

**Human-Induced Habituation and Landscape Changes at Cultural Heritage
Sites Affect the Anti-Predator Behavior of the Aegean Wall Lizard**

Podarcis erhardii

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Abstract

Predator-prey interactions are among the most common species relationships in nature, and prey will deploy a variety of anti-predator behaviors to manage levels of risk. Human activities can affect predator-prey relationships through both direct and indirect pathways.

Here, we examine the expression of a variety of key anti-predator behaviors in a common lizard species, the Aegean wall lizard (*Podarcis erhardii*, Lacertidae, Reptilia) on the Aegean Island of Naxos (Greece, NE Mediterranean Basin). To do this, we assessed a combination of three complementary anti-predator responses: Flight initiation distance towards humans (FID_H), flight initiation distance towards a mesopredator decoy (FID_D), and field autotomy rates (FAR).

Concurrently, we also obtained comprehensive metrics on the local ecosystem such as the relative abundance of humans, predators, prey, and the presence of refugia. We assessed the impact of human presence on the expression of anti-predator behaviors by comparing lizard populations using a paired experimental design in which commonly visited archaeological ruins were ranked by human presence and then divided into comparable sites of high and low human visitation.

First, we find that the expression of anti-predator behaviors depends sensitively on the existence of refugia from predation. lizards in areas that offered ample hiding places in the form of stone walls interacted more boldly with potential predators. Furthermore, lizards were able to discriminate between different threats according to their perceived risk and adjust anti-predator behaviors accordingly. Lizards in areas with a higher relative abundance of stone martens (*Martes foina*), an agile mammalian predator, displayed elevated flight distances relative to areas where this predator was uncommon. In contrast, shyness towards humans declined with increasing human visitation as lizards became habituated to a disrupting, but not particularly

dangerous, intruder. Notably, we found that increases in human visitation also resulted in a lessened anti-predator response towards stone martens. Such changes in anti-predatorial capacity are important to document as they can lead to elevated prey mortality as increased human presence results in the deployment of inappropriate anti-predator behaviors. Lastly, tail autotomy of individual lizards was also examined through binary logistic regression and, although not appearing to be significantly influenced by predation, does appear to be determined in part by the extent of human presence. Overall, this study demonstrates that human, predator, and suitable refugia abundance can significantly impact the risk perception of prey. Furthermore, this study highlights the need for further research into the effects pervasive human presence can have on predator-prey interactions.

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Dedication

This work is dedicated to my father and mother, who from a very young age have instilled in me the values of curiosity, discipline, and being a force of positivity in a world that needs more of it. These are qualities I will always carry with me in my continuing journey as a scientist.

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Introduction

Predation is a ubiquitous force in natural ecosystems, shaping the ecology and life history of most prey species. In vertebrate wildlife, predation drives the evolution of important behaviors aimed to increase survivorship (Magurán et al. 1993; Blumstein & Daniel 2005; Brock et al. 2015). Anti-predator adaptations do not just include behaviors that aim to forestall immediate predation events, but also behavioral and life history changes that aim to reduce the likelihood of predation altogether. Non-consumptive effects (NCEs) of predation shape the behavior, life history, and physiology of prey (Preisser et al. 2007). A 2011 study on NCE's found that the mere presence of predators can reduce the hatching of songbird offspring by nearly 40% (Zanette et al. 2011). Non-consumptive effects are not however limited to easily quantifiable metrics such as reproductive success in individuals. Changes in anti-predator behavior are themselves a manifestation of non-consumptive effects (Lima 1998; Caro 2005; Preisser et al. 2005). Specifically, predator presence influences prey's risk allocation abilities and boldness (Lima & Bednekoff 1999; Amo & Martín 2004). Risk allocation is defined as the time prey allot to predator avoidance instead of resource acquisition (Rodríguez-Prieto 2009). Risk allocation also influences the flight behavior of prey during predation events. When alerted, the ability for an individual to recognize a potential threat and have a fear-induced response must outweigh the energetic costs of flight (Cooper 2009). Consistent predation results in the expression of more effective anti-predator behaviors, as proper risk perception is crucial for prey survival through both evolutionary and ecological time (Lima & Dill 1990; Lima & Bednekoff 1999). Anti-predator behaviors are to varying degrees plastic, and without consistent predator presence, these behaviors can be lost (Brock et al. 2015). Moreover, numerous factors affect the expression of anti-predator behaviors in nature including predator abundance and the availability of potential

refugia (see “threat sensitivity hypothesis”: Amo et al. 2005; Camp et al. 2012; Smith et al. 2019).

Human activities can have significant impacts on the expression of anti-predator behaviors as well (Geffroy et al. 2015; Uchida et al. 2015; Lapiedra et al. 2016; Maurer et al. 2022). Increases in human presence can habituate prey, emboldening them in situations that would normally call for fear (Shannon et al. 2014; Shutt et al. 2014; Geffroy et al. 2015). Habituation to humans can influence anti-predator behavior distinctly, through direct or indirect pathways. “Human shields” act as an indirect pathway in which anti-predator behaviors may be affected by humans. This phenomenon associates areas of greater human visitation with an accompanying persecution of predators. Because of this persecution, many predatorial species tend to avoid human dominated areas. In turn, nearby prey take advantage of this reduction in predation risk and gravitate towards such high-human visitation safe regions to benefit from this “human shield” effect. Since predation risk is lower in such areas, prey will frequently downregulate their alertness and behavioral sensitivity to predators (Geffroy et al. 2015). Human shields were well documented in a 2014 study conducted in Grand Teton National Park on elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*). Ungulates that ranged in the vicinity of roadways spent more time grazing and less time in alert postures because of a reduced threat of predation from wolves (*Canis lupus*) who shy away from infrastructure (Shannon et al. 2014). However in many instances, habituation to humans can also directly change anti-predator behavior even when the predator community has not been impacted. This form of anti-predator behavioral loss is known as “behavioral spillover”. A behavioral spillover refers to the behaviors prey attribute to humans mistakenly being carried over to predators due to the positive association prey may have towards a human population (through feeding, etc.) (Geffroy et al.

2015). Drops in the production of stress hormones (i.e. corticosterone, cortisol, etc.) among individuals in low-stress environments are documented as being the physiological mechanism which induces behavioral spillovers (Shutt et al. 2014). This decrease in stress hormone production translates to an increase in boldness which may be exhibited incorrectly by prey in situations where fear would be more favorable for survival. In any case, behavioral spillovers can be distinguished from human shield effects by the fact that the latter is associated with measurable declines in predator abundance near human-dominated areas.

Human activities can also affect expressions of anti-predator behaviors indirectly through changes in the environment in which predator-prey interactions occur (Tellería et al. 2001). Past research has indicated that the expression of anti-predator behaviors depends on prey's ability to perceive risk (Lima & Bednekoff 1999). Risk in turn is influenced not just by predator presence, but also by opportunities to hide or escape (i.e. availability of refugia) (Camp et al. 2012). Therefore, one would expect that the expression of anti-predator behaviors may be correlated with the presence of refugia, whether natural or artificial (Longland & Price 1991; Wheeler & Hik 2014; Wagnon et al. 2020). Human activities have the capacity to increase or decrease the quality of suitable habitat for prey (e.g. through habitat alteration or degradation). The loss of potential refugia can change anti-predator behavior in prey due to an increased sense of vulnerability. This is because proximity to a potential refuge allows for easier escape during predation events, thus decreasing threat sensitivity and increasing boldness (Morelli et al. 2022).

The study of human activities on the expression of anti-predator behavior is complicated by the fact that human-induced influences can occur through multiple direct or indirect pathways. This creates challenges in the selection of potential study locations since many of the processes discussed here are more likely to occur in relatively intact habitats that support

abundant wildlife, but which nevertheless experience a pronounced human presence. Such locations may be sites of cultural, historical, or religious significance which draw large numbers of visitors and are located in relatively intact ecological settings.

Cultural heritage sites offer unique opportunities as natural settings to investigate how human presence can influence anti-predator behavior. As particularly little research regarding humanity's impact on reptilian anti-predator behavior exists (Batabyal et al. 2017), we took advantage of a series of archaeological sites of varying popularity to conduct a study in regard to how habituation to human visitors may affect anti-predator behavior in a model endemic island lizard species, the Aegean wall lizard (*Podarcis erhardii*). For our research, we hypothesized that increasing human visitation would lead to prey exhibiting down-regulated reactions to both humans and predators through the aforementioned pathway of human-induced behavioral spillover. We also hypothesized that changes of suitable habitat availability for prey at our study sites would affect anti-predator behavior; and that human interference will change baseline anti-predator behaviors, thus negatively influencing lizard tail autotomy rates. We quantified anti-predator behavior in the field on an Aegean Island with large amounts of seasonal tourism. We then compared observed anti-predator behaviors to relevant abiotic and biotic determining variables while also quantifying predation on lizard populations.

Methods

Study Island & Site Selection

Data collection was focused on Naxos, an island in the Cyclades Archipelago located in the Aegean Sea (Greece, Northeast Mediterranean Basin, Fig. 1). The Cycladic Islands have a typical Mediterranean climate with dry, warm summers and mild, wet winters (Gikas and

Tchobanoglous 2009). Situated on a distinct shelf, the Cyclades have been separated from the main European landmass since the Middle Pleistocene, and are occupied by a partially endemic flora and fauna (Lisiecki & Foufopoulos 2022). The archipelago has been inhabited by both humans and their domesticated affiliates, including cats and goats, for many millennia (Gizicki et al. 2017; Stewart & Campbell 2019; Li et al. 2014). Naxos, the largest Cycladic Island (429 km²), has supported thriving human communities for at least 30,000 years (Crow et al. 2011). As a result of continuous human habitation, the island's landscape has been strongly modified. Human impacts on the landscape have been persistent throughout the millennia, and are perhaps most evident in the numerous archaeological ruins found throughout the island as well as the terraces and dry-stone walls which dominate the island's ecosystems.

Archaeological sites on Naxos are typically located away from modern settlements because their presence was often dictated by past considerations like defensibility and year-round water access (Crow et al. 2011). Archaeological sites are popular with the many tourists on Naxos, and visitation rates vary greatly between well-known, or easily accessible, ruins versus others that are obscure and/or remote. Archaeological sites on Naxos typically contain abundant stone walls and other man-made structures which make them suitable habitats for wall lizards. These sites are also generally surrounded by the quintessential hilly landscape and agricultural terracing common throughout the island.

This study focused on seven archaeological sites across Naxos that were selected to be away from any modern settlements and embedded within the island's agricultural matrix in order to negate extraneous effects of urban development on our study systems. We used a paired design of sites for our study. The first member of each pair – one of the seven archaeological sites- was selected to be the high tourist visitation area. The second member of each pair,

adjacent to the respective archeological site (<1 *km* away) was matched for biotic and abiotic characteristics, except being mostly visitor-free. The seven archaeological sites –also denoted as high human visitation sites (or S1)- were themselves located along a gradient of human visitation, with some sites receiving close to a hundred visitors a day while others had close to none. All sites received the same sampling effort and shared the same general predator community. Sampling and behavioral observations were conducted under environmental conditions optimal for lizard activity: on sunny days (20-24 °C) with little to no wind from the hours of 9:00 to 16:00. Field work began in early May and ended in late June.

Measuring Vegetation & Wall Cover

Extent of suitable cover, in the form of walls or shrub vegetation, is known to be important for predator avoidance in lacertid lizards (Amo et al. 2004; Monasterio et al. 2009; López & Martin 2005). To quantify the extent of available cover, we conducted three 25 m-long vegetation transects at each of our sites (N = 42). These vegetation transects were placed in the vicinity of transects used to determine lizard density. Along each transect, and at 1 m intervals, we recorded the presence or absence of perennial woody shrubs (defined as height > 10 cm) (Gizicki et al. 2017). If shrubs were present, their height was also recorded. Vegetation cover was expressed as the percentage of the number of measurements along a transect. Individual heights of vegetation across the three transects were averaged to obtain a specific mean value. We excluded heights of less than 10 cm when calculating mean vegetation height.

To assess potential wall cover available to lizards at each site, we identified the abundance of walls using Google Earth Pro, which provides superior spatial resolution (Visser et al. 2013; Vos et al. 2019; Whalley 2021). For select sites, we then confirmed this remotely

sensed data using ground surveys. At each site, we selected three 25m-long digital transects (N = 42) placed randomly, but in the general vicinity, of lizard and vegetation transects. At every meter, the presence or absence of wall cover was indicated. We only recorded walls that were within a 50 cm distance from our transects. Once transects were established and wall presence quantified, we averaged at each site the proportions of transect measurements with walls to obtain the final estimated value of percent wall cover.

Measuring Human Visitation

We quantified the number of visitors a site received each day through repeated surveys over the course of the 2022 tourist season. One of the authors (IS), sitting near the entrance of the site, used a tally counter to record the total number of visitors per day (Wolf & Croft 2010; Li et al. 2011). We surveyed the number of visitors throughout the day for 6 hours at a time. Every site was surveyed for visitors three to five days. The daily number of visitors sampled per site was summed at the end of each day, and was subsequently averaged by the number of days visitation was recorded in the field. Averages were later square root transformed to normalize distribution.

Focal Species

Our study organism, the Aegean wall lizard (*Podarcis erhardii*), is widespread across the Southern Balkan Peninsula and the Cycladic Islands (Lymberakis et al. 2018). The species is common across a range of natural and anthropogenically modified habitats and can be encountered in particularly high densities on the dry-stone walls and agricultural terraces found across the island of Naxos. To quantify the species' abundance along such walls, we conducted

four standardized surveys on each site and the results were then averaged. These surveys involved walking a 100 m-long transect slowly while remaining at a 1 m distance from a randomly selected stone wall and recording all lizards observed (Li et al. 2014; Brock et al. 2015). To reduce observer bias, all transects were recorded by the same researcher (IS) across all sites. Lizard transects were only conducted during hours of peak lizard activity (8-11 am and 4-6 pm) and on days in which the weather was favorable (sunny, with low windspeeds <28 km/h and moderate ambient temperatures (19-25 °C)). We recorded the sex and autotomy status of each lizard (1 intact tail/ 0 regrown) before in-field experimentation (Brock et al. 2015). Methods for assessing autotomy in study lizards followed a similar methodology to Pafilis et al. (2009).

Predator Abundance

While all study sites, being located on the same island, shared the same general predator community composition, there were differences in the relative abundances of individual predators at each study location. To quantify the predation environment, we conducted multiple assessments of relative predator abundance at each site over the course of the study season. The primary predators of *Podarcis erhardii* in the Cyclades are stone martens (*Martes foina*), feral cats (*Felis catus*), two species of snake (*Vipera ammodytes*, *Eryx jaculus*), and two species of raptor (*Buteo buteo*, *Falco tinnunculus*).

To quantify aerial raptor presence, while also accounting for seasonal variation in detectability, we assessed raptor abundance on each site over the course of three different observation periods. For each one hour-long session, the same observer (IS) counted all visible raptors from an elevated location using a pair of binoculars (Kemp et al 2011). Only raptor species that are known predators of *Podarcis erhardii* were recorded.

To ascertain the relative abundance of mammalian predators (stone martens and cats) present on Naxos, we deployed camera traps (one camera trap (Wildview 12mp) per site) at each site for a period of ten days. The cameras had a 15 meter range and were mounted 1 meter above the ground to record medium sized predators (Rowcliffe et al. 2008). Cameras were placed in areas of expected high predator abundance (high prey density areas with ample vegetation cover for stalking). Additionally, we conducted two nighttime (23:00-1:00) vehicle-based roadside transects at each site on non-consecutive nights following the same 1 km route (N = 28). Two researchers were present during data collection: a driver and an observer. The driver drove at a low speed ($\sim 4\text{kmh}^{-1}$) while the observer used a handheld spotlight (Cyclops Mevo 255; 250 lumens) to search the sides of the road for the eye-shine of both feral cats and stone martens (see Li et al. 2014).

Presence of mammalian predators was further quantified using multiple scat transects at each site (Olson et al. 2012). Three scat line transects were walked per site (N = 42). Scat was surveyed over a 100 m transect along a randomly selected focal stone wall. The width of each scat transect was 3 meters per side (6 meters in total). Scat transects were walked during regular daytime data collection hours (9:00-16:00). In addition, we recorded any terrestrial predators encountered while at each field site including snakes (Santos et al. 2016).

To create comprehensive indices of relative abundance for each predator type, we integrated the metrics collected for each predator to create summary values. Both marten and cat relative abundance indices utilized various predator metrics (animals seen during nighttime roadside transects, scat transects, animals seen in daylight, and animals seen from trail cameras). We also summed the various measurements of relative abundance used for each species thus creating the value of “total predation” for all sites (Cooper and Pérez-Mellado 2012). This value

serves as a holistic summation of the total predation exerted on *Podarcis erhardii*. Additionally, we created a summary category termed “terrestrial predator abundance” (TPD) which contained relevant data on cat and marten abundances and excluded raptor abundance . To determine metrics of raptor abundance, we first averaged the number of raptors seen per site (S1 or S2). The values for each pair of sites was subsequently averaged to obtain an overall raptor score for each (paired sites were counted together). This adjustment was made to account for the large size of raptor territories which exceed the spatial extent of our study sites.

Human FID (FID_H)

To gauge the fear response of lizards towards humans, we recorded both the flight initiation distance (FID_H) and distance to refuge (DR_H) of lizards across all study sites as a response to an approaching human. This methodology has been established as a reliable means of quantifying anti-predator vigilance (see Brock et al. 2015). FID, defined as the distance at which an animal flees from a perceived threat (Fernandez-Juricic et al. 2005), was measured across all study sites. For consistency purposes, the same person (IS) conducted all surveys while wearing similar clothes (Brock et al. 2015). All FID trials were piloted early in the study season for a week to achieve methodological consistency and avoid biases (Rodriguez-Prieto et al. 2008). To limit habituation to investigators, FID assessments were not carried out on consecutive days. At any given site, we waited at least 3 days before revisiting to collect more FID data (Brock et al. 2015). At the beginning of each trial, the researcher spotted a lizard from a distance, then the lizard would be approached at a steady speed of 80 m/min with the researcher taking care to avoid any confounding shadow effects that may occur during their approach (Brock et al. 2015). After the lizard-initiated flight, we measured distance to refuge (DR), defined as the

distance between the original encounter site and the spot where the lizard entered its refuge (usually either a rock or crevice). We obtained FID_H from at least 10 lizards per site.

Decoy FID (FID_D)

To assess the reaction study lizards had towards a native predator, we measured FID and DR in response to a mounted taxidermized stone marten (*Martes foina*) decoy, fitted on top of a remote control (RC) car suited for all-terrain movement. FID_D , or the distance between the decoy and the point of flight, and DR_D , or the distance between the point of flight and the refuge that an animal escapes to, were both measured in the same manner as our FID_H experiment (i.e., from the base of the RC car to the area in which the lizard-initiated flight). We chose *Martes foina*, a widespread predator of *Podarcis erhardii* on Naxos, to be our decoy predator (Stille et al. 2021; Bakaloudis et al. 2012). The RC car we used was an ECX RC Ruckus 2WD model (Dimensions: 51 x 35 x 24 cm; 2.5 kg) with full suspension, 10-cm Shootout HT traction tires, and powered by a 3200mAh Li polymer battery. The RC allowed for easily controllable speed during directional FID_D tests in the field. The decoy itself was prepared from a freshly deceased road-killed marten that was taxidermized before being mounted onto the chassis of the RC car. The vehicle was camouflaged with a mesh-wire skirt with native vegetation woven into it (see Uchida et al. 2019 who followed similar methodology) (See Figure 2 & Image 1).

To avoid observer bias, all trials were carried out by a single researcher (IS). On average, we conducted 10 decoy trials per site. $FID_{D/H}$ trials were not conducted on consecutive days to avoid increased habituation amongst the lizards. In an effort to avoid effecting animal responses, the observer remained hidden ~10 meters away from the focal animal (Rodriguez-Prieto et al. 2008). The RC was driven directly at the lizard at an approximate speed of 25cm s^{-1} (Li et al.

2014), and we recorded the location of the RC vehicle at the moment the lizard initiated the response. Lizards perched higher than 30 cm were excluded as they would not respond to the decoy (Diego-Rasilla 2003).

Statistical Analysis & Model Selection

To assess the relationships between $FID_{D/H}$ and our independent variables, we used a generalized linear mixed model (GLMM) approach (see Brock et al. 2015; Silk et al. 2020) utilizing the following general model structure:

$$y = \beta_0 + \sum X_i \beta_i + \gamma + \varepsilon$$

where y was the dependent variable (either FID_D or FID_H) with a linear target distribution. We also used a normal distribution with an identity link (Lo & Andrews 2015). The fixed effect explanatory variables (X_i) used included predator abundance categories, wall cover, vegetation cover, lizard density, and human visitation while β_i acted as the fixed effect's scaling parameters. We denoted β_0 as the global intercept and ε as the residual variance. Distance to refuge ($DR_{D/H}$) was added to all models as a random effect, γ . Our two subjects were primary archaeological sites ($N = 7$), as well as the high and low human visitation sites which were nested within (S1 or S2) ($N = 14$). We initiated the model selection process by performing univariate mixed modeling that used all potential independent variables individually in order to assess for downstream variable input.

All models used were ranked based on best fit AIC_c values (Burnham et al. 2011). We used AIC_c values to decrease the use of unnecessary data parameters, as well as to address our finite dataset (Brock et al. 2015; Anderson & Burnham 2002). We subsequently calculated

ΔAIC_c (or Δ_i) through subtraction of the smallest AIC_c value (AIC_{min}) by the relevant model (AIC_i). Associated Akaike weight was then calculated using the formula:

$$W_i = \exp(-1/2 \Delta_i) / \sum^R \exp(-1/2 \Delta_r)$$

(See Burnham and Anderson 1998, Symonds and Moussalli 2010). This value gives the relative likelihood of each model occurring in-lieu of all other possibilities described.

Different fixed effect terms describing the local predation environment were added to candidate multivariate models one at a time to avoid pseudoreplication. We chose to test the “total predation hypothesis” (PD) (Cooper and Pérez-Mellado 2012) in our potential models to see whether fear towards a perceived predator was due to the aggregate presence of all predators rather than the most relevant predator or perceived predator (marten or human). Similarly, we tested for total terrestrial predator abundance, a sum of the scores of all terrestrial predators recorded per site. We included human visitation rates in all models in order to assess the potential for *Podarcis erhardii* being habituated to humans at our study sites. Average percent wall cover and vegetation cover were included as fixed effects as we hypothesized that these variables may correlate to a lessened perception of risk amongst prey (Camp et al. 2012; Batabyal et al. 2017). We used one-way ANOVA tables to compare average values of $FID_{D/H}$ across our seven high human visitation sites. Additionally, we used one-way ANOVA tables to compare the average values of $FID_{D/H}$ between high and low visitation sites (S1 vs. S2).

A binary logistic regression was used to investigate the relationship between tail autotomy status (coded as a binary variable intact vs. not intact) and various causative factors. All variables used in our multivariate analysis were first assessed in a univariate context through Wald testing done through logistic regression and the analysis of associated P-values (P-values < 0.25) (Bursac et al. 2008). Variables selected for multivariate analysis included: human density

(HD), raptor density (RD), and lizard density (LD). To identify the best fitting model, we used backward stepwise regression analysis with the null model containing the variables listed above. We used omnibus tests of model coefficients to find the most likely influencing variables (Doornik & Hansen 2008). Additionally, we performed a chi-squared test of association between tail autotomy and high versus low human visitation sites (S1 or S2).

Simple pairwise linear regressions were created testing all independent variables against lizard density. Additionally, a simple linear regression involving all trials of $FID_{D/H}$ tested against lizard density was done to test for covariance.

Results

Characteristics of Study Sites

Human visitation rates varied greatly across S1 sites (High Human Visitation Sites: *Mean* = 22.86, *S.E.M.* = 8.60, *Max* = 65, *Min* = 0, *N* = 7; mean human visitation at S2 sites was consistently < 2 individuals per site). We found a near-significant positive correlation between average human visitation and vegetation cover at S1 sites (High Human Visitation Sites: $r = 0.74$, $P = 0.06$, $N = 7$; Low Human Visitation Sites: $r = 0.23$, $P = 0.62$, $N = 7$). Additionally, average vegetation cover and wall cover were significantly correlated with each other, though only at high human visitation sites (High Human Visitation Sites: $r = 0.89$, $P = 0.01$, $N = 7$, Low Human Visitation Sites: $r = -0.33$, $P = 0.47$, $N = 7$). There was also a near-significant positive correlation between vegetation cover and marten abundance across all sites ($r = 0.50$, $P = 0.07$, $N = 14$) and a significant negative correlation between average vegetation cover and average raptor abundance across all sites ($r = -0.53$, $P = 0.01$, $N = 14$).

Lizard Density

Simple pairwise regressions showed that there were no significant relationships between lizard density and any independent variables considered. A linear regression between $FID_{D/H}$ and lizard density, also shows no obvious relationship ($F_{1,331} = 0.26$, $P = 0.61$, $N = 284$).

Human FID (FID_H)

As FID_H was correlated with distance to refuge (DR) ($r = 0.17$, $P = 0.03$, $N = 175$), distance to refuge was used as a covariate in both univariate and multivariate modeling. The mean value of FID_H varied significantly between high and low human visitation sites with high human visitation sites having a 14% smaller average FID (117.79 cm \pm 60.62 cm versus 136.23 cm \pm 59.32 cm; ANOVA: $F_{1,175} = 4.36$, $P = 0.04$, $N = 177$). FID_H varied significantly between individual archaeological sites as well ($F_{6,170} = 3.04$, $P = 0.01$, $N = 177$). FID_H also had a significant negative correlation with human visitation ($r = -0.59$, $P = 0.01$, $N = 175$). Across high human visitation sites, every increase of 10 visitors resulted in an associated decrease in FID_H by an average of 17 cm.

Univariate analysis documented that human visitation, as well as wall cover, have significant negative relationships with FID_H (Human Visitation: $F_{1,173} = 5.35$, $t = -2.31$, $P = 0.02$, $N = 175$; Wall Cover: $F_{1,173} = 6.32$, $t = -2.51$, $P = 0.01$, $N = 175$). All other terms, when examined singly, had non-significant relationships with FID_H ($P > 0.05$).

Our best performing multivariate model of FID_H contained raptor abundance as our sole predator predictor variable, as well as all other independent variables (lizard density, vegetation cover, wall cover, and human visitation). This model greatly outperformed all other models even when penalized for having two more fixed effect variables than the majority of other candidates

(Akaike weight = 0.94; see Table 3 in Figures & Tables section). Analysis of our best-fitting multivariate model for FID_H showed significant negative relationships existed between FID_H and human visitation as well as wall cover (Human Visitation: $F_{1,169} = 7.30$, $t = -2.70$, $P = 0.01$, $N = 175$; Wall Cover: $F_{1,169} = 6.55$, $t = -2.56$, $P = 0.01$, $N = 175$). All other terms included in our best performing multivariate model were not significantly related to FID_H ($P > 0.05$).

Decoy FID (FID_D)

As FID_D was correlated with distance to refuge (DR) ($r = 0.24$, $P = 0.01$, $N = 131$), distance to refuge was used as a covariate in both univariate and multivariate modeling. The mean value of FID_D varied significantly between high and low human visitation sites with high human visitation sites having a 13% smaller average FID_D ($77.06 \text{ cm} \pm 25.17 \text{ cm}$ versus $88.55 \text{ cm} \pm 29.99 \text{ cm}$; ANOVA: $F_{1,131} = 5.80$, $P = 0.02$, $N = 136$). FID_D did not significantly vary between individual archaeological sites ($F_{6,129} = 1.84$, $P = 0.10$, $N = 136$).

Univariate analysis revealed a significant negative relationship exists between FID_D and wall cover, as well as with human visitation (Wall Cover: $F_{1,129} = 8.06$, $t = -2.84$, $P = 0.01$, $N = 131$; Human Visitation: $F_{1,129} = 5.61$, $t = -2.37$, $P = 0.02$, $N = 131$). Univariate analysis also showed significant positive relationships exist between FID_D and total predator abundance as well as cat abundance (Σ Predator Abundance: $F_{1,129} = 8.19$, $t = 2.86$, $P = 0.01$, $N = 131$; Cat Abundance: $F_{1,129} = 5.34$, $t = 2.31$, $P = 0.02$, $N = 131$) while there was a near significant positive relationship between FID_D and marten abundance, as well as with terrestrial predator abundance (Marten Abundance: $F_{1,129} = 2.89$, $t = 1.70$, $P = 0.09$, $N = 131$; Terrestrial Predator Abundance: $F_{1,129} = 3.51$, $t = 1.88$, $P = 0.06$, $N = 13$). Total predator abundance also had a near significant positive correlation with FID_D ($r = 0.50$, $P = 0.07$, $N = 14$). FID_D did not appear to

have a significant relationship with vegetation cover, lizard density, or raptor abundance ($P > 0.05$)

Our best performing multivariate model of FID_D contained marten abundance as our sole predictor variable of predator occurrence, in addition to several other independent variables (lizard density, vegetation cover, wall cover, and human visitation). This model greatly outperformed all other models even when penalized for having two or more fixed effect variables than all other candidates models (Akaike weight = 0.91; see Table 2 in Figures & Tables Section). Crucially, this model revealed a significant positive relationship exists between FID_D and marten abundance ($F_{1,125} = 7.00$, $t = 2.65$, $P = 0.01$, $N = 131$). In this model, there was a significant negative relationship between wall cover and FID_D ($F_{1,125} = 4.78$, $t = -2.19$, $P = 0.03$, $N = 131$) as well as a near significant negative relationship between FID_D and human visitation ($F_{1,125} = 3.49$, $t = -1.87$, $P = 0.06$, $N = 131$). Neither lizard density nor vegetation cover appeared to have a significant impact on FID_D ($P > 0.05$).

Tail Autotomy

Tail autotomy rates were significantly greater at high human visitation sites ($X^2(1, N = 285) = 7.93$, $P = 0.01$). There was a statistically significant positive relationship between average tail autotomy and average marten abundance across all sites as well ($r = 0.55$, $P = 0.04$, $N = 14$).

Univariate analyses showed that tail autotomy and the independent variables human visitation, raptor abundance, and lizard density were the most statistically viable candidates for our multivariate binary logistic model based upon the conditions set forth by Bursac et al. (2008). (Human Visitation: $B = 0.22$, $S.E. = 0.10$, $Wald = 4.74$, $P = 0.03$, $N = 285$; Raptor

Abundance: $B = -0.18$, $S.E. = 0.14$, $Wald = 1.65$, $P = 0.20$, $N = 285$; Lizard Density: $B = 0.33$, $S.E. = 0.20$, $Wald = 2.72$, $P = 0.10$, $N = 285$).

Our best performing multivariate model for tail autotomy included human visitation as the sole predictor variable (Model: $X^2(1, N = 285) = 4.49$, $P = 0.03$). In this model, human visitation had a significant positive relationship with lizard tail autotomy ($B = 0.22$, $S.E. = 0.10$, $Wald = 4.74$, $P = 0.03$, $N = 285$).

Our second best performing multivariate model contained the independent variables human visitation and lizard density (Model: $X^2(2, N = 285) = 6.02$, $P = 0.05$). Human visitation had a near significant positive relationship with tail autotomy while lizard density had a non-significant positive relationship with tail autotomy (Human Visitation: $B = 0.20$, $S.E. = 0.11$, $Wald = 3.47$, $P = 0.06$, $N = 285$; Lizard Density: $B = 0.26$, $S.E. = 0.21$, $Wald = 1.54$, $P = 0.22$, $N = 285$).

Discussion

Anti-predator behavioral change is an issue of critical importance for wildlife prey as it affects population survival while also having significant management implications. Here, we investigated the factors that shape anti-predator behavior in a widespread island lizard across a range of sites which differed in quantifiable characteristics such as human visitation, refuge availability, and predator community composition. We found that the anti-predator behavior of the Aegean wall lizard, *Podarcis erhardii*, was influenced complexly by multiple distinct biotic and abiotic factors. At its most basic, anti-predator responses in this species are fundamentally shaped by the animal's perception of risk, which in turn is determined by the dual considerations of the local predation environment, as well as the availability and proximity of refugia. As a

result, the increased abundance of hiding places in the form of stone walls was broadly associated with shorter flight initiation distances in *P. erhardii* (i.e. higher lizard boldness in the face of approaching threats). Furthermore, increased presence of both native and introduced predators was correlated with greater levels of lizard-shyness, as measured in FID to a stone marten decoy. Lastly, human visitation had an analogous effect on human FID, albeit in the opposite direction: increased human visitation resulted in more tame lizards presumably as a result of habituation to a disrupting, but non-lethal, mammal (humans).

One of the main conclusions of this study is that habituation to humans occurred across *P. erhardii* populations living within the confines of investigated archaeological sites. FID_H was also on average lower at high human visitation sites relative to respective low visitation counterparts. The negative relationship between human visitation and FID_H (evident in both univariate and multivariate analysis) points towards habituation, rather than sensitization, of the animals to a recurrent disruption. In other words, this pattern suggests that human visitors are not perceived as threats, rather as disrupting factors by resident *P. erhardii* lizards. This is confirmed by similar findings from a study performed by Uchida et al. (2019) who found that Eurasian red squirrels (*Sciurus vulgaris*) in urban environments had a reduced vigilance towards humans, yet did not fully lose their risk perception. At our study sites, reoccurring observations indicated that lizards were (with possible rare exceptions) not harassed by humans visitors. Hence, this relationship shows that lizards were mostly able to discriminate between humans (being benign or low-level threats) and natural predators (Coleman et al. 2008).

We found that predator abundance was closely related to lizard flight-responses towards our predator decoy (FID_D). Previous research has suggested that predator proximity to a population of prey increased that prey population's wariness (Lima & Dill 1990). The data in this

study broadly agree with this conclusion: our best-performing model supports a significant positive relationship exists between stone marten abundance and FID towards a stone marten decoy. Other metrics of predator abundance (e.g. cat abundance, terrestrial predator abundance, and total predator abundance) used also had similar, but less strong, relationships to FID_D in worse performing multivariate models.

There was little to no influence of human visitation rates on the abundance of predators. This was true across all sites, as well as between paired high and low human visitation sites. This means that any changes in anti-predator responses are not the result of underlying, human-caused changes in predator abundance. Hence, we find little support for the “human shield” hypothesis as articulated in the literature (Isbell & Young 1993; Shannon et al. 2014). Additionally, this lack of a human shield is further supported by the observation that lizards do not seem to directly benefit from human presence. Indeed, we did not find that lizard densities increased as a result of rising human visitation as would be expected if greater visitor numbers would shield lizards from predation.

Nevertheless, our research does demonstrate that human-induced anti-predator behavioral change, by way of behavioral spillover, does occur in this study system. Indeed, we found that FID_D in high human visitation sites was significantly less than the FID_D measured at low visitation sites. This indicates that broad habituation towards humans, in the form of reduced FID_H at well-visited sites, was also spilling over and influencing other aspects of the anti-predator behavior of prey (FID_D). Given that low and high human visitation sites were ecologically similar, except for the number daily visitors, and that there was no relationship between human visitation and predator abundance, we conclude that behavioral spillover is occurring in the absence of any predator or prey population density changes. Nevertheless, it

would be beneficial to complement the findings from this study by also testing for circulating corticosterone in study lizards in order to quantify changes in stress-levels induced by human visitation.

Past research has shown that the fear response of prey is influenced by the availability of refugia (Iglesias-Carrasco et al. 2016; Dellinger et al. 2019; Ålund et al. 2022). In our study, amount of wall cover was significantly negatively associated with the mean flight response of lizards. We hypothesize that these reductions in $FID_{D/H}$ reflects a reduced perception of predation risk in areas with abundant walls. This confirms existing knowledge that *Podarcis erhardii* uses man-made structures for hiding and foraging. Moreover, recent investigations have shown that the species shifts its ecology according to the presence or absence of dry stone walls (Donihue 2016).

Unlike wall cover, vegetation cover did not have as strong of an influence on lizard $FID_{D/H}$. This may be because solid stone refuges (rocks, walls, etc.) are likely more substantial refuges than vegetation alone for lizards in flight (Batabyal et al. 2017). However, previous studies have also shown that vegetation can somewhat act as a deterrent towards predation and allow for increased escape time (Amo et al. 2007; Pietrek et al. 2009).

It appears that on Naxos, the long-term presence of humans has created an environment in which man-made structures have assumed great importance for the survival of *Podarcis erhardii*. It should be noted that there was no direct relationship between human visitation and wall cover. However, due to the ever-present human population on the island and the ancient status of Naxian walls (the oldest dating to at least 1400-1370 B.C.E; Vlachopoulos & Charalambidou 2019) it can be assumed that the behaviors displayed by study lizards are likely imparted by the historic presence of humans on the island.

Tail autotomy is often used as a metric for assessing the relative impact of predation on lizard populations (Bateman & Fleming 2008). Our study found that tail autotomy amongst *Podarcis erhardii* had a stronger relationship to human visitation than any other influencing variable. We hypothesized that this relationship reflects the underlying stress inflicted on lizards by a growing human presence. It must be further emphasized that corticosterone production regulates stress in lizards (Denardo & Licht 1993; Romero & Wikelski 2002; Langkilde & Shine 2006). Associated reductions of corticosterone can explain the potential for behavioral spillover of learned relaxed risk perception from humans to true predators (Romero & Wikelski 2002; Shutt et al. 2014).

To summarize, our research showed that differential habitat suitability and increasing human presence is associated with a down-regulation of anti-predator behavior in *Podarcis erhardii*. Conversely, the abundance of relevant predators a prey population may encounter positively influences FID. As our multivariate model showed, habituation to humans impacted the risk perception of prey towards natural predators across a gradient of human visitation.

Importantly, the complex nature of humanity's impact on the island of Naxos's ecology, specifically through the direct influence on predator-prey interactions, highlights the importance of man-made structures as preferential habitats for prey. Dry stone walls exist across the island and are a defining characteristic of the Naxian landscape. These walls were common both in our high and low human visitation sites. Based off of our findings the historic presence of humans, who change the island's landscape, acts as a strong influencer of anti-predator behavior.

This paper additionally supports the need for further research into the complex relationship between human presence and prey behavior, especially through tourism. Human visitation at studied cultural heritage sites appeared to influence the behavior of wildlife.

Invasive species invasion, or natural predator reintroductions, at these places where prey species are vulnerable due to increased boldness are also concerns which should be heeded in future management endeavors.

Figures & Tables

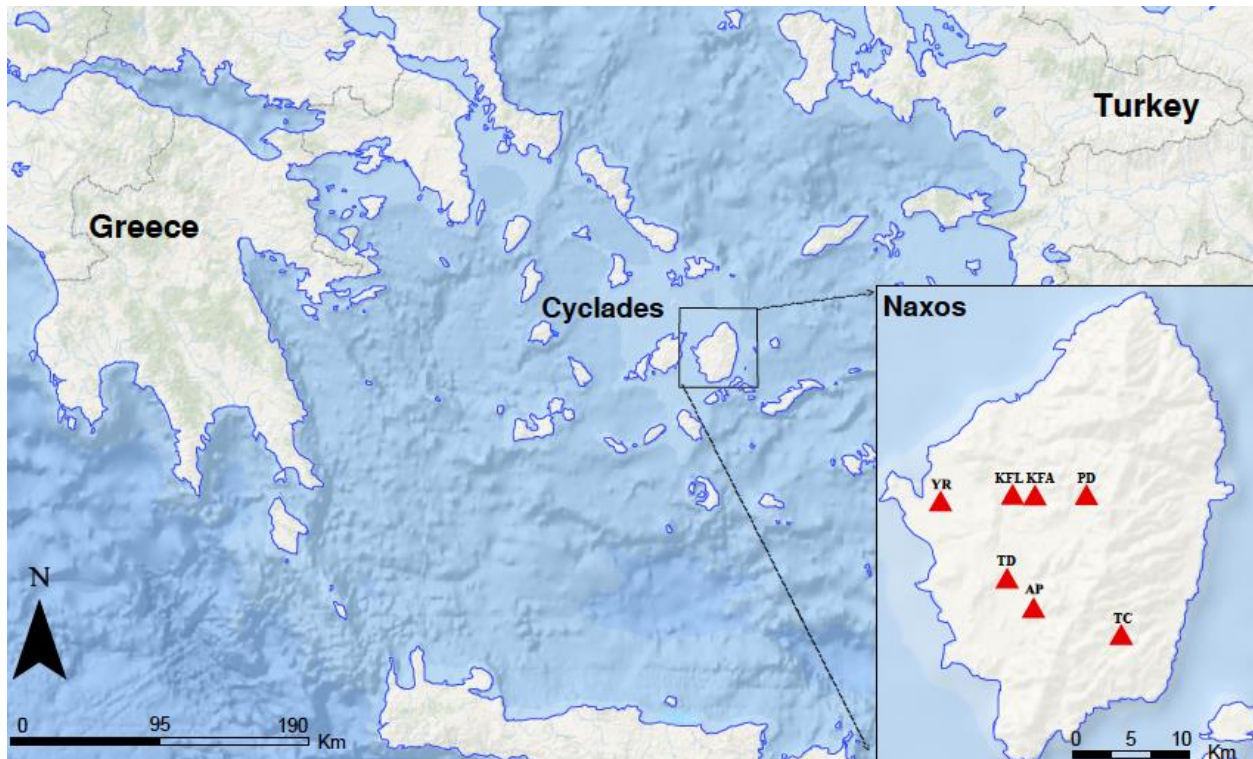


Figure 1: A map of the Aegean Sea and the Island of Naxos (where field work was carried out). The red triangles indicate seven archaeological ruins used for our study. Each ruin contained a paired high and low human visitation site in close proximity to one another (<1km) ($N = 14$). Ruin indicators represent the following places: YR = Yria (Temple of Dionysus), KFL = Kouros of Flerio, KFA = Kouros of Faranaghi, PD = Panagia Drosiani, TD = Temple of Demeter, AP = Apaliros Castle, TC = Tower of Cheimarrou.

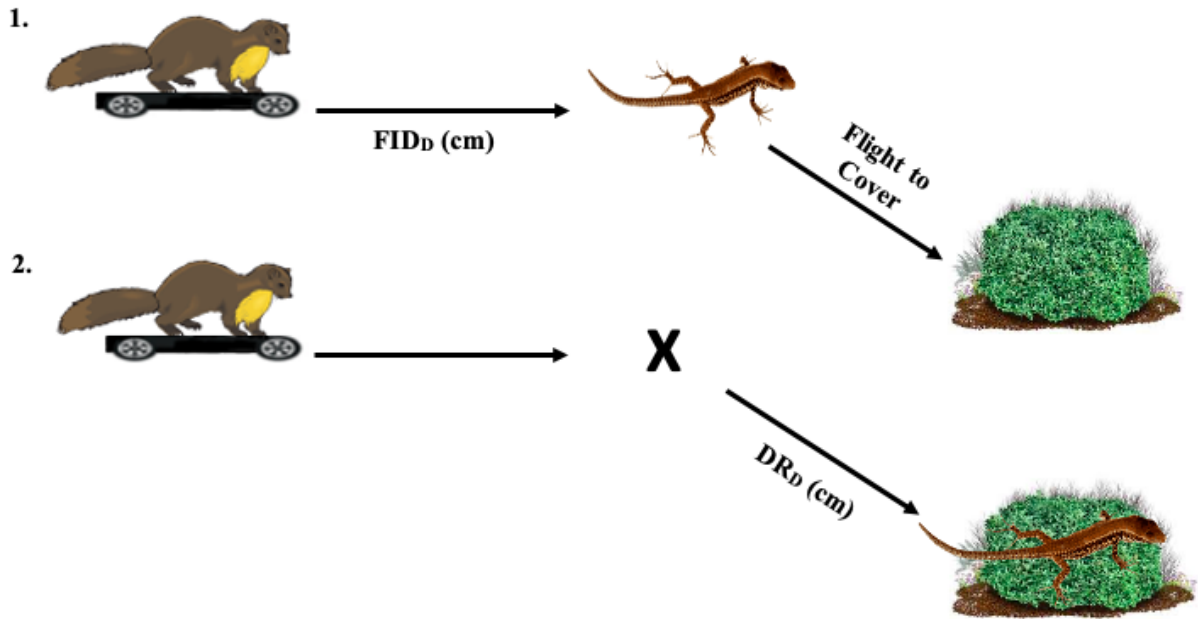


Figure 2: (1) Flight Initiation Distance (FID) is a measurement of the distance at which an animal flees from an observer or decoy. In this figure, we are measuring FID to a decoy (FID_D) in centimeters. (2) Distance to Refuge (DR) is the distance between the point of flight from said observer or decoy to a suitable refuge (wall, rock, plant biomass, etc.). In this figure, we are measuring DR to a decoy (DR_D) in centimeters (Bateman & Fleming 2011).

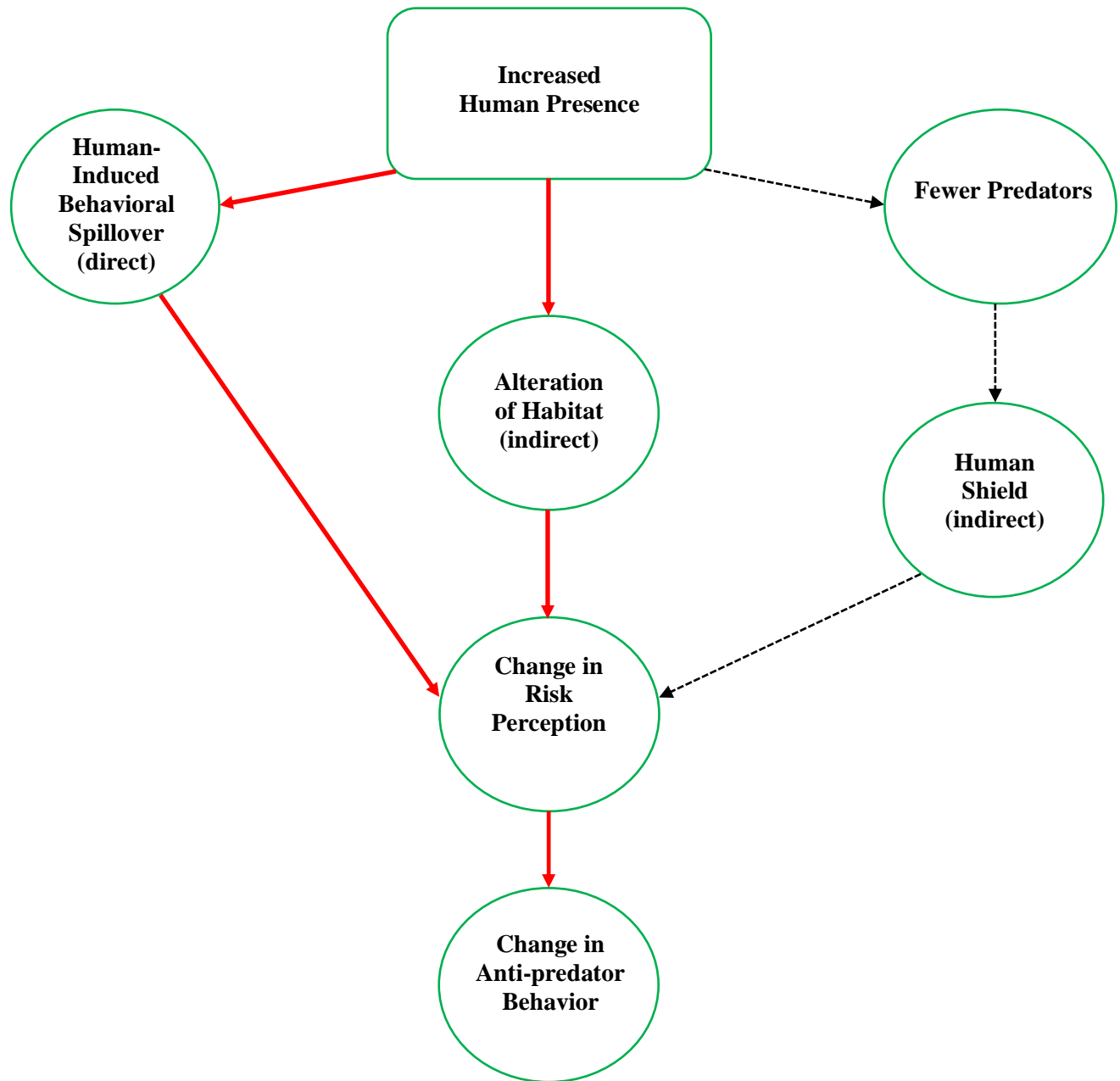


Figure 3: The above flowchart displays the known pathways of human-induced habituation and how it changes antipredator behavior through increased human presence. Our flowchart also displays the pathways expressed in our study system on Naxos (red arrows). **Pathway 1 (far left)** displays how human-induced behavioral spillover can directly affect anti-predator behavior. As there was a lack of change in the predator community across high human visitation sites, we hypothesize that this pathway is a major driver of risk perception loss in prey (as it is not dependent on predator abundance). **Pathway 2 (far right)** displays how human presence negatively influences predator abundance, which in turn encourages prey to use humans as a “human shield”. This pathway did not occur in our system as human visitation on Naxos does not seem to inhibit the predator community. **Pathway 3 (center)** displays how increased human presence changes status-quo habitat and increases available refugia for prey, in turn, increasing boldness. Pathway 3 was evident in our study as greater stone wall cover across our sites lessened the $FID_{D/H}$ of study lizards. This flowchart is influenced by figure two of Geffroy et al. (2015).

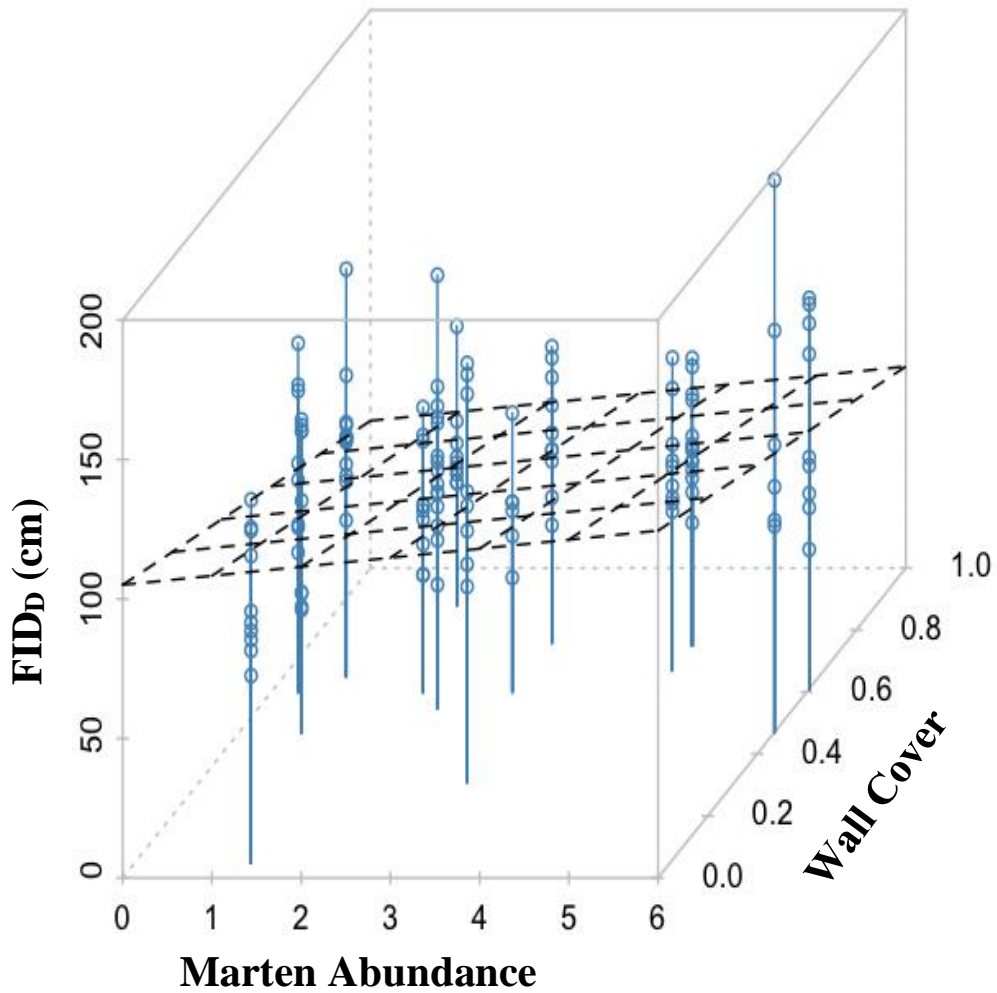


Figure 4: Scatterplot of our dependent variable FID_D (cm) in comparison to the average proportional wall cover per site ($F_{1,125} = 4.78$, $t = -2.19$, $P = 0.03$, $N = 131$) and marten abundance ($F_{1,125} = 7.00$, $t = 2.65$, $P = 0.01$, $N = 131$). FID_D increases with marten abundance and decreases with wall cover.

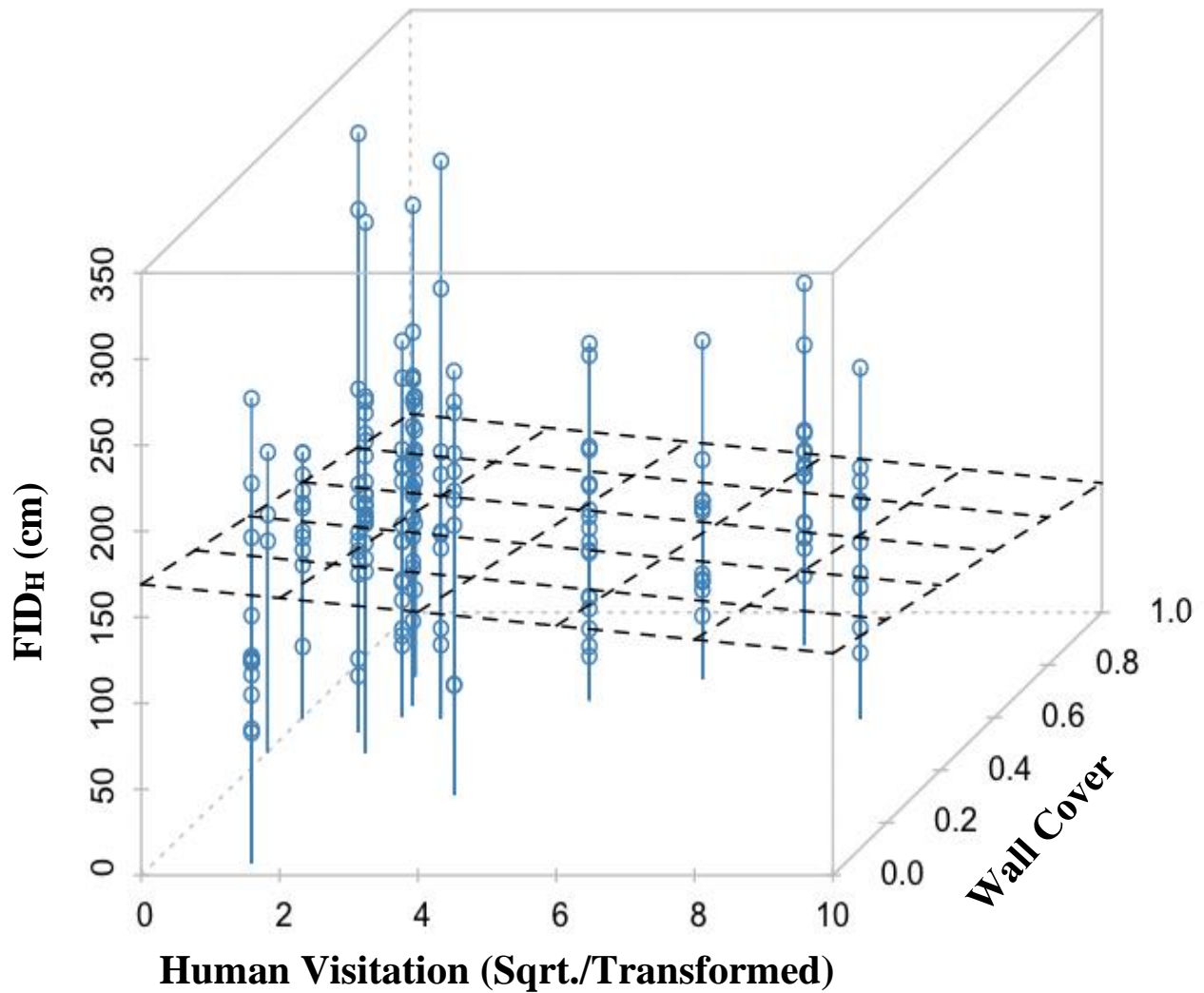


Figure 5: Scatterplot of our dependent variable FID_H (cm) in comparison to the average proportional wall cover per site ($F_{1,169} = 6.55$, $t = -2.56$, $P = 0.01$, $N = 175$) and human visitation (sqrt./transformed) ($F_{1,169} = 7.30$, $t = -2.70$, $P = 0.01$, $N = 175$). FID_H decreases with increasing wall cover and human visitation.

Site	FID _D (cm)	DR _D (cm)	FID _H (cm)	DR _H (cm)	FAR	Human Visitation (Sqrt./Transf.)	Σ Predator (R.A.)	Terrestrial Predator (R.A.)	Marten (R.A.)	Cat (R.A.)	Raptor (R.A.)	Wall Cover (%)	Vegetation Cover (%)	Lizard Density (indiv./ 100m)
Temple of Demeter (TD) (S1)	68.2 ± 6.5 (42-102) N = 10	39.9 ± 5.7 (11-64) N = 10	99.9 ± 15.2 (39-200) N = 10	23.2 ± 3.6 (5-38) N = 10	0.11 ± 0.16 N = 8	8.06	3	1.7	1.7	1.7	2	60	71	1
Temple of Demeter (TD) (S2)	107.7 ± 11.6 (50-140) N = 9	60 ± 15.5 (20-160) N = 9	127.4 ± 13.7 (40-220) N = 15	31.9 ± 5.5 (2-80) N = 15	0.09 ± 0.0 N = 15	1.4	11.3	10	6	9	2	61	89	1
Panagia Drosiani (PD) (S1)	54.2 ± 5.9 (44-100) N = 9	55.6 ± 22.4 (4-204) N = 8	95.2 ± 10.8 (40-209) N = 16	38.1 ± 17.7 (1-220) N = 16	0.16 ± 0.55 N = 25	6.2	4.7	3.3	1.3	0.3	2.3	88	67	3.5
Panagia Drosiani (PD) (S2)	76 ± 6.6 (42-106) N = 10	23.7 ± 3.9 (5-40) N = 10	147.9 ± 11.1 (50-160) N = 10	29.9 ± 7.7 (1-77) N = 10	0.07 ± 0.0 N = 20	1.0	5	3.7	2.7	1.7	2.3	76	77	1.25
Kouros of Flerio (KFL) (S1)	70.9 ± 4.5 (44-103) N = 14	73.2 ± 14.1 (15-150) N = 13	86.3 ± 13.8 (40-200) N = 11	52.8 ± 17.7 (5-153) N = 11	0.1 ± 0.04 N = 25	5.2	9.6	9.3	4.3	8.25	2.7	75	71	1.5
Kouros of Flerio (KFL) (S2)	52.6 ± 6.9 (44-155) N = 15	88.1 ± 8.2 (5-140) N = 15	134.1 ± 27.6 (35-350) N = 12	54.4 ± 17.9 (2-180) N = 12	0.04 ± 0.05 N = 27	1	7.4	6	2	6	2.7	55	60	3
Kouros of Faranaghi (KFA) (S1)	71.4 ± 6.3 (57-112) N = 9	49.1 ± 8.6 (18-102) N = 9	94.9 ± 12.3 (24-205) N = 18	16.9 ± 4.9 (2-76) N = 18	0.08 ± 0.05 N = 10	3.9	5.3	4.3	4.3	4.25	3	67	69	2.5
Kouros of Faranaghi (KFA) (S2)	87.3 ± 6.0 (56-146) N = 13	57.7 ± 14.9 (6-200) N = 13	143.9 ± 13.8 (46-290) N = 18	50.2 ± 5.3 (18-100) N = 18	0.001 ± 0.0 N = 30	1.4	2.9	0.7	0.7	0.7	3	65	48	0.5
Yria (YR) (S1)	115 ± 11.1 (70-150)	48 ± 9.5 (24-110) N = 8	152.7 ± 20.5 (60-248) N = 10	38.8 ± 14 (10-144) N = 9	0.03 ± 0.15 N = 11	3.3	9.3	8	3	8	1.7	31	55	2.75

	(N=8)													
Yria (YR) (S2)	78.9 ± 10.4 (44-112) N = 9	46.6 ± 8.8 (9-82) N = 8	167.9 ± 9.7 (101-305) N = 21	59.0 ± 8.2 (16-153) N = 20	0.07 ± 0.05 N = 29	1.4	4	2.7	0.7	2.7	1.7	47	91	4
Tower of Cheimarrou (CHE) (S1)	66.3 ± 7.9 (41-100) N = 6	22.5 ± 7.1 (8-54) N = 6	151.7 ± 30.4 (40-322) N = 9	13.2 ± 3.9 (1-32) N = 9	0.11 ± 0.09 N = 15	2.0	4.9	2.7	2.7	2.7	4.8	60	64	0.5
Tower of Cheimarrou (CHE) (S2)	113.8 ± 19.8 (74-198) N = 6	65.3 ± 23.4 (10-175) N = 6	237 ± 15.0 (125-175) N = 3	30.3 ± 6.1 (13-34) N = 3	0.6 ± 0.0 N = 9	0	8.5	6	6	5	4.8	47	85	1
Apaliros (AP) (S1)	83.8 ± 6.4 (67-120) N = 9	56.9 ± 5.8 (5-50) N = 7	114.5 ± 15.4 (77-266) N = 13	38 ± 25.6 (5-269) N = 13	0.13 ± 0.0 N = 22	1.4	7	2.3	3	1.3	10	5	51	1
Apaliros (AP) (S2)	96.1 ± 10.0 (50-130) N = 9	44.5 ± 22.3 (5-200) N = 9	136.7 ± 9.6 (40-150) N = 11	75.1 ± 9.9 (8-100) N = 11	0.04 ± 0.05 N = 20	0	5.7	0.3	0.3	0.3	10	60	46	1
Average	83.1 ± 2.4 (41-198) N = 136	51.5 ± 3.7 (4-204) N = 131	127.2 ± 4.5 (24-350) N = 177	41.5 ± 3.6 (1-269) N = 175	1.06 ± 0.14 (1-2) N = 285									

Table 1: Site characteristic data means from all 14 study sites. Sites are ranked by number of visitors with S1 (high human visitation sites) placed above their respective S2 (low human visitation) counterpart. Dependent variables (left) are FID_D, DR_D, FID_H, DR_H, and FAR (field autotomy rate) while our independent variables (right) are human visitation (Sqrt./Transformed), predator relative abundances (R.A.), vegetation cover, wall cover, and lizard density. All average values of FID, DR, and FAR (field autotomy rate) per site are accompanied by their standard error, minimum, maximum, and sample size. We also included the standard error, minimum, maximum and sample size of the average values across all sites for FID, DR, and FAR in the bottom row.

<i>Model</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>Akaike Weight</i>
HD+WC+LD+VC+MD	1196.349	-	0.9091
HD+WC+VC+MD	1201.124	4.775	0.0835
HD+WC+LD+MD	1206.841	10.492	0.0048
HD+WC+MD	1210.569	14.220	0.0007
HD+WC+CD	1210.616	14.267	0.0007
HD+WC+TPD	1210.988	14.639	0.0006
HD+WC+ PD	1211.301	14.952	0.0005

Table 2: The seven candidate mixed models for decoy flight initiation distance (FID_D) using differing combinations of fixed effects. Fixed effects used were marten density (MD), lizard density (LD), wall cover (WC), vegetation cover (VC), human density (HD), cat density (CD), terrestrial predator density (TPD), and total predator density (PD). Better fitting models are listed higher and worse ranked lower. We show the respective AIC_c, ΔAIC_c, and Akaike weight of each model. Based off of these metrics, the proposed model HD+WC+LD+VC+MD was best fitting. Human density and wall cover were included in all candidate models because both variables were known to be functionally related to FID.

<i>Model</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>Akaike Weight</i>
HD+WC+LD+VC+RD	1870.269	-	0.9409
HD+WC+VC+RD	1885.023	5.754	0.0523
HD+WC+LD+RD	1889.700	10.431	0.0051
HD+WC+RD	1894.073	14.804	0.0006
HD+WC+MD	1896.769	17.500	0.0001
HD+WC+ PD	1896.864	17.595	0.0001
HD+WC+TPD	1898.691	19.422	5.7033E-05
HD+WC+CD	1898.891	19.622	5.1605E-05

Table 3. The eight candidate mixed models for human flight initiation distance (FID_H) using differing combinations of fixed effects. Potential fixed effects used were marten density (MD), cat density (CD), terrestrial predator density (TPD), total predator density (PD), lizard density (LD), wall cover (WC), vegetation cover (VC), human density (HD) and raptor density (RD). Better fitting models are listed higher and worse listed lower. We show the respective AIC_c , ΔAIC_c , and Akaike weight for each model. Based off of these metrics, the proposed model HD+WC+LD+VC+RD was the best fitting.

<i>Model Term</i>	<i>F Stat & DF</i> <i>1,2</i>	<i>95% Confidence Interval</i>		<i>B. Coef. & Std. Error</i>	<i>t</i>	<i>Sig.</i>
		<i>Lower</i>	<i>Upper</i>			
Human Visitation (Sqrt./Transf.)	$F_{1,125} = 3.49$	-4.52	0.13	-2.20 ± 1.18	-1.87	0.06
Marten (R.A)	$F_{1,125} = 7.00$	1.31	9.10	5.20 ± 2.00	2.65	0.01
Wall Cover	$F_{1,125} = 4.78$	-57.36	-2.84	-30.10 ± 13.77	-2.19	0.03
Vegetation Cover	$F_{1,125} = 2.22$	-88.70	12.48	-38.11 ± 25.56	-1.49	0.14
Lizard Density	$F_{1,125} = 1.13$	-2.39	7.92	2.77 ± 2.61	1.10	0.29

Table 4: The above table shows the relevant statistics from our best performing multivariate mixed model for FID_D and its fixed effects. Our fixed effects for this model included (from top to bottom) human visitation, marten relative abundance, wall cover, vegetation cover, and lizard density. The statistics we have included in this table for each fixed effect respectively include (from left to right) an F-statistic and associated degrees of freedom, our confidence interval, a beta coefficient and associated standard error, a t-value, and a p-value. Based on the above, we can conclude that marten abundance and wall cover have statistically significant relationships with FID_D.

Model Term	F Stat & DF 1,2	95% Confidence Interval		B. Coef. & Std. Error	t	Sig.
		Lower	Upper			
Human Visitation (Sqrt./transf.)	$F_{1,169} = 7.30$	-10.87	-1.69	-6.28 ± 2.32	-2.70	0.01
Raptor (R.A)	$F_{1,169} = 3.52$	-18.19	0.46	-8.90 ± 4.72	-1.88	0.06
Wall Cover	$F_{1,169} = 6.55$	-115.10	-14.85	-65.00 ± 25.38	-2.56	0.01
Vegetation Cover	$F_{1,169} = 1.35$	-117.34	30.35	-43.50 ± 37.41	-1.16	0.25
Lizard Density	$F_{1,169} = 1.23$	-3.55	12.67	4.56 ± 4.11	1.11	0.27

Table 5: Statistics table for our best-performing model for human FID (FID_H). Our fixed effects for this model included (from top to bottom) human visitation, raptor relative abundance, wall cover, vegetation cover, and lizard density. The statistics we have included in this table for each fixed effect respectively include (from left to right) an F-statistic and associated degrees of freedom, our confidence interval, a beta coefficient and associated standard error, a t-value, and a p-value. Based on the above, we can conclude that human visitation and wall cover have statistically significant relationships with FID_H .

Images



1.



2.

Images 1-2: **Image one (top)** depicts our taxidermized stone marten decoy atop of our RC car. The RC is obscured by a chicken-wire mesh skirt fitted with local vegetation for concealment. The decoy was fastened to the RC atop of the car's chassis via a wooden board. **Image two (bottom)** depicts a male wall lizard sitting atop a rock watching a group of tourists pass by. This photo (captured by a trail camera) was taken near the well visited archaeological ruins of the "Kouros of Flerio".

3.



4.



5.



6.



Images 3-6: **Image three (top left)** shows the highly touristed paleo-Christian church, Panagia Drosiani. The site was heavily walled and was home to many reptiles. **Image 4 (top right)** depicts our least trafficked site, Apaliros Castle. This castle was a Byzantine sanctuary. Due to its isolated location and steep cliff faces, it is rarely frequented. The ruins have abundant wildlife and sparse vegetation. Man-made structures have fallen into disrepair and the area has largely reverted into “phrygana” (a small-woody shrub assemblage common in the Aegean (Greek word)) due to consistent goat grazing over the years. **Image 5 (bottom left)** depicts the S1 site and ruins of the Kouros of Faranaghi. This site was moderately trafficked by visitors and had many stone walls and increased vegetation surrounding the ruins. **Image 6 (bottom right)** shows the accompanying S2 site at the Kouros of Faranaghi. This site was less trafficked and had less vegetation cover. Both S1 and S2 sites at the Kouros of Faranaghi were densely walled likely due to having ruins dating back to the Archaic period of Greek history (800-480 BCE).

Appendix I

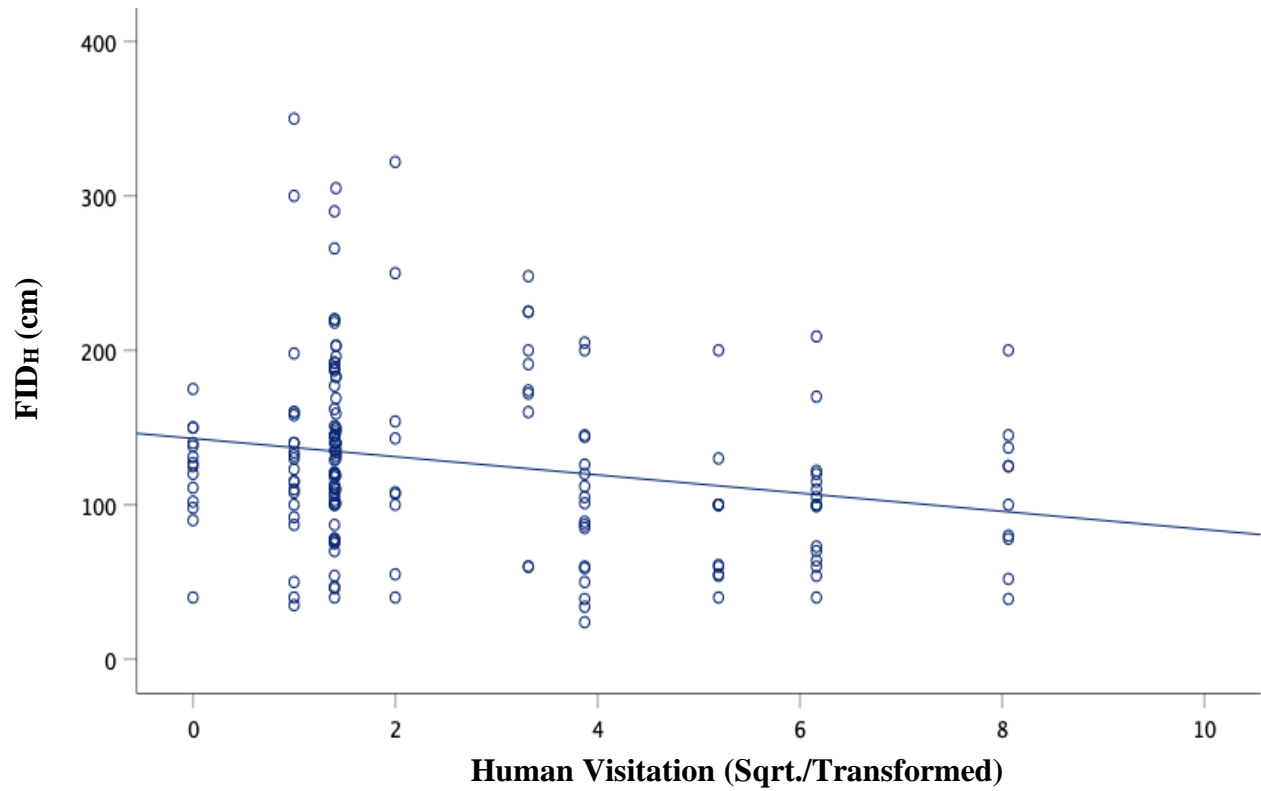


Figure 6: Relationship between human visitation (Sqrt./Transformed) and FID_H (cm) from our best performing multivariate model of FID_H ($F_{1,169} = 7.30$, $t = -2.70$, $P = 0.01$, $N = 175$). Circles represent individual lizards whom FID was measured from across sites.

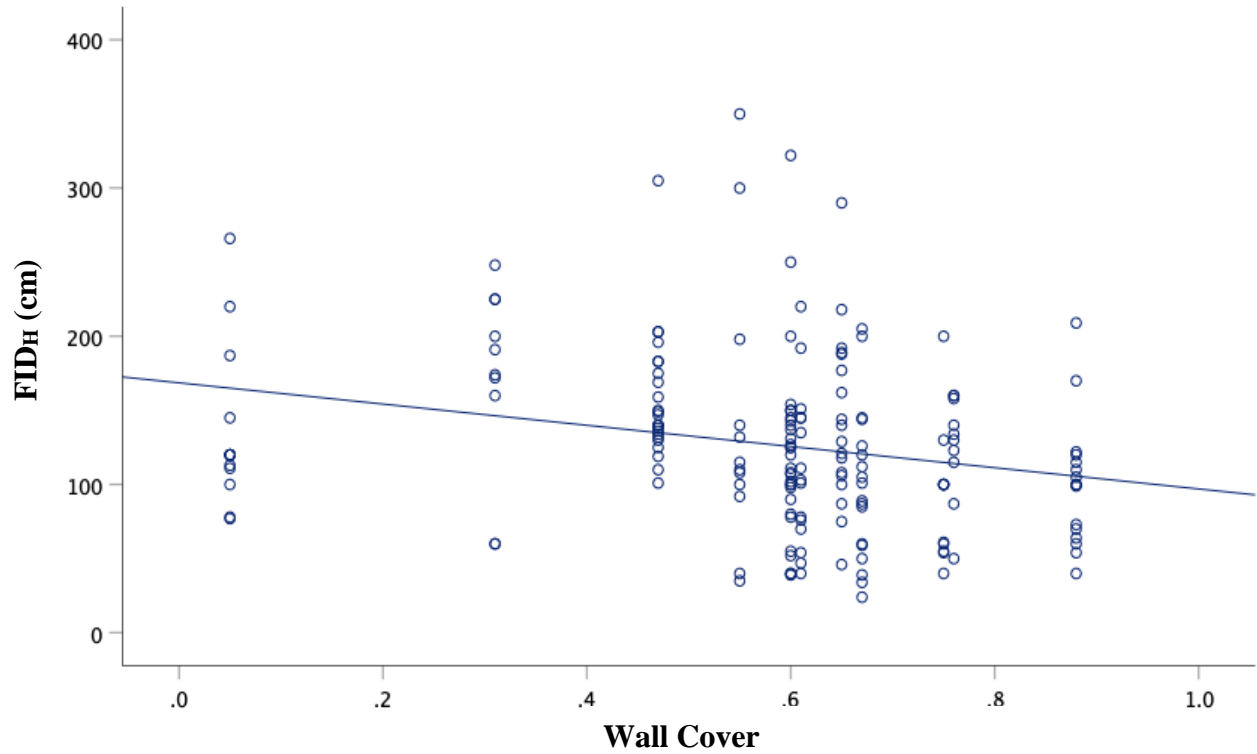


Figure 7: Relationship between FID_H and the average proportional wall cover per site from our best performing multivariate model for FID_H ($F_{1,169} = 6.55$, $t = -2.56$, $P = 0.01$, $N = 175$). Circles represent individual lizards whom FID was measured across sites.

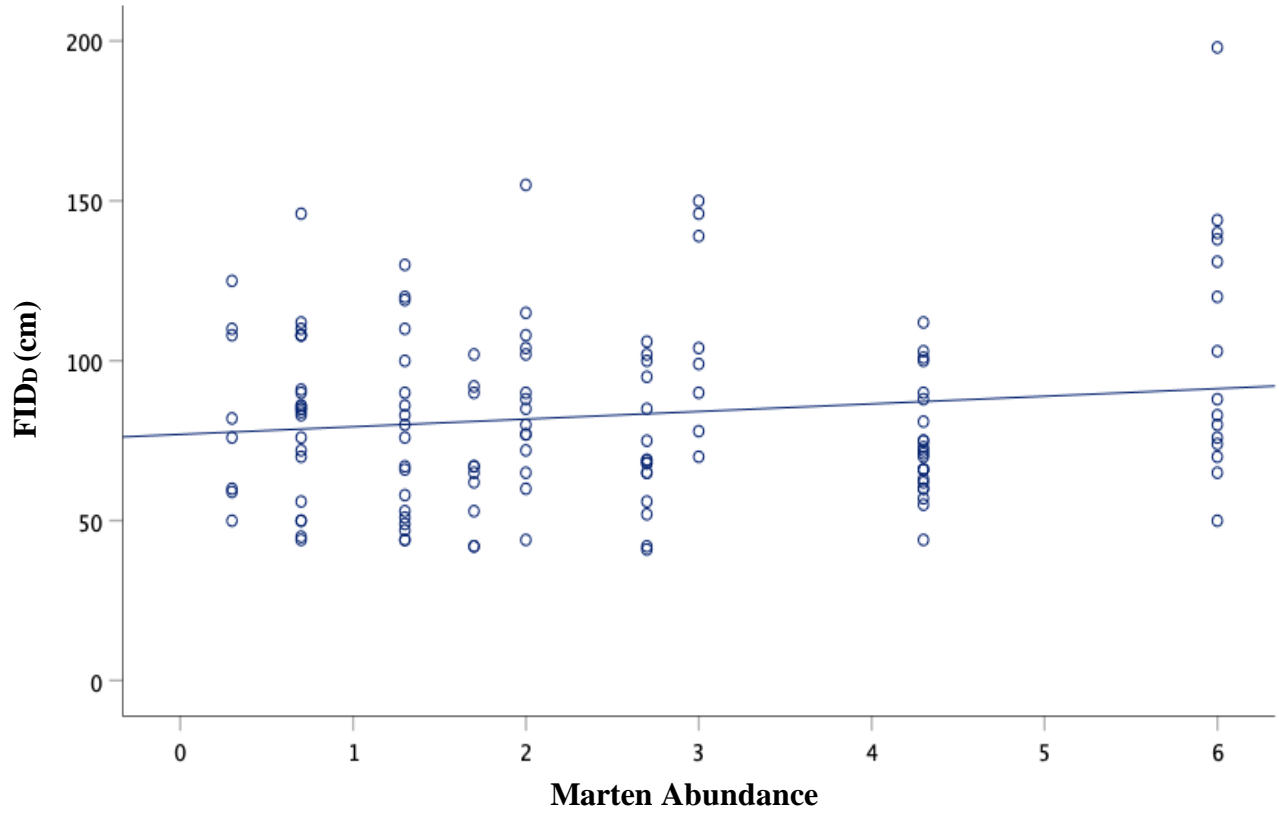


Figure 8: Scatterplot of FID_D and marten abundance across sites from our best performing multivariate model of FID_D ($F_{1,125} = 7.00$, $t = 2.65$, $P = 0.01$, $N = 131$). Individual lizards' associated FIDs are represented as blue circles on the scatterplot.

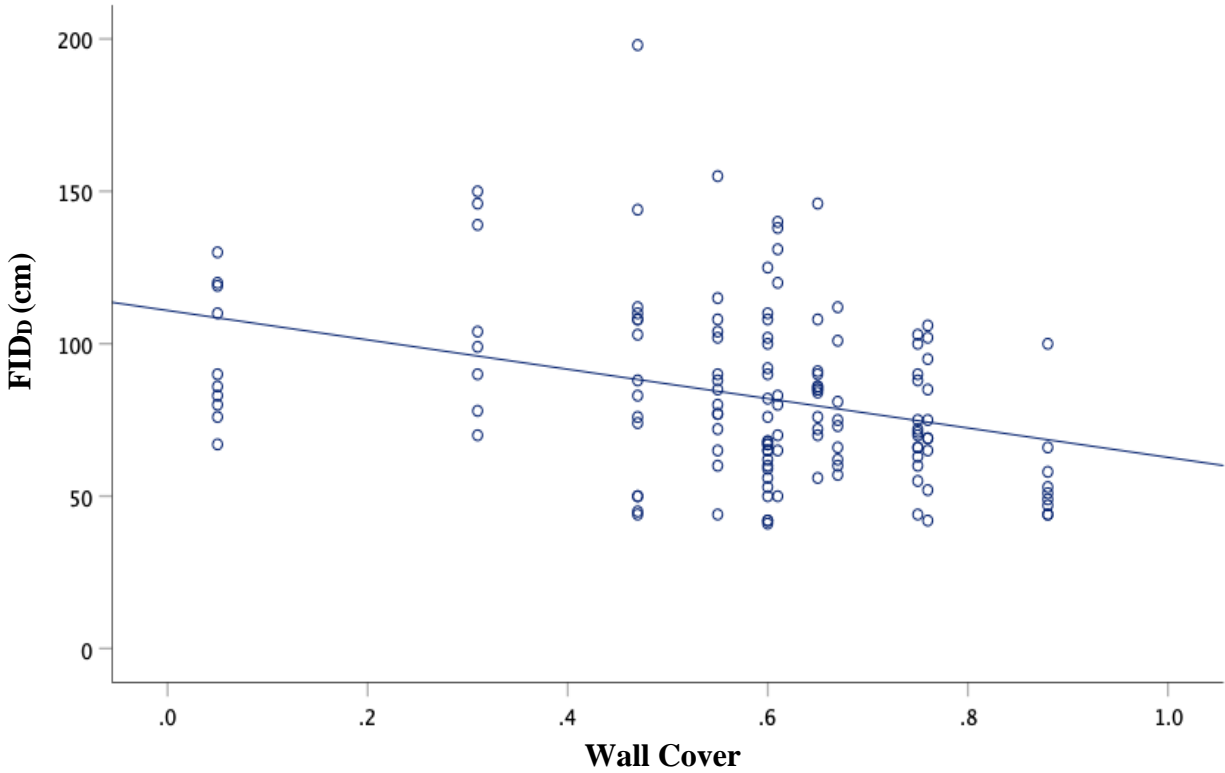


Figure 9: Relationship between FID_D and the associated average proportional wall cover from our best performing multivariate model for FID_D ($F_{1,125} = 4.78$, $t = -2.19$, $P = 0.03$, $N = 131$). Circles represent the FID_D's of individual lizards.

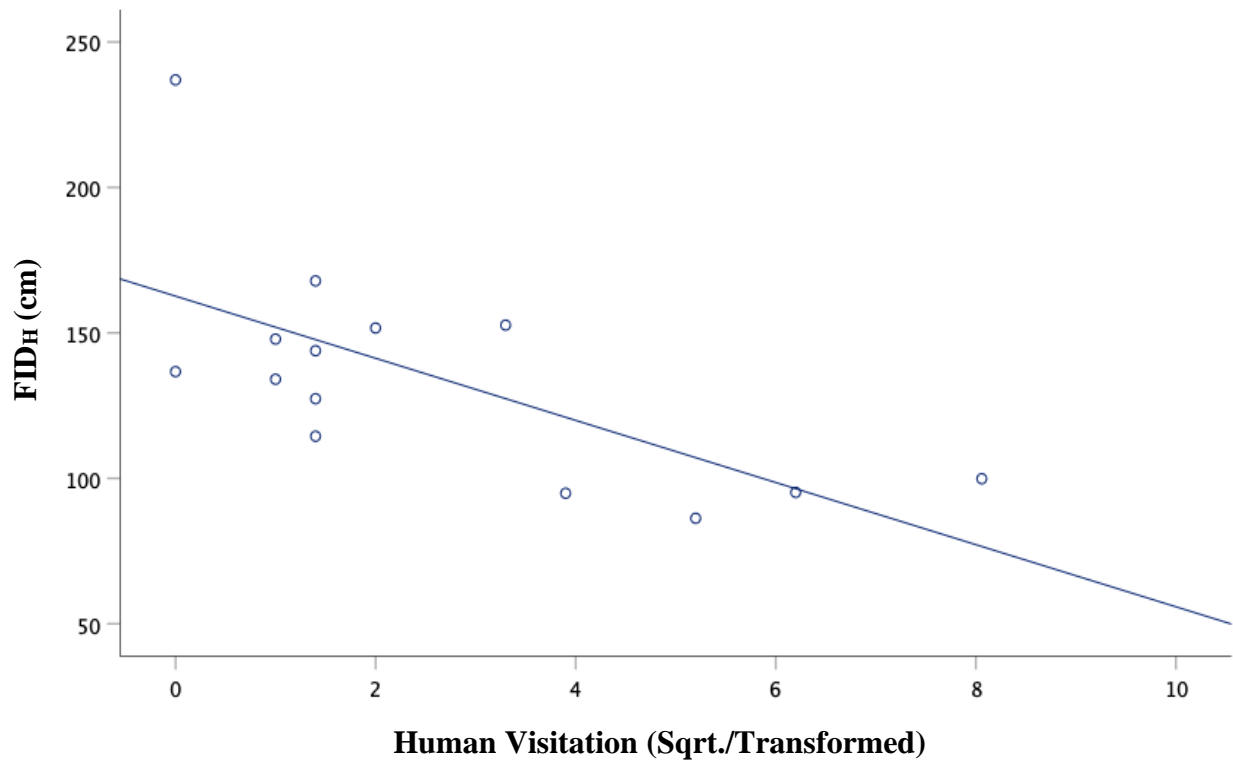


Figure 10: Scatterplot depicting the significant negative correlation between mean FID_H (cm) and human visitation (Sqrt./Transformed) per site ($r = -0.59$, $P = 0.01$, $N = 14$).

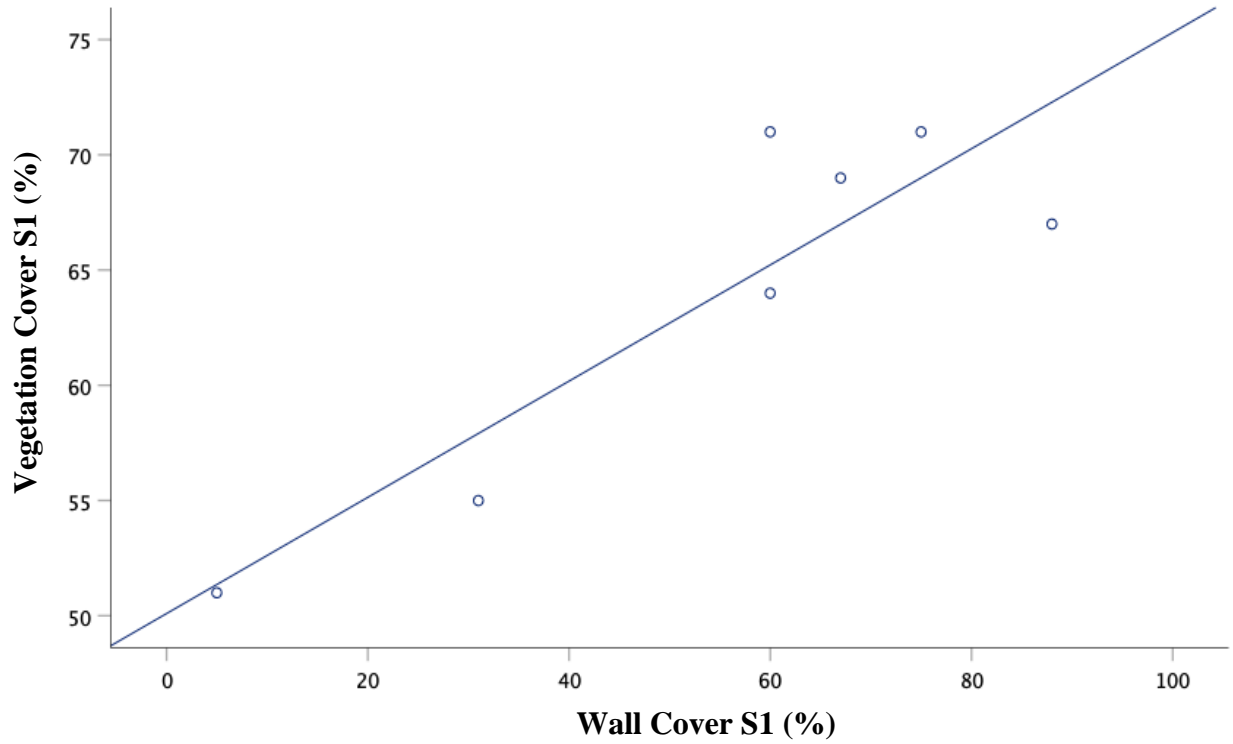


Figure 11: More walls permit more vegetation to grow at a site. Above is a scatterplot depicting the positive correlation between average wall density and vegetation cover at high human visitation sites ($r = 0.89$, $P = 0.01$, $N = 7$). Both wall cover and vegetation cover are expressed as percentages.

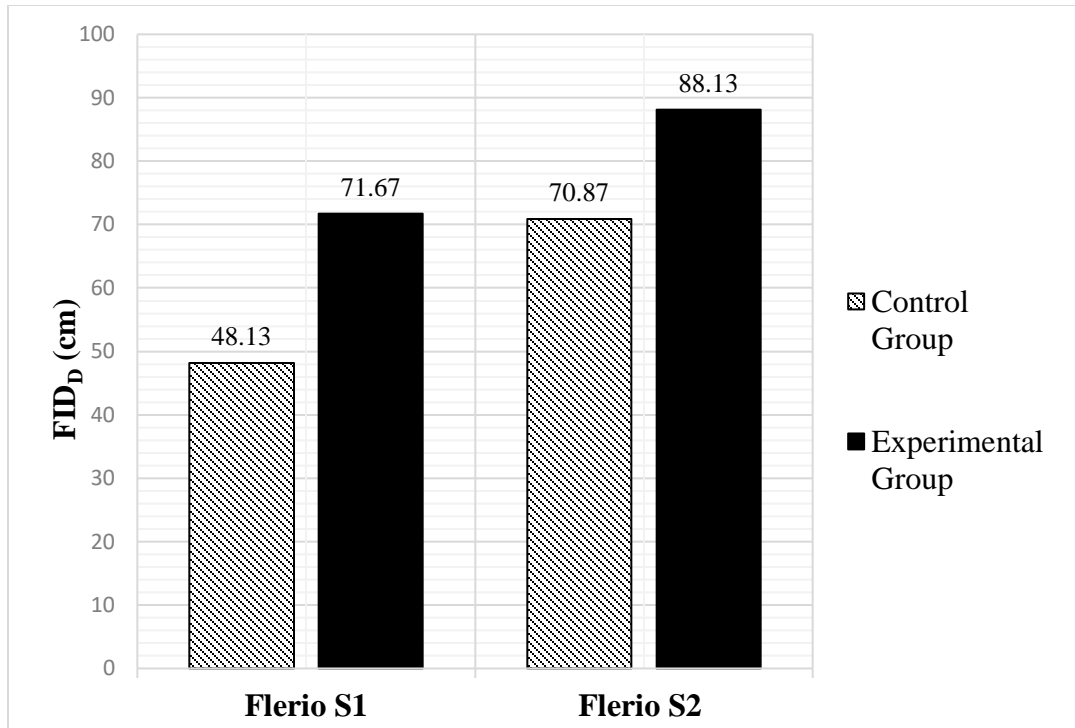


Figure 12: To test whether or not lizards responding to our FID_D trials were more concerned by our mounted decoy predator rather than our RC car, we ran an experimental set of control trials. We performed FID_D trials at the Kouros of Flerio with and without the mounted predator decoy. Above is a comparative bar graph displaying the difference between mean FID_D (cm) at the archaeological ruins of Flerio (high human visitation and low human visitation sites are represented respectively as S1/S2) (S1: $N = 15$, Mean FID_D = 48.13 cm; S2: $N = 15$, Mean FID_D = 70.87 cm). The full black bars represent the mean FID from our “control” testing at the Kouros of Flerio (S1 & S2). For these trials, our RC car was driven at lizards under the same trial parameters as all other FID_D trials, only without the stuffed marten decoy on the top of the vehicle (S1: $N = 15$, Mean FID_D = 71.67 cm; S2: $N = 15$, Mean FID_D = 88.13 cm). These control trials show that lizards had a stronger reaction to the RC with the mounted decoy than to the RC car alone. Experimental and control testing occurred with ample time in between data collection dates to avoid researcher habituation at these sites.

References

- Ålund, M., Harper, B., Kjærnested, S., Ohl, J.E., Phillips, J.G., Sattler, J., Thompson, J., Varg, J.E., Wargenau, S., Boughman, W., Keagym J. 2022. Sensory environment affects Icelandic threespine stickleback's anti-predator escape behaviour. *Proceedings of the Royal Society B*, 289(1972): 1-10.
- Amo, L., López, P., Martín, J. 2004. Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges. *Animal Behaviour*, 67(4): 647-653.
- Amo, L., López, P., Martín J. 2006. Can wall lizards combine chemical and visual cues to discriminate predatory from non-predatory snakes inside refuges? *Ethology*, 112(5): 478-484.
- Amo, L., López P., Martín, J. 2007. Habitat deterioration affects body condition of lizards: a behavioral approach (*Iberolacerta cyreni*). *Biological Conservation*, 135(1): 77-85.
- Anderson, D.R., Burnham, K.P., 2002. Model selection and interference: a practical information-theoretic approach. 2nd edition. *Springer-Verlag*.
- Bakaloudis, D.E., Vlachos, C.G., Papakosta, M.A., Bontzorlos, V.A., Chatzinikos, E.N. 2012. Diet composition and feeding strategies of the stone marten (*Martes foina*) in a typical Mediterranean ecosystem. *The Scientific World Journal*, 2012: 1-11.
- Batabyal, A., Balakrishna, S., Thaker, M. 2017. A multivariate approach to understanding shifts in escape strategies of urban lizards. *Behavioral Ecology and Sociobiology*, 71(83): 1-8.
- Bateman, P.W., Fleming, P.A. 2008. To cut a long tail short: a review of lizard caudal autotomy studies carried out over 20 years. *Journal of Zoology*, 277(1): 1-14.
- Bateman, P.W., Fleming, P.A. 2011. Does human pedestrian behaviour influence risk assessment

- in a successful urban adapter? *Journal of Zoology*. 952: 1-12.
- Blumstein D.T., Daniel, J.C. 2005. The loss of anti-predator behaviour following isolation on islands. *Proceedings of the Royal Society B*, 272(1573): 1663-1668.
- Brock, K.M., Bednekoff, P.A., Pafilis, P., Fouflopoulos, J. 2015. Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): the sum of all fears? *Evolution*, 69(1): 216-231.
- Burnham, K.P., Anderson, D.R. 1998. Practical use of the information-theoretic approach. In: Model Selection and Inference. *Springer*, New York, NY. 75-117.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65: 23-25.
- Bursac, Z., Gauss, C.H., Williams, D.K., Hosmer, D.W. 2008. Purposeful selection of variables in logistic regression. *Source Code for Biology and Medicine*, 3(17): 1-8.
- Camp, M.J., Rachlow, J.L., Woods, B.A., Johnson, T.R., Shipley, L.A. 2012. When to run and when to hide: the influence of concealment, visibility, and proximity to refugia on perceptions of risk. *Ethology*, 118(10): 1010-1017.
- Caro, T. M. 2005. Antipredator defenses in birds and mammals. *University of Chicago Press*.
- Coleman, A., Richardson, D., Schechter, R., Blumstein D.T. 2008. Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*). *Animal Behaviour*, 4: 250-252.
- Cooper, W.E.J. 2009. Theory successfully predicts hiding time: new data for the lizard *Sceloporus virgatus* and a review. *Behavioral Ecology*, 20(3): 585-592.

- Cooper, W.E.J., Pérez-Mellado, V. 2012. Historical influence of predation pressure on escape by *Podarcis* lizards in the Balearic Islands. *Biological Journal of the Linnean Society*, 107(2): 254-268.
- Crow, J., Vionis, A., Turner, S. 2011. Characterizing the historic landscapes of Naxos. *Journal of Mediterranean Archaeology*, 24(1): 111-137.
- Dellinger, J.A., Shores, C.R., Craig, A., Heithaus, M.R., Ripple, W.J., Wirsing, A.J. 2019. Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. *Oecologia*, 189: 487-500.
- Denardo, D.F., Licht, P. 1993. Effects of corticosterone on social behavior of male lizards. *Hormones and Behavior*, 27(2): 184-199.
- Diego-Rasilla, F.J. 2003. Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. *Behavioural Processes*, 63(1): 1-7.
- Donihue, C.M. 2016. Drivers of functional trait variability in *Podarcis erhardii*, the Aegean wall lizard. Available from Agricultural & Environmental Science Collection; *ProQuest Dissertations & Theses Global*.
- Doornik, J.A., Hansen, H. 2008. An omnibus test for univariate and multivariate normality. *Oxford Bulletin of Economics and Statistics*, 70(1): 927-939.
- Fernández-Juricic, E., Venier, M.P., Renison, D., Blumstein, D.T. 2005. Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biological Conservation*, 125(2): 225-235.
- Geffroy, B., Diogo, S.M.S., Eduardo, B., Blumstein, D.T. 2015. How nature-based tourism might increase prey vulnerability to predators. *Trend in Ecology & Evolution*, 30(12): 755-765.

- Gikas, P., Tchobanoglous, G. 2009. Sustainable use of water in the Aegean Islands. *Journal of Environmental Management*, 90(8): 2601-2611.
- Gizicki, Z.S., Tamez, V., Galanopoulou, A.P., Avramidis, P., Foufopoulos, J. 2017. Long-term effects of feral goats (*Capra hircus*) on Mediterranean island communities: results from whole island manipulations. *Biological Invasions*, 20: 1537-1552.
- Iglesias-Carrasco, M., Head, M.L., Cabido, C. 2016. Habitat dependent effects of experimental immune challenge on lizard anti-predator responses. *Behavioral Ecology and Sociobiology*, 70: 1931-1939.
- Isbell, L.A., Young, T.P. 1993. Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behaviour*, 45(6): 1233-1235.
- Kemp, A., Kemp, M., Thong-Aree, A. 2011. Use of lookout watches over forest to estimate detection, dispersion and density of hornbills, Great Argus and diurnal raptors at Bala Forest, Thailand, compared with results from in-forest line transects and spot maps. *Bird Conservation International*, 21(4): 394-410.
- Langkilde, T., Shine, R. 2006, How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*, *Journal of Experimental Biology*, 209(6): 1035-1043.
- Lapiedra, O., Chejanovski, Z., Kolbe, J.J. 2016. Urbanization and biological invasion shape animal personalities. *Global Change Biology*, 23(2): 592-603.
- Li, B., Belasen, A., Pafilis, P., Bednekoff, P., Foufopoulos, J. 2014. Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: insights from an ancient introduction. *Proceedings of The Royal Society B.*, 281(1788): 1-6.

- Li, J., Huang, L., Liu, C. 2011. An efficient self-learning people counting system. *IEEE*, 1: 1-6.
- Lima, S.L., Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4): 619-640.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior*. 27: 215-290.
- Lima, S.L., Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, 153(6): 649-659.
- Lisiecki, C., Foufopoulos, J. 2022. Profits vs. preservation: how can shepherds balance the social and ecological costs of livestock grazing on Naxos. *World Development Perspectives*, 26: 1-8.
- Lo, S., Andrews, S. 2015. To transform or not to transform: using generalized linear mixed models to analyze reaction time data. *Frontiers in Psychology*. 6: 1-16
- Longland, W.S., Price, M.V. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitats use? *Ecology*, 72(6): 2261-2273.
- Lymberakis, P., Pafilis, P., Poulakakis, N., Sotiropoulos, K., Valakos, E.D. 2018. Amphibians and Reptiles of the Aegean Sea. *Biodiversity of the Aegean. In Honor of Prof. Moysis Mylonas*: 169-189.
- Maguran, A.E., Seghers, B.H., Carvalho, G.R., Shaw, P.W. 1993. Evolution of adaptive variation in anti-predator behaviour. *Behavioural Ecology of Fishes*, 23(1-4): 1-8.
- Maurer, A.S., Cove, M.V., Siegal, O.M., Lashley, M.A. 2022. Urbanization affects the behavior of a predator-free ungulate in protected lands. *Landscape and Urban Planning*, 222: 104-391.

- Morelli, F., Mikula, P., Blumstein, D.T., Díaz, M., Markó, G., Jokimaki, J., Kaisanlahti-Jokimäki, M.L., Floigl, K., Zeid, F.A., Siretckaia, A., Benedetti, Y. 2022. Flight initiation distance and refuge in urban birds. *Science of The Total Environment*, 842(10): 1-8.
- Olson, S.H., Cameron, K., Reed, P., Ondzie, A., Joly, D. 2012. Maximizing nonhuman primate fecal sampling in the Republic of Congo. *Journal of Wildlife Diseases*, 48(4): 888-898.
- Pafilis, P., Meiri, S., Fougopoulos, J., Valakos, E. 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften*, 96: 1107-1113.
- Pellitteri-Rosa, D., Bellati, A., Cocca, W., Gazzola, A., Marín, J., Fasola, M. 2017. Urbanization affects refuge use and habituation to predators in a polymorphic lizard. *Animal Behaviour*, 123: 359-367.
- Pietrek, A.G., Walker, R.S., Novaro, A.J. 2009. Susceptibility of lizards to predation under two levels of vegetation cover. *Journal of Arid Environments*, 73(4-5): 574-577.
- Preisser, E. L., Bolnick, D. I., & Benard, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*. 86(2): 501-509.
- Preisser, E.L., Orrock, J.L., Schmitz, O.J. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88(11): 2744-2751.
- Rodriguez-Prieto, I., Fernández-Jurcic, E., Martín, J., Regis, Y. 2009. Antipredator behavior in blackbirds: habituation complements risk allocation. *Behavioral Ecology*, 20(2): 371-377.
- Romero, L.M., Wikelski, M. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galápagos marine iguanas. *Biological Conservation*, 108(3): 371-374.
- Rowcliffe, M., Carbone, C. 2008. Surveys using camera traps: are we looking to a brighter future? *Animal Conservation*, 11: 185-186.

- Santos, M.J., Rosalino, L.M., Matos, H.M., Santos-Reis, M. 2016. Riparian ecosystem configuration influences mesocarnivores presence in Mediterranean landscapes. *European Journal of Wildlife Research*, 62: 251-261.
- Shannon, G., Angeloni, L.M., Wittemeyer, G., Fristrup, K.M., Crook, K.R. 2014. Road traffic modifies behavior of a keystone species. *Animal Behaviour*, 94: 135-141.
- Shutt, K., Heistermann, M., Kasim, A., Todd, A., Kalousova, B., Profosouva, I., Petrzelkova, K., Fuh, T., Dicky, J.F., Bopalanzognako, J.B., Setchell, J.M. 2014. Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. *Biological Conservation*, 172: 72-79.
- Silk, M.J., Harrison, X.A., Hodgson, D.J. 2020. Perils and pitfalls of mixed-effects regression models in biology. *PeerJ*, 10: 1-20.
- Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J., Bidder, O.R., Middleton, A.D. 2019. Habitat complexity mediates the predator-prey space race. *Ecology*, 100(7): 1-8.
- Stewart, A., Campbell, J. (Eds.). 2019. A companion to the archaeology of early Greece and the Mediterranean, Two Volume Set. *John Wiley & Sons*.
- Stille, M., Gasteratos, I., Stille, B. 2021. Larger mammals of Corfu, Ionian Islands, Greece- status and potential threats. *Russian Journal of Theriology*, 20(2): 202-214.
- Symonds, M.R.E., Moussalli, A. 2010. A brief guide to model selection, multimodal inference, and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65: 13-21.
- Tellería, J.L., Virgós, E., Carbonell, R., Pérez-Tris, J., Santos, T. 2003. Behavioural

- responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos*, 95(2): 253-264.
- Uchida, K., Suzuki, K., Shimamoto, T., Yanagawa, H., Koizumi, I. 2015. Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. *Journal of Zoology*, 298(3): 225-231.
- Uchida, K., Suzuki, K., Shinamoto, T., Yanagawa, H., Koizumi, I. 2019. Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behavioral Ecology*, 30(6): 1583-1590.
- Vlachopoulos, A.G. and Charalambidou, X. 2019. Naxos and the Cyclades. In *A Companion to the Archaeology of Early Greece and the Mediterranean* (eds I.S. Lemos and A. Kotsonas).
- Visser, V., Langdon, B., Pauchard, A., Richardson, D.M. 2013. Unlocking the potential of Google Earth as a tool in invasion science. *Biological Invasions*. 16: 513-534.
- Vos, K., Splinter, K.D., Harley, M.D., Simmons, J.A., Turner, A.L. 2019. *CoastSat*: a Google Earth Engine-enabled Python toolkit to extract shorelines from publicly available satellite imagery. *Environmental Modeling & Software*. 122: 1-7.
- Wagnon, C.J., Schooley, R.L., Cosentino, B.J. 2020. Shrub encroachment creates a dynamic landscape of fear for desert lagomorphs via multiple pathways. *Ecosphere*, 11(9): 1-16.
- Whalley, W.B. 2021. Geomorphological information mapping of debris-covered ice landforms using Google Earth: an example from the Pico de Posets, Spanish Pyrenees. *Geomorphology*. 393: 1-14.
- Wheeler, H.C., Hik, D.S. 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Animal Behaviour*, 95: 1-8.

Wolf, I.D., Croft, D.B. 2010. Minimizing disturbance to wildlife by tourists approaching on foot or in a car: a study of kangaroos in the Australian rangelands. *Applied Animal Behaviour Science*, 126(1-2): 75-84.

Zanette, L.Y., White, A.F., Allen, M.C., Clinchy, M. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, 334(6061): 1398-1401.