EFFECTS OF FERAL CATS ON THE EVOLUTION OF ANTIPREDATOR BEHAVIORS IN THE AEGEAN WALL LIZARD *PODARCIS ERHARDII*

by
Binbin Li

A project submitted
in partial fulfillment of the requirements
for the degree of
Master of Science (Natural Resources and Environment)
at the University of Michigan
April 2012

Faculty advisors:
Associate Professor Johannes Foufopoulos, Chair
Professor Peter Bednekoff

ACKNOWLDGEMENTS

Foremost, I would like to express my sincere gratitude to my advisor Dr. Johannes Foufopoulos for his continuous support, enthusiasm, motivation and patience for the completion of this research. I could not have made so much progress without his help and I could not have imagined having a better advisor for my master study.

Secondly, I would like to thank Dr. Peter Bednekoff for his insightful comments, encouragement and continued support through the project. My sincere thanks also goes to Dr. Panayiotis Pafilis in University of Athens who gave me very important guidance and help while I was in the field and assisted with data collection.

I owe my deep gratitude to my fellow students: Anat Belasen, Ana Marcela Chara, Maureen Lynch, Colin Donihue for their help and feedback. And I also would like to thank School of Natural Resources and Environment and Rackham for their funding support, which gave me the chance to implement and finish this project.

I could not have made it this far without the lifelong support of my family, especially my parents Haiqing Li and Yunfeng Zhao. Thank you for giving me the life and providing me with an environment full of love, encouragement and support.

TABLE OF CONTENTS

ABSTRACT

Exotic predators such as feral cats (*Felis catus*), have been the driving force behind the extinction of many endemic species of island mammals, birds and reptiles. Island endemics appear to be exceptionally susceptible to invasive predators because of small population size and frequent lack of anti-predator defenses. The goal of this study was to determine the impacts of feral cats on the island populations of Aegean Wall lizards (*Podarcis erhardii,* Lacertidae) in relationship to the expression of anti-predator behaviors. I estimated lizard population densities in areas with low cat density sites (LCD) versus high cat density (HCD) sites by conducting 100-m transect along dry-stone walls, on the island of Naxos, as well as on surrounding islets (Cyclades, Greece). Degree of expression of antipredator behaviors was determined by measuring flight initiation distance (FID) and rates of tail autotomy both in the field and in the lab for six populations in HCD, LCD sites and four satellite islets without cat presence. I also staged controlled encounters with mounted cats decoys and quantified escaping responses from lizards from these populations. I found that feral cats had a strong negative effect on lizard population densities. Lizards adapted their antipredator behaviors in response to cat predation by extending their FIDs, increasing their capacity for tail autotomy, and by staying closer to refugia. In laboratory predation simulations, lizards from cat-free islets had significantly shorter FIDs than LCD site lizards and in particular than HCD site lizards. Furthermore, some unique islet behaviors, presumably evolved in response to lack of predators and to ameliorate chronic conditions of food shortage, appear to render islet lizards strongly susceptible to cat predation. These behaviors include rarely utilizing available refugia, and moving towards anything new, including cat decoys. Nonetheless, I found that repeated exposures over three trials led to significant increases in FIDs for all populations, indicating at least some behavioral plasticity. My results suggest that although lizards may adapt their antipredator behaviors to cope with introduced predators, this offers at best only partial protection, so that there remains strong concern about their survival in the face of expanding feral cat populations.

KEYWORDS. Anti-predator behavior, feral cat, island endemics, Mediterranean Basin

INTRODUCTION

Loss of biodiversity is one of the major global problems, with more than 40% of the world's species being threatened with extinction (Baillie *et al.,* 2004). Island species appear to be disproportionally affected (Cox *et al.*, 2006). While multiple factors predispose island species to extinction, including small population size and niche specialization, the introduction of exotic predators has been the driving factor~~s~~ behind many of these extinctions (Primack, 2004). Island endemics appear to be exceptionally susceptible to invasive predators such as feral cats, dogs and foxes because the lack of exposure to previous predators and associated low wariness (Blumstein, 2002; Bonnaud *et al.*, 2007).

Feral cats (*Felis catus*) originate from house cats which in turn descend from the African wildcat (*Felis silvestris libyca*) domesticated more than 9,500 years ago (Serpell, 2000; Driscoll *et al.*, 2009). Cats have been introduced to nearly 179,000 islands worldwide (Medina et al., 2010) and have established feral populations in many of those (Todd, 1977). Feral cats are dietary generalists and efficient predators that have adapted to a wide range of often adverse environments (Coman & Brunner 1972; Van Aarde 1986; Konecny 1987; Tabor 1983; Atkinson 1989). Their presence has been tied to extinctions of multiple taxa of endemic island mammals, birds and lizards (Iverson 1978; Kirkpatrick & Rauzon 1986; Towns et al. 1990; Donlan *et al.* 2000; Veitch 2001; Griffin *et al.*, 2000; Blumstein, 2002). They are responsible for at least 13.9% of the bird, mammal and reptile extinctions globally, and are the major threat to almost 8.2% of critically endangered birds, mammals, and reptiles on islands (Medina et al., 2011). In the Canary Islands for example, cats have been implicated in the extirpation of several giant endemic lizards (*Gallotia* sp.) (Garcia-Márquez *et al.*, 1999; Nogales & Medina, 2009). Due to their wide distribution and their detrimental effects on local biodiversity, feral cats have been listed as one of the 100 worst invasive species (Lowe *et al.,* 2001).

A critical factor exacerbating the devastating impacts of feral cats on insular species is the lack of behavioral, morphological and life-history adaptations against predators among such island taxa. Insular ecosystems usually harbor few, or no predator species so that predation pressure is unusually relaxed for most island vertebrates (MacArthur & Wilson, 1967; Pafilis *et al.*, 2009). Because antipredator defenses are costly in terms of energy and time invested, their deployment generally means reduced resources and opportunities available for foraging, mating and reproduction (Parejko, 1991; Forsgren, 1992; Hunter & Skinner, 1998; Dukas & Kamil, 2000). In the absence of substantial predation, costly antipredator defenses lose their benefits and evolutionary theory predicts their gradual loss (McNab 1994; Van Damme & Castilla 1996; Magurran 1999; Blumstein & Daniel 2005; Rödl *et al.,* 2007).

Many lizard species use wariness (measured through Flight Initiation Distances [FIDs]) and the ability to shed their tail as their main antipredator defenses. FID is defined as the distance between the prey and a predator at which the animal initiates an escape. According to the cost-benefit analysis of escape behaviors, lizards will only take off at a distance where gains outweigh the costs which are measured as the expected fitness loss if not fleeing (Ydenberg & Dill, 1986). FID increases with predation risk and decreases with the distance to refuge (Cooper *et al.*, 2009). Ease of caudal autotomy (tail-shedding) also follows a similar pattern, occurring only when the benefits exceeds the costs (Arnold 1988; Perez-Mellado *et al.*, 1997). Because intact tails are not only signifiers of social status but also play an important role in locomotion, courtship, defense, and as lipid storage sites (Avery 1974; Daniels 1984; Vitt & Cooper 1986; Ballinger *et al.*, 1979; Punzo 1982; Fox *et al.*, 1990; Salvador *et al.*, 1996; Pafilis *et al.*, 2005), retention of caudal autotomy is an inefficient strategy under conditions of relaxed predation (Pafilis *et al.*, 2005). On small islands with few or no predators, rapidity of loss of an antipredator behavior will depend on the cost of each behavior, with the most expensive behaviors being lost first (Blumstein, 2002). Beyond cost, experience necessary to perform a behavior also matters: 'hard-wired' behaviors that can be performed properly without prior experience can persist long enough after isolation from predators (Byers 1997; Coss 1999). The plasticity of a behavior also has important implications for management: If an antipredator behavior can be easily lost, then on the other hand, it will be also easily regained (Blumstein, 2002). This means that it might be possible to re-establish plastic antipredator behaviors through appropriate training schemes in captive populations slotted for re-introduction, or in behaviorally naive species of conservation concern (Griffin *et al.*, 2000; Blumstein *et al.*, 2004; Berger *et al.*, 2007). Ultimately, understanding the environmental factors that determine the loss of antipredator behaviors is important for being able to predict the vulnerability of island populations to invasive predators.

The Mediterranean Basin represents one of the world's biggest biodiversity 'hotspots' and harbors more than 461 endemic taxa of reptiles and amphibians (Cox *et al.*, 2006). In this region multiple island reptiles are today either endangered or already extinct, and invasive predators, such as feral cats, are thought to have been responsible for several of these extinctions (Perez-Mellado *et al.*, 1997). However, previous studies on impacts of feral cats on reptiles mainly focused on iguanas on the West Indies and on Fiji, and the giant lacertids on the Canary Islands (Nogales & Medina, 2009). Few studies have concentrated on reptiles of the Aegean Sea in the E. Mediterranean Basin. In this study I conduct a combined field and experimental study aiming to understand the effects of the presence of introduced predators on a widespread reptile species. In particular, I ask whether: i.) Degree of pre-existing antipredator defenses depends on the presence and number of native predators on the islands; ii.) Susceptibility to feline predation is dependent on the existence of antipredator defenses. iii.) The presence of cats has a significant impact on lizard populations on Mediterranean islands.

MATERIALS AND METHODS

1. Study area

This study was conducted on the island of Naxos (Cyclades Cluster, C. Aegean Sea, Greece) and the surrounding satellite islets (see Fig. 1, Table 1). Naxos is a large island (438 km^2) that contains a diversity of habitats ranging from dwarf bush steppe ('phrygana'), to evergreen maquis, olive groves, terraced agricultural areas and relict oak forest (Arianoutsou et al. 1997). The climate is classified as Mediterranean, characterized by warm dry summers and mild, rainy winters with total annual precipitation of approx. 375 mm (Marinos & Maris, 2006). Both climate and type of vegetation cover are representative of lowland sites in the E. Mediterranean Basin. Fieldwork was performed during the summer of 2011 (5/12-7/15). In addition to 18 sites on Naxos, I also worked on 4 nearby islets (Ovriokastro, Aspronissi (sometimes also referred to as Glaronissi), Parthenos and Mando, see Fig. 1, Table.1). Because lizards seek out dry-stone walls for thermoregulation and for refuge, for each of the Naxos locations, I focused my work on a randomly selected 100m-long segment of dry-stone wall.

The first three islets were connected to Naxos during the last ice age but were separated by rising sea levels around the same period of time (5,600-6,100 yrs bp, see Table 1.) (Foufopoulos *et al.,* 2011). In contrast, Mando Isl. was separated from Naxos by a storm in 2006 and remains isolated by a 20m wide channel. The soil is sandy and covered by sparse evergreen maquis bushes. None of the islets harbors cat or native predator populations and all of them have very high lizard population densities.

2. Cat populations

Cats (*Felis catus*) are not native to the region and were introduced to the Cyclades most likely in early historic times. The species is common on Naxos but is almost exclusively restricted to the vicinity of human settlements. Because human settlement has been traditionally clustered tightly around old village cores, presence of cats tends to be similarly aggregated around these well-defined habitation sites. Cats occur on Naxos in a spectrum of dependence on humans with many animals being fed by their owners regularly, while others appear to be largely feral. My study sites fell into three distinct categories: *i.)* Areas close to human habitations with high cat density, *ii.)* Areas at least 500m away from human habitations with low cat presence, and *iii.)* Satellite islets with no cats.

Nine sites within 300m from villages in Naxos were selected as high cat density sites, while nine sites with similar ecological conditions but away from villages were selected as low cat density sites (Fig. 1, Table 2).

3. Study species

The study focuses on the Aegean Wall lizard (*Podarcis erhardii,* Lacertidae), a species with a wide distribution throughout the ecosystems of the Aegean. *P. erhardii* is a small-sized (snout-vent length [SVL] about 70mm), terrestrial, and diurnal insectivore lizard. The species is common in the study region, inhabiting a broad spectrum of habitats ranging from undisturbed to strongly human-impacted, and is absent only from closed-canopy forest. However, these lizards have a clear preference for dry-stone walls, which separate fields and grazing properties, support agricultural terraces on sloping ground, and which constitute a ubiquitous feature of the Aegean landscape. The species escapes predators by employing vigilance behaviors and by shedding its tail when attacked. I captured these lizards by using either a noose or a mealworm (*Tenebrio* sp.) larva attached to the end of a telescopic fishing pole (Pafilis *et al*., 2009). Once captured, lizards were transported to a holding site where I recorded standard life history data (e.g. SVL, weight, sex etc.). Animals were housed in plastic terraria allowing for normal thermoregulation and were allowed to acclimatize to conditions in captivity for a minimum of two days. Lizards had free access to water and sunlight, and were fed daily *ad libitum* with mealworms (*Tenebrio* sp.).

4. Ecological measurements

To evaluate possible effects of habitat on lizard behavior and ecology, I measured canopy coverage, understory coverage, understory biomass for all 18 sites. I also designated a 100m-long transect parallel to the wall in each study area. At 10m intervals, I placed a 0.16 m^2 quadratic frame and clipped all above-ground understory plant species in it. A stopwatch was used to randomly select the distance of the quadrat from the road; the hundredth of a second designated the number of meters I traveled into the habitat from the transect. To determine arthropod populations, I deployed three pitfall traps at each site (with a minimum intertrap distance of 25m) for a period of 21 days. For each site I furthermore determined aspect, slope, wall height and each wall facing.

We selected a subset of sites from each category for in-depth behavioral comparisons of the lizard populations. I determined field FID, field autotomy rates and captured 20 individuals to conduct lab autotomy rate tests and to quantify laboratory escape behavior measurements from the following sites: three populations from low cat density sites (South slope, North Slope, Moni); three populations from high cat density sites (Filoti, Glinado and Vivlos); and four populations from satellite islets (Ovriokastro, Aspronissi, Parthenos and Mando).

5. Field methods

5.1 Cat density measurements

We determined the relative abundance of cats by carrying out standardized nocturnal spotlight counts on 1-km long road transects. This method is widely used to monitor mammals like rabbits (*Oryctolagus cuniculus*), foxes (*Vulpes vulpes*) or feral cats (Read and Bowen 2001; Reddiex *et al.,* 2004). At each site, I conducted this survey on the road nearest (average distance to the focal wall;

35m) to the focal study wall with the road transect extending 500 meters in either direction from the point of greatest proximity to the study wall. For each survey, we drove our vehicle at low speed (approx. 4 km/h) along the transect once a night for each of three nights. Both sides of the road were slowly scanned using a powerful hand-held spotlight (Cyclops CYC-9WS; Cyclops Solutions, LLC. Grand Prairie, TX, U.S.A). We identified feral cats by their eye-shine and the illuminated part of the body. To account for possible confounding effects of observer bias, time of the day and weather, surveys were conducted by the same observers (BL, AB) at the same time (21:00-00:30) during clear and windless nights.

5.2 Lizard surveys

Lizard densities were determined by surveying the population on the focal 100m-long wall segment. This was done by walking along the wall at 1m-distance and recording the number of lizards seen either on the wall or on the nearby ground. On each site, I repeated the survey at the same time on three consecutive days; survey results were averaged.

5.3 Measurements of Flight Initiation Distance (FID) and field autotomy rate

We determined Flight Initiation Distances (FIDs) by collecting data on at least 30 focal animals from each site in a standardized fashion. After sighting an animal while walking slowly across a study site, I approached it at an intermediate speed of approximately of 45m/min. I recorded the distance to the observer at which each lizard initiated an escape, the distance covered to reach the refuge, as well as the sex the focal animal. I also quantified field tail autotomy rates for each site by determining the fraction of the animals with regenerated tails. Because a regenerated tail has a different shape and color than an unshed one, a field observer can determine readily autotomy status by using a pair of binoculars.

5.4 Laboratory measurements of autotomy rates

Field autotomy rates can be shaped on the one hand by the innate ‘ease’ of tail-shedding of a lizard population, and on the other hand by the number of opportunities to do so, as well as the demographic structure of a population. To isolate the innate component of autotomy, I followed Perez-Mellado *et al.* (1997) who used a standardized laboratory procedure to quantify intrinsic ability for tail-shedding. In brief, I simulated the attack of a predator by using a pair of calipers to grasp an animal’s tail, 20mm from the coala. To standardize the measurement, I applied just enough pressure to depress the tail to half of its original thickness, and this was maintained for 20s. A coarse mat was provided to maintain traction for the animals. If an animal shed its tail within the 20s period, I also recorded the duration of post-autotomy movement, from the moment of autotomy to the time where all movement ceased (Pafilis *et al.*, 2005). The autotomy rate for a population was calculated as the ratio of number of automized individuals over the total number of tested lizards. Because previous history of autotomy may affect the ease of tail-shedding (P. Pafilis, pers. comm.), I only did this experiment on individuals with intact tails. At the end of this experiment, all the animals were released back into their territory.

5.5 Laboratory escape behavior measurements

Although field FID has been shown to be a representative measure of awareness and fear in a population, it may be confounded by various environmental factors, such as temperature, habitat openness or familiarity with humans. To quantify antipredator responses specifically towards feral cats, while controlling for possibly confounding factors, I subjected lizards from different populations to a simulated predation event using a mounted cat decoy.

Predation simulations where conducted in a indoor arena, that allowed lizards to observe an approaching cat decoy and then decide when to escape into a readily available refugium.
We prepared the cat decoy using standard taxidermy methods (Pray, 1982) from an animal that had died in a car accident and that was set in a natural, crouching position. The completed decoy was then mounted on a low, 20 x 40cm big-wheeled platform that could be pushed from the back by a 3m long attached pole.

The arena was consisted of two parts: a long corridor (35 cm wide and 3m long) and a trapezoid enclosure (50cm wide and 60cm long) attached to the one end of the corridor. Focal animals were placed into the enclosure which was surrounded by 30cm high walls and whose floor was covered with fresh sand to obscure olfactory cues. Enclosure and corridor were separated by a glass window, which enabled the lizard to observe the cat decoy approaching in the corridor. Two 10 x 7 cm bricks with holes were placed at the corners of the enclosure and acted as refugia for the lizards. A 100W incandescent light bulb was hung 8 cm above the center of the enclosure to provide warmth and to create species-appropriate thermal gradients. After introducing a focal lizard to the arena I allowed the animal to familiarize itself with the area for 10 minutes before starting the experiment. At that moment, one of us (BL) started pushing the cat decoy along the corridor towards the enclosure at a constant speed of 25cm/s. To avoid affecting lizard behavior, the observer remained out of sight of the lizard, but was able to observe the animal through a mirror mounted above the arena. All lizard responses in relationship to the approaching decoy were recorded using an overhead digital video camera (Sony HDR-CX550). I noted (1) the first reaction of the focal animal when it noticed the approaching decoy, (2) whether or not it escaped into a refuge, and (3) the distance to the decoy at which a lizard initiated its escape. All trials were done during the normal activity periods of the lizards (9:00-16:00) while the temperature was kept at between 21-25℃. Lizard body temperature was measured before each trial was used as a covariate in the analyses.

We conducted this experiment for 20 individuals (10 females and 10 males) from each of the 10 study sites (Three high cat density sites, three high cat density sites and four islets). Each lizard was tested one trial per day for three consecutive days.

RESULTS

1. Site comparisons

The vegetation type on the study islets was in general similar to the correspondin sites on Naxos. However, islet habitats tended to be more open and had fewer walls. Since the fauna and flora composition of the islets was not comparable to Naxos sites, which in turn affected food availability, predator numbers, availability of refuge, diseases etc., I did not compare lizard population densities between Naxos and the islets.

Both vegetation structure and arthropod biomass did not differ between High Cat Density (HCD) and Low Cat Density (LCD) sites. I also did not find significant differences in canopy cover (Mann-Whitney U test, Z=-0.222, *p*=0.436, n=27), understory coverage (Mann-Whitney U test, Z=-0.808, *p*=0.863, n=27), understory biomass (Mann-Whitney U test Z=-0.697, *p*=0.486, n=27), and mean arthropod biomass (Mann-Whitney U test, Z=-0.605, *p*=0.545, n=27) between these two kinds of sites (Table 3). Lastly, there were no differences in the structure of the refugia present, with dry stone wall heights not differing significantly between high and low density cat sites (HCD vs. LCD sites: 102.1±9.35cm vs. 91.1±4.66cm; Mann-Whitney U test, Z=-.751, p=0.489, n=27).

We documented significant differences in the number of cats between HCD and LCD sites, with a 1.63±0.25 cats seen on average cumulatively over the course of the three survey nights for HCD sites; in contrast no cats were ever detected during the corresponding surveys at the LCD sites (Mann-Whitney U test, *Z*=-5.802, *p*<0.001, n=27). Nonetheless, the absence of cat observations during the night surveys should not be interpreted as complete absence of cats from LCD sites as cats are notorious for being both cryptic and persisting at very low densities. Underscoring this point, a single cat was observed once at one LCD site (Moni) during regular daytime fieldwork hours. No cats were ever observed on the islet sites. In contrast to LCD sites, islets can be assumed to be cat free, being too small and too isolated to support even single cats.

2. Lizard population density

The survey results of lizard population density were highly repeatable across three visits of each site. There was no significant difference between the three measurements (χ^2=2.800, df=2, p=0.247, Friedman Test) and the results of individual surveys were highly correlated (e.g. between first and second survey: r=0.767, p<0.01, n=18, Pearson). I found significant differences in lizard population densities between high and low cat density sites. At low cat density sites lizard densities were 110.8% higher than at high cat density sites (10.32±1.29 individuals/100m of wall vs. 4.90±1.10 individuals/100m wall in high density cat density sites; Mann-Whitney U, Z=-2.475, p=0.013, n=27). Across all sites, lizard density was negatively correlated with cat density (r=-0.54, *p*=0.021, n=18, Spearman).

Lizard population density was positively related to wall height, though I detected a significant interaction between wall height and cat presence. Whereas in low cat areas lizard densities rose with increasing wall height (r=0.692, *p*=0.039, n=9, Pearson), in high cat areas, lizard densities remained low independently of wall height (r=0.049, *p*=0.900, n=9, Pearson, Fig. 2).

Lizards' use of space was associated with presence of cats. In particular, closeness of association with dry stonewalls, which constitute important refugia for *P. erhardii*, co-varied with the occurrence of cats. A significantly higher proportion (86.67%±6.49%) of lizards living in HCD areas was seen on walls compared to lizards found at LCD sites (51.18%±4.87%)(Mann-Whitney U, Z=-2.475, p=0.013).

3. Anti-predator behaviors

3.1.a Autotomy Rates - Field

While a higher fraction of lizards encountered in HCD sites had autotomized tails relative to those living in LCD or islet sites, this relationship was not significant (p>0.1), except in the case of female lizards where it approached significance (χ^2= 5.561, df=2, p=0.061, Kruskal-Wallis).

3.1.b Autotomy rates - Laboratory

Caudal autotomy rates measured in the lab differed significantly between lizard populations living under divergent cat predation regimes. In particular, the stronger the presence of cats in a population, the more easily lizards from that population shed their tails during standardized predation simulation trials (see Fig. 3) (one-way ANOVA, *p*<0.001; p<0.05 for all post-hoc comparison pairs, Tukey). Thus, autotomy rates in LCD and in HCD areas were respectively 47.2% and 164.4% above those observed in lizards from the cat-free islets. There duration of post-autotomy movement was significantly shorter for HCD sites (225.1±63.7s) than for LCD (302.0±18.3s) and islets (318.3±25.8s) (one-way ANOVA, F=8.194, *p*=0.001; Dunnett's C post-hoc test: p<0.05 between HCD and the others; p>0.05 between other pairs).

3.2. Field Flight Initiation Distances

Fear behaviors measured in the field also differed significantly between the three types of predation regimes. At all sites, flight initiation distance (FID) significantly correlated to the distance the lizard had to cover to reach its hiding place (refuge distance, RD) though the strength of this relationship varied between predation regimes (No Cats: r=0.311 n=145, p<0.001; LCD: r=0.192 n=131, p<0.028; HCD: r=0.402 n=101, p<0.001; Pearson)(Fig. 4). There were significant differences between the three predation regimes both for RD (One-way ANOVA, F=18.208, p<0.001), as well as

FID (One-way ANOVA, F=31.257, $p<0.001$)(Fig 4.). Post-hoc tests indicated that in both the cases of FID and RD, all three categories differed significantly from each other ($p<0.05$, Dunnett's C)(Fig. 5a, 5b). Thus lizards from HCD sites tended to stay closer to refugia and had greater FID than lizards from LCD sites, and this trend was even more pronounced when compared to lizards from islet populations.

4. Cat predation experiment

4.1 Flight Initiation Distance (FID)

During standardized laboratory predation simulation trials I found that lizard responses (average 3-trial FID) to an approaching cat decoy were significantly associated with the prevailing predation regime at their site of origin (One-way ANOVA, F=10.022, $p<0.001$). Hence, lizards from high cat density areas had significantly bigger FIDs than lizards living under either one of the other predation regimes; however there were no significant differences between LCD and no predation (islet) sites ($p<0.05$ between HCD sites and the other two, $p>0.05$ between LCD sites and islets; Dunnett's C post-hoc tests, Fig.6). Lizard FIDs increased progressively over the course of the study (One-way ANOVA, F=6.522, $p=0.002$, Fig. 7). FIDs in the first trial were significantly shorter than those in second and third trials ($p<0.05$, Dunnett's C post-hoc test) although the differences between the second and the third trial were not significant ($p>0.05$, Dunnett's C post-hoc test).

4.2 Escape behaviors

During the cat predation simulations, in addition to FIDs, I also scored two other aspects of predator-relevant behavior. First, I recorded the number of times that a lizard sought refuge when encountering a cat decoy over the course of three trials. Significant differences existed between lizards originating in different predation environments with fewer lizards from islet populations seeking a refuge relative to LCD or HCD sites (one-way ANOVA, F=7.365, $p=0.001$)(Fig. 8). While 78.3% of lizards from HCD and 80.0% of LCD used the provided refugia at least once over the course of three predator simulation trials, only 51.3% of the lizards from islets did so (island lizards vs LCD or HCD $p<0.05$; LCD vs HCD $p>0.05$, Dunnett's C post-hoc test). In the first trials only 28.1% of individuals used the refuge, which was lower than the second and third trials with 37.1% and 37.3% of individuals respectively. However, there was no significant difference between trials (one-way ANOVA, F=2.671, $p=0.07$).

Second, a substantial fraction of lizards instead of fleeing, moved towards the approaching decoy. I scored the number of times that a lizard approached the decoy over the course of the three cat predation simulation trials. I detected pronounced differences in this approach behavior between lizards coming from different predation regimes (one-way ANOVA, F=13.886, $p<0.001$; Dunnett's C post hoc test: $p<0.05$ for all pairs)(Fig. 9). Lizards from lower predation regimes approached a cat decoy more frequently than those from higher predation regimes. Thus, a higher fraction of lizards from LCD sites approached the mounted decoy at least once relative to lizards from High Cat density sites; this tendency was even more pronounced among lizards originating on the islets (35.0% HCD vs. 64.4% LCD vs. 75.7% from the islets). I found that 24% of the individuals in the first trial, 25% in second trial and 28% in the third trial showed approach behaviors when pooling the data of HCD, LCD and islets. However, there was no significant difference among the three trials (one-way ANOVA, F=2.671, $p>0.05$).

4.3 Rapidity of loss of anti-predator behavior

Lizards from predator-free Mando Isl., which was separated from Naxos only five years ago, offer an opportunity to evaluate the rapidity with which antipredator behaviors are being lost. FIDs of Mando lizards were significantly different from islets populations and were more similar to Naxos populations (one-way ANOVA, F=30.817, $p<0.01$, Mando vs. Other Islets, $p<0.05$; Mando vs. LCD or HCD, $p>0.05$; Dunnett's C post-hoc test). In contrast, lab autotomy rates of Mando lizards were more similar to those of other islets rather than any of the Naxos' populations (Fig. 10-11).

DISCUSSION

My comparison of HCD and LCD sites demonstrated that cat presence is associated with both reduced densities of lizard populations, as well as increased anti-predator behaviors. In contrast, there was no significant difference between LCD and HCD sites on Naxos in terms of understory coverage, understory biomass, canopy cover, arthropod biomass or wall height, all of which are thought to be important ecological determinants of lizard density.

Cats were found almost exclusively around human habitations (<1 km radius). Impromptu field observations suggest that while some cats were fed by their owners, others had to fend for themselves via regular visits to village garbage bins. In either case, most cats, whether fed or not, will hunt size-appropriate wildlife if given the opportunity, and we witnessed on several occasions cats preying on wall lizards. Although I never observed cats far away from human habitations, one cannot assume that Naxos predation pressure on lizards away from villages is negligible. While feral cats are known to be both cryptic and to roam widely, they have been shown to affect prey populations significantly even at low densities (Peck *et al.*, 2008). In addition, there are other native predators, such as stone martens (*Martes foina*) or aerial predators, which although rare, have the potential to affect lizard populations. Although reptiles constitute only a relative small proportion of the diet of feral cats on Mediterranean islands compared to small mammals and birds (Bonnaud *et al.*, 2010; Medina & Nogales, 2008), in this study I found that the focal species was still significantly impacted by cats. Overall, HCD areas had on average less than half the wall lizard density of LCD sites despite being otherwise ecologically indistinguishable, thus highlighting the ability of cats to suppress lizard populations.

My study also reveals that dry-stone walls act as important predation avoidance sites for lizards. In areas with cats, lizards tended to stay on, or in the immediate vicinity, of dry-stone walls. Because of their complex three-dimensional structure, dry-stone walls act as refugia from predation, and possibly also as areas that facilitate thermoregulation. Both in HCD or LCD sites, I found a strong association of lizards with walls as they sought walls as basking sites and refugia. However, relative to LCD sides I recorded in HCD sites a much higher proportion of lizards that stayed on walls *per se* rather than on the ground or in bushes near walls. Wall height was positively correlated with lizard population density at LCD but not at HCD sites (Fig. 2). Thus at HCD sites, even at relatively high walls, lizard density never rose past a thresh hold density of approx. 10 liz./100m. of wall. This suggests that cats were capable of killing lizards and depressing their densities to a certain thresh hold no matter how high a wall was. Consequently, dry-stone walls are best viewed as critical, though incomplete refugia from cat predation for lizards. As a matter of fact, during fieldwork we witnessed a feral cat successfully attack and kill a lizard that had ventured only 20 cm away from the base of such a wall.

In addition to altering lizard densities and use of the landscape, cats also had strong effects on lizard antipredator behaviors. Lizards at HCD sites had longer FIDs and a strongly elevated ease of caudal autotomy. Furthermore, in line with other studies (Perez-Mellado *et al.*, 1997; Pafilis *et al.* 2009), I found that all populations from Naxos shed their tails more easily than the islet populations living under relaxed predation conditions. While the high tail loss rate can help lizards avoid the predation of cats, this defense is also energetically expensive and can impact territorial protection, social status, reproduction, and effective thermoregulation (Pafilis *et al.*, 2005; Perez-Mellado *et al.*, 1997; Ballinger *et al.*, 1979; Punzo, 1982; Martin & Salvador, 1993a, 1993b, 1993c; Salvador *et al.*, 1996). The inability to deploy the tail as an anti-predator mechanism and the reduction in locomotory ability (Perez-Mellado *et al.*, 1997; Daniels, 1983; Brown *et al.*, 1995; Formanowica *et al.*, 1990) represents additional costs. Interestingly, while the differences in laboratory autotomy rates were quite pronounced between lizards from the three different predation regimes, the corresponding rates in field autotomy rates were not statistically significant. This was because islet lizards had more autotomized tails in the field than what would one predict based on their general inability to shed their tail during staged laboratory autotomy trials. My field observations shed light on this unusual pattern. Whereas predation pressure is essentially absent in small but high-density islet populations, I did regularly witness lizards attacking each other's tails during intra-specific acts of aggression. On several occasions this lead to autotomy, in which case the autotomized tail was consumed. This means that this phenomenon of intra-specific parasitism is most likely responsible for the unexpectedly high autotomy rates observed in islet populations.

While field experiments indicated that FIDs on islets were significantly smaller than on Naxos, this pattern was less pronounced in the laboratory trials. In reality there are multiple aspects in the pattern of activity beyond FIDs of islet lizards that render them very susceptible to cat predation. Islet lizards roam further away from refugia than mainland Naxos animals, which means they are more likely to never reach them during an encounter with a predator. As a matter of fact, about 50% of islet lizards did not even seek a refuge during at least one of the predation encounters. Furthermore, almost 80% of all islet lizards actually first approached the moving cat decoy before fleeing. This unusual neophilic behavior is also evident in the field where islet lizards will quickly investigate all new objects placed into their territory. This is best explained by the fact that on small islets, lizard population densities are very high and animals are constantly in the process of searching for food items. In general, the lack of fully developed escape behaviors, as well as the inability to recognize new predators as threats, makes islet populations very susceptible to invasive cats.

Despite the general lack of effective antipredator behaviors in relaxed-predation environments, my cat predation trials suggest that escape behavior is plastic and can be re-acquired through repeated exposures. Lizards from all three types of predation regimes increased their FIDs between first and third exposure to a cat decoy (Fig. 7). This increase was most pronounced in the islet group where FIDs more than doubled and rose by the third trial to the baseline levels of the HCD lizards. This plasticity in anti-predator behavior is important from a conservation perspective as it shows that lizards can learn to recognize and avoid introduced predators, especially if given the benefit of multiple encounters. It also suggests that predator avoidance training programs for endangered lacertids are likely to be successful. Such programs, used in endangered taxa or captive species slated for re-introductions have taught animals to recognize predators and to enhance their initially low-level anti-predator responses in order to bolster their probabilities of survival in nature (Miller *et al.*, 1994; Maloney & Mclean, 1995; McLean *et al.*, 1996; Griffin *et al.*, 1999).

Whereas the laboratory predation trials reveal the ability of lizards to quickly regain fear behaviors, a comparison of the lizards from Mando Isl. also highlights the ease with which such behaviors can also be lost. Mando lizards became isolated from larger Naxos only about five years ago and have been living in a predator-free environment only for this short period of time. While FIDs of these animals, still resemble those of nearby Naxos, tail autotomy rates already approach those of the islets (Fig. 11). This disjunction between different anti-predator responses reflects predictions from evolutionary theory which postulates that in the face of relaxed predation, energetically ‘expensive’ behaviors such as caudal autotomy will be lost much sooner than ‘cheap’ behaviors like longer FIDs (Maloney & McLean, 1995; Blumstein & Daniel, 2005; Beauchamp, 2004; Berger *et al.*, 2007).

In summary, the results of this study indicate that expression of lizard antipredator behaviors closely mirrors the severity of local predation pressure. They also reveal that feral cats are important predators to island lizards and are able to severely depress lizard populations despite a broad suite of antipredator behaviors that these animals deploy. The efficiency of cat predation in combination with the general absence of effective antipredator behaviors in small islet lizards indicates that these populations are extremely susceptible to feral cats and will likely disappear rapidly if cats are introduced there. As a result, if native reptile populations are to survive, Mediterranean island ecosystems need to me managed in a manner that prevents the introduction of novel predators to them.

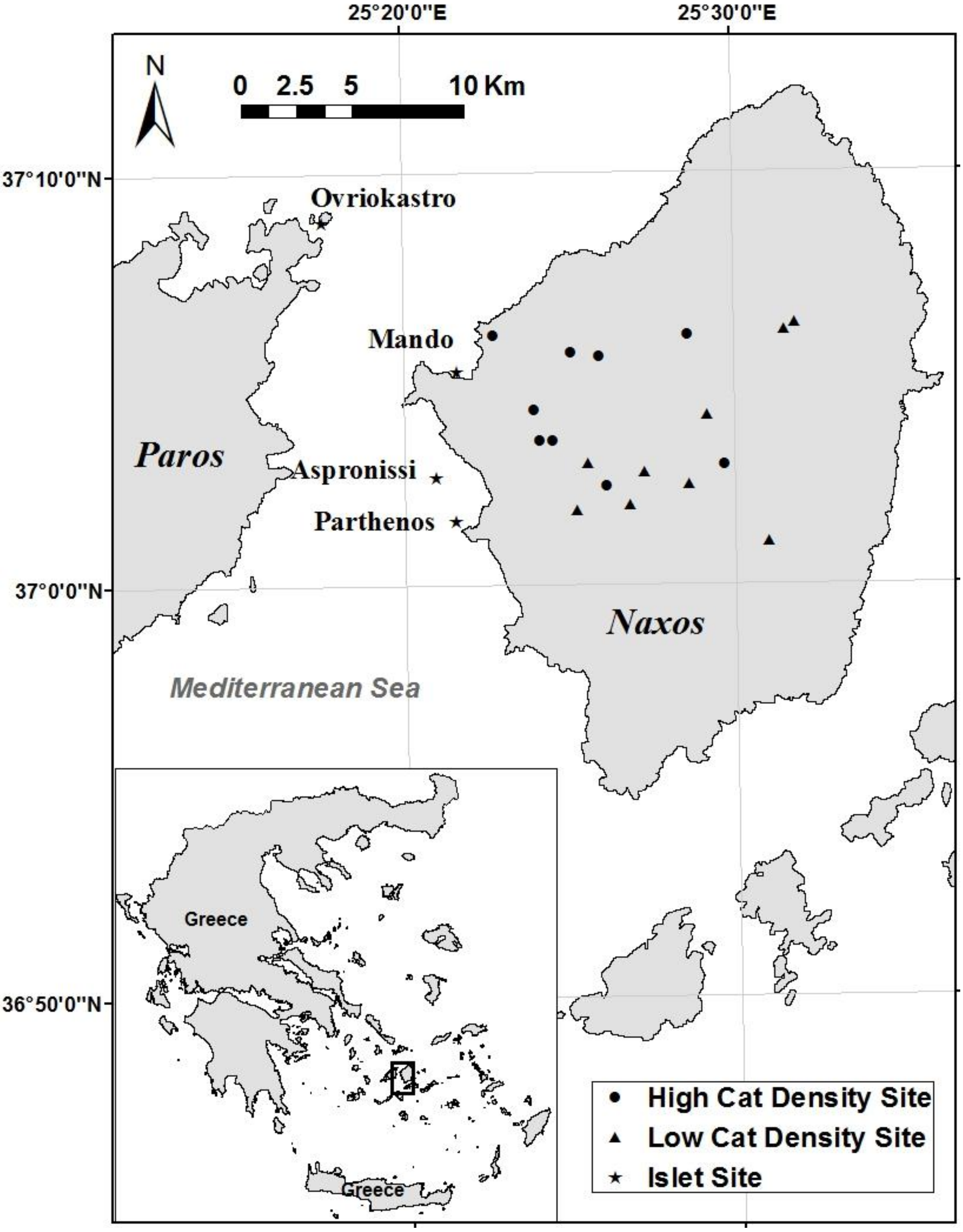

Fig. 1 Map of the study area (Naxos and surrounding islets, Cyclades Cluster, Greece). High cat density sites are indicated with triangles, Low cat density sites with round dots and Islets with stars.

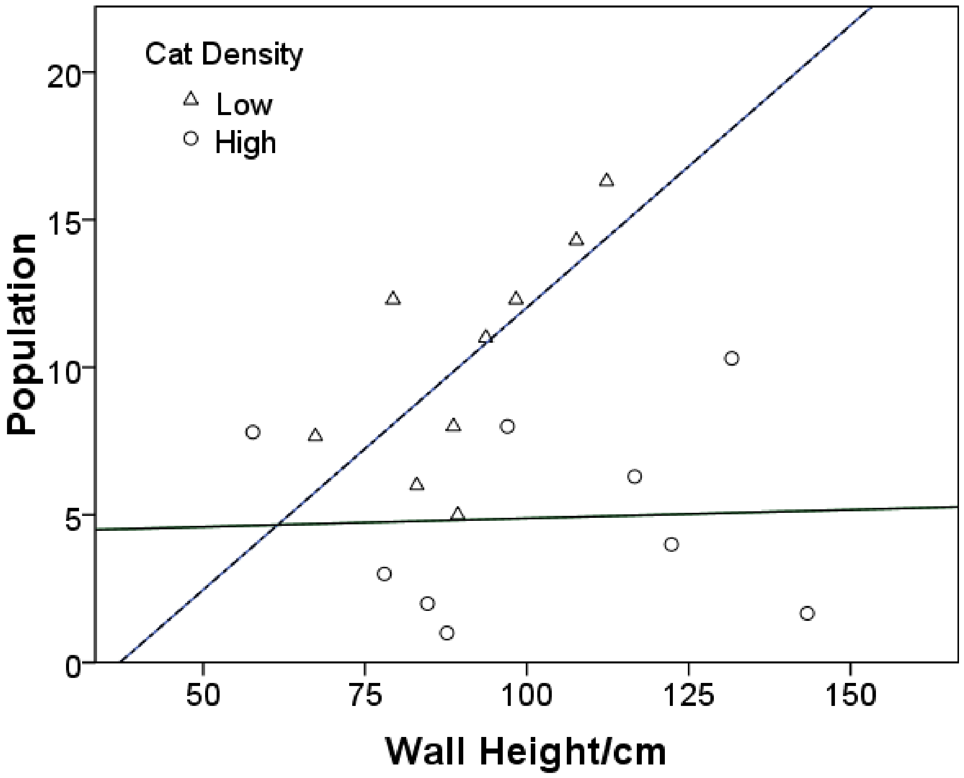

Fig. 2 The correlation between wall height and lizard population. The population in low cat density sites showed a positive correlation with wall height while lizards found in high cat density environments did not show the same trend.

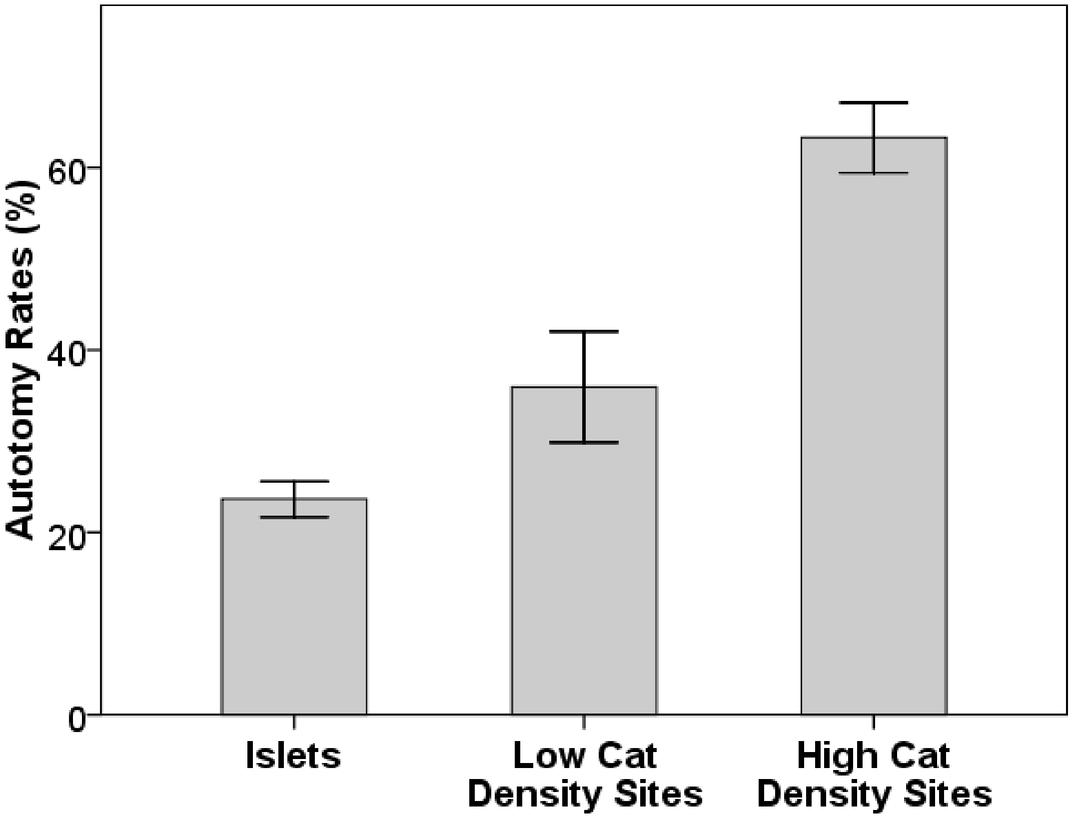

Fig. 3 Laboratory autotomy rates, expressed as percent of animals in a population that shed their tails. Data pooled for all lizard populations living under the same predation regimes. (Mean ±2SE).

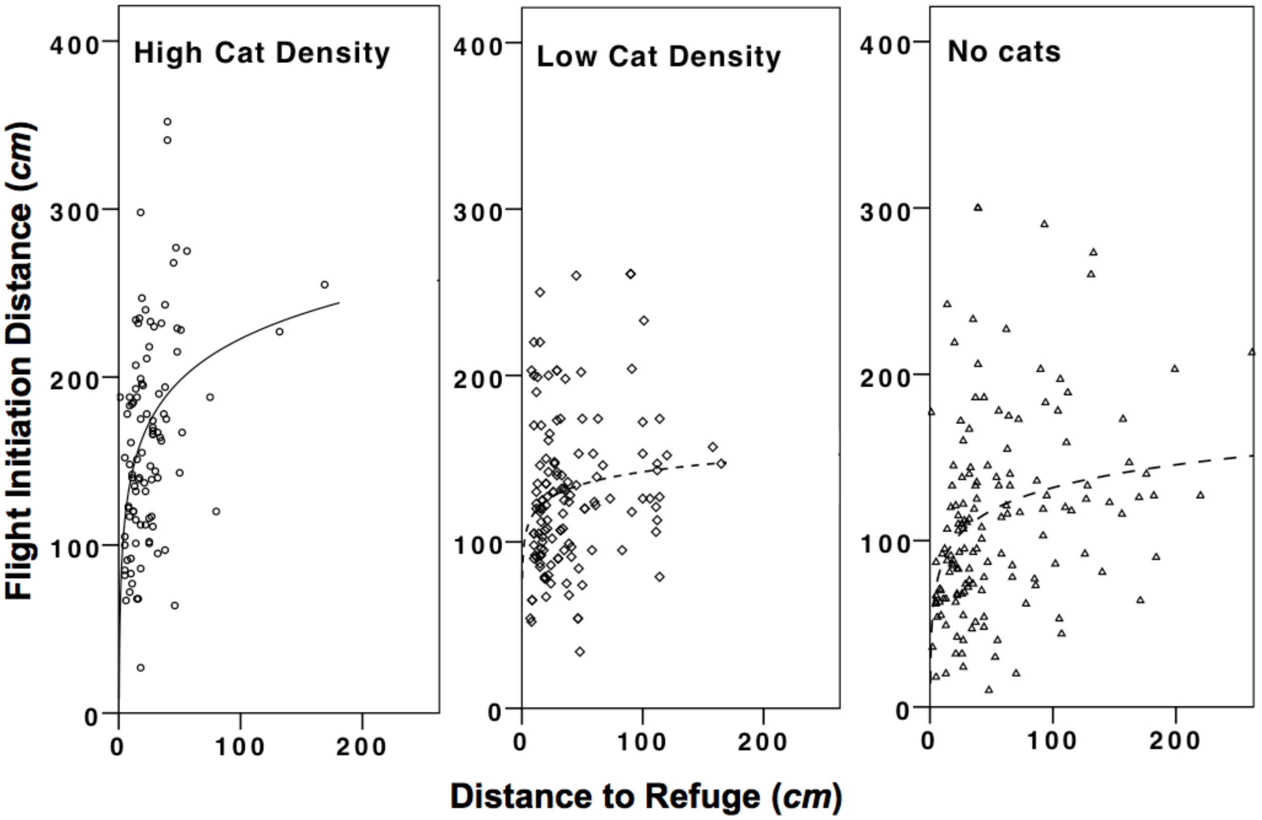

Fig. 4 The pattern between Flight Initiation Distance and Refuge Distance for HCD sites, LCD sites and Islets (No cats). Logarithmic curves fit the data best, and are shown in the figures.

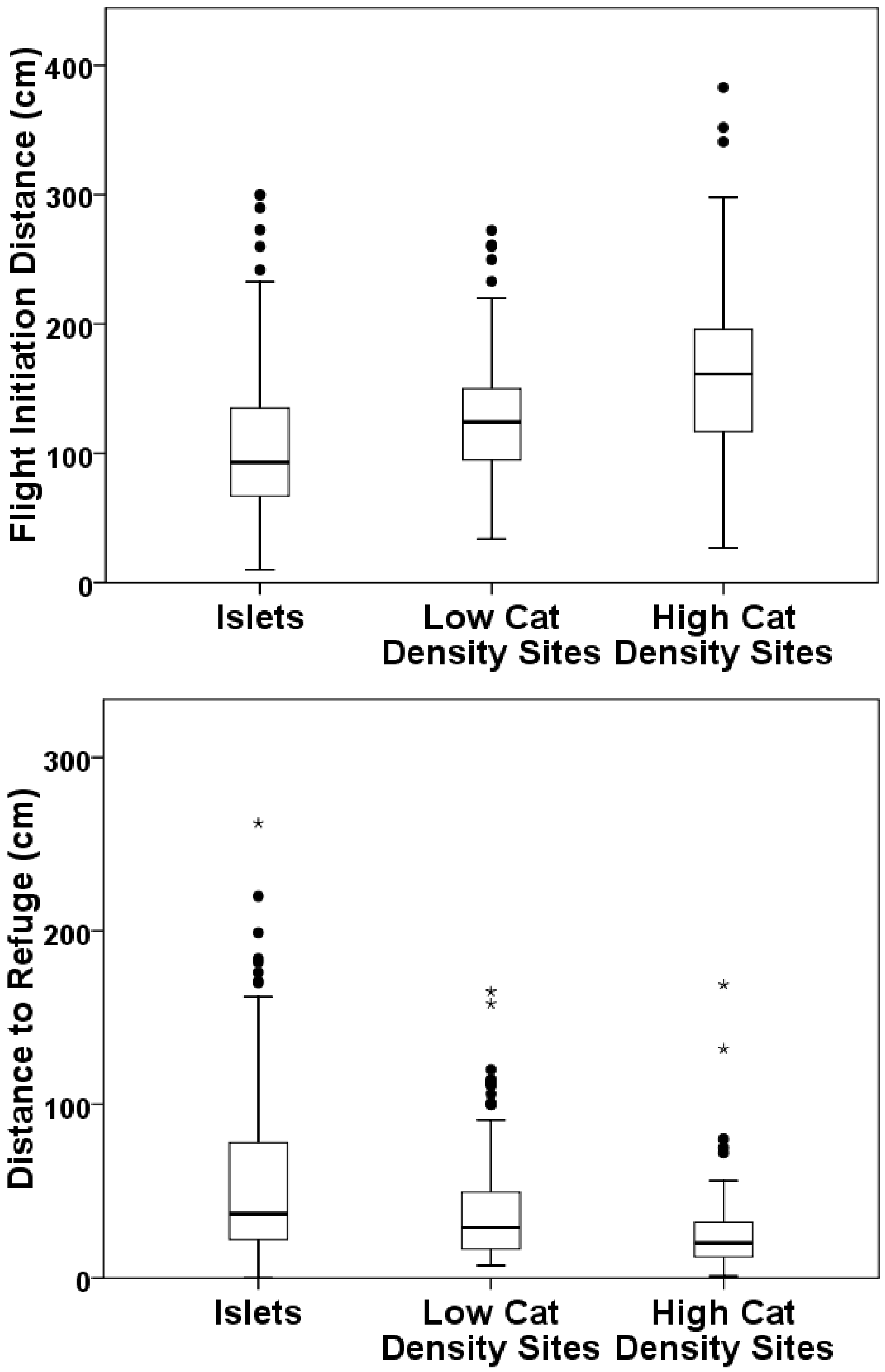

Fig. 5 Box plots of Flight Initiation Distance (a) and Refuge Distance (b) based on field observations.

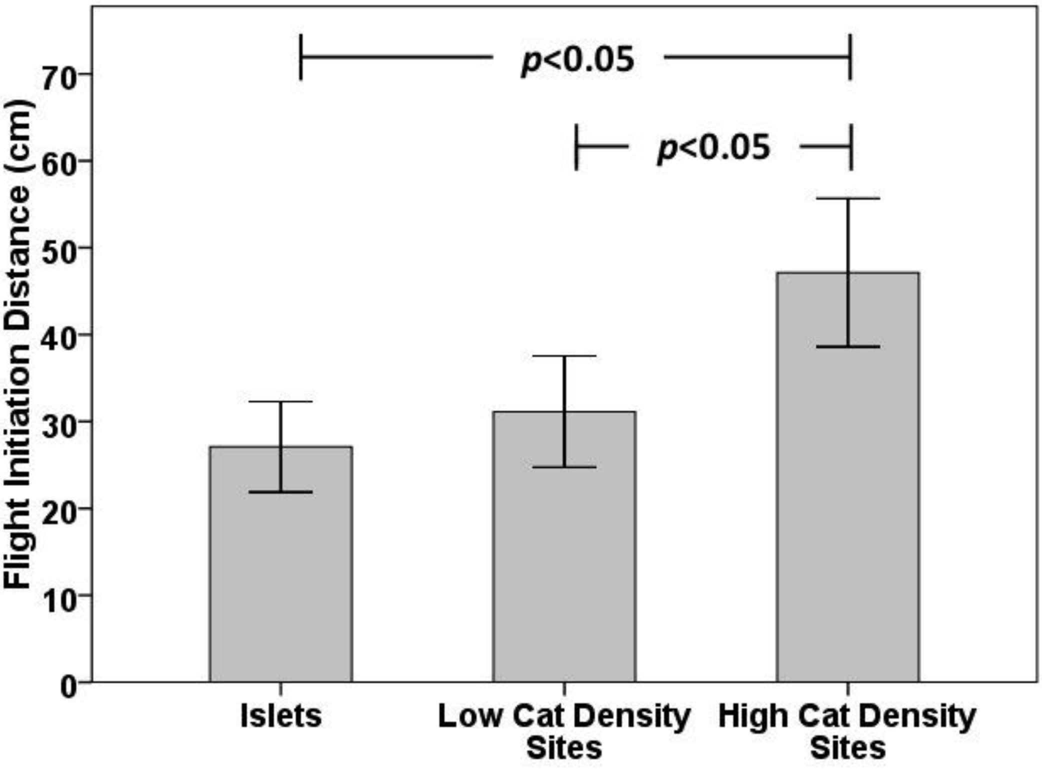

Fig. 6 Flight Initiation Distance (FID) to a simulated predation event. Bars represent means ±2SE. Only significant post-hoc test differences ($p<0.05$) are identified.

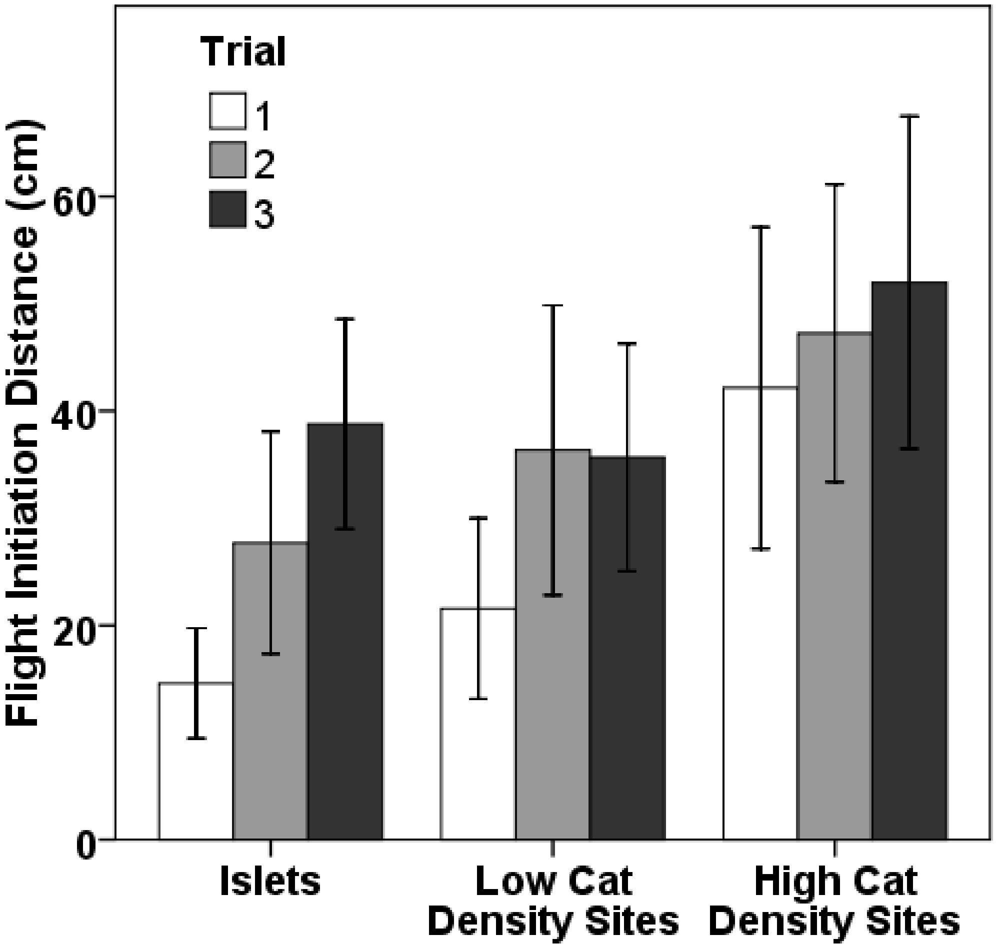

Fig. 7 Flight Initiation Distance (FID) for three trials of a cat predation simulation. Figure shows means for each trial ± 2SE.

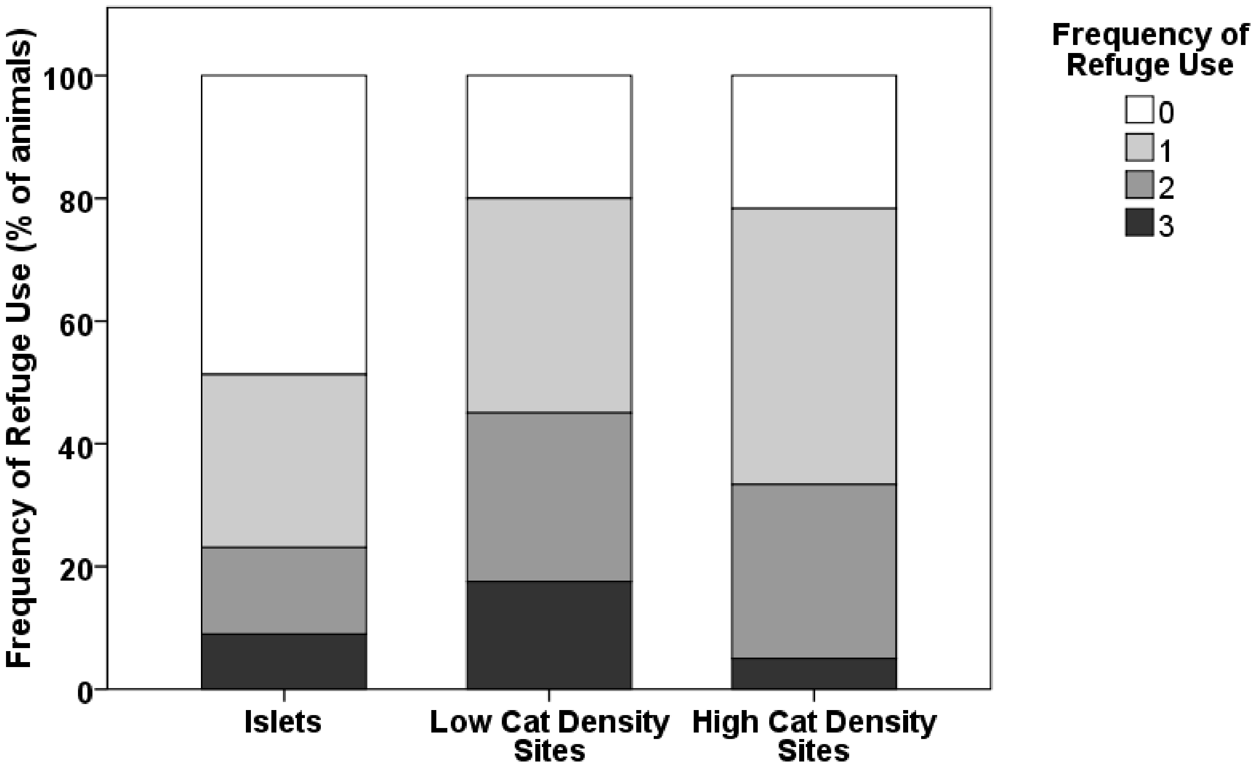

Fig. 8 The percentage of the frequency to use refuge across the three trials of the laboratory cat predation experiment.

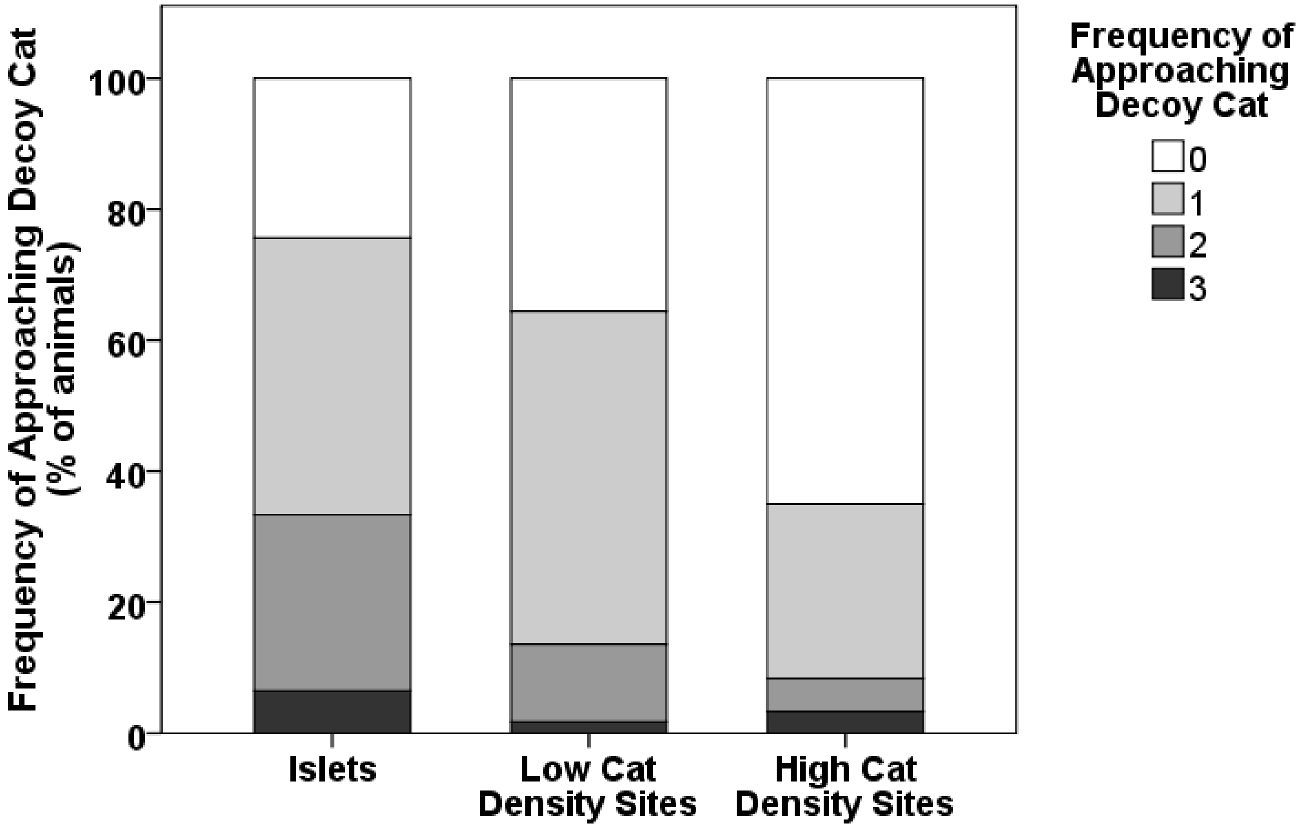

Fig. 9 The percentage of the frequency of approach behavior over the course of the three predation simulation trials.

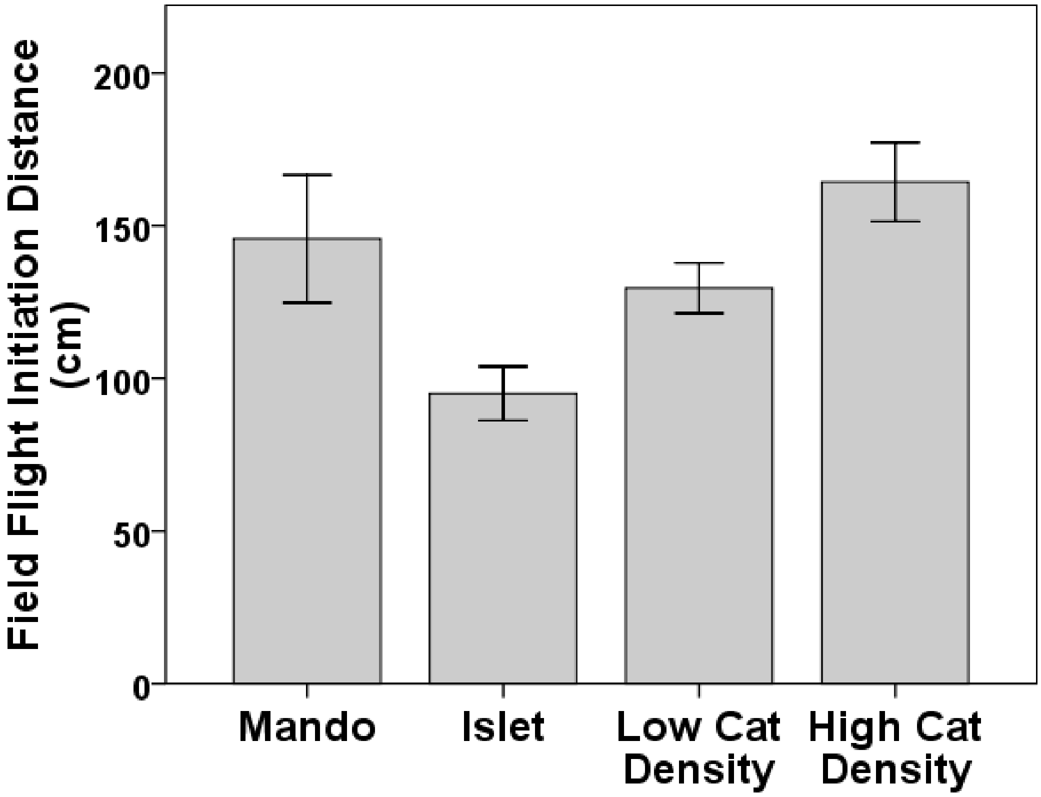

Fig. 10 Comparison of field Flight initiation distance between Mando Isl., other islets, and low cat density and high cat density sites.

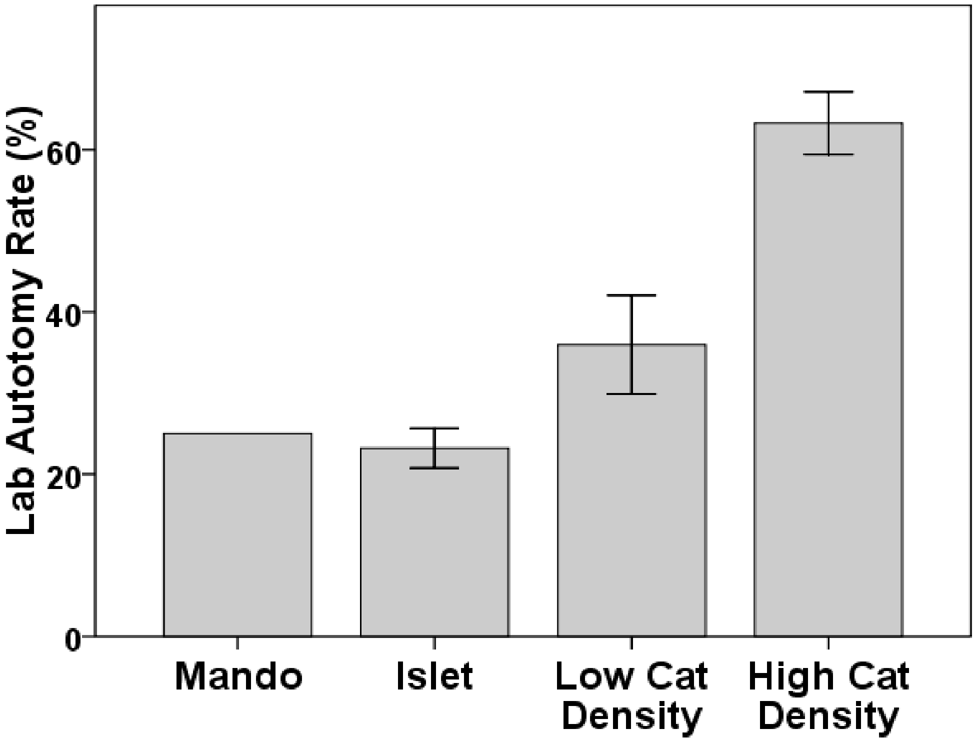

Fig. 11 Comparison of field Flight initiation distance between Mando, other islets, low cat density and high cat density sites.

Table 1. Geographic information for islets sampled

Island name	GPS Location		Area (km^2)	Maximum Island Elevation (*m*)	Distance from closest landmass (*m*)	Maximum Water Depth (*m*)	Duration of isolation (*yr*)
	North	West					
Ovriokastro	37°9.1´	25°17.7´	0.22	23	732	7.2	5,600
Aspronissi	37°2.8´	25°21.1´	0.01	6	333	11	6,100
Parthenos	37°1.7´	25°21.6´	0.004	9	116	8	5,650
Mando	37°5.3´	25°21.7´	0.025	11	20	0.4	5

Table 2. Information on physical aspects of the study sites on Naxos.

Site	Abbreviation	Elevation (*m asl.*)	GPS Location		Slope Aspect	Wall Direction
			North	West		
Low Cat Density Sites						
1. South Slope	SO	642	37°6.5´	25°32.0´	South	East to West
2. North Slope	NS	636	37°6.3´	25°31.6´	Northeast	NE to SW
3. Moni Olive	MO	304	37°4.3´	25°29.3´	0	East to West
4. Marina	MR	370	37°2.2´	27°27.1´	Northwest	NE to SW
5. Small Slope	SS	214	37°2.1´	25°26.9´	West	North to South
6. Gas Station	GS	251	37°2.9´	25°27.4´	West	North to South
7. Kanakali	KN	87	37°3.1´	25°25.7´	North	North to South
8. Halkio Olive	HA	224	37°2.6´	25°28.7´	0	North to South
9. Well	WE	170	37°2.0´	25°25.3´	North	East to West
High Cat Density Sites						
10. Glinado	GL	77	37°4.4´	25°24.1´	North	East to West
11. Filoti	FL	361	37°3.1´	25°29.8´	0	NE to SW
12. Vivlos	VI	130	37°3.7´	25°24.5´	West	North to South
13. Plantation	PL	190	37°2.6´	25°26.2´	0	East to West
14. Angidia	AG	11	37°5.7´	25°26.0´	0	North to South
15. Kinidaros	KN	433	37°6.2´	25°28.7´	West	North to South
16. Naxos	NA	95	37°6.4´	25°22.8´	0	North to South
17. Ag. Thaleleos	AT	98	37°5.8´	25°25.2´	South	East to West
18. Vivlos 2	VI2	135	37°3.7´	25°24.6´	South	North to South

Table 3. Comparison of environmental factors in high cat density sites versus low cat density sites on Naxos (Mann-Whitney U test)**.**

	Low cat density sites	**High cat density sites**	***p* value**
Canopy coverage (%)	0.17±0.09	0.30±0.10	0.436
Understory coverage (%)	0.66±0.03	0.66±0.03	0.863
Understory biomass (g/m^2)	227.94±6.69	243.75±6.25	0.486
Arthropod biomass (g/pitfall)	4.71±1.12	4.95±0.97	0.545

APPENDICES

Appendix 1.

Site characteristics given as means ± S.E.

Site name	Wall Height (cm)	Canopy Cover (%)	Understory Coverage (%)	Understory Biomass (g/0.16m^2)	Arthropods Biomass (g/pitfall)	Cat Density (cats/km)	Lizard density (lizards/100m wall)
LCD sites							
South Slope	112.3 ±4.1	0.43±0.03	0.83±0.03	52.61±8.41	7.166±3.627	0	16.3±1.2
North Slope	79.3±9.4	0.67±0.13	0.57±0.12	22.23±7.54	8.663±6.542	0	12.3±0.7
Moni Olive	107.7±3.3	0.67±0.13	0.07±0.07	1.90±1.01	0.164±0.060	0	14.3±1.2
Marina	83.0 ±12.5	0.27±0.03	0.30±0.06	10.17±5.54	1.061±0.690	0	6.0±1.0
Small Slope	67.3 ±11.8	0.00±0.00	0.73±0.03	22.30±6.40	0.607±0.274	0	7.7±0.3
Gas Station	88.7± 7.8	0.03±0.03	0.97±0.03	46.26±12.20	11.304±2.433	0	8.0±1.0
Kanakali	93.7 ±1.2	0.07±0.07	0.97±0.03	54.98±5.05	5.642±2.008	0	11.0±2.1
Halkio olive	98.3±8.5	0.53±0.09	0.57±0.12	46.43±2.74	0.286±0.097	0	12.3±0.7
Well	89.3±8.1	0.00±0.00	0.90±0.06	71.39±7.66	7.526±2.665	0	5.0±1.2
HCD sites							
Glinado	116.7±15.3	0.03±0.03	0.70±0.06	40.31±5.57	1.759±0.514	1.3±0.9	6.3±1.2
Filoti	97.0±5.7	0.70±0.06	0.33±0.03	25.89±5.59	0.670±0.699	3.7±0.9	8.0±2.9
Vivilos	57.7±5.0	0.03±0.03	0.93±0.03	54.10±3.35	2.273±1.220	1.7±0.3	7.8±0.3
Plantation	78.0±3.2	0.03±0.03	0.90±0.06	46.17±13.37	4.467±2.011	2.3±0.9	3±0.6
Angidia	84.7±9.9	0.07±0.07	0.53±0.07	47.92±14.66	21.796±13.666	0.7±0.3	10.3±1.8
Kinidaros	122.3±3.7	0.00±0.00	0.97±0.03	64.20±7.47	2.985±1.006	0.7±0.3	4.0±1.5
Naxos	87.7±3.8	0.00±0.00	0.73±0.03	36.80±2.25	4.776±1.789	1.7±0.3	1±0.6
Ag.Thaleios	131.7±7.3	0.03±0.03	0.47±0.09	30.53±2.42	3.613±0.335	2.3±0.3	2±0.6
Vivlos 2	143.3±12.0	0.60±0.06	0.37±0.07	5.12±1.10	0.820±0.385	0.3±0.3	1.7±1.2

Appendix 2.

Behavioral data and antipredator defenses in the field and in the laboratory. Field autotomy rates were quantified as the fraction of individuals with autotomized tails observed in the field, while laboratory autotomy rate was the fraction of individuals that shed their tails during a standardized autotomy test. Refuge use and approach behaviors in the cat experiment were recorded as mean percentage of refuge use or approaches towards the decoy over the course of three trials.

name	Field FID (cm)	Field RD (cm)	Field Autotomy Rate (fraction)	Laboratory Autotomy Rate (fraction)	Cat Experiment-FID (cm)	Cat Experiment-Refuge Use (%)	Cat Experiment-Approaching (%)
LCD sites							
South Slope	137.0±8.7	30.2±3.1	0.268	0.357	28.6±6.1	0.472±0.059	0.271±0.058
North Slope	119.9±5.8	37.8±4.5	0.100	0.300	24.6±5.0	0.400±0.064	0.200±0.052
Moni	131.4±4.1	60.5±7.7	0.360	0.400	40.2±5.5	0.550±0.065	0.333±0.061
HCD sites							
Glinado	171.5±15.3	27.8±5.4	0.300	0.632	51.5±7.6	0.333±0.061	0.250±0.056
Filoti	155.7±7.1	25.8±3.7	0.571	0.667	38.4±6.9	0.467±0.065	0.133±0.044
Vivɨlos	168.0±62.2	26.1±15.6	0.308	0.600	51.5±7.7	0.367±0.063	0.083±0.036
Islets							
Aspronissi	111.4±7.5	43.4±6.4	0.228	0.256	18.0±4.5	0.267±0.058	0.300±0.060
Ovriokastro	123.6±9.8	46.6±7.7	0.217	0.222	13.2±3.1	0.067±0.032	0.300±0.060
Parthenos	68.7±4.3	47.8±6.0	0.146	0.217	38.1±6.1	0.283±0.059	0.450±0.065
Prokopios	145.7±10.5	89.6±10.9	0.256	0.250	40.6±5.7	0.519±0.069	0.500±0.069

BIBLIGRAPHY

Arianoutsou M., P. Delipetrou, P. Dimopoulos, P. Konstantinidis, E. Economidou & G. Tsiourlis. 1997 Habitat types in Greece. In: *The Greek "Habitat" project Natura 2000: An overview* (ed. Daphis S. et *al.*), pp. 402 - 434.

Arnold E. N. 1988 Caudal autotomy as a defense. In: *Biology of the Reptilia. Vol. 16. Ecology B: Defense and Life History* (ed. C. Gans & R.B. Huey), pp. 235–273. New York.

Atkinson I. A. E. 2001 Introduced mammals and models for restoration. *Biol. Conserv*. **99**: 81-96.

Avery R. A. 1974 Storage lipids in the lizard *Lacerta vivipara*: a quantitative study. *J. Zool. (London)* **173**: 419–425.

Baillie, J. E. M., Hilton-Taylor, C. & Stuart, S.N. (ed.) 2004 2004 IUCN Red List of Threatened Species. A Global Species Assessment. IUCN, Gland, Switzerland and Cambridge, UK. xxiv + 191 pp.

Ballinger, R.E., Nietfeldt, J**.**W. & Krupa, J. J. 1979 An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). *Herpetologica* **35**: 114 - 116.

Beauchamp, G. 2004 Reduced flocking by birds on islands with relaxed predation. *Proc. R. Soc. Lond. B.* **271**: 1039-42.

Berger, S., Wikelski, M., Romero, L. M., Kalko, E. K. V., & Rödl, T. 2007 Behavioral and physiological adjustments to new predators in an endemic island species, the Galápagos marine iguana. *Horm. Behav*. **52**: 653-63.

Blumstein, D. T. 2002 Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *J. Biogeography*. **29**: 685-692.

Blumstein, D. T. & Daniel, J. C. 2005 The loss of anti-predator behaviour following isolation on islands. *Proc. R. Soc. Lond. B.* **272**: 1663-1668.

Blumstein, D. T., Daniel, J. C., & Springett, B. P. 2004 A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethol*. **110**: 919-934.

Bonnaud, E., Bourgeois, K., Vidal, E., Kayser, Y., Tran-chant, Y. & Legrand, J. 2007 Feeding ecology of a feral cat population on a small Mediterranean island. *J. Mammal.* **88**: 1074-1081.

Bonnaud, E., Medina, F. M., Vidal, E., Nogales, M., Tershy, B., Zavaleta, E., C.J. Donlan, B. Keitt, M. Le Corre, S.V. Horwarth. 2010 The diet of feral cats on islands: a review and a call for more studies. *Biol. Invasions.* **13**: 581-603.

Brown, R. M., Taylor, D. H. & Gist, D. H. 1995 Effect of caudal autotomy on locomotor performance of wall lizards *(Podarcis muralis). J. Herpetol.* **29**: 98-105.

Byers, J. A. 1997 *American pronghorn: social adaptations and the ghosts of predators past.* University Chicago Press, Chicago.

Coman, B. J. & Brunner, H. 1972 Foods habits of the feral house cat in Victoria. *J. Wildl. Manage.* **36**: 848-853.

Cooper, W. E. 2009 Optimal escape theory predicts escape behaviors beyond flight initiation distance: risk assessment and escape by striped plateau lizards (*Sceloporus virgatus*). *Curr. Zool.* **55**: 123-131.

Coss, R. G. 1999 Effects of relaxed natural selection on the evolution of behavior. Geographic variation in *behavior: perspectives on evolutionary mechanisms* (ed. S.A. Foster and J.A. Endler), pp. 180–208. Oxford University Press, Oxford.

Cox, N., J. Chanson & S. Stuart. 2006 *The status and distribution of reptiles and amphibians of the Mediterranean Basin.* International Union for Conservation of Nature, Gland, Switzerland.

Daniels, C. B. 1983 Running: an escape strategy enhanced by autotomy. *Herpetologica.* **39**: 162-165.

Daniels C. B. 1984 The importance of caudal lipids in the gecko *Phyllodactylus marmoratus*. *Herpetologica.* **40**: 337–344.

Donlan, C. J., B. R. Tershy, B. S. Keitt, B. Wood, J. A. S´ anchez, A. Wein- stein, D. A. Croll & J. L. Aguilar. 2000 Island conservation action in northwest Mexico. in *Proceedings of the fifth California Islands symposium* (ed. D. H. Browne, H. Chaney, and K. Mitchell), pp. 330-338 Santa Barbara Museum of Natural History, Santa Barbara, California.

Driscoll, B. C. A., Clutton-brock, J., Kitchener, A. C., & Brien, S. J. O. 2009 The taming of the cat. *Sci. Am.* **6:** 68-75.

Dukas, R. & Kamil, A. C. 2000 The cost of limited attention in blue jays. *Behav. Ecol.* **11**: 502-506.

Formanowicz, D. R., Brodie, E. D. & Bradley, P. J. 1990 Behavioural compensation for tail loss in the ground skink, *Scincella lateralis. Anim. Behav.* **40**: 782-784.

Forsgren, E. 1992 Predation risk affects mate choice in a gobiid fish. *Am. Nat.* **140**: 1041-1049.

Fox S.F., N. A. Heger & L. S. Delay. 1990 Social cost of tail loss in Uta stansburiana: lizard tail as status signaling badges. *Anim. Behav.* **39**: 549–554.

Garcia-Márquez, M., A. Caetana, I. Bello, L. F. López-Jurado & J. A. Mateo. 1999 Ecología del gato cimarrón en el ecosistema termófilo de El Hierro (Islas Canarias) y su impacto sobre el Lagarto Gigante (Gallotia simonyi). *Monografias de Herpetologia* **4**: 207-222.

Griffin, A. S., Blumstein, D. T., & Evans, C. S. 2000 Training Captive-Bred or Translocated Animals to Avoid Predators. *Conserv. Biol.* **14**: 1317-1326.

Hunter, L. T. B. & Skinner, J. D. 1998 Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour* **135**: 195–211.

Iverson, J. B. 1978. The impact of feral cats and dogs on populations of the West Indian rock iguana, Cyclura carinata. *Biol. Cons.* **14**: 63-73.

Kirkpatrick, R. D. & M. J. Rauzon. 1986 Foods of feral cats *Felis catus* on Jarvis and Howland Islands, central Pacific Ocean. *Biotropica.* **18**: 72-75.

Konecny M. J. 1987 Food habits and energetics of feral house cat in the Galapagos Islands. *Oikos* **50**: 24-32.

Lowe, S., M. Browne, S. Boudjelas & M. De Poorter. 2001 *100 of the world's worst invasive alien species: a selection from the global invasive species database*. Species Survival Commission, World Conservation Union, Auckland, New Zealand.

MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton University Press, Princeton.

Madn, J. & Salvador, A. 1993a T. hermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour.* **124**: 123-136.

Madn, J. & Salvador, A. 1993b Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola. Behav. Ecol. Sociobiol.* **32**: 185-189.

Madn, J. & Salvador, A. 1993c Tail loss and foraging tactics of the Iberian rock-lizard, *Lacerra monticola. Oikos.* **66:** 318-324.

Magurran, A.E. 1999 The causes and consequences of geographic variation in antipredator behavior: perspectives from fish populations. In *Geographic variation in behavior: perspectives on evolutionary mechanisms* (ed. S.A. Foster & J.A. Endler), pp. 139-163. Oxford University Press, New York.

Maloney, R & McLean, I. 1995 Historical and experimental learned predator recognition in free-living New-Zealand robins. *Anim. Behav*. **50**: 1193-1201.

McLean, I. 1996 Teaching an endangered mammal to recognize predators. *Biol. Cons*. **75**: 51-62.

McNab, B. K. 1994 Energy conservation and the evolution of flightlessness. *Am. Nat.* **144**: 628-642.

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., Keitt, B. S., Lecorre, M., Horwath, S. H., Nogales, M. 2011 A global review of the impacts of invasive cats on island endangered vertebrates. *Global. Change. Biol*. **17**: 3503-3510.

Medina, F. M., & Nogales, M. 2008 A review on the impacts of feral cats (Felis silvestris catus) in the Canary Islands: implications for the conservation of its endangered fauna. *Biodiversity Conserv.* **18**: 829-846.

Miller, B., D. Biggins, L. Hanebury, A. Vargas. 1994 Reintroduction of the black-footed ferret (Mustela nigripes). in *Creative conservation: interactive management of wild and captive animals* (ed. P. J. S. Olney, G. M. Mace, A. T. C. Feistner), pp. 455-464. London: Chapman and Hall.

Nogales, M., & Medina, F. M. 2009 Trophic ecology of feral cats (*Felis silvestris f. catus*) in the main environments of an oceanic archipelago (Canary Islands): An updated approach. *Mamm. Biol.* **74**: 169-181.

Pafilis, P., Foufopoulos, J., Poulakakis, N., Lymberakis, P., & Valakos, E. D. 2009. Tail shedding in island lizards (Lacertidae, Reptilia): decline of antipredator defenses in relaxed predation environments. *Evolution*. **63**: 1262-78.

Pafilis, P., Valakos, E. D., & Foufopoulos, J. 2005 Comparative postautotomy tail activity in six Mediterranean lacertid lizard species. *Physiol. Biochem. Zool.* **78**: 828-38.

Parejko, K. 1991 Predation by chaoborids on typical and spined Daphnia pulex. *Freshwater Biol.* **25**: 211–217.

Peck, D. R., Faulquier, L., Pinet, P., Jaquemet, S., & Corre, M. L. 2008 Feral cat diet and impact on sooty terns at Juan de Nova Island , Mozambique Channel. *Anim. Conserv*. **11**: 65-74.

Pérez-Mellado, V., Corti, C. & Lo Cascia, P. 1997 Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and mainland populations. *J. Zool. (Lond.)* **243**: 533–541.

Pray L. L. 1949 *Taxidermy,* pp. 45-61. New York : Outing publishing company.

Primack R. B. 2004 *A primer of conservation biology.* Sinauer, Sunderland, Massachusetts

Punzo, F. 1982 Tail Autotomy and Running Speed in the Lizards Cophosaurus texanus and Uma notate. *J. Herpetol.* **16**: 329-331

Read, J. & Bowen, Z. 2001 Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife. Res.* **28**: 195–203.

Reddiex, B., Forsyth, D. M., McDonald-Madden, E., Einoder, L. D., Griffioen, P. A., Chick, R. R. & Robley, A. J. 2004 *Review of existing red fox, wild dog, feral cat, rabbit, feral pig, and feral goat control in Australia.* I. Audit. Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, Melbourne.

Rödl, T., Berger, S., Romero, L. M., and Wikelski, M. 2007. Tameness and stress physiology in a predator-naive island species confronted with novel predation threat. *Proc. R. Soc. Lond. B Biol. Sci.* **274**: 577-582.

Salvador A., J. Martin, P. Lopez & J. Veiga. 1996 Long-term effect of tail loss on home-range size and access to females in male lizards (*Psammodromus algirus*). *Copeia.* **1996**: 208–209.

Serpell, J. A. 2000 Domestication and history of the cat. in *The domestic cat: the biology and its behaviour* (ed. D. C. Turner and P. Bateson), pp. 179–192. Cambridge, United Kingdom: Cambridge University Press.

Tabor, R. K. 1983 *The wild life of the domestic cat*. London: Arrow Books.

Todd, L. 1977 Cats and commerce. *Sci. Am.* **237**: 100-107.

Towns, D. R., I. A. E. Atkinson & C. H. Daugherty. 1990 *Ecological restoration of New Zealand islands: papers presented at conference on ecological restoration of New Zealand islands 1989.* New Zealand: Department of Conservation,Wellington.

Van Aarde RJ. 1986 A case study of an alien predator (*Felis catus*) introduced on Marion Island: selective advantages. *S. African. J. Antarc. Res.* **16**: 113-114

Van Damme, R. & Castilla, A.M. 1996 Chemosensory predator recognition in the lizard Podarcis hispanica: effects of predator pressure relaxation. *J. Chem. Ecol.* **22**: 13-22.

Veitch, C. R. 2001 The eradication of feral cats (*Felis catus*) from Little Barrier Island, New Zealand. *New Zeal. J. Zool.* **28**: 1-12.

Vitt L.J. & W.E. Cooper. 1986 Tail loss, tail colour, and pred- ator escape in Eumeces (Lacertilia: Scincidae): age-specific differences in costs and benefits. *Can. J. Zool.* **64**: 583–592.

Ydenberg, R.C. & Dill, L.M. 1986 The economics of fleeing from predators. *Adv. Stud. Behav.* **16**: 229-249.