers as a driving factor underlying the retention of autotomy on islands with few other predators (Pafilis et al. 2009a). In our sample, vipers only occurred on large, predator-rich islands. Given this potential confounding factor, we performed a post-hoc test that compared the correlation of the entire sample ($r = 0.825$, $P < 0.001$, $N = 28$, linear regression) with one that excluded islands with vipers ($r = 0.672$, $P < 0.001$, $N = 22$). Given that the correlation remained robust, we conclude that vipers contribute to the relationship of laboratory autotomy to predator diversity, but that autotomy rates are shaped by predation pressure beyond the presence of vipers.

RELATIONSHIPS BETWEEN MEASURES OF DEFENSE

Against expectation, field autotomy rates were not correlated with laboratory rates (Spearman’s rho 0.088, $P = 0.655$, $N = 28$). Average FID per island was positively correlated with LAR (Pearson $r = 0.644$, one-tailed $P < 0.001$, $N = 28$) but was not obviously related with field autotomy rate (Pearson $r = -0.024$, one-tailed $P = 0.449$, $N = 32$).

EFFECTS OF ISOLATION ON ANTIPREDATOR BEHAVIOR

Lizards from islets that were directly separated from larger, more predator diverse islands had shorter FIDs than lizards from the larger islands (average difference of 67.81 cm, $N = 17$). Further, populations isolated for the longest period of time displayed shorter than average FIDs (Fig. 5A). A comparison of two mixed models (one with and one without isolation period) revealed that “Predation + Isolation” had the best fit for FID ($\Delta AIC_c = 309.4$, Table 4). Thus, our results suggest duration of isolation has an effect on flight behavior in addition to the prevailing predation environment (Pearson $r = -0.477$, one-tailed $P = 0.036$, $N = 17$), with the most extreme cases of island age driving the pattern (the youngest and second-oldest islands, Mando and Chtenia, respectively). Current predator diversity of an island was not correlated with duration of isolation (Ln-transformed, $r = -0.177$, $P = 0.497$, $N = 17$).

Lizard populations occurring on islets that became separated from predator-rich islands were less likely to shed the tails in laboratory tests (19% average, $N = 12$). However, in contrast to the results for FID, the addition of isolation time did not improve autotomy models (see Fig. 5B and Table 4).

Discussion

In this study, we examined factors underlying the erosion of ancestral antipredator behaviors in isolated populations living in island

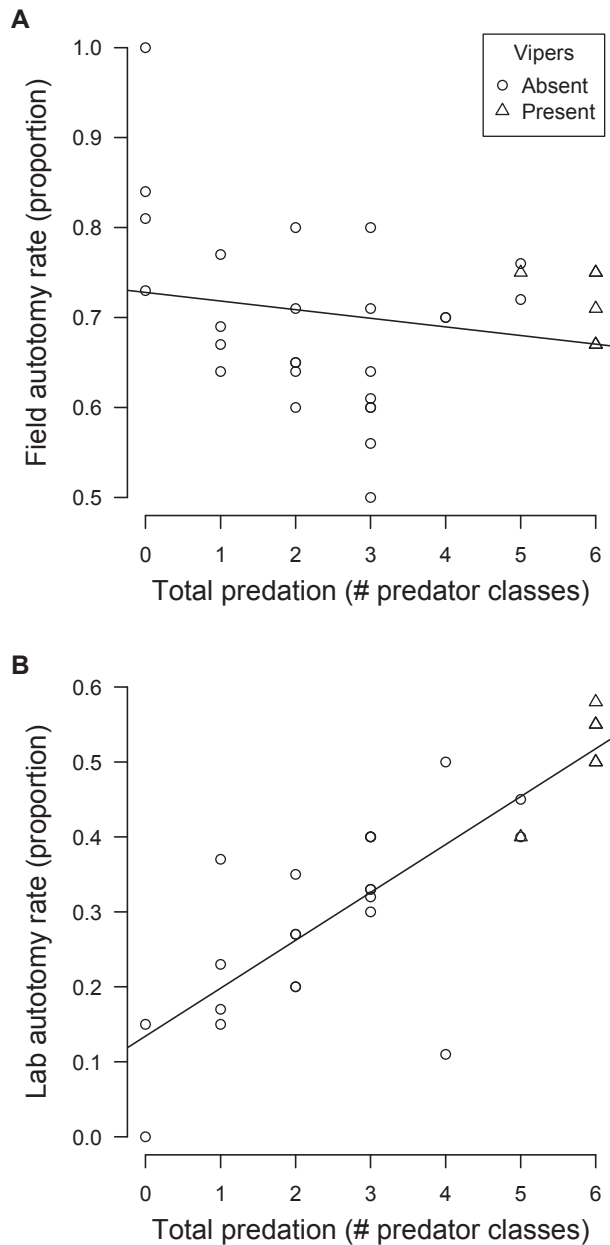


Figure 4. (A, top) Field autotomy rate (FAR) versus total number of predator categories per island (Total Predation). Field autotomy rates did not increase with rising predator diversity ($R^2 = 0.039$, $P = 0.279$, 95% CI Σ Predation = -0.027 to 0.008 , $df = 1$, $N = 32$). Conversely, predator-free islands had significantly higher FARs than islands with any amount of predation (mean ranks of predator-free vs. predator islands were 28.75 and 14.75, respectively, $U = 7.000$, $Z = -2.798$, $P = 0.005$, $N = 32$, Mann–Whitney U -test). Because past work (Pafilis et al. 2009a) suggested a special effect of viperids on autotomy rates, islands inhabited by vipers are marked with triangles. (B, bottom) Laboratory autotomy rate (LAR) versus total amount of predator categories per island (Total Predation). LARs increased steadily with increased number of predator categories present ($R^2 = 0.680$, $P < 0.001$, 95% CI Σ Predation = 0.046 – 0.082 , $df = 1$, $N = 28$). Triangles represent islands with vipers, and circles islands without vipers.

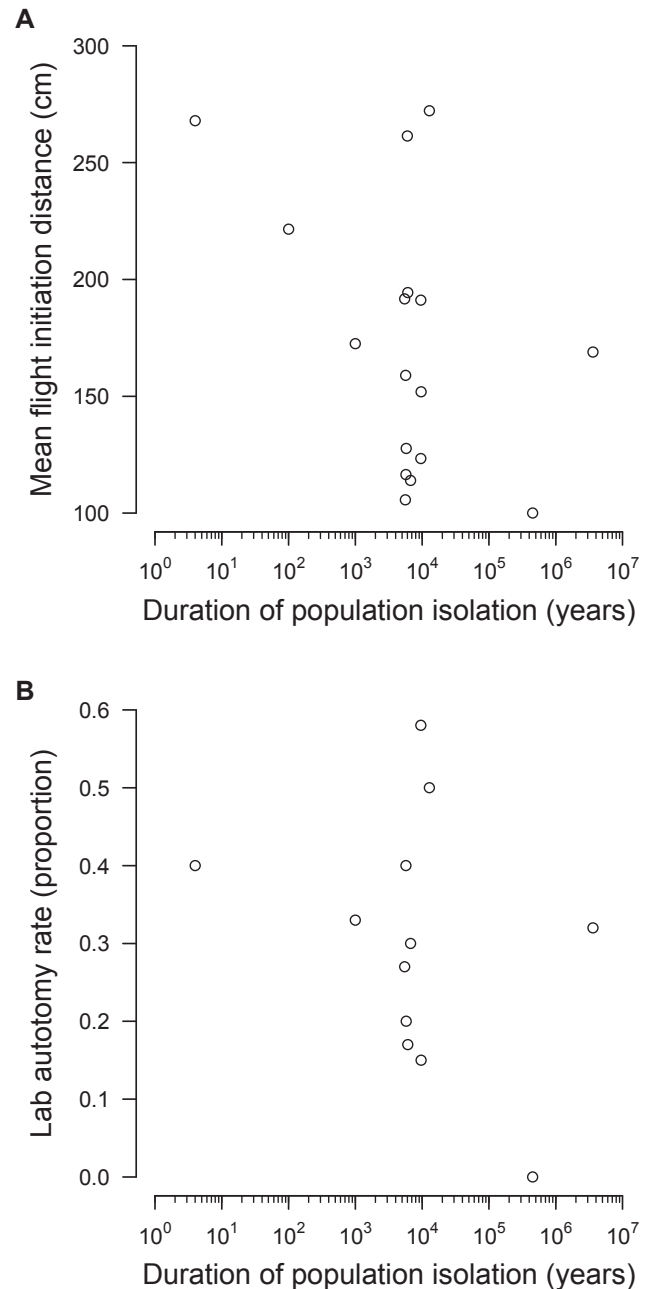


Figure 5. (A, top) Average flight initiation distance (cm) on islets against duration of isolation (Ln-transformed) from the main island landmass ($R^2 = 0.200$, Pearson $r = -0.477$ (one-tailed), $P = 0.036$, $N = 17$). (B, bottom) Laboratory autotomy rates against duration of isolation (Ln-transformed) (linear regression $R^2 = 0.094$, Pearson $r = -0.306$, $P = 0.333$, $N = 12$). This represents the relationship between antipredator defenses with increasing period of isolation.

environments. We predicted that flight behavior would vary across distinct island populations of lizards, and decrease with loss of predator types. Results match our predictions for two main lizard antipredator defenses, flight response and laboratory autotomy (Figs. 2 and 4B). For FID, each predator type had an impact, with

more predator-diverse islands having the strongest responses. For autotomy ability, predator diversity predicted ease of autotomy with no special effect of vipers apparent, counter to our second prediction. Finally, lizard populations from islets that had been isolated for the longest period of time under conditions of reduced predator diversity indeed displayed decreased expression of flight behavior.

Predator diversity was positively correlated with longer FID, and the absence of mammalian and avian predators had a strong effect on the erosion of flight behavior in particular (Figs. 2, 3, 5A). Presence of either mammalian or avian predation increased lizard FID on average by 60 cm and 40 cm, respectively (Fig. 3). 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 to an attack. Feral cats (*F. catus*) and stone martens (*M. 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; Smith 1976). These approaches differ dramatically from snake predators in this island system. Vipers usually employ a sit-and-wait hunting strategy and all snake species remain relatively close to the ground before striking prey (Valakos et al. 2008; Pafilis et al. 2009a). Hence, the reliance on speed to approach a prey item from afar means that lizards that escape early reap the largest benefits. However, it is important to emphasize that chemosensory cues, although not evaluated in this study, may be more important for detecting at least some types of predators (Cooper 2003). Nonetheless, the candidate model that simply summed the number of predator categories present (Σ Predation), had the least predictive power, whereas the model that considered all predator categories separately had a model weight close to 1, even after the penalty AIC_c imposes for the inclusion of six explanatory variables (Table 2). This suggests that predator categories are not all interchangeable and that each is important in a distinct manner in determining the expression of flight behavior (Table 2), and that simply aggregating the number of predator groups is not sufficient to predict FIDs.

Populations of *P. erhardii* showed declines in flight behavior with increasing duration of isolation, particularly on predator-poor islands isolated for millennia, suggesting that time tells us something more about antipredator behavior than current predator community alone (Fig. 5A, Table 4). 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; Cooper et al. 2014). Although these studies have shown that isolated populations have lost some of their antipredator defenses, they provide little insight into the rate at which behaviors change (see Cooper et al. 2014). Reduced flight behavior was particularly

evident during visits to very old islands (see Fig. 5A and B): lizards from some of the oldest islands (450,000 years and older) were tame enough to approach within arm's reach, and would sit in one's hand after capture without attempting to flee (K. M. Brock, pers. obs.). Because flight behavior is largely recognized as an "experience-dependent" antipredator behavior (Blumstein 2002; Blumstein and Daniel 2005; Rödl et al. 2007), tameness on islands with limited predation is probably due to an inability to adequately identify predators and correctly respond. Previous work has suggested that loss of vigilance, a type of antipredator behavior, can occur rapidly (Blumstein 2002; Li et al. 2014). We found that short-term isolation (4–1000 years) of populations experienced marginal reduction in FID (8–61 cm), with a greater loss occurring over thousands of years (15–176 cm). Further, the inability for insular populations to mount an adequate endocrine stress response could also be related to the tameness we observed on our oldest islands (see Rödl et al. 2007). An effect of isolation remains even if predator diversity is taken into account (Table 4), thus suggesting an impact of duration of isolation directly on the extent of FID erosion. Extreme tameness on islands is probably the result of a combination of decreased predator diversity (especially hawks and mammals) and subsequent loss of predator experience and recognition, an effect that increases with period of isolation.

Researchers have long debated whether the highest incidences of autotomy should occur in areas with inefficient predators (because failed attacks are likely to result in autotomy and escape), or areas with the greater diversity of predators (Cooper et al. 2004; Pafilis et al. 2009a; Bateman and Fleming 2011; reviewed in Bateman and Fleming 2009). In contrast to other studies on Mediterranean herpetofauna (Diego-Rasilla 2003; Cooper et al. 2004; Pafilis et al. 2008, 2009a), we found that field autotomy rates did not reflect prevailing predation levels (in terms of predator diversity), nor were they correlated with standardized laboratory autotomy trials. Counterintuitively, the highest rates of autotomy were actually observed on islets completely isolated from predators, suggesting that autotomy on predator-free islets was driven by intraspecific aggression and not by predation. Increased intraspecific aggressiveness on islets without predators is likely a product of intensified competition for food, territory, and mates (Castilla and Van Damme 1996; Pafilis et al. 2009b; Raia et al. 2010; Capula and Aloise 2011). Our results also suggest that intraspecific aggression is more intensive among male individuals in predator-free environments. In an effort to prevail over their (extremely numerous in the case of dense populations) rivals, male lizards attack conspecifics (Kneill 2009). These fierce battles regularly result in amputated body limbs (Jennings and Thompson 1999; Kneill 2009; Pafilis et al. 2009b; Vervust et al. 2009), and may include cannibalism (Elgar and Crespi 1992; Bonsall and Klug 2011). Thus, it is possible the high rates of field autotomy

Table 4. Selection criteria for alternative models investigating the importance of duration of isolation on antipredator behaviors.

Measure	Model	AIC _c	Δ AIC _c	Akaike weight
Field autotomy	0 Predation	-19.283	-	0.91158
	0 Predation + Isolation	-14.617	4.666	8.84×10^{-2}
Laboratory autotomy	Σ Predation	-21.617	-	0.81967
	Σ Predation + Isolation	-18.607	3.01	1.8×10^{-1}
Flight initiation distance (+DR)	R + SB + B + M + Isolation	3930.11	-	0.99999
	R + SB + B + M	4239.51	309.4	1×10^{-10}

Winning models are boldfaced. Both field autotomy rate ($N = 12$), and laboratory autotomy rate ($N = 12$) predation models did not improve by adding period of isolation, possibly due to small sample size and the penalty AIC_c imposes on additional explanatory variables. However, adding duration of isolation (Ln-transformed) as a covariate (in addition to distance to refuge) did improve our best predator model of flight initiation distance ($N = 371$). Because these analyses were performed on a subset of islands that directly split from larger, more predator diverse islands, there are no vipers (V) or other saurophagus Colubrid snakes (OS) present, thus we did not include them in our isolation mixed models.

we observed on predator-free islands could be due to intraspecific agonistic encounters, although our results do not indicate a direct correlation between population density and field autotomy. However, this result could be due to small sample size or factors unaccounted for in this study. This phenomenon should be investigated more specifically in the future, by taking into account factors such as sex ratio, islet carrying capacity, food abundance, marines subsidies, etc.

In contrast to a similar study of autotomy in Mediterranean lizards by Pafilis et al. (2009a), we found no relationship between field and LARs, which likely reflects that none of that study's locations (with the exception of Dragonada) were small enough for small-islet intraspecific aggression effects to come into account. Interestingly, only the lizards from Dragonada, the one island ecologically similar to the present predator-free islets, displayed the same contrasting pattern of high field and low LARs as seen in the present study (see Pafilis et al. 2009a). Small islet populations of *P. erhardii* may differ in age structure because lizards are not being killed by predators, and therefore contain, on average, older individuals that have likely encountered more aggressive events and thus have more regenerated tails (Bateman and Fleming 2009; Pafilis 2009a; Pleguezuelos et al. 2010). Further investigation is required into intraspecific dynamics, food availability, and intraspecific interactions on predator-free islands to explain why these predator-free populations have such high autotomy rates in the field and yet low rates in standardized trials.

LARs increased linearly with predator diversity. In distinct departure from field autotomy, LARs declined linearly with the loss of any predator category (Fig. 4B). Of our three competing hypotheses, the model that added all predator types captured the most variation in LARs (Table 3). A post-hoc investigation of the influence of vipers supports the claim that overall predator diversity, and not viper presence alone, has a strong relationship with retained autotomic abilities. Thus, even after the removal of islands where vipers were present from our analysis, we found a linear relationship between LARs and number of predator types.

Indeed, nonviperid snakes, as well as mammalian predators including rats, will attack lizards and induce autotomy (McCallum 1986; Hare and Miller 2010, J. Foufopoulos, pers. obs.), and it appears that all predator categories can exert selective pressure on the maintenance of tail autotomy.

In general, islets that were isolated for longer periods of time lost more predator types, specifically vipers, mammals, other saurophagus Colubrid snakes, and hawks, although there was no statistically significant relationship between predator diversity and island isolation (see Table 1 and Appendix S1). This pattern is consistent with other island systems around the world that have fewer predator species relative to mainland areas of comparable size and habitat type (Darwin 1839; MacArthur and Wilson 1967; Blumstein and Daniel 2005; Foufopoulos et al. 2011; Cooper and Pérez-Mellado 2012). LARs were not correlated with prolonged duration of isolation (Fig. 5B), which was surprising given the lifetime fitness costs of autotomy (Ballinger and Tinkle 1979; Vitt and Cooper 1986; Pafilis et al. 2009a; Cromie and Chapple 2013). Although our model that accounted for isolation period and predation performed somewhat worse than our model that considered only predation (Table 4), we feel that this issue would be worth revisiting with a larger sample size containing more islands younger than 6000 and older than 9000 years. Although a less-refined fear response and reduced ability for tail autotomy may be advantageous to a lizard's fitness in a less-diverse predation environment (Cooper et al. 2004, 2014; Rödl et al. 2007), individuals may not have the capacity to adapt if a novel predator were suddenly introduced (Beauchamp 2003; Baillie et al. 2004; Blackburn et al. 2004; Losos et al. 2006; Bonnaud et al. 2010). Our data suggest that when it comes to susceptibility to invasive predators (cats and rats in our case), the smaller and older the population, the more likely that population will be susceptible to predation.

We demonstrated 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 practiced behaviors, such as FID. A basic yet novel finding was that FID, a main antipredator behavior, decayed largely according to period of isolation from intense predation pressure. Interestingly, the current predation regime of an island effectively predicts the degree of expression of antipredator behavior, but for FID, the duration of isolation improves our understanding of this trajectory. Taken together, our results suggest that tameness is strongly selected for on predator-free islands, where the energetic and fitness costs of maintaining antipredator behaviors greatly outweigh the benefits. Costly antipredator behaviors may fade away quickly in the absence of selective pressure; however, extreme tameness may result from many years of isolation from predators.

ACKNOWLEDGMENTS

This study would not have been possible without financial support from the University of Michigan School of Natural Resources & Environment, University of Michigan Museum of Zoology, University of Michigan International Institute, The SNRE Envoys, and the University of Michigan Marching Band. Generous statistical advice was given by Drs. D. Costello, K. Welch, and I. Ibáñez. Supplies for field work were provided by G. Schneider and the Herpetology Division of UMMZ. We appreciate the visual consultation given by J. Estrada and Drs. A. Davis-Rabosky and D. Rabosky. Our sincerest thanks to the wonderful field and laboratory assistants who worked many hours to ensure this project was successful: M. White, C. Weber, W.-C. Cheng, C. Bergman, C. Donihue, J. Jozlin, F. Elias, and the entire Foskolos family.

DATA ARCHIVING

The doi for our data is 10.5061/dryad.bt52f.

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Associate Editor: E. B. Rosenblum

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. This file contains supplemental analyses and statistics referenced in the main text.