Human Subsidies Facilitate Hyperpredation of Mediterranean Island Wildlife by Outdoor Cats

by

Jeffrey Ferrer

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Thesis Committee:

Johannes Foufopoulos, Associate Professor (Chair)

John Vandermeer, Associate Professor

Abstract

Domestic cats (*Felis catus*) are avid wildlife predators and one of the most harmful invasive species, having been a causal factor in over 60 species extinctions worldwide (Doherty et al., 2016). The lethal impacts of an introduced predator such as cats on wildlife can be further exacerbated by the introduction of an additional abundant non-native prey species capable of supporting an exceptionally dense predator population, a phenomenon known as hyperpredation. A special case of hyperpredation involves human food subsidies, when an invasive predator impacting native wildlife is supported not by another invasive taxon, but by human-derived food sources. To test whether access to anthropogenic food subsidies by cats is causing hyperpredation, mark-recapture methodology was used to measure twelve cat populations experiencing a gradient of human subsidies on the Mediterranean island of Naxos, Greece. Line-transect surveys were conducted at each site to measure reptile population abundance across this gradient, and other factors including human density and distance of reptiles from villages were considered as well. Strong evidence was found that the population size of cats is a direct result of the density of anthropogenic food available to them, and a corresponding decline in the size of reptile populations as cat density increased was observed. It was also shown that as cat populations exceed the available supply of human food, the negative effects of cat density on reptile populations are exacerbated. These results demonstrate that access to anthropogenic subsidies has allowed cat populations to expand to exceptional levels, driving hyperpredation on island wildlife.

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1. Introduction

1.1 Invasive Species and Cats

Invasive species are one of the greatest threats to biodiversity worldwide (Wilcove et al., 1998, Tilman et al., 2017, Hald-Mortensen 2023). Invasive species have been implicated in over 50% of all modern extinctions whose causes are known, and in about 20% of total cases, invasive species have been identified as the sole driver of extinction (Clavero & García-Berthou 2005, Bellard et al., 2016). One of the most harmful groups of invasive species are mammals, who currently threaten more IUCN listed critically endangered terrestrial vertebrate species than any other group, an impact driven primarily by black rats (*Rattus rattus*) and domestic cats (*Felis catus*) (Dueñas et al., 2021).

Cats have been linked to ≥ 63 vertebrate extinctions (Doherty et al., 2016) and are recognized as one of the most harmful invasive species due to their global distribution and devastating impacts on wildlife (Loss et al., 2022). In the United States alone, it has been estimated that cats kill billions of birds, mammals, and reptiles each year, with mortality driven primarily by unowned free-roaming cats, rather than pets (Loss et al., 2013). In addition to direct predation, cats can have many other negative effects on wildlife such as influencing prey behavior by increasing prey wariness and decreasing foraging time (Stone 1994, Li et al. 2014), transmission of diseases such as rabies, toxoplasmosis, cutaneous larval migrans, tularemia, and plague (Gerhold & Jessup 2013), and loss of genetic integrity in native species such as the Eurasian wildcat (*Felis silvestris silvestris*) through hybridization (Beutel et al., 2017).

The damaging effects of cats are particularly prevalent on islands (Medina et al., 2011). Despite making up only 5.3% of the Earth's landmass, 61% of all known extinctions have occurred on islands, and invasive species have been cited as the most frequent cause of insular species extinctions (Tershy et al., 2015). Island communities are disproportionately affected by invasive mammalian predators, and especially cats, where a general lack of native predators typically results in down-regulated antipredator responses, rendering island wildlife relatively tame and easy to capture (Courchamp et al. 1999). Cats have emerged as the causal factor in at least 33 extinctions of insular vertebrate species (Loss et al., 2013), and because they have already been introduced to most suitable islands worldwide (Medina 2011), they represent a threat to numerous additional island endemics (Stone 1994).

1.2. Hyperpredation

The impacts of an introduced predator on native prey can be exacerbated by the introduction of an additional non-native prey species, a phenomenon known as hyperpredation (Smith & Quinn 1996, Bonsall & Hassell 1997, Courchamp et al., 2000, Courchamp et al., 2000). When this occurs, a rapidly reproducing non-native prey species supports an unusually dense population of predators. This can have severe consequences for the native prey species, which may be decimated by the resulting increase in predators. For example, the extinction of the endemic Macquarie Island Parakeet (*Cyanoramphus*

novaezelandiae erythrotis) is thought to have occurred following cat hyperpredation. Although cats were introduced onto Macquarie Island within ten years of its discovery in 1810, the native parakeet withstood predation and remained numerous there until about 1880. Then in 1879, European rabbits (*Oryctolagus cuniculus*) were released onto the island and reproduced rapidly. Within a few years, cat populations persisting primarily on rabbits expanded rapidly, and the parakeet was last definitively seen in 1890 (Taylor 1979, Smith & Quinn 1996, Courchamp 2000). Hyperpredation has since been recorded in several systems (Imber et al., 2000, Roemer et al., 2001, Pope et al., 2008, Carpio et al., 2015), and understanding how to predict and manage it will only increase in importance as the spread of invasive species is expected to increase with the expansion of global trade networks (Levine & D'Antonio 2003).

1.3. Subsidized Predators

A related situation can occur when an invasive predator, impacting native wildlife, is supported not by another invasive taxon, but by human-derived food sources (Maeda et al., 2019, see Fig. 1). In many urban environments, densities of predators increase simply through ease of access to anthropogenic resources like trash and hand-outs. (Liberg et al., 2000, Fedriani et al., 2001, Newsome et al., 2015). For example, while cats are typically solitary and territorial hunters, the presence of large quantities of a stable food resource can alter their behavior by reducing their home-range size and territoriality, increasing tolerance of home-range overlap, and leading to the formation of cat colonies (Izawal & Ono 1982MacDonald 1983). While densities of cats can vary greatly, Liberg et al. (2000) found that densities above 100 cats/km^2 are only found in urban areas with a constant source of anthropogenic food supplementation. These unnaturally high densities of cats can potentially result in a unique form of hyperpredation where the introduced 'prey' that is supplementing the predator population is simply anthropogenically derived food. As cats have been shown to have high fidelity to a single feeding site (Izawal & Ono 1982), it is expected that the number of feeding sites available to cats should be correlated with the size of the cat population. However, this has yet to be demonstrated, and the extent to which increased food supplementation affects greater impacts on wildlife remains unclear as for example, more subsidies may simply result in a switch away from wildlife to anthropogenic sources.

1.4 Research Goals

Cats were first introduced to the Mediterranean islands thousands of years ago (Serpell 2000, Vigne et al., 2004, Driscoll et al., 2009) and are playing an important predator role in both urban and rural Mediterranean ecosystems (More et al., 2019, Krawczyk et al., 2019) where they have been implicated in significant wildlife mortality (Bonnaud et al., 2007, Bonnaud et al., 2012, Li et al., 2014). The goals of this study were to establish which factors support cat populations in a representative Mediterranean ecosystem (the island of Naxos in the Aegean Sea, Greece), and to determine how cats are affecting resident wildlife populations while considering other factors that may shape a possible relationship between cats and wildlife.

Methods used to answer these questions included, 1) obtaining population and density estimates of twelve discrete cat populations experiencing a range of food supplementation, 2) quantifying the amount of food supplementation available to each cat population, 3) surveying reptile communities in the natural habitat in the immediate vicinity of each of these locations, and 4) providing visual support through the development of heat maps showing the spatial distribution of cats.

By investigating these population level relationships along a gradient of food supplementation within a representative island system, this study is taking a novel and fine-grained approach that will allow a quantitative demonstration of the connection between human food subsidies and decreases in wildlife in Mediterranean wildlife.

2. Methods

2.1 Study Site

Field work was conducted during the months of May and June 2024 on the Aegean Island of Naxos, Greece. Naxos (430km^2) is the largest island in the Cyclades archipelago with a typical Mediterranean climate consisting of warm dry summers, and mild moist winters. The landscape of Naxos is characterized by xeric *phrygana*, a type of thorny summer-deciduous Mediterranean cushion scrub community dominated by *Sarcopoterium spinosum* and *Genista acanthoclada*, as well as high evergreen *maquis* dominated by *Quercus coccifera* and *Juniperus turbinata*. The wide distribution of these communities is consistent with a long history of disturbance and degradation of the original oak forest habitats through grazing and agricultural activities on the island (Sarika et al., 2015). Areas near villages consist of a mosaic of these communities mixed with irrigated gardens, grainfields, as well as olive groves.

Cycladic wildlife is dominated by reptiles which, by virtue of their life history, are particularly well suited for the Mediterranean climate (Valakos 2008). Naxos is home to 13 reptile species, including two introduced species (*Hemidactylus turcicus* and *Chalcides ocellatus*). While reptiles are overall common, communities on the island are dominated by the Aegean wall lizard (*Podarcis erhardii*), hereafter "wall lizard", which can easily be observed. Both wall lizards and other reptile taxa occur in particularly high densities along the drystone walls and terraces which act as focal points of reptile activity, and are a ubiquitous feature of the Mediterranean landscape (Solomou et al., 2022, Nossan 2023). Reptile populations in the region are likely shaped by a combination of both bottom-up, as well as top-down effects. Among lizard predators, snakes are probably the most important (Pafilis et al., 2009). The only other mammalian predator besides cats are stone martens (*Martes foina*), although because of their strictly nocturnal activity pattern, they do not likely encounter the broadly heliothermic reptiles. Because of this high aggregate biomass, reptiles are a particularly important component of Cycladic ecosystems and constitute an ideal system to investigate the impacts of cats on local species communities.

Naxos contains over 30 towns and villages that range in population size from being essentially abandoned, to the capital of Chora (with ca. 6000 inhabitants) (Hellenic

Statistical Authority. n.d.). Naxian settlements have traditionally been built in a very compact manner, facilitating defense against pirate raids (Semple 1916). They typically encompass a dense network of stone-lined footpaths that allow access to every part of the village. Household refuse is collected in select sites located at the edge of a settlement where garbage truck access is possible, creating distinct hot spots of waste accumulation. At the same time, there is a clear border and very sharp transition from the last outer row of houses to the surrounding agricultural matrix where resident wildlife occurs.

Cats can be found in large numbers in nearly every town on Naxos. At the same time, because of Naxos' arid landscape, cats are present but rare in the remote countryside, especially more than 1-2km away from human habitations (Li et al., 2014). They appear to be highly dependent on the shelter of human settlements where they readily consume nutritionally dense cat food provided by residents as well as garbage from open dumpsters (see Appendix B, Image 1). These conditions are representative of many coastal areas around the Mediterranean Basin (Krawczyk et al., 2019). Within villages, cats exist across a spectrum of associations with humans, ranging from fully domesticated and fed to completely ignored and even persecuted (personal observation). Even when affiliated with a household, cats on Aegean islands are traditionally kept as outdoor pets and are allowed to roam freely. Because they are typically fed in a yard or in the street, and because of the open nature and dense path network of island villages, it is possible to obtain a good estimate of the extent of food supplementation in each village.

This study focuses on 12 representative villages selected randomly as study sites (Fig. 2) while ensuring that the following criteria were met: 1) presence of a discrete village edge and a sufficiently dense network of village paths allowing easy access and high visibility to the entire settlement, and 2) the presence of dry-stone walls extending radially away from the village into the surrounding habitats to facilitate reptile surveys. Two of these rock walls ($\geq$ 200m in length) were randomly selected for surveys for each village, except for one smaller village that contained a single wall.

2.2 Reptile Surveys

Reptile population abundance for each village were quantified through standardized surveys. Each survey was conducted along 200-meter transects parallel to drystone walls, which have been shown to act as foci for reptile activity in the region (Li et al., 2014, Donihue 2016). All surveys were completed during the months of May and June 2024 during peak reptile activity time (8am – 12pm), and under favorable weather conditions (Catsadorakis 1984). Weather metrics (temperature, wind speed, relative humidity, cloud cover) were collected at the beginning and end of each survey (Kestrel 5000 Environmental Meter, 2024, Nielsen-Kellerman Company, Boothwyn, Pennsylvania). Surveys began at the edge of a village and were conducted by slowly walking along the length of the drystone wall. Species name and distance (m) from the origin were recorded (Garmin, 2024, GPSMAP® 65s Handheld GPS device, Olathe, Kansas) for all reptiles observed on the wall or on the ground within 1 meter from the wall (using 'unknown' if no species ID was possible). Each wall received four surveys spread over the duration of the field season.

2.3 Cat Surveys

Cat surveys were conducted for three consecutive nights within each village. Surveys were performed in the evening during the time of peak cat activity (5pm – 8pm) and under appropriate weather conditions (Konecny 1987). Surveys were conducted by walking along every path in a village once, and taking a picture and recording the GPS location of every cat observed. Survey tracks were recorded and uploaded into ArcGis Pro (ESRI, 2024, Redlands, California) to confirm comprehensive coverage of each village. Great individual variability in terms of cat color, size, condition, and unique markings allowed cats to be identified to the level of individual (Elizondo & Loss 2016). Each cat was given a unique identifier code, and on the second and third survey nights, cats were designated as new individuals or recaptures from previous nights. Cat population size in each village was calculated using the Schnabel Index, a method used to estimate population size in mark-recapture studies when multiple sampling events are conducted (Schnabel 1938, Carvalho et al., 2013)**.** Kittens were also recorded in the surveys but were excluded from the population size calculation due to their secretive nature making comprehensive identification difficult.

2.4 Additional field data

During the first cat survey conducted at each village, the locations of all food available to cats in the form of either pet food dishes or communal garbage dumpsters were recorded. The aggregate number of food dishes and dumpsters were combined into a number of 'food stations.' Human population data for every community on the island were provided by the municipality of Naxos and confirmed through a review of the Greek National Statistical Agency. The area of each village (ha) was quantified in ArcGIS Pro v.3.4 by manually digitizing the perimeter of each village. Larger villages have more cats, as well as humans and feeding sites, necessitating the need to establish a correction for community size. To correct for area effects, cat population, number of food stations, and human population were divided by the village surface area.

3. Statistical Analyses

Statistical analysis were performed in R version 4.4.2 (packages (R Core Team 2024) with the following the packages, lme4 (Bates et al., 2015), AICcmodavg (Mazerolle 2023)

3.1 Cat Density

Ordinary least squares regression (OLS) was used to first explore univariate associations between cat density, human density, and food station density and then to develop more complex models that included combinations of these predictors and their interactions. Corrected Akaike information criterion (AICc) (McQuarrie & Tsai 1997) was used to determine the best fit model.

3.2 Reptile Populations

A cat 'satiation index' was calculated for each village as the residuals of the regression of cat density against food density. Positive residuals were interpreted as cats being in a food deficit, and therefore hungrier, while negative residuals were interpreted as cats being in a food surplus and more satiated. The residual values were rescaled so that the most satiated (index = 0) had a value of 0, and higher positive values indicated lower satiation, or increased hunger. This index was used as a model parameter to investigate whether level of cat satiation influenced reptile populations.

To analyze the overall effect of distance from a village on reptile populations, all reptile observations were combined, and the total number of reptiles observed at each 1-meter interval on the transects were calculated. These data met the assumptions of a linear regression, with a linear relationship between count and distance, normally distributed residuals, and homoscedasticity. Therefore, OLS was performed to analyze the association between distance and reptile counts for the combined dataset. Surveys for the village that only had one rock wall were given twice as much weight to prevent reptile counts for this village to be smaller due to reduced sampling effort. To further test whether cat density influenced the effect of distance on reptile counts, the number of reptiles observed at each 1-meter interval were summed within each village, and a Poisson regression was ran for each village with reptile counts regressed against distance. The coefficient for distance was exponentiated to obtain a slope, and the slopes were regressed against cat density to investigate the association between cat density and the change in reptile counts with distance.

The association between reptile counts and cat density, cat satiation, and distance were analyzed in two separate analyses. For analysis one, Reptile counts in each village were grouped into eight 25-meter distance bins. Then, through Poisson generalized linear mixed effect models (GLMM), with village ID included as a random effect, combinations of model parameters were explored to determine the best fit model, with AICc criteria used to determine model fit. An interaction term between cat density and satiation index was included in model exploration as well. For analysis two, reptile counts were analyzed at the survey level, through Poisson generalized linear mixed effect models (GLMM) with village ID included as a random effect. These models were used to analyze the association between the number of reptiles observed in each survey and cat density and cat satiation index across all villages without distance. An interaction term between cat density and satiation index was explored in this analysis as well.

4. Results

4.1 Cat Density Analysis

Cat densities in all villages were higher than what is normal for the species under rural or natural conditions (see Fig. 3, see Appendix B, Image 2) (Liberg et al., 2000), except for one village with no cats that also had no additional food supplementation or permanent human residents.

Cat density was significantly positively associated with both predictor variables when analyzed independently- food density (adjusted $R^2 = 0.66$, $p = 0.009$, $n = 12$, OLS, Fig. 3), and human density (adjusted $R^2 = 0.45$, $p = 0.001$, $n = 12$, OLS Fig. 4). When multiple predictor variables were included in model selection, two models showed nearly equal fit for predicting cat density. The first model (Model A) included only food density as a predictor (AICc = 65.54, AICcWt = 0.67, Log Likelihood = -28.27, Table 1) and the second model (Model B) included both food density and human density (AICc = 67.47, AICcWt = 0.26, Log Likelihood = -26.88, Table 1). Food density was significantly positively associated with cat density in both models (adjusted $R^2 = 0.657$, $p = 0.0001$ for Model A and adjusted $R^2 = 0.698$, $p = 0.014$ for Model B, Multiple Regression, Table 2), while human density was not significant in the model that included it. When the type of feeding supplementation (garbage bins and food dishes) was separated, cat density was significantly positively associated with both density of garbage bins (adjusted $R^2 = 0.28$, $p = 0.044$, OLS, Fig. 5) and density of feeding dishes (adjusted $R^2 = 0.73$, $p = 0.0002$, OLS, Fig. 6).

4.2 Reptile Population Analysis

A significant positive correlation was found between reptile counts and distance from the village edge, indicating that reptile numbers declined closer to human habitations and cats (Pearson's R = .2176, $p = 0.002$, OLS, $n = 200$, Fig. 7).

For analysis 1, when variables with the binned dataset were examined individually, Poisson GLMM's showed that both cat density (marginal $R^2 = 0.33$, conditional $R^2 = 0.82$, $p = 0.007$, $n = 96$, Poisson GLMM), and satiation index (marginal $R^2 = 0.38$, conditional $R^2 = 0.82$, $p = 0.002$, $n = 96$, Poisson GLMM) were significantly negatively associated with reptile counts. When models that included different combinations of predictor variables and their interactions were compared, the model that best fit the data included all of the predictor variables; distance ($p = 0.0003$), cat density ($p = 0.053$), satiation index ($p = 0.212$), as well as the interaction between cat density and satiation index ($p = 0.001$) (marginal $R^2 = 0.67$, conditional $R^2 = 0.83$, AICc = 569.11 and AICcWt = 0.87, Tables 3 & 4, compared to next best model AICc = 574.91, and AICcWt = 0.05,). Hence, distance and the interaction term were found to be significant, while cat density and satiation index were not.

For analysis 2, when variables were examined individually, cat density (marginal $R^2 = 0.33$, conditional $R^2 = 0.83$, $p = 0.008$, $n = 96$, Poisson GLMM, Fig. 8) and cat satiation (marginal $R^2 = 0.39$, conditional $R^2 = 0.82$, $p = 0.002$, $n = 96$, Poisson GLMM, Fig. 9) were significantly negatively associated with the number of reptiles observed in a survey . The full model that best fit the data included cat density ($p = 0.047$) cat satiation ($p = 0.218$), and the interaction between cat density and cat satiation ($p = 0.001$) (marginal $R^2 = 0.67$, conditional $R^2 = 0.83$, AICc = 686.08 and AICcWt = 0.89, Tables 3 & 5, compared to the next best model AICc = 692.09 and AICWt = 0.04, Table 3). In this model, cat satiation was not significant, cat density was significant, and there was a significant negative interaction between cat density and cat satiation.

4.3 Heat Maps

Heat maps showing the spatial distribution of cats, dumpsters, and food dishes were created for each village in ArcGIS Pro to provide visual supplementation to these results. Heat maps include every cat observation across all three surveys in each village. These heat maps clearly show that cats form high density aggregations near human-derived food resources. Due to large cat population size, these results were best visually observed in the village of Vivlos (Fig. 10), where the highest cat density regions (red regions) are all associated with a dumpster or a food dish, while none of the lowest cat density areas (blue regions) had a detectable source of human-derived food within them. Results from heat maps from other villages with smaller populations were consistent with these findings.

5. Discussion

Cats pose an increasingly pressing ecological problem across most island ecosystems globally (Medina et al., 2011, Medina et al 2014), yet managers and local decisionmakers still have a poor understanding of the magnitude of the impacts, as well as the causative factors. By surveying outdoor cats along a gradient of increasing food supplementation at twelve discrete sites within a single representative Mediterranean ecosystem, this study demonstrated that cat population size is the direct product of the quantity of human-derived food resources available to them. It was found that food resources come primarily in the form of food scraps or dry cat food (Fig. 6) placed by local residents in their yards or village paths. Equally important are the communal dumpster bins that are usually overflowing with garbage and surrounded by groups of stray cats (Fig. 5). These results demonstrate that cat densities in villages are correlated with the density of both these resources. Beyond density of food resources, a separate and distinct effect of human population on cat density was detected, potentially reflecting additional benefits in the form of shelter and medical care some cats derive from a subset of each community's inhabitants. While previous studies have shown that cats will congregate and form high density colonies around easily accessible food resources (Liberg 1980, Izawa et al., 1982, Mirmovitch 1995), these results further demonstrate that cats are not just simply reorganizing themselves spatially around these resources (Fig. 4 & 10), but rather that population level cat density readily rises to match bottom-up human supplementation effects.

These analyses are based on the assumption that the cat population within each village constitute a discrete unit. The existing literature indicates that while the home range size of cats varies widely (, Jones & Coman 1982, Mirmovitch 1995), home range decreases with increasing productivity of the landscape (Bengsen et al., 2016). The high density of food dishes and garbage sites within each village in this study (Fig. 10) indicates that sufficient resources are available to collapse home ranges and congregate cats within the individual village. The cat surveys, conducted over three consecutive nights demonstrate high level of philopatry of individual cats with most animals not moving more than a few dozen meters from day to day. The assumption of closed village populations was further supported by a conspicuous absence of cats away from human settlements. These observations agree with past research (Li et al., 2014) and indicate that cats are not roaming the landscape of Naxos or travelling between villages in significant numbers, but rather

remain close to their within-village food sources. Consequently, increases in cat density within a village are the result of local legacies rather than the result of extensive inter-village movement.

Is it possible that the association between cats and food dishes is simply the result of increased provisioning by compassionate locals in response to rising cat populations, rather than the other way around? While some of this cannot be completely ruled out, field observations suggest instead that feeding intended for a local house pet ends up inadvertently supporting other stray cats and hence promotes population increases. Furthermore, cat populations closely reflect the density of garbage dumpsters, the number of which certainly is not determined by cat density. In summary, the existing evidence suggests that intentional or unintentional supplementation of cats drives population numbers rather than vice versa.

We find that cat population density is negatively correlated with resident reptile population abundance, indicating substantial levels of predation on lizards and snakes. This corroborates regular but *ad hoc* observations during the study of cats consuming wildlife (see Appendix, Image 1). While data collection in this study focused on reptiles, parallel trends are known to occur within birds as well (Krawzcyk et al., 2019).

This study also reveals that while cat impacts on local wildlife are both pervasive and density-dependent, they are also modulated by the degree of cat satiation. Because cat populations do diverge somewhat from what would be predicted based on available resources, the residuals of this relationship were used as a metric of the relative resources available per cat capita, essentially obtaining an index of over/under provisioning (termed cat satiation). The results indicate that not only is the extent to which cat satiation is proportional to decreases in wildlife populations independent from cat density (Fig. 9), but also that the interaction between cat density and satiation is particularly important. Hence, cat numbers are more negatively associated with wildlife populations when satiation indices are high, i.e. cats are hungry. This is consistent with a scenario where cats preferentially consume human-derived resources and switch to preying local wildlife when these are not sufficient. Despite the strong evidence of direct cat impact on reptiles through predation, a different explanatory process cannot be completely excluded. In this scenario, higher cat density and reduced provisioning results in reptiles that are more wary, more cryptic, and less active, therefore reducing detectability during surveys.

A clear linear rise in reptile abundance with increasing distance from a village edge was found (Fig. 7). Reptile counts increased on average by ~40% from the immediate edge of the village to 200 meters away from a village, suggesting that proximity to villages was detrimental to reptiles. While this pattern is consistent with increased cat-induced mortality close to villages, there was no relationship between cat density and how rapidly reptile numbers rose with increasing distance from a village. Hence, the steepness of this decline in reptile abundance when approaching a village was not significantly related to cat density or cat satiation, perhaps because of insufficient sample sizes or non-linear relationships. While the possibility that cats do not influence the effect of distance is not being ruled out, alternative causes may be that 1) as lizards are predated by cats, the high density of highly

active lizards means that the new spaces created by cat predation are readily filled by a lizard from further away and 2) the increase in reptiles away from villages could be attributed to other factors such as habitat suitability increasing with greater distance from human settlements.

Because anthropogenic food subsidies are critical for cat population growth, and increasing cat population size has proportional negative impacts on resident wildlife population sizes, this study strongly indicates that human subsidies are facilitating hyperpredation of wildlife on Naxos. As a result, in many Mediterranean regions, human supplementation drives the impacts of an artificially elevated cat population on resident wildlife.

Management recommendations

Public opinion regarding free-ranging cats on the Aegean islands varies greatly, with some residents considering them pests while others taking care of them through regular feeding (personal observation). On Naxos and other islands, cats are increasingly becoming a source of amusement for tourists, and cat-themed merchandise can be found on sale in many retail stores. Local businesses have also capitalized on the tourist's affection for cats by selling bags of cat food to allow for a petting zoo-like experience with the local strays. Over the last several years, there has been a pronounced shift in public opinion regarding cat welfare away from the past *laissez-faire* attitude toward a more compassionate stance. As a matter of fact, it is the attitude of support and consequent feeding that has resulted in the present-day ballooning of cat populations on Aegean islands. Concurrently, there is a growing realization that cat overpopulation is a problem, primarily due to animal welfare rather than wildlife conservation reasons, and cat population control programs are increasingly discussed.

This study has shown that increasing cat densities translate directly into higher mortality for reptiles, and that the negative impacts of cats is strongest when human food becomes limiting, and cats are forced to rely more on wildlife for nutrition. These results may be interpreted as providing conflicting management suggestions. While in the short term, overprovisioning of cats reduces predation of wildlife, in the long term this will result in accelerated reproduction and expanding cat populations. This conflict between short-term benefits versus long-term detriments can best be navigated through a carefully balanced approach. If cat populations are to be managed as to reduce wildlife mortality, several steps need to be taken including expansion of existing trap-neuter-release programs, as well as reduction in supplemental feeding of unsterilized cats to reduce reproductive potential. More specifically, proposed recommendations include 1) improving waste management policies to decrease accessibility of this resource to cats, 2) increasing trap-neuter release efforts, and 3) providing local education about the deleterious impacts of cats on wildlife and encouraging both residents and tourists to only feed sterilized cats. This last point is significant, as keeping only sterilized cats fed will decrease their dependence on wildlife while also not contributing to cat population growth. The reduced access to human-derived food by unsterilized cats through recommendations 1 and 3 may cause them to consume wildlife more in the short term, but the loss of easily available human food resources should also reduce their reproductive output. While controversial, it is worth mentioning that

humane cat culling is an option as well, as it has been shown to be highly effective, especially on islands (Nogales et al., 2004). Additionally, the implementation of cat management needs to be followed by close environmental monitoring to assess unintended consequences such as mesopredator release of rats following cat population declines (Courchamp et al., 1999).

6. Conclusion and future research directions

As global biodiversity continues to be lost at an alarming rate (Wilson 1989), the importance of understanding the mechanisms driving species extinction is increasing. The conclusions of this study should be applicable to numerous regions in the Mediterranean Basin, at least those where cats impact small- and medium- bodied vertebrates. Further research efforts need to center on investigating how the extent of human subsidies influences that distance cats will roam from a village, and stable-isotope analysis of scat can help elucidate how the ratio of anthropogenic and natural food sources vary along this gradient. Lastly, this study focused on the high tourism summer period when large numbers of visitors come to the island. Extending the study to the winter months when less food supplementation is available can help to understand the true impact on resident wildlife.

Figures

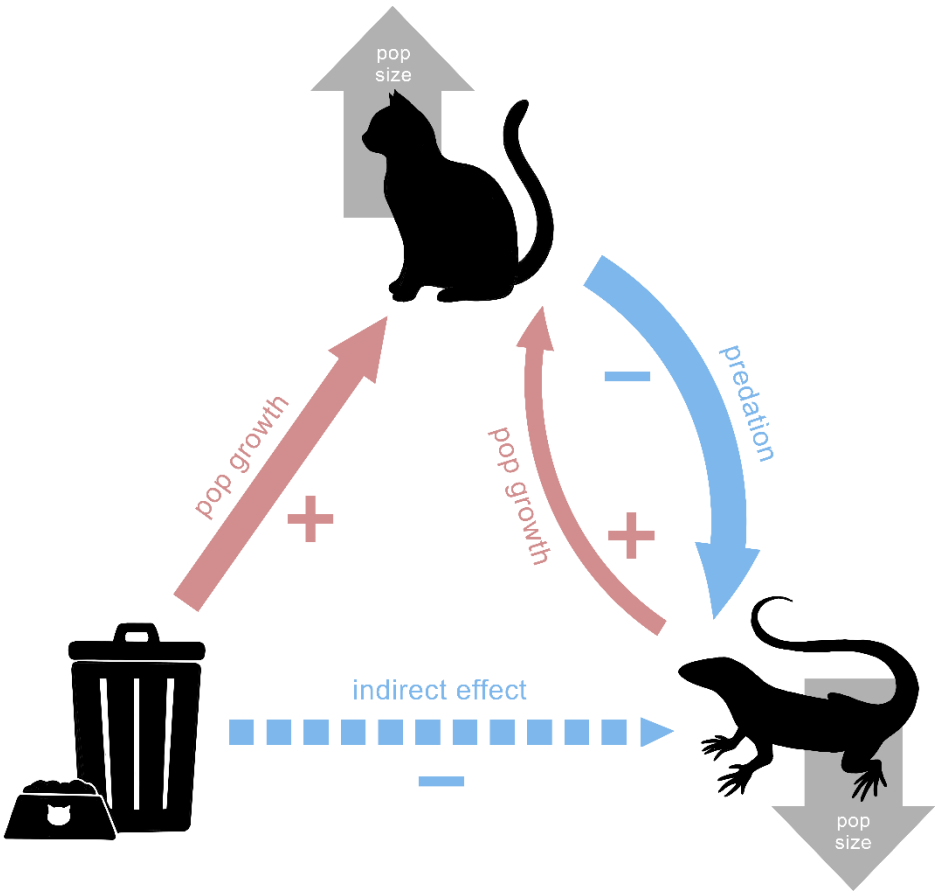


Figure 1. *Conceptual diagram showing how the addition of anthropogenic food supplementation into a predatory-prey relationship can result in hyperpredation on wildlife.*

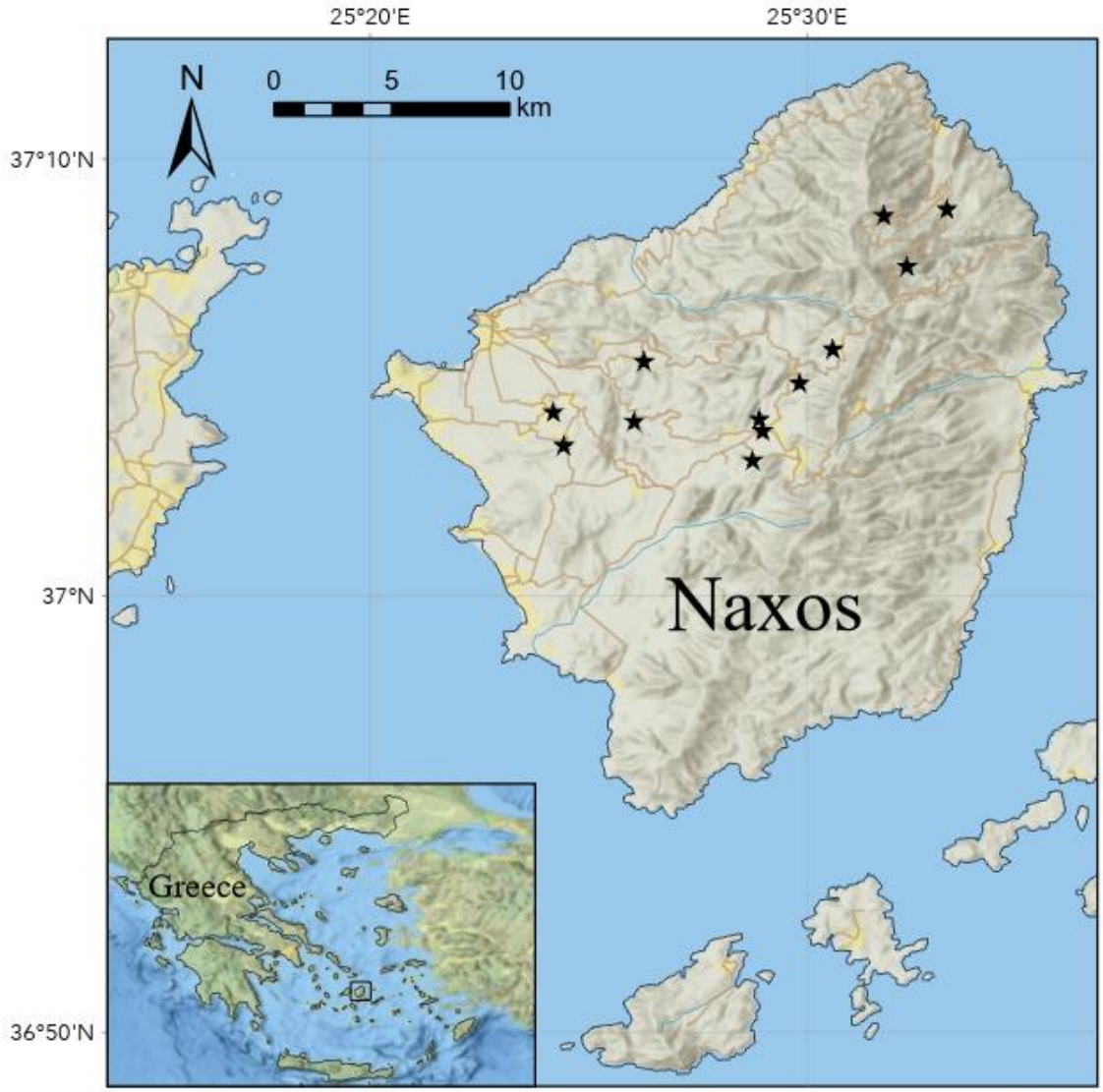


Figure 2. *Map of the study area with survey locations indicated by black stars. Naxos, Greece and surrounding islets shown in main map. Entire country outlined in the inset, with a square around Naxos for reference) Map created in ArcGIS Pro v3.4 (2024). Produced with custom ESRI National Geographic Basemap (2025)*

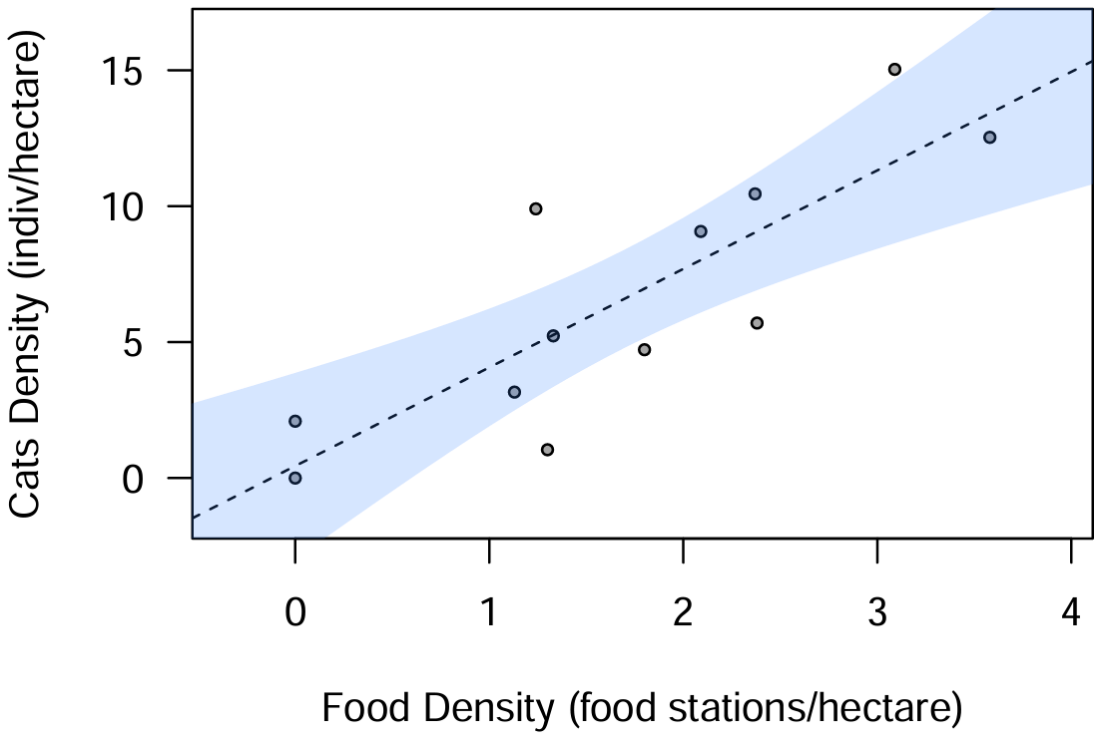


Figure 3. *Ordinary least squares regression showing association between cat density and feeding density ($p = 0.0008$, adjusted $R^2 = 0.66$). Shaded region represents 95% confidence interval.*

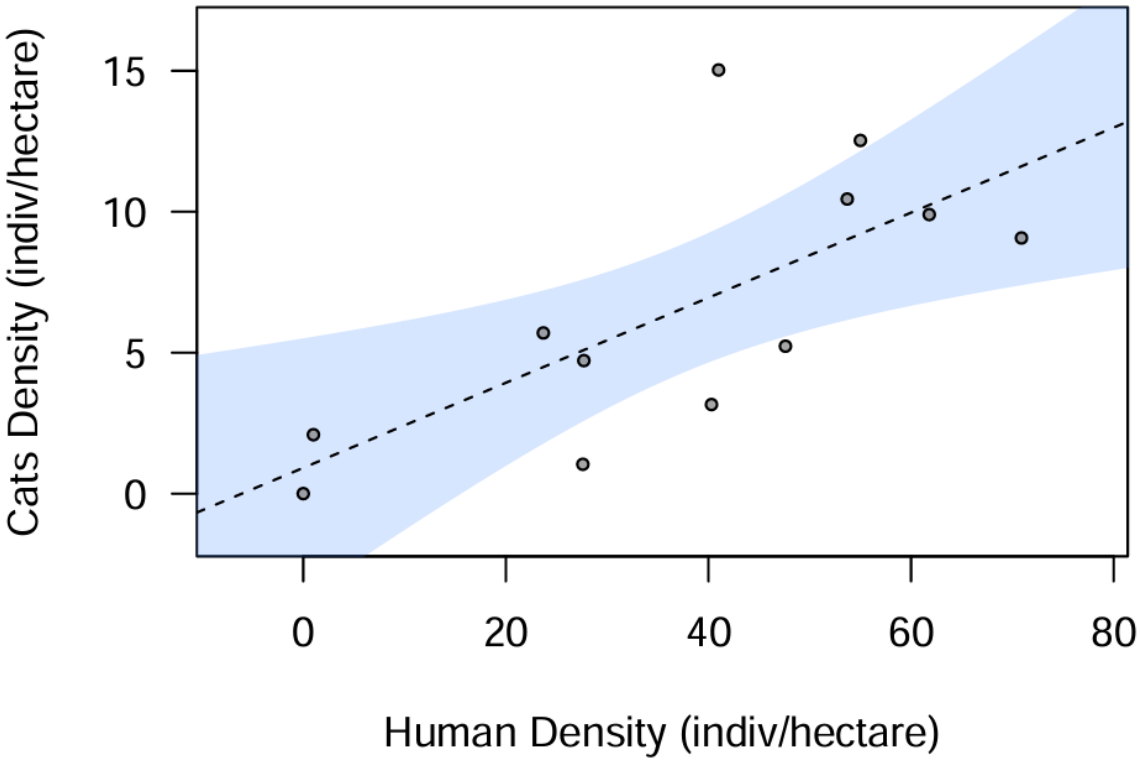


Figure 4. *Ordinary least squares regression showing association between cat density and human density ($p = 0.01$, adjusted $R^2 = 0.45$). Shaded region represents 95% confidence interval.*

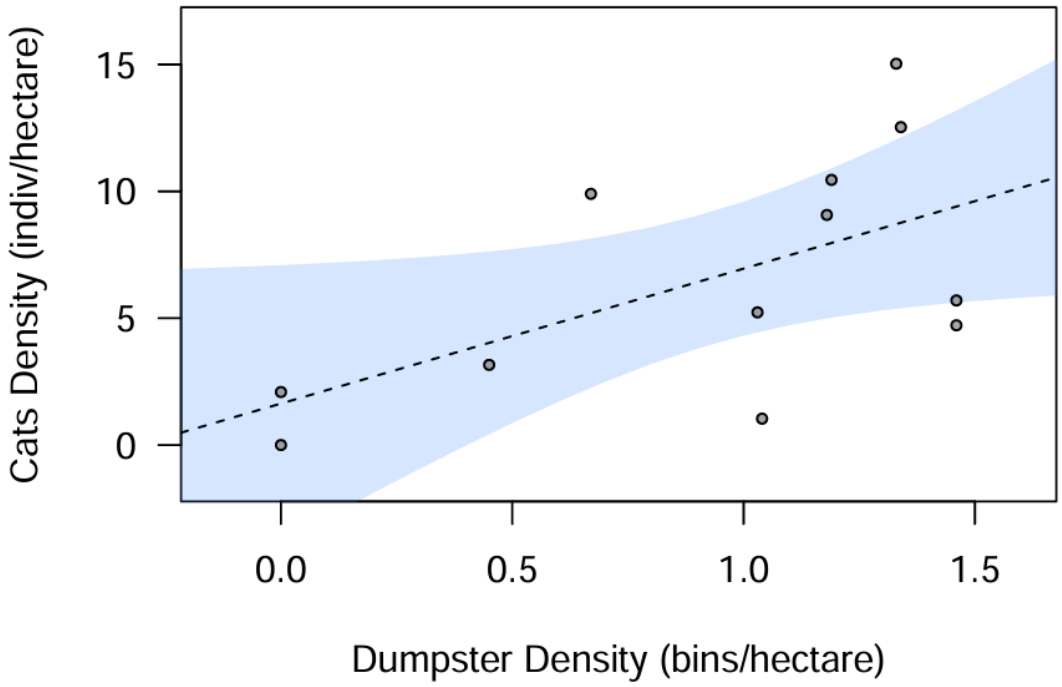


Figure 5. *Ordinary least squares regression showing association between cat density and density of dumpster bins ($p = 0.044$, adjusted $R^2 = 0.28$). Shaded region represents 95% confidence interval*

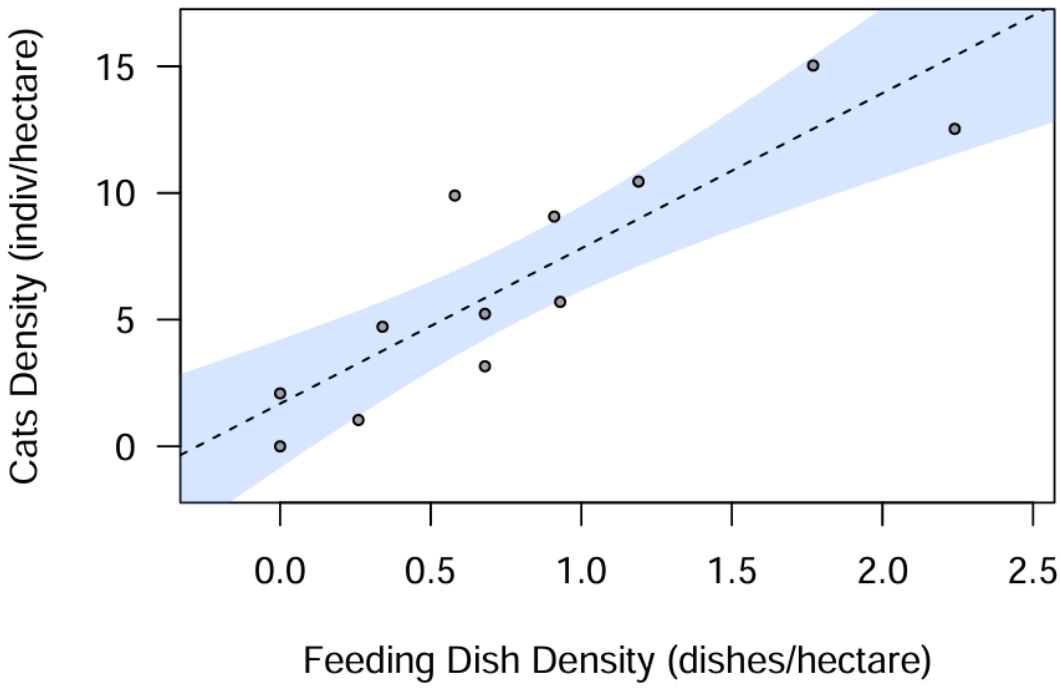


Figure 6. *Ordinary least squares regression showing association between cat density and density of food dishes ($p = 0.0002$, adjusted $R^2 = 0.73$). Shaded region represents 95% confidence interval.*

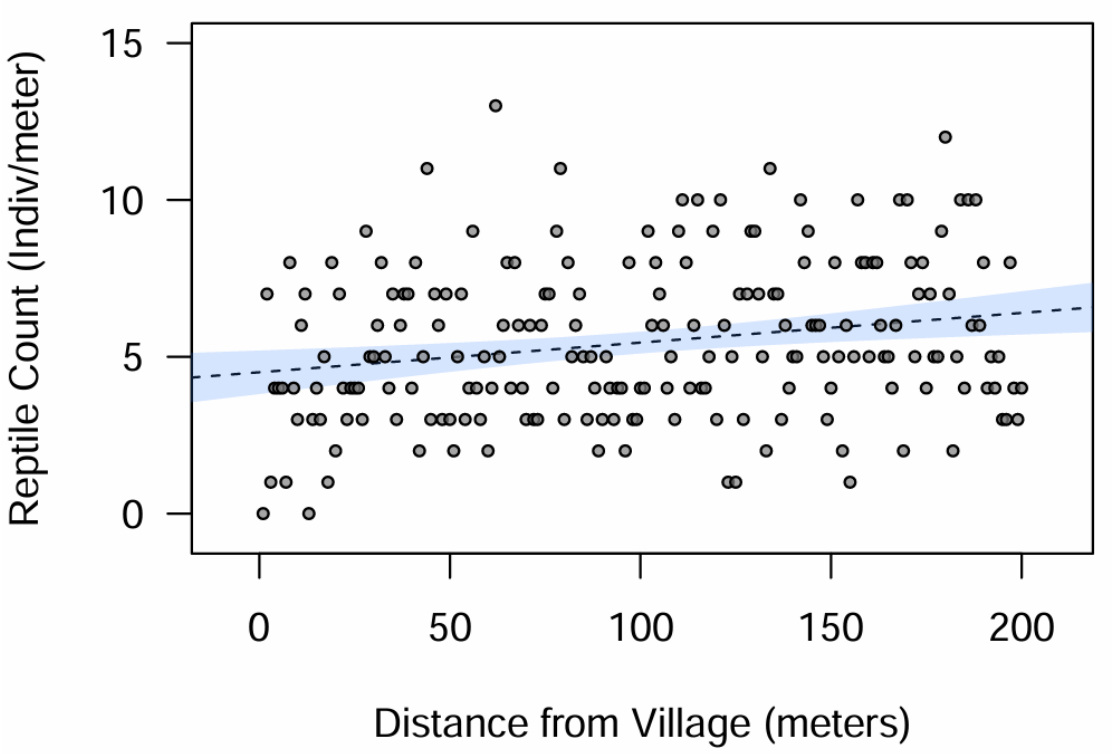


***Figure** 7. Ordinary least squares regression showing association between the number of reptiles observed at each 1-meter interval distance from village for the entire study ($p = 0.002$, adjusted $R^2 = 0.43$). Shaded region represents 95% confidence interval.*

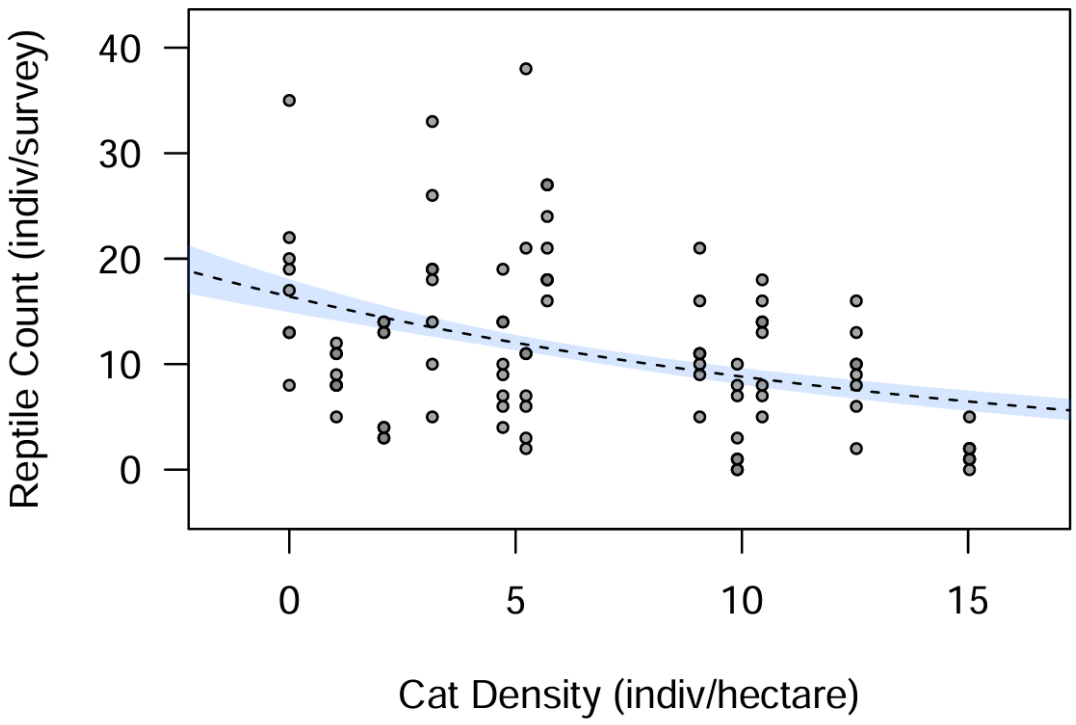


Figure 8. *Poisson generalized linear model showing association between reptile counts per survey and cat density. Shaded region represents 95% confidence interval for fixed effects, p = 2e-16, null deviance = 544.02 on 95 degrees of freedom, residual deviance = 462.78 on 94 degrees of freedom.*

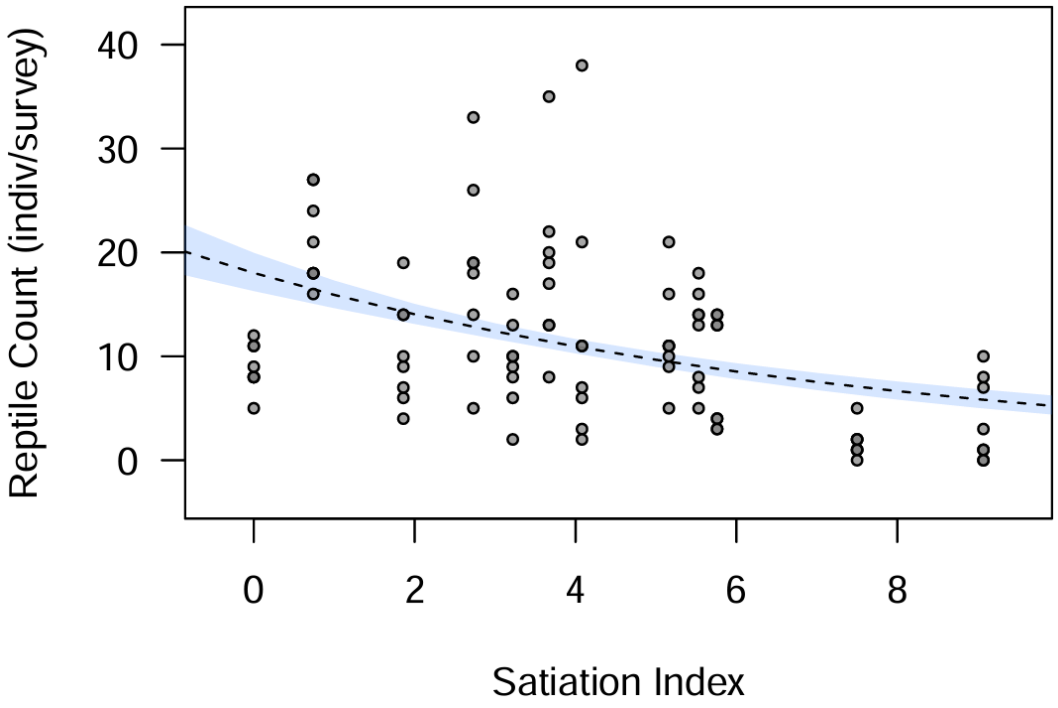


Figure 9. *Poisson generalized linear model showing association between reptile counts per survey and satiation index. Shaded region represents 95% confidence interval for fixed effects, p = 2e-16, null deviance = 544.02 on 95 degrees of freedom, residual deviance = 440.90 on 94 degrees of freedom.*

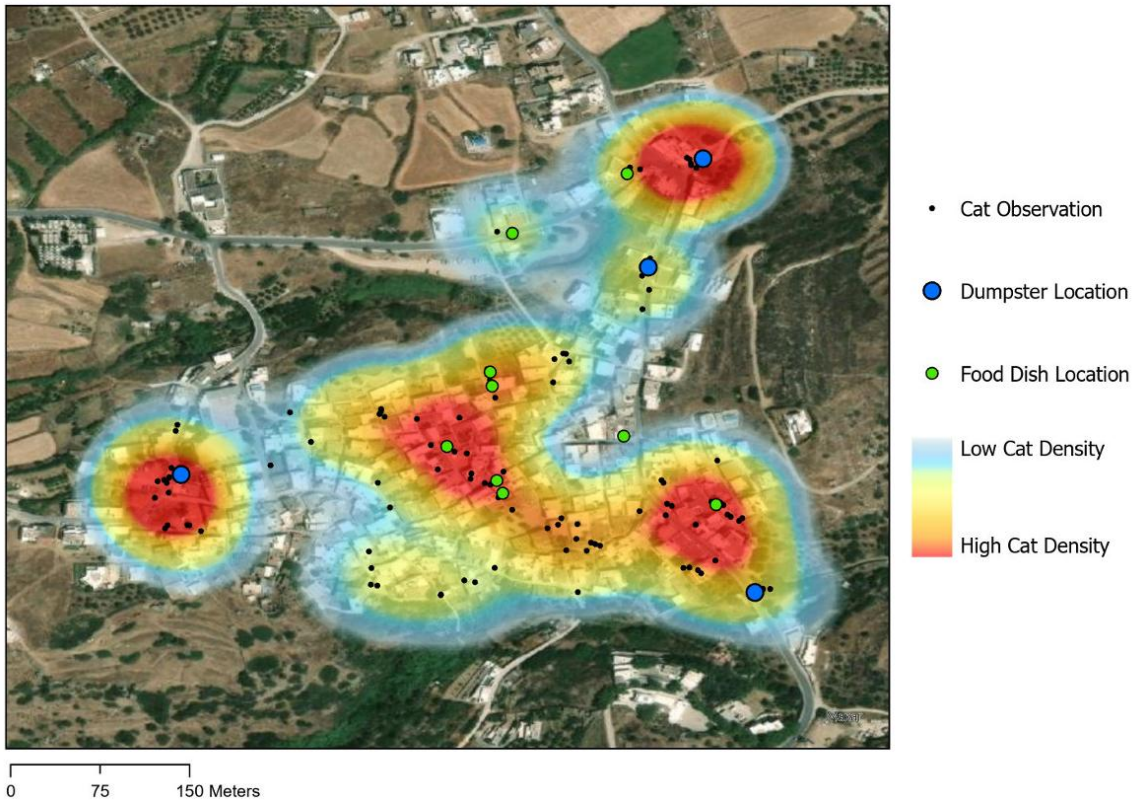


Figure 10. *Heat map showing the spatial distribution of cats (n = 171 cat observations) in relationship to human subsidies in a typical Naxian village (Vivlos). Black dots show all cat observations made during three nights of surveys. Cats typically stayed in close proximity to sources of food, whether deeding dishes or dumpsters Map created in ArcGIS Pro v3.4. Produced with ESRIi World Image WGS1983 World Image Base Map (2025).*

Tables

Table 1*: Model selection for factors predicting density of cats, Models are ranked in ascending order by corrected Akaike corrected information criteria (AICc). ΔAICc, AICc weight, and Log Likelihood are provided for each model. Bold selections show models with near equal fit. Model variables include food density, human density, and an interaction between food.*

Predictors	**AICc**	**ΔAICc**	**AICcWt.**	**Log Likelihood**
Cat Density				
~food density	**65.54**	**0.00**	**0.67**	**-28.27**
~human density + food density	**67.47**	**1.93**	**0.26**	**-26.88**
~human density	71.2	5.66	0.04	-31.10
~ human density + food density + interaction	72.16	6.62	0.02	-26.08
null model	75.87	10.33	0.00	-35.27

***Table 2**: Results for cat density analysis using multiple linear regression showing two models with similar fit for predicting cat density. Asterisks indicate significant predictors (p-value <0.05). Estimates, standard errors, and z-values are also shown. Model A adjusted $R^2 = 0.657$. Model B adjusted $R^2 = 0.698$.*

	Statistic	Estimate	Std. Error	t-value	p-value
Model A.					
	Intercept	0.443	1.534	0.289	0.779
	Food Density	3.624	0.771	4.702	**0.0001***
Model B.					
	Intercept	-0.675	1.6`4	-0.418	0.779
	Human Density	0.068	0.045	1.532	0.160
	Food Density	2.769	0.914	3.031	**0.014***

***Table 3**: Model selection for factors predicting number of reptile observations from two different analyses. Model A shows results from reptile analysis 1 and Model B shows results from reptile analysis 2. Models are ranked in ascending order by corrected Akaike corrected information criteria (AICc). ΔAICc, AICc weight, and Log Likelihood are provided for each model. Model variables include distance (model A only), cat density, cat satiation, and an interaction between cat distance and cat satiation.*

	Reptile Count ~	AICc	ΔAICc	AICcWt.	Log Likelihood
A	*Reptile Analysis 1*				
	~ distance + cat density + cat satiation + interaction	**569.11**	**0.00**	**0.87**	**-278.09**
	~ distance + cat satiation	574.91	5.79	0.05	-283.23
	~ distance + cat density + cat satiation	575.04	5.93	0.04	-282.19
	~ cat density + distance	576.16	7.05	0.03	-283.86
	~ cat density + cat satiation + interaction	579.63	10.51	0.00	-284.48
	~ distance	579.83	10.71	0.00	-286.78
	~ cat satiation	585.52	16.4	0.00	-289.63
	~ cat density + cat satiation	585.61	16.49	0.00	-288.58
	~ cat density	586.77	17.66	0.00	-290.26
	null model	590.48	21.37	0.00	-293.18
B	*Reptile Analysis 2*				
	~ cat density + cat satiation + interaction	**686.08**	**0.00**	**0.89**	**-337.71**
	~ cat satiation	692.09	6.01	0.04	-342.91
	~ cat density + cat satiation	692.24	6.16	0.04	-341.90
	~ cat density	693.59	7.51	0.02	-343.66
	null model	697.27	11.2	0.00	-346.57

***Table 4**: Reptile analysis 1 results using a Poisson Generalized Linear Mixed Model with village ID included as a random effect. Reptiles observations from all surveys in a village were combined and separated into eight 25-meter distance bins (n = 96). Asterisks indicate significant predictors (p-value <0.05). Estimates, standard errors, and z-values are shown as well. Marginal R^2 = 0.67, conditional R^2 = 0.83*

Statistic	Estimate	Std. Error	z -value	p-value
Intercept	2.090	0.299	7.000	< 2e-16*
Distance	0.047	0.013	3.577	**0.0003***
Cat Density	0.095	0.049	1.933	0.053
Cat Satiation	0.096	0.077	1.247	0.212
Cat Density * Cat Satiation	-0.031	0.010	-3.283	**0.001***

Table 5: *Reptile analysis 2 results using a Poisson Generalized Linear Mixed Model with village ID included as a random effect. Reptile counts were grouped by number of reptiles observed in each transect (n = 96). Asterisks indicate significant predictors (p-value of <0.05). Estimates, standard errors, and z-values are also shown. Marginal R^2 = 0.67, conditional R^2 = 0.83.*

Statistic	Estimate	Std. Error	z-value	p-value
Intercept	2.307	0.292	7.910	< 2e-16*
Cat Density	0.097	0.049	1.983	**0.047***
Cat Satiation	0.095	0.077	1.232	0.218
Cat Density * Cat Satiation	-0.032	0.010	-3.331	**0.001***

Literature Cited

Bates D., Maechler M., Bolker B., Walker S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67(1)*, 1-48.

Bellard, C., Cassey, P., & Blackburn, T. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, *12*(2).

Bengsen, A. J., Algar, D., Ballard, G., Buckmaster, T., Comer, S., Fleming, P. J. S., Friend, J. A., Johnston, M., McGregor, H., Moseby, K., & Zewe, F. (2016). Feral cat home-range size varies predictably with landscape productivity and population density. *Journal of Zoology*, *298*(2), 112–120.

Beutel, T., Reineking, B., Tiesmeyer, A., Nowak, C., & Heurich, M. (2017). Spatial patterns of co-occurrence of the European wildcat *Felis silvestris silvestris* and domestic cats *Felis silvestris catus* in the Bavarian Forest National Park. *Wildlife Biology*, *2017*(1).

Bonnaud, E., Berger, G., Bourgeois, K., Legrand, J., & Vidal, E. (2012). Predation by cats could lead to the extinction of the Mediterranean endemic Yelkouan Shearwater *Puffinus yelkouan* at a major breeding site. *Ibis*, *154*(3), 566–577.

Bonnaud, E., Bourgeois, K., Vidal, E., Kayser, Y., Tranchant, Y., & Legrand, J. (2007). Feeding Ecology of a Feral Cat Population on a Small Mediterranean Island. *Journal of Mammalogy*, *88*(4), 1074–1081.

Bonsall, M. B., & Hassell, M. P. (1997). Apparent competition structures ecological assemblages. *Nature*, *388*(6640), Article 6640.

Carpio, A. J., Tortosa, F. S., & Barrio, I. C. (2015). Rabbit Abundance Influences Predation on Bird Nests in Mediterranean Olive Orchards. *Acta Ornithologica*, *50*(2), 171–179.

Carvalho, D. de A., Collins, P. A., & Bonis, C. J. D. (2013). The mark–recapture method applied to population estimates of a freshwater crab on an alluvial plain. *Marine and Freshwater Research*, *64*(4), 317–323.

Catsadorakis, G. (1984). Aspects of Ecology and Behaviour in the lizard *Podarcis erhardii. Biologia Gallo-Hellenica, 11,* 99-110.

Clavero, M., & García-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, *20*(3), 110.

Courchamp, F., Langlais, M., & Sugihara, G. (1999). Cats protecting birds: Modelling the mesopredator release effect. *Journal of Animal Ecology*, *68*(2), 282–292.

Courchamp, F., Langlais, M., & Sugihara, G. (1999). Control of rabbits to protect island birds from cat predation. *Biological Conservation*, 89(2), 219–225.

Courchamp, F., Langlais, M., & Sugihara, G. (2000). Rabbits killing birds: Modelling the hyperpredation process. *Journal of Animal Ecology*, *69*(1), 154–164.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*(40), 11261–11265.

Donihue, C. M. (2016). Drivers of Functional Trait Variability in *Podarcis erhardii*, the Aegean Wall Lizard. Yale University.

Driscoll, C. A., Clutton-Brock, J., Kitchener, A. C., & O'Brien, S. J. (2009). The Taming of the Cat. *Scientific American*, *300*(6), 68–75.

Dueñas, M.-A., Hemming, D. J., Roberts, A., & Diaz-Soltero, H. (2021). The threat of invasive species to IUCN-listed critically endangered species: A systematic review. *Global Ecology and Conservation*, *26*, e01476.

Elizondo, E. C., & Loss, S. R. (2016). Using trail cameras to estimate free-ranging domestic cat abundance in urban areas. *Wildlife Biology*, *22*(5), 246–252.

ESRI (2025) World Image WGS1983 World Image Base Map. California: ESRI, Inc.

ESRI. (2024). ArcGISPro v3.4. California: ESRI, Inc.

ESRI. (2025). National Geographic World Map. California: ESRI, Inc.

Fedriani, J. M., Fuller, T. K., & Sauvajot, R. M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, *24*(3), 325–331.

Gerhold, R. W., & Jessup, D. A. (2013). Zoonotic Diseases Associated with Free-Roaming Cats. *Zoonoses and Public Health*, *60*(3), 189–195.

Hald-Mortensen, C. (2023). The Main Drivers of Biodiversity Loss: A Brief Overview (SSRN Scholarly Paper 4579821). Social Science Research Network.

Hellenic Statistical Authority. (n.d.). https://www.statistics.gr/en/home/

Imber, M., Harrison, M., & Harrison, J. (2000). Interactions between petrels, rats and rabbits on Whale Island, and effects of rat and rabbit eradication. *New Zealand Journal of Ecology*, *24*(2), 153–160.

Izawa, M., Doi, T. & Ono, Y. (1982). Grouping patterns of feral cats living on a small island in Japan. *Japan Journal of Ecology*, 32, 373-82.

Jones, E., & Coman, B. J. (1982). Ecology of the Feral Cat, *Felis catus* (L.), in South-Eastern Australia III.* Home Ranges and Population Ecology in Semiarid North-West Victoria. *Wildlife Research*, *9*(3), 409–420.

Krawczyk, E., Hedman, H., Pafilis, P., Bergen, K., & Foufopoulos, J. (2019). Effects of touristic development on Mediterranean island wildlife. *Landscape Ecology*, *34*.

Levine, J. M., & D'Antonio, C. M. (2003). Forecasting Biological Invasions with Increasing International Trade. *Conservation Biology*, *17*(1), 322–326.

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: Biological Sciences*, *281*(1788), 20140339.

Liberg, O. (1980). Spacing Patterns in a Population of Rural Free Roaming Domestic Cats. *Oikos*, *35*(3), 336–349.

Liberg, O., Sandell, M., Pontier, D., & Natoli, E. (2000). Density spatial organisation and reproductive tactics in the domestic cat and other felids. In D. C. Turner & P. Bateson (Eds.), *The domestic cat: The biology of its behavior. 2nd edition: Vol.* (pp. 119–148). Cambridge University Press.

Loss, S. R., Boughton, B., Cady, S. M., Londe, D. W., McKinney, C., O'Connell, T. J., Riggs, G. J., & Robertson, E. P. (2022). Review and synthesis of the global literature on domestic cat impacts on wildlife. *Journal of Animal Ecology*, *91*(7), 1361–1372.

Loss, S. R., Will, T., & Marra, P. P. (2013). The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications*, *4*(1), Article 1.

Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature*, *301*(5899), 379–384.

Maeda, T., Nakashita, R., Shionosaki, K., Yamada, F., & Watari, Y. (2019). Predation on endangered species by human-subsidized domestic cats on Tokunoshima Island. *Scientific Reports*, *9*, 16200.

Mazerolle M.J. (2023). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)_ R package version 2.3.3

McQuarrie, A., Shumway, R., & Tsai, C. L. (1997). The model selection criterion AICu. *Statistics & probability letters*, *34*(3), 285-292.

Medina, F. M., Bonnaud, E., Vidal, E., & Nogales, M. (2014). Underlying impacts of invasive cats on islands: Not only a question of predation. *Biodiversity and Conservation*, *23*(2), 327–342.

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., Keitt, B. S., Le Corre, M., Horwath, S. V., & Nogales, M. (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, *17*(11), 3503–3510.

Mirmovitch, V. (1995). Spatial Organisation of Urban Feral Cats (*Felis Catus*) in Jerusalem. *Wildlife Research*, *22*(3), 299–310.

Mori, E., Menchetti, M., Camporesi, A., Cavigioli, L., Tabarelli de Fatis, K., & Girardello, M. (2019). License to Kill? Domestic Cats Affect a Wide Range of Native Fauna in a Highly Biodiverse Mediterranean Country. *Frontiers in Ecology and Evolution*, *7*.

Natoli, E. (1985). Spacing pattern in a colony of urban stray cats (*Felis catus* L.) in the historic centre of Rome. *Applied Animal Behaviour Science*, *14*(3), 289–304.

Natoli, E., & De Vito, E. (1991). Agonistic behaviour, dominance rank and copulatory success in a large multi-male feral cat, *Felis catus* L., colony in central Rome. *Animal Behaviour*, *42*(2), 227–241.

Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, *24*(1), 1–11.

Nogales, M., Martín, A., Tershy, B. R., Donlan, C. J., Veitch, D., Puerta, N., Wood, B., & Alonso, J. (2004). A Review of Feral Cat Eradication on Islands. *Conservation Biology*, *18*(2), 310–319.

Nossan, H. (2023). Biodiversity Implications of Agricultural Terrace Abandonment in a Mediterranean Landscapes. Master's Thesis. University of Michigan.

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*(5), 1262–1278.

Pope, K. L., Garwood, J. M., Welsh, H. H., & Lawler, S. P. (2008). Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. *Biological Conservation*, *141*(5), 1321–1331.

R Core Team (2024). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria.

Roemer, G. W., Coonan, T. J., Garcelon, D. K., Bascompte, J., & Laughrin, L. (2001). Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. *Animal Conservation Forum*, *4*(4), 307–318.

Sarika, M., Bazos, I., Zervou, S., Christopoulou A. (2015). Flora and vegetation of the European-network "Natura 2000" habitats of Naxos island (GR4220014) and of nearby islets Mikres Kyklades (GR4220013), Central Aegean (Greece). *Plant Sociology*, *52 (2)*, 3–56.

Schnabel, Z. E. (1938). The Estimation of the Total Fish Population of a Lake. *The American Mathematical Monthly*, *45*(6), 348–352.

Semple, E. C. (1916). Pirate Coasts of the Mediterranean Sea. *Geographical Review*, *2*(2), 134–151.

Serpell, J. A. (2000) Domestication and history of the cat. In *The domestic cat: the biology of its behaviour* (eds DC Turner, P Bateson), pp. 179– 192. Cambridge, UK: Cambridge University Press.

Smith, A. P., & Quin, D. G. (1996). Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation*, *77*(2), 243–267.

Solomou, A., Proutsos, N., Karetsos, G., Tsagari, K., & Chatzipavlis, N. (2022). Micrometeorology of the agricultural terraces and stone walls and impacts on biodiversity in the Mediterranean landscape of Greece. *International Journal of Agricultural Resources, Governance and Ecology*, *18*(1–2), 3–21.

Stone, P. A., Snell, H. L., & Snell, H. M. (1994). Behavioral Diversity as Biological Diversity: Introduced Cats and Lava Lizard Wariness. *Conservation Biology*, *8*(2), 569 573.

Taylor, R. H. (1979). How the Macquarie Island parakeet became extinct. *New Zealand Journal of Ecology*, 42-45.

Tershy, B. R., Shen, K.-W., Newton, K. M., Holmes, N. D., & Croll, D. A. (2015). The Importance of Islands for the Protection of Biological and Linguistic Diversity. *BioScience*, *65*(6), 592–597.

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, *546*(7656), 73–81.

Vigne, J.D., Guilaine, J., Debue, K., Haye, L., & Gérard, P. (2004). Early Taming of the Cat in Cyprus. *Science*, *304*(5668), 259–259.

Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying Threats to Imperiled Species in the United States: Assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. *BioScience*, *48*(8), 607–615.

Wilson, E. O. (1989). Threats to Biodiversity. *Scientific American*, *261*(3), 108–117.

Valakos, E. D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., Foufopoulos, J. (2008). *The amphibians and reptiles of Greece*. Ed. Chimaira.

Appendix

Appendix A (following page). Summary table showing data used in this study. Area and density columns are in hectares, total food density column is equal to the summation of dish density and dumpster density, the reptile count column shows the average and standard deviation of total reptile counts observed at the corresponding village across all surveys.

Village	Location (Lat/Long)	Village Area	Human Density	Cat Density	Cat Satiation	Dish Density	Dumpster Density	Total Food Density	Reptile Count (mean ± SE)
Monitsia	37.07, 25.48	0.9	0	0	3.67	0	0	0	18.38 ± 1.01
Chalkio	37.06, 25.48	7.55	23.7	5.7	0.74	0.93	1.46	2.38	21.13 ± 0.54
Damarionas	37.05, 25.48	8.867	40.3	3.16	2.73	0.68	0.45	1.13	18 ± 1.10
Melanes	37.09, 25.44	9.749	47.6	5.23	4.08	0.31	1.03	1.33	12.38 ± 1.49
Glynado	37.07, 25.40	12.022	61.8	9.9	9.07	0.58	0.67	1.25	3.75 ± 0.5
Vivlos	37.06, 25.41	11.024	70.9	9.07	5.16	0.91	1.18	2.09	11.75 ± 0.6
Kato Potamia	37.07, 25.43	2.235	55	12.53	3.22	2.24	1.34	3.58	9.25 ± 0.53
Moni	37.08, 25.50	4.211	53.7	10.45	5.53	1.19	1.19	2.37	11.88 ± 0.58
Skado	37.13, 25.54	3.846	27.6	1.04	-0.74	0.26	1.04	1.3	9 ± 0.28
Sifones	37.09, 25.51	0.955	1	2.09	0	0	0	0	8.5 ± 0.67
Mesi	37.15, 25.55	2.262	41	15.03	7.5	1.77	1.33	3.09	1.75 ± 0.19
Koronida	37.15, 25.55	8.895	27.7	4.72	1.86	0.34	1.46	1.8	10.375 ± 0.62

Appendix B. Field photos taken by Jeffrey Ferrer May-June 2024 on Naxos, Greece



Image 1. A. Outdoor cats line a set of dumpsters in Chalkio. B. Outdoor cats feed out of a feeding dish in Vivlos. C. Cat predates a Eurasian Collared Dove in Chora. D. Cat predates a wall lizard in Moni.



Image 2. Photo taken in Glynado demonstrating the exceptional densities cats can achieve in urban environments.



Image 3. Example of a rock wall used for conducting reptile line-transect surveys on Naxos

Appendix C. R code used for analyses and figures

```
library(AICcmodavg)
library(lme4)


##############################
#-------Cat Density Analysis----------#
##############################


data_1 <- read.csv('cat_density_analysis.csv')


#building models to find best combination of predictors for cat density
#run summary() with models to see individual model summary statistics

interaction_mod <- lm(cat_density ~ human_density + food_density + human_density *
food_density, data = data_1)

human_food_dens_mod <- lm(cat_density ~ human_density + food_density, data =
data_1)

human_dens_mod <- lm(cat_density ~ human_density, data = data_1)

food_dens_mod <- lm(cat_density ~ food_density, data = data_1)

null_mod <- lm(cat_density ~ 1, data = data_1)

#developing AIC table for model comparison

model_list <- list(model_1 = interaction_mod, model_2 = human_food_dens_mod,
                   model_3 = human_dens_mod, model_4 = food_dens_mod,
                   model_5 = null_mod)


aic_table <- aictab(cand.set = model_list, modnames =
          c("human density + food density + interaction",
          "human density + food density",
          "human density","food density",
          "null model"))

print(aic_table)

##################################
#-------------Reptile Analysis 1-------------#
##################################


data_2 <- read.csv('binned_data.csv')
```

```
#building models to find best combination of predictors for cat density
#run summary() with models to see individual model summary statistics

full_mod <- glmer(count ~ distance + cat_density + satiation + (1|village), family =
'poisson', data = data_2)


full_mod_interaction <- glmer(count ~ distance + cat_density + satiation +
cat_density*satiation + (1|village), family = 'poisson', data = data_2)


dens_mod <- glmer(count ~ cat_density + (1|village), family = 'poisson', data = data_2)


dense_satiat_mod <- glmer(count ~ cat_density + satiation + (1|village), family =
'poisson', data = data_2)

satiat_mod <- glmer(count ~ satiation + (1|village), family= 'poisson', data = data_2)

dist_mod <- glmer(count ~ distance + (1|village), family = 'poisson', data = data_2)

dist_satiat <- glmer(count ~ distance + satiation + (1|village), family = 'poisson', data =
data_2)

interaction_mod <- glmer(count ~ cat_density + satiation + cat_density * satiation +
(1|village), family = 'poisson', data = data_2)

dist_dense_mod <- glmer(count ~ distance + cat_density + (1|village), family = 'poisson',
data  = data_2)

null_mod <- glmer(count ~ 1 + (1|village), family = 'poisson', data = data_2)


##developing AIC table for model comparison


model_list <- list(model_1 = full_mod, model_2 = full_mod_interaction,
                   model_3 = dens_mod, model_4 = dense_satiat_mod,
                   model_5 = satiat_mod, model_6 = dist_mod,
                   model_7 = dist_satiat, model_8 = interaction_mod,
                   model_9 = dist_dense_mod, model_10 = null_mod)


aic_table <- aictab(cand.set = model_list, modnames =
                      c("Distance + Cat density + Cat Satiation",
                        "Distance + Cat Density + Satiation + Interaction",
                        "Cat Density",
                        "Cat Density + Cat Satiation",
                        "Cat Satiation", "Distance",
                        "Distance + Cat Satiation",
```

```
                "Cat Density + Cat Satiation + Interaction", "Null Model",
                "Cat Density + Distance"))
print(aic_table)

################################################
#--------------Reptile Analysis 2------------#
################################################

data_3 <- read.csv('transect_totals.csv')

#building models to find best combination of predictors for cat density
#run summary() with models to see individual model summary statistics

interaction_mod <- glmer(reptile_count ~ cat_density + satiation + cat_density*satiation
+ (1|village), family = 'poisson', data = data_3)


dens_satiat_mod <- glmer(reptile_count ~ cat_density + satiation + (1|village), family =
'poisson', data = data_3)


dens_mod <- glmer(reptile_count ~ cat_density + (1|village), family = 'poisson', data =
data_3)


satiat_mod <- glmer(reptile_count ~ satiation + (1|village), family = 'poisson', data =
data_3)


null_mod <- glmer(reptile_count ~ 1 + (1|village), family = 'poisson', data = data_3)


model_list <- list(model_1 = interaction_mod, model_2 = dens_satiat_mod,
            model_3 = dens_mod, model_4 = satiat_mod, model_5 = null_mod)


aic_table <- aictab(cand.set = model_list, modnames = c("Cat Density + Cat Satiation +
Interaction",
'Cat Density + Cat Satiation',
'Cat Density',
'Cat Satiation',
 'Null Model'))

print(aic_table)

############################################################
#------Schnabel Index for Cat Population Estimates------#
############################################################

cat_data <- read.csv("raw_cat_data.csv")
cat_data<- cat_data[cat_data$kitten == 'no',]
```

```
village <- c(unique(cat_data$village))
pop_vec <- rep(NA, length(village))


for (i in 1:length(village)){

  survey <- cat_data[cat_data$village == village[i],]

  if(sum(is.na(survey$cat_code)) == 0){

    survey_1 <- survey[survey$survey_number == '1',]
    survey_2 <- survey[survey$survey_number == '2',]
    survey_3 <- survey[survey$survey_number == '3',]
    survey_1_2 <- survey[survey$survey_number == '1' | survey$survey_number == '2',]

    pop_vec[i] <- (nrow(survey_1) * nrow(survey_2) +
length(unique(survey_1_2$cat_code)) * nrow(survey_3))/
      (sum(survey_2$recap == 'yes') + sum(survey_3$recap == 'yes'))
  }

  else if (sum(is.na(survey$cat_code)) == 3){

    pop_vec[i] <- 0
    cat('this is village', village[i])

  }

  else{

    survey_1 <- survey[survey$survey_number == '1',]

    survey_2 <- survey[survey$survey_number == '2',]

    pop_vec[i] <- (nrow(survey_1) * nrow(survey_2))/sum(survey_2$recap == 'yes')

  }
}

pop_vec

names(pop_vec) <- village


################################################
#---------Calculating Satiation Index-------#
################################################

satiation <- residuals(lm(cat_density ~ food_density, data = data_1))
satiation <- round(satiation, 2)
satiation <- satiation + 4.11
```

```
##############################################
#--------Garbage and Food Dish Analysis-----#
##############################################

cat_dens_garb <- lm(cat_density ~ garbage_density, data = data_1)

cat_dens_dish <- lm(cat_density ~ dishes_density, data = data_1)

##############################################
#------------------Figures-----------------#
##############################################

############################################################
#--------Figure 3. Cat Density vs Food Density-----------#
############################################################

model <- lm(cat_density ~ food_density, data = data_1)
newdata <- data.frame(food_density = seq(-6,6,.1))
predictions <- predict(model, newdata = newdata, interval = 'confidence', level = 0.95)

lower_bound <- predictions[, "lwr"]
upper_bound <- predictions[, "upr"]

# Adjust xlim and ylim to add some padding around the points
xlim_padding <- 0.1 * (max(data_1$food_density) - min(data_1$food_density))
ylim_padding <- 0.1 * (max(data_1$cat_density) - min(data_1$cat_density))

# Create the plot with adjusted limits
plot(NA,
    xlab = 'Food Density (food stations/hectare)',
    ylab = 'Cats Density (indiv/hectare)',
    las = 1,
    xlim = c(min(data_1$food_density) - xlim_padding, max(data_1$food_density) +
xlim_padding),
    ylim = c(min(data_1$cat_density) - ylim_padding, max(data_1$cat_density) +
ylim_padding))

#shaded region
polygon(c(newdata$food_density, rev(newdata$food_density)),
       c(lower_bound, rev(upper_bound)),
       col = rgb(0.2, 0.5, 1.0, 0.2),
       border = NA)

# Add the regression line
abline(lm(data_1$cat_density ~ data_1$food_density), lty = 2)

# Add Data Points

points(data_1$food_density, data_1$cat_density, pch = 21, col = rgb(0, 0, 0, 1), bg =
rgb(0.5, 0.5, 0.5, 0.7), cex = .6)
```

```
#######################################################
#-----Figure 4. Cat density vs human density------#
#######################################################

model <- lm(cat_density ~ human_density, data = data_1)
newdata <- data.frame(human_density = seq(-20,90,.1))
predictions <- predict(model, newdata = newdata, interval = 'confidence', level = 0.95)

lower_bound <- predictions[, "lwr"]
upper_bound <- predictions[, "upr"]

# Adjust xlim and ylim to add some padding around the points
xlim_padding <- 0.1 * (max(data_1$human_density) - min(data_1$human_density))
ylim_padding <- 0.1 * (max(data_1$cat_density) - min(data_1$cat_density))

# Create the plot with adjusted limits
plot(NA,
    xlab = 'Human Density (indiv/hectare)',
    ylab = 'Cats Density (indiv/hectare)',
    las = 1,
    xlim = c(min(data_1$human_density) - xlim_padding, max(data_1$human_density) +
xlim_padding),
    ylim = c(min(data_1$cat_density) - ylim_padding, max(data_1$cat_density) +
ylim_padding))

#shaded region
polygon(c(newdata$human_density, rev(newdata$human_density)),
       c(lower_bound, rev(upper_bound)),
       col = rgb(0.2, 0.5, 1.0, 0.2),
       border = NA)

# Add the regression line
abline(lm(data_1$cat_density ~ data_1$human_density),lty = 2)

# Add data points

points(data_1$human_density, data_1$cat_density, pch = 21, col = rgb(0, 0, 0, 1), bg =
rgb(0.5, 0.5, 0.5, 0.7), cex = .6)

#############################################################
#--------Figure 5. Cat Density vs Dumpster Density-------#
#############################################################

model <- lm(cat_density ~ garbage_density, data = data_1)
newdata <- data.frame(garbage_density = seq(-2, 2.5, .1))
predictions <- predict(model, newdata = newdata, interval = 'confidence', level = 0.95)

lower_bound <- predictions[, "lwr"]
upper_bound <- predictions[, "upr"]

# Adjust xlim and ylim to add some padding around the points
```

```
xlim_padding <- 0.1 * (max(data_1$garbage_density) - min(data_1$garbage_density))
ylim_padding <- 0.1 * (max(data_1$cat_density) - min(data_1$cat_density))

# Create the plot with adjusted limits
plot(NA,
    xlab = 'Dumpster Density (bins/hectare)',
    ylab = 'Cats Density (indiv/hectare)',
    las = 1,
    xlim = c(min(data_1$garbage_density) - xlim_padding,
max(data_1$garbage_density) + xlim_padding),
    ylim = c(min(data_1$cat_density) - ylim_padding, max(data_1$cat_density) +
ylim_padding))

#shaded region
polygon(c(newdata$garbage_density, rev(newdata$garbage_density)),
       c(lower_bound, rev(upper_bound)),
       col = rgb(0.2, 0.5, 1.0, 0.2),
       border = NA)

# Add the regression line
abline(lm(data_1$cat_density ~ data_1$garbage_density), lty = 2)

# Add Data Points

points(data_1$garbage_density, data_1$cat_density, pch = 21, col = rgb(0, 0, 0, 1), bg =
rgb(0.5, 0.5, 0.5, 0.7), cex = .6)

############################################################
#--------Figure 6. Cat Density vs Food Dish Density-------#
############################################################

model <- lm(cat_density ~ dishes_density, data = data_1)
newdata <- data.frame(dishes_density = seq(-1, 3, .1))
predictions <- predict(model, newdata = newdata, interval = 'confidence', level = 0.95)

lower_bound <- predictions[, "lwr"]
upper_bound <- predictions[, "upr"]

# Adjust xlim and ylim to add some padding around the points
xlim_padding <- 0.1 * (max(data_1$dishes_density) - min(data_1$dishes_density))
ylim_padding <- 0.1 * (max(data_1$cat_density) - min(data_1$cat_density))

# Create the plot with adjusted limits
plot(NA,
    xlab = 'Feeding Dish Density (dishes/hectare)',
    ylab = 'Cats Density (indiv/hectare)',
    las = 1,
    xlim = c(min(data_1$dishes_density) - xlim_padding, max(data_1$dishes_density) +
xlim_padding),
    ylim = c(min(data_1$cat_density) - ylim_padding, max(data_1$cat_density) +
ylim_padding))
```

```
#shaded region
polygon(c(newdata$dishes_density, rev(newdata$dishes_density)),
        c(lower_bound, rev(upper_bound)),
        col = rgb(0.2, 0.5, 1.0, 0.2),
        border = NA)

# Add the regression line
abline(lm(data_1$cat_density ~ data_1$dishes_density), lty = 2)

# Add Data Points

points(data_1$dishes_density, data_1$cat_density, pch = 21, col = rgb(0, 0, 0, 1), bg =
rgb(0.5, 0.5, 0.5, 0.7), cex = .6)


##########################################################
#-----Figure 7. All Reptile Counts vs Distance------#
##########################################################

data_4 <- read.csv('raw_herp_data.csv')

abundance_vec <- rep(NA, 200)

for (i in 1:length(abundance_vec)){
  abundance_vec[i] <- sum(data_4$distance == i)
}

distance <- c(1:length(abundance_vec))

model <- lm(abundance_vec ~ distance)
#use summary on above model to see analysis results

newdata <- data.frame(distance = seq(-20,220,.1))
predictions <- predict(model, newdata = newdata, interval = 'confidence', level = 0.95)

lower_bound <- predictions[, "lwr"]
upper_bound <- predictions[, "upr"]

# Adjust xlim and ylim to add some padding around the points
xlim_padding <- 0.05 * (max(distance) - min(distance))
ylim_padding <- 0.05 * (max(abundance_vec) - min(abundance_vec))

# Create the plot with adjusted limits
plot(NA,
     xlab = 'Distance from Village (meters)',
     ylab = 'Reptile Count (Indiv/meter)',
     las = 1, cex = 1,
     xlim = c(min(distance) - xlim_padding, max(distance) + xlim_padding),
     ylim = c(min(abundance_vec) - ylim_padding, 15))
```

```
#shaded region
polygon(c(newdata$distance, rev(newdata$distance)),
        c(lower_bound, rev(upper_bound)),
        col = rgb(0.2, 0.5, 1.0, 0.2),
        border = NA)

# Add the regression line
abline(lm(abundance_vec ~ distance), lty = 2)

points(distance, abundance_vec, pch = 21, col = rgb(0, 0, 0, 1), bg = rgb(0.5, 0.5, 0.5,
0.7), cex = .6)


##########################################################
#------Figure 8. Reptile Count vs Cat Density-------#
##########################################################

model <- glm(reptile_count ~ cat_density, family = 'poisson', data = data_3)

x <- seq(-5,20,.1)

# Predict the mean response and confidence interval
new_data <- data.frame(cat_density = x)

predictions <- predict(model, newdata = new_data, type = "link", se.fit = TRUE)

# Calculate the confidence intervals on the link scale
alpha <- 0.05
z_value <- qnorm(1 - alpha / 2)

# Upper and lower CI on the link scale
link_fit <- predictions$fit
link_se <- predictions$se.fit
ci_lower_link <- link_fit - z_value * link_se
ci_upper_link <- link_fit + z_value * link_se

# Convert the confidence intervals to the response scale
ci_lower <- exp(ci_lower_link)
ci_upper <- exp(ci_upper_link)
response_fit <- exp(link_fit)


# Adjust xlim and ylim to add some padding around the points
xlim_padding <- 0.1 * (max(data_3$cat_density) - min(data_3$cat_density))
ylim_padding <- 0.1 * (max(data_3$reptile_count) - min(data_3$reptile_count))


plot(NA,
    xlab = 'Cat Density (indiv/hectare)',
    ylab = 'Reptile Count (indiv/survey)',
    las = 1,
```

```
    xlim = c(min(data_3$cat_density) - xlim_padding, max(data_3$cat_density) +
xlim_padding),
    ylim = c(min(data_3$reptile_count) - ylim_padding, max(data_3$reptile_count) +
ylim_padding))

# Create the shaded polygon for the confidence interval
polygon(c(x, rev(x)), c(ci_lower, rev(ci_upper)), col = rgb(0.2, 0.5, 1.0, 0.2), border = NA)

# Add the predicted line in response scale
lines(x = seq(-5,20,.1), response_fit, lty = 2)

# Add data points
points(data_3$cat_density, data_3$reptile_count, pch = 21, col = rgb(0, 0, 0, 1), bg =
rgb(0.5, 0.5, 0.5, 0.7), cex = .6)

#######################################################
#-----Figure 9. -Reptile Count vs Cat Satiation---#
#######################################################

# Fit the Poisson regression model
model <- glm(reptile_count ~ satiation, family = 'poisson', data = data_3)

x <- c(-4:10)

# Predict the mean response and confidence interval
new_data <- data.frame(satiation = x)
predictions <- predict(model, newdata = new_data, type = "link", se.fit = TRUE)

# Calculate the confidence intervals on the link scale
alpha <- 0.05
z_value <- qnorm(1 - alpha / 2)

# Upper and lower CI on the link scale
link_fit <- predictions$fit
link_se <- predictions$se.fit
ci_lower_link <- link_fit - z_value * link_se
ci_upper_link <- link_fit + z_value * link_se

# Convert the confidence intervals to the response scale
ci_lower <- exp(ci_lower_link)
ci_upper <- exp(ci_upper_link)
response_fit <- exp(link_fit)

# Adjust xlim and ylim to add some padding around the points
xlim_padding <- 0.05 * (max(data_3$satiation) - min(data_3$satiation))
ylim_padding <- 0.1 * (max(data_3$reptile_count) - min(data_3$reptile_count))


plot( NA,
     xlab = 'Satiation Index',
     ylab = 'Reptile Count (indiv/survey)',
```

```
     las = 1, cex = 1,
     xlim = c(min(data_3$satiation) - xlim_padding, max(data_3$satiation) +
xlim_padding),
     ylim = c(min(data_3$reptile_count) - ylim_padding, max(data_3$reptile_count) +
ylim_padding))


# Create the shaded polygon for the confidence interval
polygon(c(x, rev(x)), c(ci_lower, rev(ci_upper)), col = rgb(0.2, 0.5, 1.0, 0.2), border = NA)


# Add the predicted line in response scale
lines(x, response_fit, lty = 2)


points(data_3$satiation, data_3$reptile_count,  pch = 21, col = rgb(0, 0, 0, 1), bg =
rgb(0.5, 0.5, 0.5, 0.7), cex = .6)
```