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RESEARCH

Effects of the introduction of an herbivore on an endangered lizard

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Abstract
Sanitja Island, the northernmost land of the Balearic Islands, is occupied by a population of Lilford's Wall Lizard, *Podarcis lilfordi*, under extreme environmental conditions. It is an islet of less than 10 hectares, with low plant diversity and a complete absence of shrubs. During long-term monitoring, we studied lizard abundance over a period of approximately 40 years. Throughout several years, a group of domestic goats were introduced into the islet, leading to a collapse of the lizard population, with important collateral effects on their trophic ecology. On Sanitja Island, we observed the only case of a population of *P. lilfordi* in which the trend of the time series of abundance was significantly negative. The analysis of the time series indicated a lack of effect of the abiotic factors. The only factor that had a detectable effect on the population was the presence of goats. The introduction of goats caused the impoverishment of trophic resources for lizards and the change to a more diverse diet, with significantly lower consumption of plant matter. The removal of goats resulted in a partial recovery of lizard density, the recovery of a more specialized diet and the restoration of foraging behaviour on the dominant vascular plant, the sea fennel *Crithmum maritimum*. This foraging behaviour allows the pollination syndrome between the sea fennel and *P. lilfordi.* This study shows the dramatic effect of the introduction of an herbivorous competitor in an insular lizard population.

Keywords Insular lizards · Balearic Islands · *Podarcis lilfordi* · Lizard density · Invasive goats

Introduction

Large fluctuations in lizard populations pose a problem from a conservation viewpoint. It is about distinguishing between natural fluctuations, particularly declines, attributable to biotic or abiotic factors, or declines directly related to anthropogenic perturbations. This distinction can be difficult, even with long-term studies of more than a decade (Andrews and Wright 1994). Most published studies are generally based on estimates of the abundance or density of species and their variability over time. There are several studies on the sensitivity of reptiles to environmental perturbations (Bohm et al. 2016). However, these assessments are frequently hindered by a lack of species- or threat-specific data (Brooks et al. 2024). In this work, we study the dramatic effect of an identified perturbation in a population of Lilford's Wall Lizard.

Within the framework of long-term sampling of all known populations of Lilford's Wall Lizard, *Podarcis lilfordi* (Günther 1874), we had the opportunity to estimate the abundance of this species over several years, constructing long-term time series (Pérez-Cembranos and Pérez-Mellado 2024 and submitted). Thus, we were able to obtain estimations of lizard densities with a comparable methodology and, for several populations, over the last ten years. These surveys were comparatively analysed to detect population trends and establish the conservation status of each population (Pérez-Cembranos and Pérez-Mellado 2024). One of the populations under study was that from Sanitja Island, the northernmost island of the Balearic Archipelago (Fig. 1). This population lives in extreme conditions, relying on poor plant cover from the point of view of plant diversity, without shrub formations and exposed to the harsh meteorological conditions of northern Menorca Island (Brown and Pérez-Mellado 1994). Lizards from Sanitja Island showed a period of more than 12 h of daily activity, even longer than the period known from other populations of Lilford's Wall lizard (Ortega et al. 2014 and references therein). In Sanitja, lizards presented greatly elevated metabolism during their activity, almost 6 times greater than resting metabolic levels,

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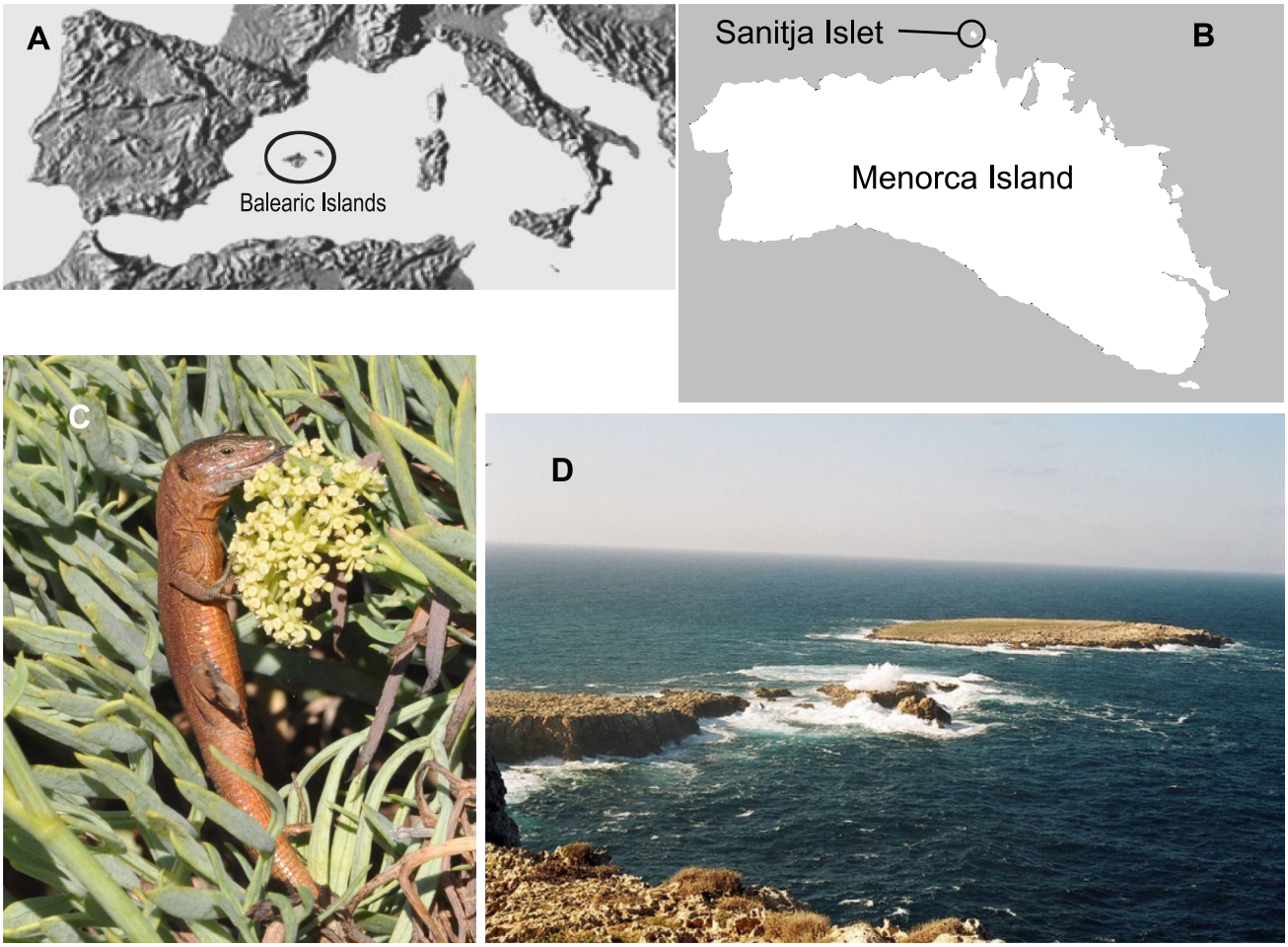


Fig. 1 **A** situation of the Balearic Islands in the western Mediterranean; **B** situation of Sanitja Islet on the northern coast of Menorca Island; **C** an adult female of *Podarcis lilfordi* foraging on a sea fennell, *Crithmum maritimum*, inflorescence in Sanitja Islet; **D** Sanitja Islet, the northernmost land of the Balearic Islands

which is rare in lacertid lizards (Brown et al. 1992). In fact, the summer field metabolic rate (FMR) was close to the values reported only for intensively foraging lizards, which have the highest FMRs yet are found in lizards (Brown et al. 1992 and references therein). From the calculation of FMR, we estimated that lizards of this population were operating during daily activities at approximately 75% of their maximum aerobic capacity and, most importantly, during a long daily activity period (Brown et al. 1992). In addition, we know that the Balearic lizard is a nonterritorial species (Pérez-Mellado 1998, 2009), and consequently, daily activity is devoted mainly to intense foraging (Brown et al. 1992; Brown & Pérez-Mellado 1994). If food availability is a major constraint on population density, we can expect that the introduction of an endothermic herbivore would reduce vegetation cover and insect biomass, posing a serious threat to the survival of this population (Brown et al. 1992).

A variable group of domestic goats, *Capra hircus* Linnaeus 1758, was introduced on Sanitja Island on an unknown date. It was an illegal introduction because the islet belongs to the state, and no official permit allowed such private introduction. We surveyed Sanitja Island beginning in 1982, but only in 1989 did we detect goats for the first time. Then, every year, goats were present on the island in a variable number, with the highest numbers recorded during the 1992 and 1997 surveys (17 goats recorded, personal observations). Finally, in 2002, we detected goats for the last time, and at the next visit, during the summer of 2005, goats were absent from the island. Thus, the final removal of goats took place during this period, owing to the efforts of the officials of Nature Conservation from the Balearic Government (Conselleria de Medi Ambient, Govern de les Illes Balears), after several claims by researchers and people involved in conservation.

Our objective in this long-term survey was to study the effects of goat introduction on Sanitja Island. In particular, the effects of the presence of goats on lizard abundance and lizard foraging ecology were investigated. Like all

other organisms, lizards have evolved to cope with stochastic and unpredictable environments (Brooks et al. 2024). This is the usual situation in the small coastal islets where Lilford's Wall Lizard lives. Environmental conditions vary dramatically from one year to the next so that populations can experience significant annual fluctuations (Pérez-Cembranos and Pérez-Mellado 2024 and submitted). However, the sudden introduction of a group of herbivores into a small population, such as Sanitja, could be an intense disturbance to lizards. Our hypothesis is that the resiliency of this population has allowed it to survive during the period of goat presence on the island. Obviously, fluctuations in the abundance of lizards can have another origin, so we analysed the role of abiotic factors in these fluctuations in density, with the objective of ruling out the potential effects of other factors.

Materials and methods

Study period and study area

Sanitja is an island of 8.59 hectares located at the northernmost point of the Menorca coast (Fig. 1; Balearic Islands, Spain). Menorca has a Mediterranean climate, with mild temperatures and very seasonal rainfall, abundant rains in winter and very dry summers. There are frequent and strong winds, principally from the north (Jansa 2019). As the northernmost land of the Balearic Islands, Sanitja is exposed to the extreme weather conditions of the northern coast, with frequent storms, especially during the winter, and almost constant winds, mainly from the north and northeast. The north wind causes saline aerosols that significantly affect the vegetation north of the Menorca coast (Jansa 2019), particularly the plant cover of the whole surface of Sanitja Island. The result is that no more than 30 vascular plants were observed on the island, with two dominant species: the sea fennel, *Crithmum maritimum*, which is found mainly in coastal areas, and *Allium ampeloprasum*, which covers the inner areas. Trees and shrubs are absent. This poor plant cover included, at least during the period with goats, some nitrophillous plant species, such as *Chrysanthemum coronarium, Silybum marianum* and *Sonchus asper* (De la Torre pers. com.).

Lizards from Sanitja Island were surveyed from 1987–2024, with several estimations of lizard densities (Pérez-Mellado 1989; Brown et al. 1992; Pérez-Cembranos and Pérez-Mellado 2024) as well as some studies of foraging ecology, energy expenditure and pollination ecology (Brown et al. 1992; Brown and Pérez-Mellado 1994; Pérez-Mellado and Casas 1997).

The lizard

Podarcis lilfordi (Günther, 1874) (Squamata, Lacertidae) is a medium-sized lizard (Fig. 1C) with a maximum snout-vent length of 81 mm in males and 75 mm in females. It inhabits the coastal islets of Menorca, Mallorca, and the Cabrera archipelago (Pérez-Cembranos et al. 2020). This lizard reaches high densities in several populations (Pérez-Mellado et al. 2008; Pérez-Cembranos and Pérez-Mellado 2024). Lilford's Wall Lizard is an active and omnivorous forager that captures insects and other invertebrates, but it also consumes vegetal matter, carrion, or conspecifics (Pérez-Cembranos et al. 2016). *Podarcis lilfordi* is an endemic and endangered species of the Balearic Islands and one of three species of terrestrial vertebrates from the prehuman Plio-Pleistocenic fauna of the archipelago (Bover et al. 2014).

Lizard densities

The densities of lizards from Sanitja Island were intermittently estimated from 1987–2024, resulting in a time series from 25 different years, with consecutive annual sampling from 2015–2024 (Table S1 and Fig. 2). Abundance estimates of lizards were carried out with the line transect methodology. In Sanitja, line transects cover almost the entire island surface with vegetation cover, with paths of approximately 200–250 m in length from several consecutive line transects of 70 m (Pérez-Cembranos and Pérez-Mellado 2024). In all the cases, we carried out line transects with a bandwidth of 2 m on each side of the line, estimating the perpendicular distance of each lizard to the central line of the transect (Burnham et al. 1980; Buckland et al. 2015; Schmidt et al. 2022). Some published densities from Sanitja (Pérez-Mellado 1989; Brown et al. 1992; Pérez-Mellado and Casas 1997) were not included in this study, as they were carried out only in the western areas of the island with an extraordinarily high local density of lizards. The western area of the island is densely covered by the sea fennel *C. maritimum*. In addition, these previous analyses were done with the limited statistical tools available at that time. The reliability of the line transect can be comparable to that of other density estimation methods, such as capture, marking, and recapture, if it is applied rigorously, respecting the premises of the estimation models and by observers with enough experience (Mazerolle et al. 2007; Ficetola et al. 2018).

Density calculations were carried out with the *unmarked* package in the R environment (Fiske and Chandler 2011; R Core Team 2024). This package works with N-mixture models that allow precise estimates of abundance in small vertebrates (Ficetola et al. 2018). To build the abundance model, we used the "distsamp" function, which fits a multinomial Poisson model to the distance data (Royle et al. 2004). The probability of detection in the density estimation

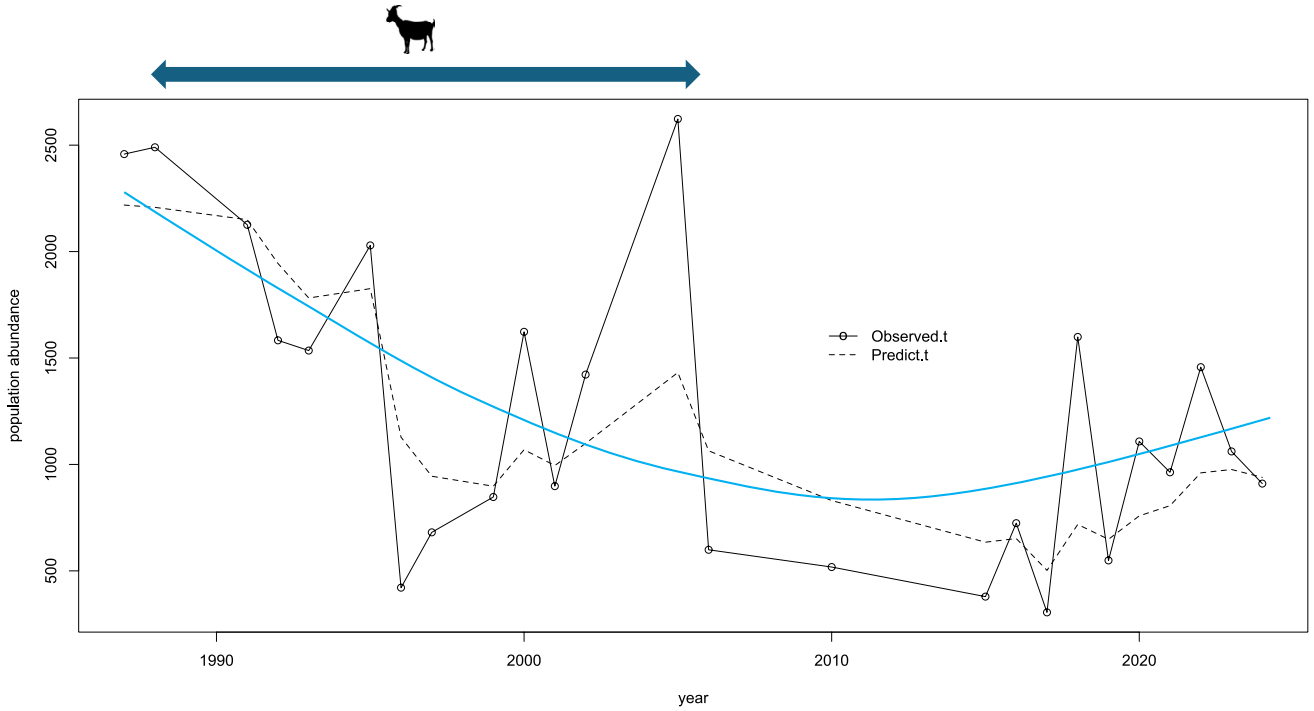


Fig. 2 Time series of population abundance (individuals/hectare) of *Podarcis lilfordi* from Sanitja Island. The dotted line indicates the predicted densities from the EGSS model. The blue line indicates the smoothed trend of the populations obtained with the loess function. The horizontal arrow marks the period of a goat's presence on the island (goat silhouette from Keesey 2024; see more details in the text)

was modelled as a function of the perpendicular distance (d) to the observer, using the "half-normal" detection function of *unmarked* (Fiske and Chandler 2011). For each estimate, we include the density as the number of individuals per hectare ± the standard error (SE). In all transects, we included adult individuals of both sexes together, and a very small fraction of individuals, owing to their body size, were classified as juveniles or subadults. This juvenile fraction was extremely small in most transects. The line transects corresponding to the years 1987, 1988, 1990, 1991 and 1992, made around the entire island surface, have been reanalysed again with the *unmarked* package, leading to some different results from those previously published (Brown et al. 1992; Pérez-Mellado 1989; Pérez-Mellado et al. 2008).

Climatic information

The values of monthly rainfall, monthly temperature, relative humidity, and atmospheric pressure were obtained from public data provided by AEMET (Spanish Meteorological Agency n.d.). The data were obtained from the weather station of Menorca airport. With this information, we calculate what we call"valid"rainfall, that is, the total precipitation of 12 months prior to April of a given year, as the start of the main period of lizard activity. We consider that during this period, from May of the previous year to April of the current year, the rainfall with the greatest influence on primary productivity occurs and, therefore, on plant and animal productivity. We also recorded the average temperature of the warmest month of the valid year (Table S1). This approach is similar to the procedure employed by several authors when analysing the effects of precipitation on time series of abundances in animal populations (Selonen et al. 2021 and references therein). Likewise, for valid months of each year, we calculated the Sahin's aridity index Iq (Sahin 2012), which is defined as follows:

$$I_q = P/S_h$$

where P represents the valid annual rainfall (mm) and S_h represents the valid annual mean specific humidity (g/kg). S_h can be easily computed with annual mean temperature, relative humidity and local pressure values that are currently available from local weather stations (see more details in Sahin 2012).

With these environmental variables, we analysed their relationships with the annual abundance of lizards on Sanitja Island. We built multiple regression models where density (number of individuals per hectare) was the dependent variable, while the environmental variables (valid average temperature of warmest month, valid annual rainfall and valid aridity index) were the continuous explanatory variables. From this saturated model, we eliminated, step by

step, nonsignificant interactions and nonsignificant quadratic terms. Afterwards, we used ANOVA to compare the models produced by that term reduction. Thus, we have finally obtained the minimum adequate model (Crawley 2013; Jones et al. 2023).

Time series analysis

Our density data are discrete, with observations of abundance through density estimation at specific times and spaced by variable intervals, with a single annual estimate. This is, therefore, an irregular time series because, except in the last ten years, we have not been able to undertake annual monitoring on Sanitja Island.

We explored whether there were observable trends by applying the "lowess" function from the basic R package, which smooths a previously defined time series (Cleveland 1979, 1981). With the Mann−Kendall test (Mann 1945; Kendall 1975), we studied the presence or absence of a monotonic linear trend in a time series (Hirsch et al. 1982). The null hypothesis is that there is no monotonic trend in the population. One of the assumptions of the Mann−Kendall test is that when there is no trend, the time series data must be independent. This means that, in our case, the annually recorded abundances should not be strongly correlated, which must be tested initially with the "acf" function. For these tests, we used the "Kendall" package of the R environment (ver. 2.2.1, McLeod 2022).

According to Auger-Méthé et al. (2021), state-space models (SSMs) are the appropriate framework for time series analysis because they are a better alternative to trend analysis of a time series via log-linear regression. Dennis et al. (2006) and Humbert et al. (2009) showed that the use of an EGSS model, which jointly considers the existence of observation errors and process noise, provides significantly more reliable estimates of population trends. Thus, the model assumes that population growth is governed by a stochastic process independent of density such that the observed abundances result from log-normal sampling errors (Dennis et al. 2006).

The Bayesian approach to time series analysis, instead of looking for the best possible model, builds an average model as a synthesis of many probable models. This technique is called Bayesian model averaging (BMA) and allows the analysis of the trend of a time series and the detection of abrupt changes via a Bayesian estimator of abrupt changes and the trend algorithm (BEAST; Zhao et al. 2019). Thus, BEAST is an algorithm that detects abrupt changes and trends through fuzzy detection of the probability of occurrence of a perturbation of the time series at any point in time. BEAST combines many possible models by decomposing the time series instead of relying on a single model (Hu et al. 2021). The result is presented in the form of a multiple graph in which the general trend of the analysed time series, the situation of points of abrupt changes and their probability of occurrence, if such changes have been detected and the proportion of trends to stability are represented (Fig. S1).

Diet

Dietary information from Sanitja lizards was obtained from 1024 scats collected from 1991–2023. This sample included data from spring and summer 1991–2023, with small subsamples from fall (October) and winter (March). For the comparison of periods with or without goats, the samples were divided into two groups: years with goats (1991, 1993, 1995, 1996, 1997, 1999 and 2002) and years without goats (2005, 2006, 2010, 2018, 2019, 2020, 2021 and 2023). From these years, we consider a subsample with only feces from spring and summer (see below). Scats were obtained directly from the ground or from captured lizards employed in other studies (e.g., Brown et al. 1992; Brown and Pérez-Mellado 1994) that defecated during handling. Lizards were released at the exact point of capture. We analysed the fecal samples under a binocular dissecting microscope. In lizards, diet reconstruction based on meticulous faecal pellet analysis has been found to be highly comparable to diet reconstructions based on gastric contents removed from dissected stomachs, with soft-bodied prey and particularly insect larvae being equally represented in faecal pellets and gut contents (Pérez-Mellado et al. 2011). Furthermore, faecal pellet analysis is a standard method to quantify diet with the added advantage of not compromising animal well-being. Each individual fecal sample was spread in a thin layer of less than 0.5 mm over the entire surface of a Petri dish with some drops of 70° ethylic alcohol. The percentage of vegetal matter was then visually estimated according to the surface occupied by vegetal remains in the Petri dish. The plants were recognized at the species, genus, or family level. Prey remains were identified up to their order or, exceptionally, at the family level. The prey number for each fecal pellet was conservatively estimated by counting only identifiable remains. The consumption of carcasses from birds and mammals was detected by the presence of feathers or hairs, employing the work of Teerink (1991) for hair identification.

The diet was described as the contribution of each prey item. We calculated prey abundance (%n) as the percentage of a given prey type in relation to the total prey number and the relative prey or plant presence (%p) as the percentage of feces containing a given prey type or plant. The diets of lizards from the two periods, with and without goats, were compared via permutational multivariate analysis of variance (permutational MANOVA, Anderson 2001) via the 'adonis' function from the 'vegan' R package (Oksanen et al. 2015). The multivariate homogeneity of group dispersions (variances) was tested with the function 'betadisper' from

the 'vegan' package, a multivariate analogue of Levene's test for homogeneity of variances. We estimated and compared diet diversities via the approach proposed by Pallmann et al. (2012). Instead of describing diet diversity through a given index, we converted these "raw" indices into "true" diversities, which all belong to one and the same mathematical family. That is, different measures are considered special cases of Hill's general definition of diversity measures (Hill 1973). In this way, to study differences in diversity among diets of years with or without goats, we performed two-tailed tests for integral Hill numbers. This selection included the transformed versions of the three following indices: the species richness index, H_{sr} ($q = 0$); the Shannon entropy index, H_{sh} ($q \rightarrow 1$); and the Simpson concentration index, H_{is} ($q = 2$; Magurran 2004). All comparisons among diversities were made with Tukey-like contrasts employing a resampling procedure. We performed 5000 bootstrap replications to obtain reliable p values. The methods described here are implemented in the R package "simboot" (Scherer et al. 2014).

Owing to the heterogeneity of variances among samples (Fligner test, $\chi^2 = 307.82$, d.f. $= 6$, $p = 2.2 \times 10^{-16}$), the percentages of plant matter in the diet were compared with a Kruskal–Wallis test. In feces where we were able to identify plant species, the proportion of a plant species between periods with or without goats was compared with a G test (Hervé 2023). All calculations were performed in R version 4.0.3 (R Core Team 2024).

Results

Lizard densities

We analysed an irregular time series with 25 annual data points (Table S1). We did not detect a density dependence in lizards from the Sanitja population (PBRLT test, L = —3.2416, $p = 0.366$). We did not find any significant relationship between annual lizard abundance and the Iq aridity index ($p = 0.581$) or between the average temperature of the warmest month or annual valid rainfall and lizard abundance ($p = 0.345$).

Among all known populations of Lilford's Wall Lizard, Sanitja Island is the only population where we detected a time series with a negative and statistically significant trend ($\tau = -0.287$, $p = 0.047$). Visually (Fig. 2), this trend was negative from approximately 1987–1989 to 2009–2010, covering the period of presence of goats on the island and some years after eradication. Approximately 2005, we detected an abundance peak, but then, the recovery of the population was slow and occurred mainly from 2010–2011, never reaching the extremely high densities recorded before 1990 (Fig. 2). The negative trend gradually changed during the last 20 years. From our point of view, the main factor affecting the population of Lilford's Wall Lizard from Sanitja Island was the presence of goats during this long period (Fig. 2). This is the only change we observed on the island during a survey of more than 40 years. We did not observe any introduction of a terrestrial predator or human use of the island, except for the introduction of goats.

In addition, the Bayesian analysis with Rbeast, with a reasonably good fit of the average model ($R^2 = 0.646$), detected an abrupt change in Sanitja approximately 1999, with an acceptable probability (Pr = 0.46, Fig. S1). Over the years, the time series is a combination of stable (green color) and negative (blue color; Fig. S1) trends. The most severe effects of the introduction of goats likely occurred a few years after the first year of introduction, when the consumption of vegetation intensified and the collateral effects on general trophic availability were significant.

Foraging and diet

The diet of Sanitja lizards is dominated by the consumption of clumped prey, particularly ants and Homoptera (overall diet in Table 1 and Fig. 3). This dominance of ants is also clear when we compare the diet during years with or without goats (Table 1 and Fig. 4). Some differences are interesting. Hymenoptera were present mainly during years without goats, whereas Homoptera, Dermaptera and Gastropoda showed the opposite trend. This result revealed that diets significantly differed between periods with or without goats (permutational MANOVA, $F_{1,849} = 3.3926$, $p = 0.03$).

In a first comparison of Hill's numbers among seasons, we detected some significant differences between the fall and winter diets and between the winter and summer diets. However, we did not detect significant differences between the summer and spring diets ($p > 0.05$). For this reason, we make all comparisons between groups of years with or without goats with a subsample of 850 feces from spring and summer (June, July and August). Diet diversity significantly differed between the two periods (with goats, Shannon diversity = 1.1729 ± 0.0008; without goats, Shannon diversity = 1.168 ± 0.001). In a comparison of Hill's numbers, $q = 0$, $p = 0.0332$; $q = 1$, $p = 0.0346$; and $q = 2$, $p = 0.0382$).

The average plant matter volume was also significantly lower during years with goats (with goats: $\bar{x} = 14.06 \pm 1.39\%$, $n = 498$; without goats: $\bar{x} = 43.11 \pm 2.27\%$, $n = 352$; Kruskal–Wallis test, $\chi^2 = 136.93$, $p = 2.2 \times 10^{--16}$). In addition, from feces with positive identification of plant species, we detected that the sea fennel *Crithmum maritimum* was present in a significantly greater proportion of fecal samples from years without goats, with 95.15% (n = 103) of feces from the period without goats and only 13.16%

Table 1 Diet of Lilford's Wall Lizard on Sanitja Island

Taxa	Overall diet				With goats				Without goats			
	Frequency		**Presence**		**Frequency**		**Presence**		**Frequency**		**Presence**	
	n	**n%**	**np**	**%p**	**n**	**n%**	**np**	**%p**	**n**	**n%**	**np**	**%p**
Gastropoda	70	1.3521	70	6.7829	37	1.2239	37	7.4297	7	0.3941	7	1.9886
Pseudoscorpionida	7	0.1352	7	0.6783	0	0	0	0	6	0.3378	6	1.7045
Opiliones	2	0.0386	2	0.1938	2	0.0662	2	0.4016	0	0	0	0
Araneae	62	1.1976	61	5.9108	29	0.9593	28	5.6225	22	1.2387	22	6.2500
Isopoda	180	3.4769	180	17.4419	84	2.7787	84	16.8675	73	4.1104	73	20.7386
Diplopoda	1	0.0193	1	0.0969	0	0	0	0	1	0.0563	1	0.2841
Orthoptera	1	0.0193	1	0.0969	0	0	0	0	0	0	0	0
Dictyoptera	62	1.1976	62	6.0078	40	1.3232	40	8.0321	8	0.4504	8	2.2727
Isoptera	66	1.2749	38	3.6822	26	0.8600	16	3.2128	40	2.2523	22	6.2500
Dermaptera	104	2.0089	97	9.3992	50	1.6540	46	9.2369	7	0.3941	7	1.9886
Homoptera	323	6.2391	54	5.2325	294	9.7254	30	6.0241	6	0.3378	6	1.7045
Heteroptera	10	0.1932	10	0.9690	4	0.1323	4	0.8032	6	0.3378	6	1.7045
Diptera	72	1.3908	60	5.8139	54	1.7863	42	8.4337	12	0.6757	12	3.4090
Lepidoptera	43	0.8306	38	3.6822	20	0.6616	15	3.0120	19	1.0698	19	5.3977
Coleoptera	151	2.967	133	12.8876	61	2.0179	58	11.6466	58	3.2658	48	13.6364
Hymenoptera	208	4.0178	23	2.2287	6	0.1985	6	1.2048	198	11.1486	13	3.6932
Formicidae	3654	70.5814	668	64.7287	2225	73.6024	343	68.8755	1282	72.1847	256	72.7273
Arthropoda undet	40	0.7726	40	3.8760	3	0.5623	17	3.4136	6	0.3378	6	1.7045
Larvae	37	0.7147	37	3.5853	1	0.3639	11	2.2088	21	1.1824	21	5.9659
Birds	4	0.0773	4	0.3876	2	0.0662	2	0.4016	2	0.1126	2	0.5682
Lizards	5	0.0966	5	0.4845	1	0.1323	4	0.8032	1	0.0563	1	0.2841
Mammals	5	0.0966	5	0.4845	5	0.1654	5	1.0040	0	0	0	0
Seeds	70	1.3521	38	3.6822	52	1.7201	35	7.0281	1	0.0563	1	0.2841
Total	6797	100			2996	100			1776	100		

Frequency, n: prey frequency of each taxon, n%: percentage of prey of each taxon in relation to prey number. Presence, np: number of scats in which each taxon is present and %p: percentage of scats in which each taxon is present. The number of prey items from a given taxon is estimated from the count of significant elements (see more details in the text)

(n = 38) of feces from the period with goats (G test, G = 94.741, $p = 2.2 \times 10^{-16}$).

Discussion

Turner (1977) summarized the few available data on annual lizard density changes at that time. These data revealed relatively modest year-to-year changes, rarely exceeding 100% increases or 50% reductions in numbers (Turner 1977). Thus, lizard densities seem to be stable, at least in some populations of *P. lilfordi* (see also Barbault 1975). In the case of Lilford's Wall Lizard, we detected idiosyncratic responses to environmental factors across all the populations of Mallorca and Menorca (Pérez-Cembranos and Pérez-Mellado 2024 and submitted).

Overall, herbivorous and omnivorous reptiles constitute a relatively high proportion of at-risk species, mainly because of the impact of anthropogenic drivers, particularly invasive species (Atwood et al. 2020). Lilford's Wall Lizard can be included in this trophic group of squamate reptiles. Sanitja is particularly interesting because it is a very isolated population, with lizards living in a pristine habitat and an almost null human presence (Pérez-Cembranos and Pérez-Mellado 2024). This was probably the situation over hundreds of years. However, an absurd farming practice then appeared, and a small population of domestic goats was introduced into the islet over the years. Our results indicate that the introduction of a small group of goats had a dramatic effect on the lizard population of Sanitja. This effect was clear not only in the collapse of lizard density but also in foraging ecology and diet.

Feral goats are considered pests in several areas, such as semiarid regions of Australia (Parkes et al. 1996; Choquenot et al. 1998). In insular ecosystems, the eradication of goats is essential for preserving biodiversity loss (Campbell and Donlan 2005; Coblentz 1978; Schofield 1989). The negative effects on vegetation cover seem to be particularly

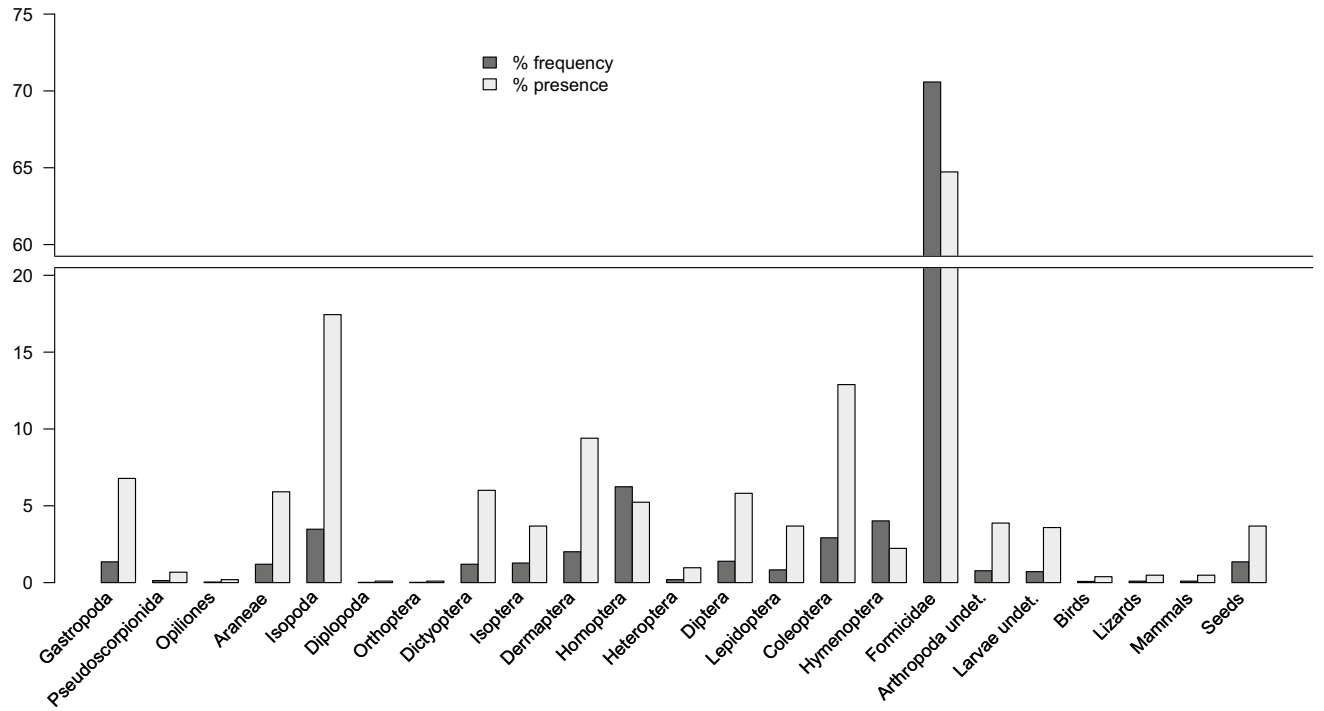


Fig. 3 The general diet of *Podarcis lilfordi* on Sanitja Island. We show the percentage of each prey item (% frequency) and the percentage of feces with this prey type (% presence)

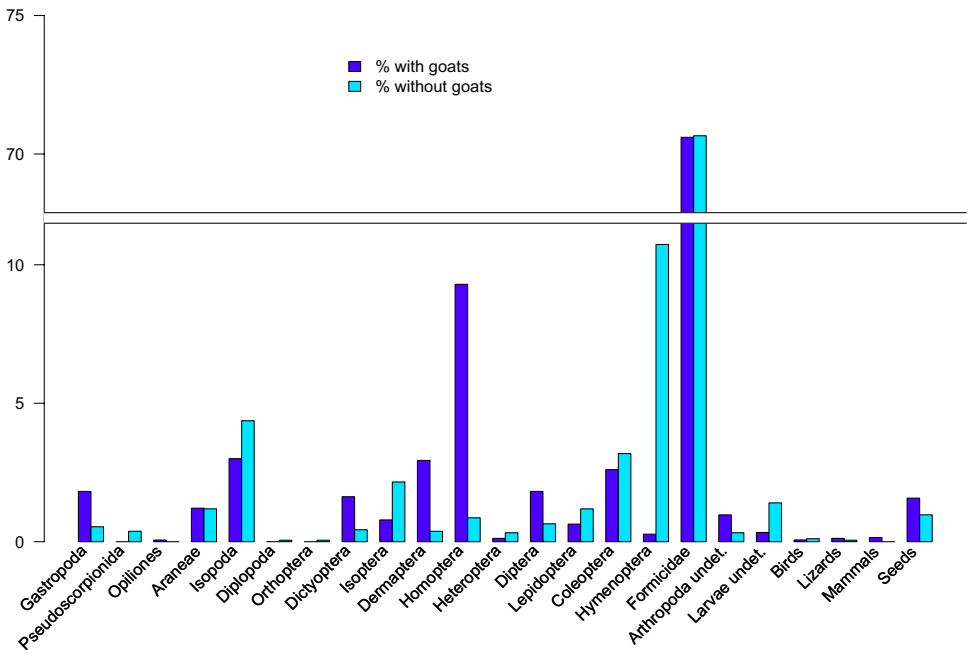


Fig. 4 Diet of *P. lilfordi* during years with goats and without goats. We show the percentage of each prey item (see more details in the text)

severe, as has been shown in the Galápagos Islands (Hamann 1979; Desender et al. 1999) and Canary Islands (Arévalo et al.2011). It is well known that introduced goats are responsible for the near extinction of some endemic plants from the Canary Islands (Gangoso et al. 2006). The almost complete eradication of goats on the large Es Vedrà Island (Ibiza, Balearic Islands), with more than 62 hectares, has led to an extraordinary recovery of vegetation, especially of the island's endemic plants, which are intensively consumed by goats (Capó et al. 2018). However, Rosa-García et al. (2012)

reported that few studies have investigated the influence of goats on vegetation. The negative effects of other herbivore species on the abundance of squamate reptiles have also been recognized. For example, the effects of grazing of feral horses, *Equus caballus*, have been studied in the American Great Basin, where Beever & Brussard (2004) reported greater absolute species richness of squamate reptiles and a greater abundance of the most common lizard species at horse-removed sites.

The density of lizards in Sanitja was spectacular in the 1980 s (Pérez-Mellado 1989). The introduction of goats marked a turning point, with the population collapsing for more than 15 years (Fig. 2). The effects of the goats were likely combined with some years of strong predation pressure by kestrels, *Falco tinnunculus,* which, in the 1990 s, came to the islet almost daily, sometimes in large groups (Pérez-Mellado 2009 and pers. obs.). However, the presence of kestrels, as the main specialized avian predator on lizards, is common in almost all populations of the two endemic species of lizards of the Balearic Islands (Pérez-Mellado 2009) and does not seem to be a significant factor in the annual fluctuations in lizard abundance (Pérez-Cembranos and Pérez-Mellado 2024).

From the perspective of foraging behaviour, the diet of the period when goats were present on the island included a greater proportion of terrestrial prey, such as Gastropoda or Dermaptera, whereas Hymenoptera, which are captured on plants, especially sea fennel (Brown and Pérez-Mellado 1994; Pérez-Mellado and Casas 1997), are notably more common in the years when goats were absent, both before (Brown and Pérez-Mellado 1994) their introduction and after their definitive removal (Fig. 4). Thus, the presence of goats, which removes an important part of the vegetation cover of the islet, apparently causes a significant change in the diet of the lizards. All theoretical models of foraging strategies predict that the lower the absolute abundance of food is, the greater the range of items that should be taken (MacArthur and Pianka 1966; Schoener 1971 and references therein). We can expect that the foraging activity of goats caused a decrease in plant food resources, as well as a negative effect on the populations of arthropods linked to these resources. In such a situation, lizards broaden their trophic spectrum, including rarer or less profitable prey types, thus increasing trophic diversity. In an optimal situation, in the absence of goats, lizards select the most profitable prey types, and this specialization leads to a decrease in trophic diversity. An island impoverished in its resources by the presence of goats would give rise to a less specialized and more diverse diet (MacArthur and Pianka 1966) than the optimal diet observed in the absence of goats.

We observed another significant effect on the foraging ecology of Lilford's Wall Lizard, which was associated with the negative effect of goats on vegetation cover. Goats disturb the foraging behaviour of lizards on blooming sea fennels in a direct way (Pérez-Mellado and Corti 1993; Pérez-Mellado and Casas 1997). Before the introduction of goats, during summer, the foraging of lizards on inflorescences of *C. maritimum* and *A. ampeloprasum* was extremely intense, leading to a high pollen load on the body surfaces of lizards (Pérez-Mellado et al. 2000). In samples from the summers of 1987 and 1988, approximately 70% of the fecal content was anther, nectar, and pollen from *C. maritimum*. The large amount of pollen transported ventrally by lizards means that they are among the main pollinators of sea fennel, as experimentally shown (Pérez-Mellado and Casas 1997). During these years prior to goat arrival, the average volume of plant matter in scats was 27.53% during spring and 72.61% during summer (Pérez-Mellado and Corti 1993), which is far from the values of plant matter volume reported in years with goats (see above).

Resiliency is the ability to recover from a perturbation because of built-in redundancy or robustness (Holling 2001; Redford et al. 2011). However, as Brooks et al. (2024) noted, even the most resilient species can cross the threshold beyond which the new state is extinguished. Sanitja is a fully isolated population of lizards of a microendemism that can collapse and become extinct. Fortunately, the goats were removed from the island between 2002 and 2005, and the density of lizards gradually recovered, as did the usual foraging patterns. This also indicates the recovery of the unique interaction between Lilford's Wall Lizard and the sea fennel, which has given rise to one of the few examples of pollination of a vascular plant by a squamate reptile (Pérez-Mellado and Casas 1997). In summary, Sanitja is an illustrative example of the harmful effect that the introduction of a competing species can have on a small population, especially in the case of a native omnivorous species that faces the arrival of a broad-spectrum herbivore, such as the domestic goat.

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Author contributions VPM and APC conceived the ideas and designed the methodology. VPM collected the data from 1987–2010, and both authors collected the data from 2015–2024. VPM and APC analysed the data and led the writing of the manuscript. Both authors contributed critically to the draft and gave final approval for publication.

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Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Competing interests The authors declare no competing interests.

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