

Article

Food versus Disturbance: Contradictory Effects of Human Activities on an Opportunistic Seabird Breeding in an Oligotrophic Marine System

Rachael A. Carlberg ^{1,2,*} , Georgios Karris ³ , Manish Verma ⁴  and Johannes Foufopoulos ¹

¹ School for Environment & Sustainability, University of Michigan, Ann Arbor, MI 48109, USA; jfoufop@umich.edu

² National Conservation Training Center, US Fish & Wildlife Service, Shepherdstown, WV 25443, USA

³ Department of Environment, Ionian University, 29100 Zakynthos, Greece; gkarris@ionio.gr

⁴ Consulting for Statistics, Computing & Analytics Research, University of Michigan, Ann Arbor, MI 48109, USA; manishve@umich.edu

* Correspondence: rachael_carlberg@fws.gov

Abstract: The islands of the Aegean Sea are areas of high biodiversity and endemism and harbor globally important seabird communities. Resident seabirds breed on offshore islands, where they often form strong nesting colonies. Breeding seabirds are important determinants of an island's ecosystem function while also being exposed to a plethora of human activities. Understanding how anthropogenic activities impact such populations is not just essential for seabird conservation but is also critically important for the management of small insular ecosystems and the native species communities they support. We quantify the effect of human activities on the size and locations of Yellow-legged Gull (*Larus michahellis*) colonies from the Cyclades and Sporades archipelagos. We gathered data on variables suspected to influence seabird colonies, including physical islet characteristics, resource availability, and type and extent of human disturbance. Analyses were conducted on the local (islet) and on the regional (island cluster) levels to identify proximate and ultimate factors shaping the breeding population sizes of resident colonies. On the local level, we identify a clear negative effect of the presence of invasive rats on gull nesting density. Similarly, the presence of feral grazing mammals such as goats and rabbits has negative impacts on gull populations, an effect that appears to be primarily mediated through nest disturbance. Access to landfills and fishing vessels both had positive impacts on gull nesting density. The presence of olive groves was also positively associated with the size of resident Yellow-legged Gull populations, highlighting the role of these anthropogenic food resources in gull diets. Our results suggest approaches to managing Yellow-legged Gull populations in the Mediterranean Basin by taking into consideration the roles of introduced mammals, fishing activities, and open-air landfills on seabirds in the region.

Keywords: disturbance; invasive species; island communities; *Larus michahellis*; Mediterranean; PAFS (predictable anthropogenic food subsidies); seabirds



Citation: Carlberg, R.A.; Karris, G.; Verma, M.; Foufopoulos, J. Food versus Disturbance: Contradictory Effects of Human Activities on an Opportunistic Seabird Breeding in an Oligotrophic Marine System. *Diversity* **2022**, *14*, 421. <https://doi.org/10.3390/d14060421>

Academic Editor: Michael Wink

Received: 20 April 2022

Accepted: 23 May 2022

Published: 25 May 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Island ecosystems have emerged as critically important areas of conservation interest due to the high levels of biodiversity and endemism they harbor [1,2]. Because of their isolation, such island ecosystems are often the only places where native wildlife can find refuge to reproduce and survive [3]. Nonetheless, human-induced changes such as the introduction of invasive species, disturbance by human visitors, and climate change are increasingly putting these areas at risk [4,5]. The proper functioning of small island ecosystems depends on the maintenance of local biodiversity and especially of breeding seabird communities [3]. Seabirds serve as globally significant island keystone taxa, largely due to the nutrients they deposit on land in the form of guano, food scraps, and carcasses,

which ultimately serve to stimulate primary productivity [6,7]. For remote or very small islets, seabirds can be the sole link between marine ecosystems and nutrient-poor terrestrial breeding grounds. This activity makes them a critical component for the maintenance of endemic islet communities. Nutrient deposits benefit island flora as well as organisms of higher trophic levels, such as insects or small reptiles, which depend on robust plant communities for their establishment [8,9]. Understanding the factors that shape seabird breeding presence on islands is therefore important not just for the conservation of these species but also for the successful management of island ecosystems in general.

The Aegean Sea lies at the biogeographic crossroads located at the vertex of three continents, and its high number of endemic species makes it an area of high environmental value [10]. The marine ecosystem is oligotrophic and characterized by low levels of annual primary productivity [11] and chlorophyll [12]. The region experiences a typical Mediterranean maritime climate with modest annual precipitation levels, warm summers, and temperate winters [13]. The islands are covered with aridity-adapted Mediterranean heath communities. Species are often summer-deciduous, aromatic, and spinose, such as *Salvia* spp., *Thymus* spp., *Juniperus* spp., and *Cistus* spp. Olive cultivation is an important part of the traditional economy of the region, and groves of *Olea europaea* can be found throughout the region's inhabited islands.

Regarding seabirds, the Aegean has exceptional conservation importance as it harbors substantial breeding populations of several rare or ecologically important species, notably Yelkouan shearwater (*Puffinis yelkouan*) and Audouin's gull (*Larus audouinii*) [14]. The region is characterized by a very large number of islands (>7500) of which a small minority (<200) are inhabited by humans [15]. The absence of permanent human presence on islands has historically offered important refugia from human disturbance and unfavorable conditions for sensitive wildlife. Especially on smaller islets, species communities have evolved in the absence of terrestrial mammals and are not well adapted to herbivory or predation [16,17]. However, human activities have increasingly led to the introduction of non-native mammals such as rats, feral cats, goats, and rabbits, which have large impacts on native communities through changes in soil, vegetation, and predation pressure [18–20]. The most populous and ecologically important seabird species native to the region is the Yellow-legged Gull (*Larus michahellis*) (Figure 1) [14]. It is a generalist, colonial, ground-nesting seabird with a wide distribution across the western Palearctic [21]. Over the past several decades, large population increases have led to expansions of its range throughout Europe, despite concurrent increases in human populations and development [22].

Like many other seabirds, Yellow-legged Gulls live in nesting colonies, which can vary greatly in size and density. While some individuals exhibit migratory behavior, residents in the Aegean can be found year-round [14,23]. In this area, Yellow-legged Gulls typically nest on small, uninhabited islets and forage utilizing the resources of nearby larger, human-inhabited islands. Thus, their distributions are not only affected by the characteristics of the islets on which they nest but also by the surrounding areas that supply the resources needed for reproduction. Similar to other large gull species, Yellow-legged Gulls consume a varied diet consisting of fish, crustaceans, and other marine organisms, as well as carcasses and human refuse [14]. The species has a foraging range up to 40–50 km and is rarely found to travel any further from their colony sites, even as human development encroaches into current foraging ranges [24,25].

While colonies of the Aegean are located in uninhabited areas, the exact extent of human activity and impact on seabirds nesting on uninhabited islets has yet to be determined. Since the species feeds in the areas surrounding breeding islets, it may compete with birds from other, nearby colonies, making it necessary to consider all colonies of a region as an aggregate for accurate biological interpretation. By combining islet-level analysis with regional-level investigation, this study elucidates for the first time the functional relationships driving seabird breeding occurrence at both scales. These relationships are particularly of interest in the Aegean, given the regional economy's dependence on fisheries

and the common presence of open landfill sites for waste collection, both potential seabird resources [26,27].

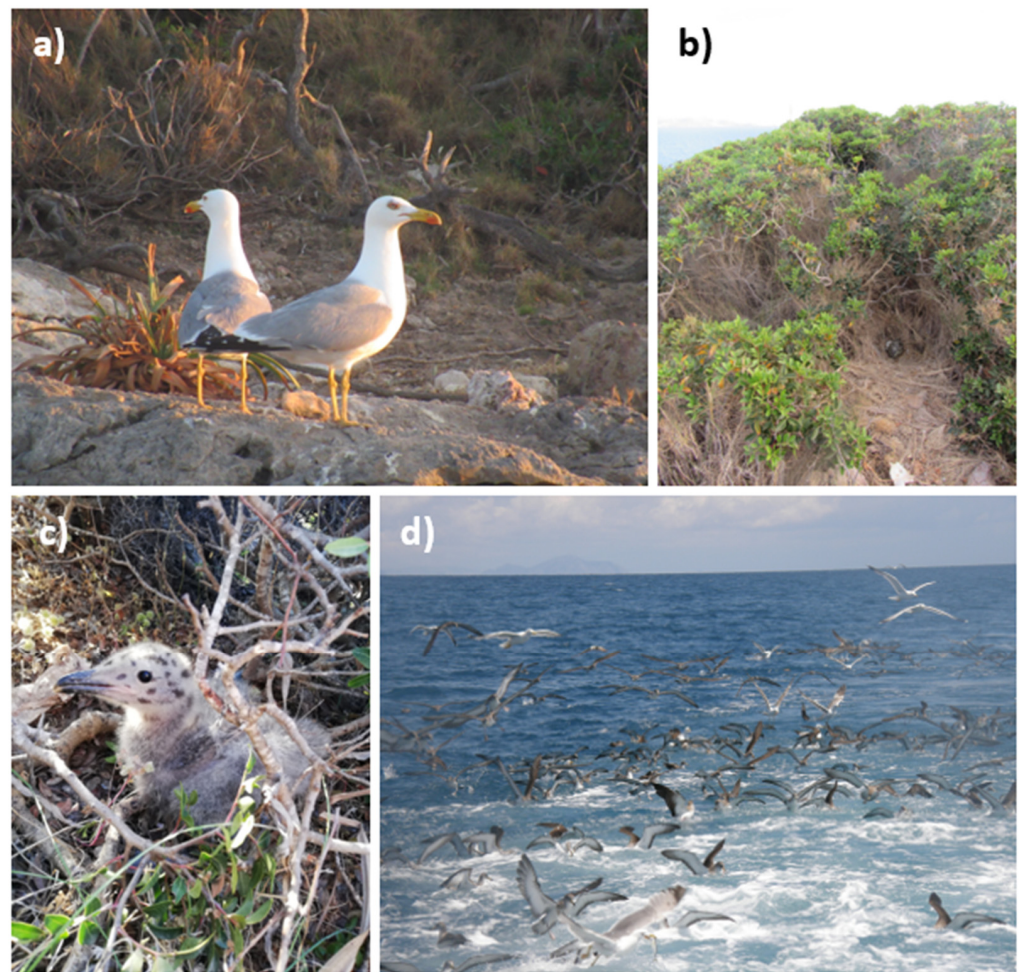


Figure 1. Photos of typical *L. michahellis* activity: (a) adult breeding pair, (b) ground nest with egg, (c) *L. michahellis* chick, (d) mixed flock foraging in the wake of a fishing vessel. Photos: Georgios Karris.

Human activity throughout Mediterranean islands, such as fishing and the introduction of feral mammals, has already impacted endemic species [18,28]. We hypothesize that human disturbances on the islet-level will constrain the size of *L. michahellis* breeding colonies by decreasing the numbers of pairs. In contrast, at a regional level, it is expected that the steadily increasing availability of Predictable Anthropogenic Food Subsidies (PAFS) [29], particularly fisheries activity, will be a key factor in the increase in Yellow-legged Gull numbers of the eastern Mediterranean. To disentangle these potentially contradictory effects, we perform two complementary analyses. To understand how proximate, islet-level factors affect the willingness of birds to nest on an island, we perform an analysis on islet-level effects impacting individual breeding colony size. On a larger, island-group scale, we complete exploratory investigations and analyses to gain an understanding of how the presence of PAFS may affect aggregate breeding population size on all surrounding colonies sharing the same main island resources. Ultimately, the results of this study can be used to target and shape regional strategic conservation planning.

2. Materials and Methods

2.1. Study Area

This study focuses on Greek islands of the northeast Mediterranean Sea with a particular emphasis on two large archipelagos: the Cyclades in the southern Aegean and the

Sporades in the northern Aegean (Figure 2). Within each island cluster, there are typically a few large islands (10,000 hectares or larger on average) inhabited by humans, each surrounded by multiple small islets (ranging from <1 to 1500 hectares) lacking any regular human presence, on which seabirds nest. Satellite island gull populations depend upon and share resources of the central island, which represents the closest and most easily accessible food source. Each satellite islet sampled in this study contained a single Yellow-legged Gull breeding colony.

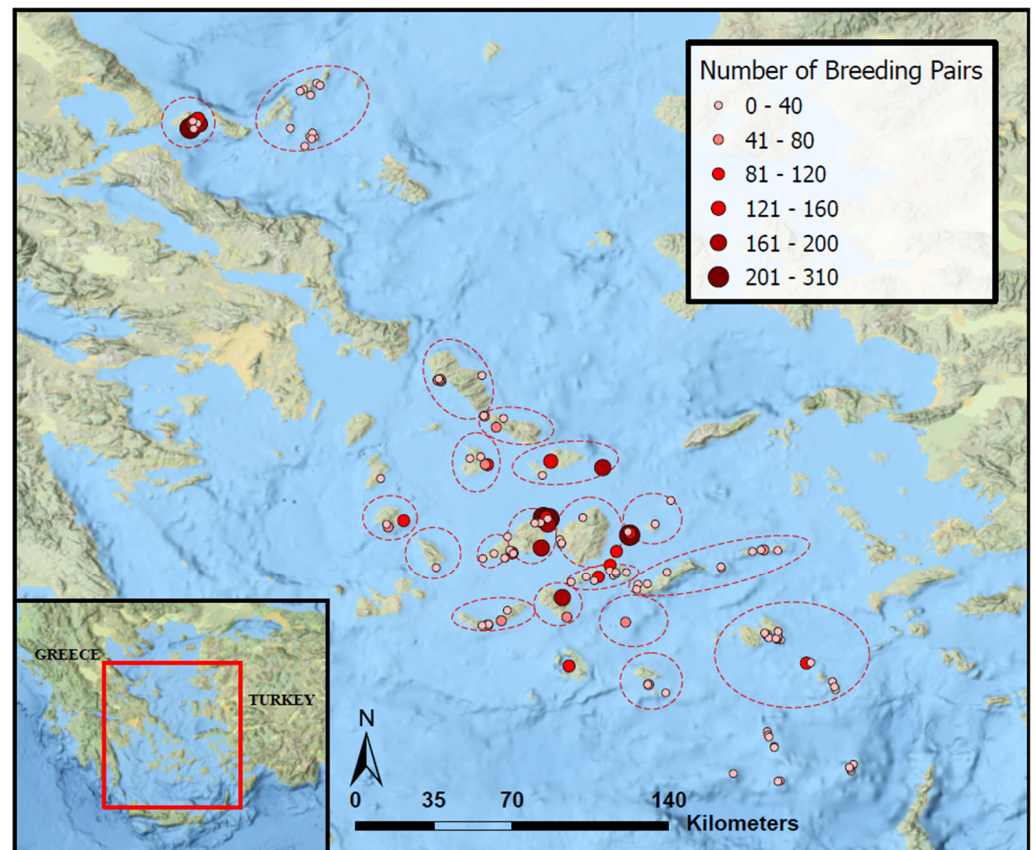


Figure 2. Locations and sizes (number of breeding pairs) of sampled *L. michahellis* colony sites located in the Aegean Sea. Regional boundaries are shown with dashed red lines and have been simplified for effective viewing. Base map sources: Esri, USGS, HERE, Garmin, FAO, NOAA, CGIAR.

2.2. Wildlife

Due to the isolation of many islands and lack of large native mammals, island endemic taxa are naïve to grazing or predation pressures from introduced taxa [13,14]. There are several mammals in the region that have been introduced to islands through human activities. Cats kept as pets are widespread on larger islands, and when not fed properly, will become feral and hunt wildlife to the point of impacting local populations [30–32]. Releases of livestock (goats (*Capra hircus*) and, less commonly, sheep (*Ovis aries*)) on islets are timed to coincide with the annual spring flush of vegetation. While goat and sheep flocks are usually left on small islets only seasonally, the timing corresponds with the Yellow-legged Gull breeding season and likely affects the nesting success of the birds [15]. Rabbits (*Oryctolagus cuniculus*) are also released on islets for hunting purposes, where they reproduce and devastate vegetation through consumption of aboveground tissues and digging of burrows, which destroys underground plant organs and loosens soil, leading to increased wind erosion.

2.3. Human Land and Resource Use

The expansion of human populations on large islands has led to key changes such as an increase in organized fishing over the past 50 years. Both the number of boats operating and the amount of gear deployed increased steeply throughout the 1970s and 1980s [33] and have remained relatively stable since then. Individual fishermen and larger trawling vessels both discard bycatch at sea, and resident gulls can regularly be seen foraging behind boats on fishing refuse [34,35]. Urbanization has led to the establishment of open-air landfills on almost every inhabited island of the Aegean. These sites are visited daily by large numbers of gulls using refuse as a food source—we, therefore, speculated that the distance to a landfill site is likely a factor determining nesting willingness in *L. michahellis* see [36–38]. Lastly, olive groves are an important part of traditional agriculture on the larger islands and gulls can be seen foraging in them. Clusters of regurgitated olive pits can be found on breeding islets in the vicinity of gull nests [39,40]. As a result, we investigated whether the extent of olive groves has an impact on gull populations.

2.4. Data Collection

Between 2016 and 2021, we censused 152 islets for the presence of Yellow-legged Gulls. The islands were visited during the gull nesting period from May to June using standardized seabird quantification protocols [41]. The small size of the nesting islets and the spatially delimited presence of gull colonies allowed for the completion of visual whole-colony counts of breeding pairs (Figure 2).

We also collected data for 14 selected variables that have the potential to influence Yellow-legged Gull colony size and distribution based on the literature and our own empirical assessment of species biology. The variables include information on physical island characteristics, human populations, resource (PAFS) availability, and local anthropogenic activities (see Tables S1 and S2 for full variables lists). We categorized each variable as a local (islet-specific) or regional metric. Physical landscape characteristics such as islet area, coastline length, and distance to the nearest inhabited island and colony site were measured from aerial imagery. Information on human populations was retrieved from the Hellenic Statistical Authority 2011 Greek Census [42].

The number of non-native grazing species occurring on an islet (European rabbits and goats; range of values 0–2) was determined through direct identification of animals, or more rarely through the presence of fresh signs, active burrows, or recent carcasses and confirmed through interviews with local shepherds and hunters. In addition, we quantified percent vegetation cover of an islet using randomized transects (see [15] for detailed methods). The presence or absence of the two main invasive rat species in the area (*Rattus rattus* and *R. norvegicus*) was determined through a literature review [43] and confirmed by visual surveys.

We determined resource availability for each colony, assuming a 50-km maximum foraging range [44]. We measured the distance from each colony to the nearest landfill site. We retrieved information from the United Nations Food and Agriculture Organization on registered fishing vessels to determine the number of vessels registered to each port [45]. We also measured each colony's distance to the nearest active fishing port. Lastly, we accessed landcover data from the CORINE Landcover Inventory to determine the area of olive groves falling within each region [46]. All spatial analysis was completed in ArcGIS Pro v2.7.1 (Esri, Redlands, CA, USA). All data can be found in Tables S3 and S4.

2.5. Statistical Analysis

Because our collection period spanned five years, we examined our data for potential sources of temporal bias. This study mainly examines the impact of human activities (access to landfills, fishing vessels, and olive groves), which show a lack of predictable temporal heterogeneity. We also assume that physical islet characteristics that may affect breeding success remain constant over time. However, population outbreaks of feral grazing mammals may affect the breeding success of Yellow-legged Gulls on a temporal

scale. As these outbreaks are unpredictable, we were unable to include a predictor to account for them in our models.

A previous study has indicated that using nested spatial scales is effective in determining seabird habitat selection [47]. Consequently, data analysis was completed on two levels to determine significant factors at the islet-level scale and at the regional island cluster scale. For the islet-level model, we calculated Pearson correlation coefficients to determine collinearity among continuous independent variables (Table S5). Variables with high levels (>0.50) of collinearity were not included in the same model. To account for the overdispersion of our count data, a negative binomial model (link = log) where $\ln(y) = \ln(\text{islet area}) + \beta_0 + \beta_1 x_1 + \beta_2 x_2 \dots$ was chosen, where y is the expected count of gull pairs. We used the natural logarithm of the islet area as an offset in each tested model to account for the wide range of sampled islet sizes [48]. We tested nested models, and the best was selected by considering the Akaike Information Criterion (AIC).

To establish a regional dataset, we took advantage of the spatial clustering of the islands to aggregate data into 19 biologically relevant units. Regions were centered around the large, inhabited islands, while islets were assigned to regions based on known gull behavior and established foraging activity. The number of fishing vessels registered to a cluster was established by adding the number of vessels at each port in that cluster. Colony distances to the nearest fishing port were weighted by colony size to obtain a combined average cluster value; this process was repeated for landfills. Other variables were only gathered at the regional scale (human population and olive grove area). Two regions without sufficient data (Kithnos and Santorini) were excluded from the analysis.

Due to the low sample size of the regional cluster units, we did not have enough statistical power to test multivariate models on a regional scale. Instead, we present correlations between total cluster gull populations and the corresponding independent variables to explore the functional relationships between regional factors and gull breeding populations. Before calculating Pearson's correlation coefficients (Table S6), each predictor variable was plotted against the total regional gull population to verify a linear relationship and assess for outliers. To avoid false-positive results inherent to conducting multiple simultaneous tests on the same dataset, we have applied the Bonferroni correction to assess the significance of p -values [49]. All statistical analysis was completed in R 4.0.3 [50]. Packages 'MASS' [51] and 'ggplot2' [52] were used for analysis and data visualization.

3. Results

3.1. Local (Islet-Level) Analysis

The average number of breeding pairs per islet was 37 (Range 1–310, $n = 152$). After testing several models, the two best models had a ΔAIC of 2. (For full R output of all models, see Figures S1–S5). Previous studies [53,54] recommend selection of the simplest model when multiple nested models are within 2 AIC units of each other. Our selected model (AIC = 1205) includes the variables of rat presence, presence of non-native grazing species, percent vegetation cover, and distance in kilometers to the nearest landfill (Table 1).

Table 1. AIC and ΔAIC values for islet-level models tested.

Model	AIC	ΔAIC
Gull Pairs ~ Rats + Grazers + Veg_cover + Dist_landfill + Fishing vessels	1203	
Gull Pairs ~ Rats + Grazers + Veg_cover + Dist_landfill	1205	2
Gull Pairs ~ Rats + Grazers + Veg_cover	1215	12
Gull Pairs ~ Rats + Grazers	1308	105
Gull Pairs ~ Rats	1317	114

Due to the inclusion of the islet area as an offset in the model, the output β -values are related to the natural logarithm of breeding pair density rather than the number of breeding pairs. To understand the effect size, the β -value for each variable has been exponentiated

and included in Table 2. The model results show a significant negative relationship between breeding colony density and the presence of non-native rats ($\beta = -1.21$, $p = 0.00029$), as well as presence of introduced grazing species ($\beta = -0.78$, $p = 0.027$ for one grazer present, $\beta = -1.23$, $p = 0.0081$ for two grazers present) (Figure 3). Percent vegetation cover showed a positive, but nonsignificant, relationship with gull density ($\beta = 0.72$, $p = 0.196$). Distance to the nearest landfill showed a negative relationship with colony density ($\beta = -0.039$, $p = 0.00002$).

Table 2. Coefficients and error estimates for islet-level gull density model. Those marked with an asterisk (*) are significant with a p -value less than 0.05, those marked with two asterisks (**) are significant with a p -value less than 0.01, and those marked with three asterisks (***) are significant with a p -value less than 0.001.

Variable	β	Effect Size (e^β)	SE	t	p-Value
Intercept	3.57	35.5	0.43	8.30	<0.001 ***
Islet Rats	−1.21	0.30	0.33	−3.63	<0.001 ***
1 Grazer	−0.78	0.46	0.35	−2.21	0.027 *
2 Grazers	−1.23	0.29	0.47	−2.65	0.008 **
Vegetation_Cover	0.72	2.05	0.56	1.29	0.20
Distance_landfill	−0.039	0.96	0.0091	−4.27	<0.001 ***

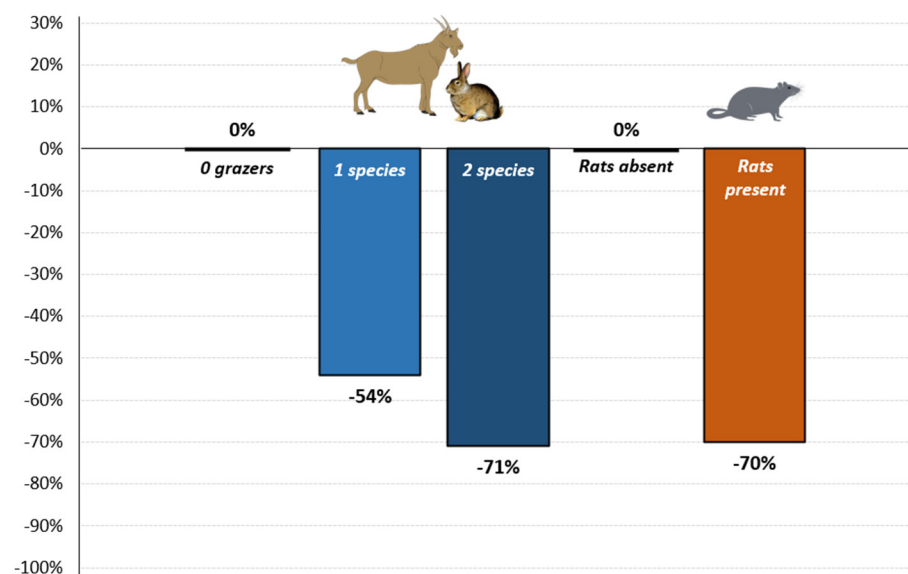


Figure 3. Changes in baseline density of islet breeding colonies based on disturbance type. Baseline density of islet colonies is calculated using the intercept of the islet-level model, and subsequent changes to the baseline are determined using the β -values for the presence of one grazing species, 2 grazing species, and rats.

3.2. Regional Analysis

The average total number of breeding pairs inhabiting a cluster was 256 (Range 7–836, $n = 19$). Upon application of the Bonferroni correction to avoid false-positive results from seven correlation tests, we used a p -value of 0.007 to assess the significance of relationships. At the regional level, the total number of Yellow-legged Gull pairs was significantly related to the number of fishing vessels registered to that particular cluster ($r = 0.75$, $p = 0.00019$) (Table 3). No other regional covariates were found to be significant.

Table 3. Pearson’s correlation coefficients between regional variables and the total number of nesting pairs in a region. Those marked with an asterisk (*) are significant with a *p*-value less than 0.007.

Variable	Correlation Coefficient	<i>p</i> -Value
Main (inhabited) island area	0.34	0.16
Human population	0.42	0.07
Total islet area	0.14	0.56
Fishing vessels	0.75	<0.001 *
Olive grove area	0.49	0.03
Average distance to nearest port	−0.14	0.56
Average distance to nearest landfill	−0.13	0.35

4. Discussion

We investigated both islet-specific and regional factors, which have the potential to influence the size of nesting colonies of Yellow-legged Gulls in the Aegean Sea. The results demonstrate that humans have, through a diversity of direct and indirect means, a strong effect on gull populations. As human presence continues to grow and development expands into new areas, Yellow-legged Gulls show two divergent responses to anthropogenic changes.

At the islet level, breeding activity responds sensitively to the presence of several exotic mammalian species. The presence of mammal predators dramatically reduces the suitability of an island as a breeding site. Out of 152 islets visited, only nine appear to harbor any mammal predators (other than rats), and gulls appear to potentially co-occur with mammal predators on only two sites, or 1.3% of the sampled colonies (Ano Fira (near Antiparos), and Kalo Livadi (off Kythnos)). The two main relevant predators include one native species, the stone marten (*Martes foina*), and one human commensal, the feral cat (*Felis catus*). Both predators are essentially absent from small, uninhabited islets [43]. Cats occur in various stages of nutritional dependence on humans in the vicinity of permanent human settlements [31] but can also be found on the largest islets in a feral state away from humans [55]. While mammal predators were not explicitly included in this analysis due to the exceedingly low number of seabird islets where they may exist, these clear distributional patterns serve to illustrate the overwhelming negative influence predator presence has on colony site selection for seabirds [32]. These patterns also argue that any reductions in feral cats will likely translate into important conservation gains in colony site dynamics and habitat use by wildlife on small islands.

The islet-level analysis also revealed that the presence of exotic rats reduces the densities of breeding Yellow-legged Gull colonies. Exotic rats were widespread, inhabiting 54% of sampled islets and 100% of regions. Our model corroborates the previously documented negative impact that rats have on seabirds, particularly ground-nesting species whose eggs and chicks are relatively easy prey [16]. Rat impacts depend on both the rat species and seabird species affected, with small-bodied species (e.g., *Hydrobates*) being more impacted by rats than large ones [56]. In the Mediterranean Basin in particular, a long history of co-occurrence of rats and seabirds appears to have allowed at least some species to adapt to rat presence [17]. Because Yellow-legged Gulls are relatively large-bodied and aggressive, rat presence may be an even larger deterrent for other Aegean seabirds compared to what is documented here. Completing population eradications of rats from small islands should therefore be a high conservation priority in the Mediterranean, as they have strong negative effects both on Yellow-legged Gulls as well as on smaller, less aggressive species such as Scopoli’s shearwater (*Calonectris diomedea*) and Yelkouan shearwater (*Puffinus yelkouan*) [57–60].

Beyond predation, we found that the introduction of non-native grazing species also has a clear impact on *L. michahellis*. Recent research has shown the pervasive effects that introduced herbivores have on Mediterranean ecosystems, including dramatic declines in shrub vegetation cover and shifts in plant community composition towards grazing-resistant species [15]. Soil disturbance through trampling and burrowing leads to elevated

levels of erosion, resulting in irreversible soil loss. Consequently, observed effects on nesting gulls are mediated either directly through trampling and nest disturbance or indirectly through soil damage and destruction of vegetation beneficial for nesting [59].

The data here argue for effects through direct nest disturbance as nesting density was not significantly related to the extent of perennial vegetation cover. Field observations indicate that Yellow-legged Gulls prefer the presence of shade for breeding; hence, more research is needed to ascertain the relative importance of the two mechanisms. As shown in Figure 3, the presence of a single grazing species (either rabbits or goats) reduces the baseline density of a colony by about 54%. The addition of a second grazing species further reduces the density of a colony to about 71% below the model baseline, indicating an additive effect of non-native grazer presence. The reduction in gull numbers by grazers is likely ecologically significant for the region [60], and grazing was extensive throughout the study area, with 55% of sampled islets containing at least one grazing species, and 17% containing two. Seabird presence and guano deposits on land are often depended upon for the recovery of overgrazed areas [61]. A decrease in seabird numbers likely lessens the chance of ecological recovery of endemic plant communities after the grazing species are moved or eradicated. Our results indicate an urgent need for policy prohibiting grazer releases to be put in place to avoid further reductions in seabird nesting, as well as the eradication of feral grazing individuals from small islets to restore potential nesting habitats.

Colony densities were also constrained by the distance to the nearest landfill site, with density decreasing by 4% for each additional kilometer of distance. These results quantify the importance of Predictable Anthropogenic Food Subsidies (PAFS) in the Aegean, which provide gulls with sources of stationary, relatively low-effort food year-round. Our results mirror those seen in other regions of the Yellow-legged Gull's range, highlighting once again the extensive and widespread impact of PAFS on seabirds see [37,38,62–64].

Because of the feeding ecology of Yellow-legged Gulls, it is important to examine not only colony-specific factors but also regional variables impacting multiple colonies at once. At the regional scale, the most significant factor impacting aggregate gull population size was the number of registered fishing vessels in that region (Figure 4). The presence of fishing vessels acts as an abundant, predictable high-quality food source for gulls by providing bycatch and offal [62,65]. We found no evidence that the total islet area in a region is related to the number of breeding pairs. This result suggests that PAFS such as fishery discards may have a larger effect on colony size than habitat availability. Due to our low sample size of regions, we cannot definitively quantify this relationship and encourage future study.

The functional relationships uncovered by this study (Figure 5) are important for Yellow-legged Gull population management but also have implications for Aegean Island species communities in general. The rapid population growth of Yellow-legged Gulls reflects their ability to exploit a variety of resources. Because of their behavioral flexibility, Yellow-legged Gulls are uniquely suited to take advantage of a diversity of PAFS, including landfills, fishing discards, and olive groves. At the same time, they are known to exhibit high levels of aggression [66] and have also been shown to compete with other species for food and display kleptoparasitic behavior [24,67,68]. The rising populations of Yellow-legged Gulls exacerbate the effects of their behavioral dominance and increasingly present a threat to other, rarer Aegean seabirds such as shearwaters and Audouin's Gulls (*Larus audouinii*), which are not characterized by behavioral flexibility and are more susceptible to predation. Another factor of concern is the link between the use of PAFS, ingestion of plastics, and disease spread such as Salmonella [69,70]. As increasing numbers of gulls congregate into small areas to compete for food, there is a rising risk of pathogen transmission both at the feeding site and at colony islets, where other species may be impacted. As Yellow-legged Gulls reap the benefits of these food sources in the Aegean, their rising populations, aggressive behavior, and disease spread may become constraints on other native seabirds.

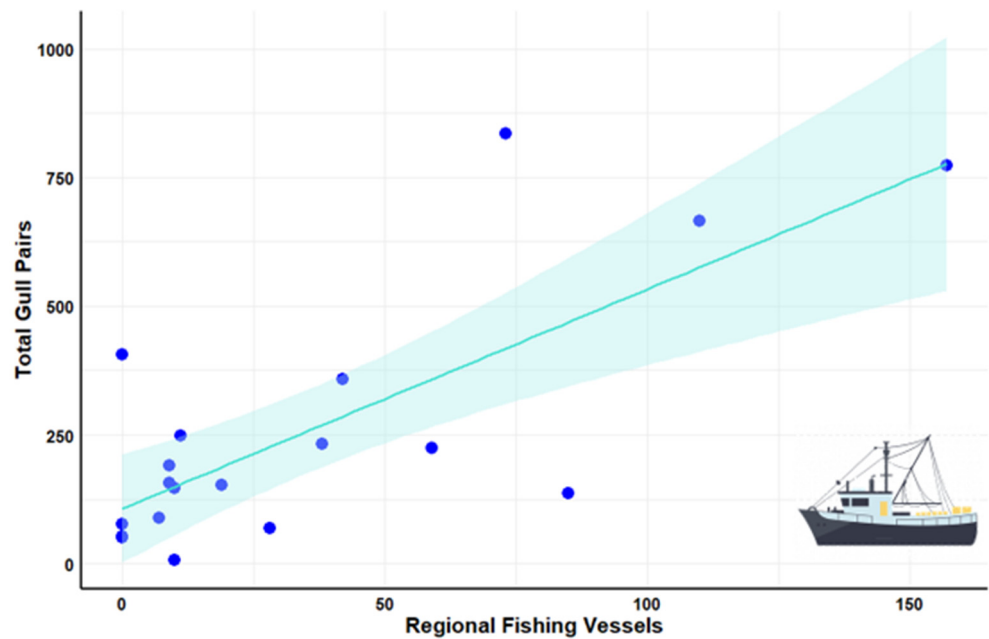


Figure 4. Plot illustrating the relationship between registered fishing vessels versus the total number of Yellow-legged Gull pairs inhabiting a region.

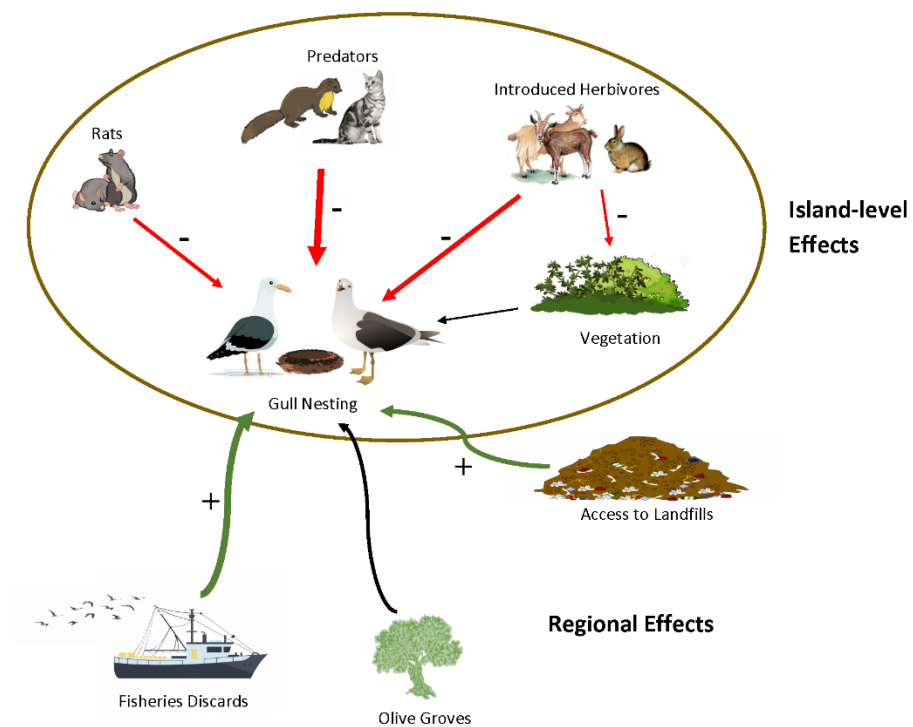


Figure 5. Conceptual diagram depicting functional interactions for a typical *Larus michahellis* colony in the Aegean Sea Region, including island-level and regional relationships with the potential to affect colony size and density. Red arrows represent expected negative effects, while green arrows suggest positive impacts.

As human populations are expected to continue increasing in the future, their impacts on local ecosystems are expected to become more pronounced. By having a solid knowledge of the factors that constrain and increase Yellow-legged Gull numbers, species populations can be better monitored and controlled. Past population control efforts for Yellow-legged

Gulls such as culls have been unreliable [71,72], indicating the need for different methods. Currently, there is no large-scale rat eradication effort in the Aegean, and the release of grazers onto islets is largely unregulated. While a comprehensive plan to control the spread of rats and designate where grazing species can be released may have positive impacts on Yellow-legged Gull numbers, more importantly, it could critically benefit other seabirds that nest on the same islets (particularly *L. audouinii*). Impacts of an eradication effort for rats and grazers may also benefit endemic plants and invertebrates, which depend on robust seabird communities for nutrient deposition. Policies on mitigation measures for fisheries bycatch and landfill waste, as well as the banning of fishery discards by imposing an obligation to land unwanted catch (according to the Common Fishery Policy reform proposed by the European Commission in 2013) could help curb further Yellow-legged Gull population increases, allowing other seabirds that are less competitive in utilizing bycatch to better compete for breeding territory, leading to more diverse seabird communities on islets of the region. We propose further research into the interactions between Yellow-legged Gulls and other native seabirds in the oligotrophic Aegean marine ecosystem to ascertain the impact that Yellow-legged Gull population expansions have on other species. This knowledge could further guide best practices to preserve healthy seabird communities and whole-island ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14060421/s1>, Table S1: Name, description, and source of all islet-level variables tested; Table S2: Name description, and source of all regional-level variables tested; Table S3: Islet-level data; Table S4: Regional data; Table S5: Pearson’s correlation coefficients for islet-level continuous independent variables; Table S6: Pearson’s correlation coefficients for regional-level independent variables; Figures S1–S5: R output for all islet-level models tested.

Author Contributions: Conceptualization, R.A.C., J.F. and G.K.; methodology, R.A.C., J.F. and G.K.; formal analysis, R.A.C., M.V. and J.F.; data curation, J.F. and R.A.C.; writing—original draft preparation, R.A.C.; writing—review and editing, J.F., G.K. and M.V.; supervision, J.F.; funding acquisition, R.A.C. and J.F. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the School for Environment & Sustainability, University of Michigan, and Matthaei Botanical Gardens and Nichols Arboretum, University of Michigan.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data is included in the Supplementary Materials.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

References

1. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853–858. [[CrossRef](#)] [[PubMed](#)]
2. Russell, J.C.; Kueffer, C. Island biodiversity in the Anthropocene. *Annu. Rev. Environ. Resour.* **2019**, *44*, 31–60. [[CrossRef](#)]
3. Mulder, C.P.H.; Anderson, W.B.; Towns, D.R.; Bellingham, P.J. *Seabird Islands: Ecology, Invasion, and Restoration*; Oxford University Press: Oxford, UK, 2011.
4. Klöck, C.; Fink, M. *Dealing with Climate Change on Small Islands: Towards Effective and Sustainable Adaptation*; Göttingen University Press: Göttingen, Germany, 2019.
5. Martin, J.-L.; Thibault, J.-C.; Bretagnolle, V. Black rats, island characteristics, and colonial nesting birds in the Mediterranean: Consequences of an ancient introduction. *Conserv. Biol.* **2000**, *14*, 1452–1466. [[CrossRef](#)]
6. Anderson, W.B.; Polis, G.A. Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **1999**, *118*, 324–332. [[CrossRef](#)]
7. Wainright, S.C.; Haney, J.C.; Kerr, C.; Golovkin, A.N.; Flint, M.V. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants of St. Paul, Pribilof Islands, Bering Sea, Alaska. *Mar. Biol.* **1998**, *131*, 63–71. [[CrossRef](#)]
8. Croll, D.A.; Maron, J.L.; Estes, J.A.; Danner, E.M.; Byrd, G.V. Introduced predators transform Subarctic islands from grassland to tundra. *Science* **2005**, *307*, 1959–1961. [[CrossRef](#)]

9. Sánchez-Piñero, F.; Polis, G.A. Bottom-up dynamics of allochthonous input: Direct and indirect effects of seabirds on islands. *Ecology* **2000**, *81*, 3117–3132. [\[CrossRef\]](#)
10. Medail, F.; Quezel, P. Hot-Spots for Conservation of Plant Biodiversity in the Mediterranean Basin. *Ann. Mo. Bot. Gard.* **1997**, *84*, 112–127. [\[CrossRef\]](#)
11. Bosc, E.; Bricaud, A.; Antoine, D. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Glob. Biogeochem. Cycles* **2004**, *18*, GB1005. [\[CrossRef\]](#)
12. Gotsis-Skretas, O.; Pagou, K.; Moraitou-Apostolopoulou, M.; Ignatiades, L. Seasonal horizontal and vertical variability in primary production and standing stocks in phytoplankton and zooplankton in the Cretan Sea and Straits of the Cretan Arc (March 1994–January 1995). *Prog. Oceanogr.* **1999**, *44*, 625–649. [\[CrossRef\]](#)
13. Gikas, P.; Tchobanoglous, G. Sustainable use of water in the Aegean Islands. *J. Environ. Manag.* **2009**, *90*, 2601–2611. [\[CrossRef\]](#)
14. Fric, J.; Portolou, D.; Manolopoulos, A.; Kastritis, T. *Important Areas for Seabirds in Greece*; Hellenic Ornithological Society (HOS/BirdLife Greece): Athens, Greece, 2012.
15. Triantis, K.A.; Mylonas, M. Greek islands, biology. In *Encyclopedia of Islands*; Gillespie, R., Glague, D.A., Eds.; University of California Press: Berkeley, CA, USA, 2009; pp. 388–392.
16. Blumstein, D.T.; Daniel, J.C. The loss of anti-predator behavior following isolation on islands. *Proc. R. Soc. B* **2005**, *272*, 1663–1668. [\[CrossRef\]](#) [\[PubMed\]](#)
17. Coblentz, B.E. The effects of feral goats (*Capra hircus*) on island ecosystems. *Biol. Conserv.* **1978**, *13*, 279–286. [\[CrossRef\]](#)
18. Gizicki, Z.S.; Tamez, V.; Galanopoulou, A.P.; Avramidis, P.; Foufopoulos, J. Long-term effects of feral goats (*Capra hircus*) on Mediterranean island communities: Results from whole island manipulations. *Biol. Invasions* **2018**, *20*, 1537–1552. [\[CrossRef\]](#)
19. Jones, H.P.; Tershy, B.R.; Zavaleta, E.S.; Croll, D.A.; Keitt, B.S.; Finkelstein, M.E.; Howald, G.R. Severity of the effects of invasive rats on seabirds: A global review. *Conserv. Biol.* **2008**, *22*, 16–26. [\[CrossRef\]](#)
20. Ruffino, L.; Bourgeois, K.; Vidal, E.; Duhem, C.; Paracuellos, M.; Escribano, F.; Sposimo, P.; Baccetti, N.; Pascal, M.; Oro, D. Invasive rats and seabirds after 2000 years of an unwanted coexistence on Mediterranean islands. *Biol. Invasions* **2009**, *11*, 1631–1651. [\[CrossRef\]](#)
21. Harrison, P.; Perrow, M.R.; Larsson, H. *Seabirds: The New Identifications Guide*; Lynx Edicions: Barcelona, Spain, 2021.
22. Vidal, E.; Medail, F.; Tatoni, T. Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. *Biodivers. Conserv.* **1998**, *7*, 1013–1026. [\[CrossRef\]](#)
23. Keller, V.; Herrando, S.; Voříšek, P.; Franch, M.; Kipson, M.; Milanese, P.; Martí, D.; Anton, M.; Klvaňová, A.; Kalyakin, M.V.; et al. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*; European Bird Census Council & Lynx Edicions: Barcelona, Spain, 2020.
24. Arizaga, J.; Herrero, A.; Galarza, A.; Hidalgo, J.; Aldalur, A.; Cuadrado, J.F.; Ocio, G. First-year movements of Yellow-legged Gull (*Larus michahellis*) from the Southeastern Bay of Biscay. *Waterbirds* **2010**, *33*, 444–450. [\[CrossRef\]](#)
25. Mendes, R.F.; Ramos, J.A.; Palva, V.H.; Calado, J.G.; Matos, D.M.; Ceia, F.R. Foraging strategies of a generalist seabird species, the yellow-legged gull, from GPS tracking and stable isotope analyses. *Mar. Biol.* **2018**, *165*, 168. [\[CrossRef\]](#)
26. Egúnez, A.; Zorrozuza, N.; Aldalur, A.; Herrero, A.; Arizaga, J. Local use of landfills by a yellow-legged gull population suggests distance-dependent resource exploitation. *J. Avian Biol.* **2018**, *49*, e01455. [\[CrossRef\]](#)
27. Karris, G.; Ketsilis-Rinis, V.; Kalogeropoulou, A.; Xirouchakis, S.; Machias, A.; Maina, I.; Kavadas, S. The use of demersal trawling discards as a food source for two scavenging seabird species: A case study of an eastern Mediterranean oligotrophic marine ecosystem. *Avian Res.* **2018**, *9*, 26. [\[CrossRef\]](#)
28. Coll, M.; Piroddi, C.; Steenbeek, J.; Kaschner, K.; Ben Rais Lasram, F.; Aguzzi, J.; Ballesteros, E.; Bianchi, C.N.; Corbera, J.; Voultsiadou, E. The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats. *PLoS ONE* **2010**, *5*, 11842. [\[CrossRef\]](#) [\[PubMed\]](#)
29. Oro, D.; Genovart, M.; Tavecchia, G.; Fowler, M.S.; Martínez-Abraín, A. Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* **2013**, *16*, 1501–1514. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Krawczyk, E.; Hedman, H.; Pafilis, P.; Bergen, K.; Foufopoulos, J. Effects of touristic development on Mediterranean island wildlife. *Landscape Ecol.* **2019**, *34*, 2719–2734. [\[CrossRef\]](#)
31. Li, B.; Belasen, A.; Pafilis, P.; Bednekoff, P.; Foufopoulos, J. Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: Insights from an ancient introduction. *P. R. Soc. B* **2014**, *281*, 20140339. [\[CrossRef\]](#)
32. Medina, F.M.; Bonnaud, E.; Vidal, E.; Tershy, B.R.; Zavaleta, E.S.; Donlan, C.J.; Keitt, B.S.; Le Corre, M.; Horwath, S.V.; Nogales, M. A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Chang. Biol.* **2011**, *17*, 3503–3510. [\[CrossRef\]](#)
33. Fishery Country Profile: Greece. Food and Agriculture Organization (FAO) of the United Nations. Available online: <https://www.fao.org/fishery/en/facp/grc?lang=en> (accessed on 19 April 2021).
34. Arcos, J.M.; Oro, D.; Sol, D. Competition between the yellow-legged gull *Larus cachinnans* and Andouin's gull *Larus audouinii* associated with commercial fishing vessels: The influence of season and fishing fleet. *Mar. Biol.* **2001**, *139*, 807–816.
35. Cama, A.; Abellana, R.; Christel, I.; Ferrer, X.; Vieites, D.R. Living on predictability: Modelling the density distribution of efficient foraging seabirds. *Ecography* **2012**, *35*, 912–921. [\[CrossRef\]](#)
36. Bosch, M.; Oro, D.; Ruiz, X. Dependence of Yellow-legged Gulls (*Larus cachinnans*) on food from human activity in two Western Mediterranean colonies. *Avocetta* **1994**, *18*, 135–139.

37. Duhem, C.; Vidal, E.; Legrand, J.; Tatoni, T. Opportunistic feeding responses of the Yellow-legged Gull *Larus michahellis* to accessibility of refuse dumps. *Bird Study* **2003**, *50*, 61–67. [\[CrossRef\]](#)
38. Duhem, C.; Roche, P.; Vidal, E.; Tatoni, T. Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. *Popul. Ecol.* **2008**, *50*, 91–100. [\[CrossRef\]](#)
39. Battisti, C. Heterogeneous composition of anthropogenic litter recorded in nests of Yellow-legged gull (*Larus michahellis*) from a small Mediterranean island. *Mar. Pollut. Bull.* **2020**, *150*, 110682. [\[CrossRef\]](#) [\[PubMed\]](#)
40. Oro, D. Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. *Mar. Ecol. Prog. Ser.* **1996**, *132*, 43–46. [\[CrossRef\]](#)
41. Hutchinson, A.E. Estimating numbers of colonial nesting seabirds: A comparison of techniques. *Proc. Colon. Waterbird Group* **1980**, *3*, 235–244.
42. General Population Census 2011. Hellenic Statistical Authority (ELSTAT), 2011. Available online: <https://www.statistics.gr/en/2011-census-pop-hous> (accessed on 9 August 2020).
43. Masseti, M. *Atlas of Terrestrial Mammals of the Ionian and Aegean Islands*; de Gruyter GmbH: Berlin, Germany, 2012.
44. Arizaga, J.; Aldalur, A.; Herrero, A.; Cuadrado, J.F.; Díez, E.; Crespo, A. Foraging distances of a resident yellow-legged gull (*Larus michahellis*) population in relation to refuse management on a local scale. *Eur. J. Wildl. Res.* **2014**, *60*, 171–175. [\[CrossRef\]](#)
45. General Fisheries Commission for the Mediterranean—Fleet Register. Food and Agriculture Organization (FAO) of the United Nations. Available online: <http://www.fao.org/gfcm/data/fleet/register/en/> (accessed on 29 June 2020).
46. European Union Corine Land Cover 2018. Copernicus Land Monitoring Service, European Environment Agency (EEA). Available online: <https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download> (accessed on 7 October 2020).
47. Vidal, E.; Roche, P.; Bonnet, V.; Tatoni, T. Nest-density distribution patterns in a yellow-legged gull archipelago colony. *Acta Oecol.* **2001**, *22*, 245–251. [\[CrossRef\]](#)
48. Cox, S.; West, S.G.; Aiken, L.S. The Analysis of Count Data: A Gentle Introduction to Poisson Regression and Its Alternatives. *J. Pers. Assess.* **2009**, *91*, 121–136. [\[CrossRef\]](#)
49. Dunn, O.J. Multiple Comparisons among Means. *J. Am. Stat. Assoc.* **1961**, *56*, 52–64. [\[CrossRef\]](#)
50. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020. Available online: <https://www.R-project.org/> (accessed on 20 May 2022).
51. Venables, W.N.; Ripley, B.D. *Modern Applied Statistics with R*, 4th ed.; Springer: New York, NY, USA, 2002.
52. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*; Springer: New York, NY, USA, 2016.
53. Symonds, M.R.E.; Moussalli, A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behav. Ecol. Sociobiol.* **2011**, *65*, 13–21. [\[CrossRef\]](#)
54. Burnham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference*, 2nd ed.; Springer: New York, NY, USA, 1998.
55. Cheke, A.S.; Ashcroft, R.E. Mammals and butterflies new to Amorgos (Kiklades), with notes on reptiles and amphibians. *Parnass. Arch.* **2017**, *5*, 11–27.
56. Latorre, L.; Larrinaga, A.R.; Santamaria, L. Rats and Seabirds: Effects of egg size on predation risk and the potential of conditioned taste aversion as a mitigation method. *PLoS ONE* **2013**, *8*, e76138. [\[CrossRef\]](#) [\[PubMed\]](#)
57. Igual, J.M.; Forero, M.G.; Gomez, T.; Orueta, J.F.; Oro, D. Rat control and breeding performance in Cory’s shearwater (*Calonectris diomedea*): Effects of poisoning effort and habitat features. *Anim. Conserv.* **2006**, *9*, 59–65. [\[CrossRef\]](#)
58. Lago, P.; Santiago Cabello, J.S.; Varnham, K. Long term rodent control in Rdum tal-Madonna Yelkouan shearwater colony. In *Island Invasives: Scaling up to Meet the Challenge*; Veitch, C.R., Clout, M.N., Martin, A.R., Russel, J.C., West, C.J., Eds.; Occasional Paper of the IUCN Species Survival Commission: Gland, Switzerland, 2019; pp. 196–199.
59. Hata, K.; Osawa, T.; Hiradate, S.; Kachi, N. Soil erosion alters soil chemical properties and limits grassland plant establishment on an oceanic island even after goat eradication. *Restor. Ecol.* **2018**, *27*, 333–342. [\[CrossRef\]](#)
60. Pafilis, P.; Anastasiou, I.; Sagonas, K.; Valakos, E.D. Grazing by goats on islands affects the populations of an endemic Mediterranean lizard. *J. Zool.* **2013**, *290*, 255–264. [\[CrossRef\]](#)
61. Jones, H.P. Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an island archipelago. *Ecol. Appl.* **2010**, *20*, 1204–1216. [\[CrossRef\]](#)
62. Calado, J.G.; Matos, D.M.; Ramos, J.A.; Moniz, F.; Cela, F.R.; Granadeiro, J.P.; Palva, V.H. Seasonal and annual differences in foraging ecology of two gull species breeding in sympatry and their use of fishery discards. *J. Avian Biol.* **2017**, *49*, 1–12. [\[CrossRef\]](#)
63. Ramos, R.; Ramírez, F.; Sanpera, C.; Jover, L.; Ruiz, X. Diet of Yellow-legged Gull (*Larus michahellis*) chicks along the Spanish Western Mediterranean coast: The relevance of refuse dumps. *J. Ornithol.* **2009**, *150*, 265–272. [\[CrossRef\]](#)
64. Real, E.; Oro, D.; Martínez-Abraín, A.; Igual, J.M.; Bertolero, A.; Bosch, M.; Tavecchia, G. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. *J. Avian Biol.* **2017**, *48*, 1462–1470. [\[CrossRef\]](#)
65. Garthe, S.; Scherp, B. Utilization of discards and offal from commercial fisheries by seabirds in the Baltic Sea. *ICES J. Mar. Sci.* **2003**, *60*, 980–989. [\[CrossRef\]](#)
66. Bracho Estévez, C.A.; Prats Aparicio, S. Competitive inter- and intraspecific dominance relations in three gull species. *Revista Catalana d’Ornitologia* **2019**, *35*, 21–29.

-
67. Martínez-Abraín, A.; González-Solis, J.; Pedrocchi, V.; Genovart, M.; Abella, J.C.; Ruiz, X.; Jiménez, J.; Oro, D. Kleptoparasitism, disturbance, and predation of yellow-legged gulls on Audouin's gulls in three colonies of the western Mediterranean. *Sci. Mar.* **2003**, *67*, 89–94. [[CrossRef](#)]
 68. Skórka, P.; Wójcik, J.; Martyka, R. Colonization and population growth of Yellow-legged Gull *Larus cachinnans* in southeastern Poland: Causes and influence on native species. *Ibis* **2005**, *147*, 471–482. [[CrossRef](#)]
 69. Malekian, M.; Shagholian, J.; Hosseinpour, Z. Pathogen presence in wild birds inhabiting landfills in Central Iran. *Eco-Health* **2021**, *18*, 76–83. [[CrossRef](#)] [[PubMed](#)]
 70. Navarro, J.; Grémilet, D.; Afán, I.; Miranda, F.; Bouten, W.; Gorero, M.G.; Figuerola, J. Pathogen transmission risk by opportunistic gulls moving across human landscapes. *Sci. Rep.* **2019**, *9*, 10659. [[CrossRef](#)]
 71. Baxter, A.T.; Allan, J.R. Use of Raptors to Reduce Scavenging Bird Numbers at Landfill Sites. *Wildl. Soc. B.* **2006**, *34*, 1162–1168. [[CrossRef](#)]
 72. Bosch, M.; Oro, D.; Cantos, F.J.; Zabala, M. Short-term effects of culling on the ecology and population dynamics of the yellow-legged gull. *J. Appl. Ecol.* **2000**, *37*, 369–385. [[CrossRef](#)]