


Article

Collapse of the endemic lizard *Podarcis pityusensis* on the island of Ibiza mediated by an invasive snake

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Abstract

The invasive snake *Hemorrhois hippocrepis* colonized the island of Ibiza (Balearic Islands) in 2003 as stowaways inside trunks of olive trees imported for gardening. It has quickly spread since 2010, posing a threat to the island's only remaining endemic vertebrate, the Ibiza wall lizard *Podarcis pityusensis*. We map the yearly expansion rate of the snake and estimate via transect surveys how severely it affects the distribution and abundance of the endemic lizard. As well, we surveyed 9 of 30 small lizard populations on islets surrounding Ibiza that have been isolated since the Last Glacial Maximum. Snakes had invaded 49% of Ibiza's land area by 2018, and censuses show a critical contrast in lizard abundance between areas with and without snakes; almost all censuses in areas without snakes show lizard presence whereas nearly all censuses in areas with *H. hippocrepis* lack lizard sightings. Moreover, at least one subspecies previously thriving on one of the off-shore islets has become extinct, and there have been several snakes recorded swimming between Ibiza and the surrounding islets. Therefore, lizard populations have been dramatically reduced or have vanished within the range of the snake, and our results quantitatively support upgrading this species' threat level for extinction. This study can inform to programs to manage invasive snake populations and to conservation actions to recover the endemic lizard.

Key words: Balearic Islands, conservation, extinction, *Hemorrhois hippocrepis*, lizard census

Biological invasions are among the biggest threats to biodiversity (Wilcove et al. 1998; Mehring and Stoll-Kleeman 2008; Simberloff et al. 2013; Bellard et al. 2016; Courchamp et al. 2017), and they are especially damaging on islands (Reaser et al. 2007; Jones et al. 2016), where endemism rates among native biota are often high (Kier et al. 2009) and disappearance of a species is, as a rule, an extinction (Smith et al. 2012). Island organisms are frequently vulnerable to invasive predators (Cohen 2002; Whittaker and Fernández-

Palacios 2006; Simberloff et al. 2013; Van Moorlegheem et al. 2020), many of which may belong to ecological guilds or taxa never before encountered in the evolutionary history of insular natives. Consequently, there are numerous examples of extinctions on islands due to invasive species, both for plants and animals (e.g., Blackburn et al. 2004; Sax and Gaines 2008; Bellard et al. 2016).

The Balearic Islands, in the western Mediterranean Sea, have suffered several extinctions due to human introductions (Alcover et al.

1999; Palmer et al. 1999). The extirpation of the endemic lizard *Podarcis lilfordi* on both main islands of Mallorca and Menorca was caused by human-mediated introductions of carnivorous mammals and snakes (*Mustela nivalis*, *Martes martes*, *Macroprotodon mauritanicus*, *Aterix algirus*, *Genetta genetta*, among others; Alcover et al. 1999; Pinya and Carretero 2011). The lizard's remaining populations are currently restricted to the surrounding islets. On the island of Ibiza, a dwarf viper vanished coincident with the arrival of the first humans and their cohort of introduced predators 4,000 years ago (Torres-Roig et al. 2020).

At the beginning of the 21st century, hundreds of large ornamental olive trees were imported from the southern Iberian Peninsula to the Balearic Islands to cater to a fad for Mediterranean landscaping. These trees brought with them to Ibiza three species of stowaway snakes: *Malpolon monspessulanus*, which appears to have disappeared; *Zamenis scalaris*, which maintains a small but stable population on the island; and *Hemorrhois hippocrepis*, which has rapidly expanded (Álvarez et al. 2010; Silva-Rocha et al. 2018). On Ibiza, *H. hippocrepis* has a diet mainly (56% in frequency) composed of the endemic Ibiza wall lizard (*Podarcis pityusensis*; Hinckley et al. 2017). This degree of lizard consumption is the highest documented for any population of *H. hippocrepis* (Hinckley et al. 2017), and, together with the abundance of the newcomer, may negatively impact the endemic lizard. The first individual *H. hippocrepis* was seen on 17 May 2003 escaping from the trunk of an imported olive tree (Servei d'Agents de Medi Ambient 2003). During the following years, snake populations were detected in the surroundings of tree nurseries in San Lorenzo and Santa Eularia, but after 7 years these invaders started to spread and were seen farther afield (Servei d'Agents de Medi Ambient 2014; Montes et al. 2015). Since 2010, environmental officers and rural residents of the island have increasingly commented on the disappearance of *P. pityusensis*, and—considering the history of reptile extinctions in the Balearic Islands—the threat to the endemic lizard by the introduced snake became of concern. Moreover, 30 of the islets surrounding Ibiza maintain isolated populations of *P. pityusensis* partitioned among 22 subspecies and deserve some concern: In addition to being a skilled hitch-hiker, *H. hippocrepis* is a competent swimmer, and its trans-marine swimming range includes the range of many of the islets (1.17 km average distance from the coast, and a maximum of 5 km away [Hinckley et al. 2017]). From 2015 to 2020, there have been 10 records—including videos and pictures—of *H. hippocrepis* swimming in the sea within a distance of 10–1,000 m off the coast of Ibiza (Supplementary Figures S1 and S2 and Supplementary Video S1).

Ecological impacts from the *H. hippocrepis* invasion remain to be fully determined. Invasive snakes have led to or contributed to numerous extinctions elsewhere, including of lizards (Fritts and Rodda 1998; Rodda and Savidge 2007; Cheke and Hume 2008; Smith et al. 2012). However, mere presence of *P. pityusensis* in the diet of *H. hippocrepis* would not necessarily signify a strong impact on lizard populations, inasmuch as the lizards might be demographically resilient to snake predation. Evolutionary or behavioral changes in native species in response to selection from alien predators may include new anti-predator defenses (e.g., Griffiths et al. 1998; Schley and Griffiths 1998; Ortega et al. 2017) or habitat changes that allow native species to persist in the invaded area (Strauss et al. 2006). Therefore, a focal study assessing if *P. pityusensis* populations are decreasing becomes necessary to determine if the snakes are having a population-level impact instead of merely an impact on individual lizards (cf., Blackburn et al. 2014; Hawkins et al. 2015). Although we lack pre-invasion data on lizard numbers or

densities, we nonetheless know that prior to snake invasion the lizard ranged extensively throughout the island and was quite common (Cirer and Serapio 2015, p. 13; Salvador 2015). Furthermore, snakes have not yet colonized the entire island, and this allows us to compare current lizard numbers between areas with and without established snake populations. Our research objectives in this study are to a) assess the range progression of the invasive snake; b) assess lizard abundance in snake-present versus snake-absent areas to evaluate the impact of snake presence on the lizard populations, and c) confirm the status of some of the islet lizard populations. Demonstration of negative impacts to lizard populations could serve to improve programs to manage the invasive snake and recover the endemic lizard, as well as protect the unique populations on surrounding islets.

Materials and Methods

Study area

The island of Ibiza is located in the Balearic Archipelago, in the western Mediterranean Sea. Ibiza, Formentera and surrounding smaller islands form the Pityusic Islands, the southwesternmost portion of the Balearic Islands. Ibiza has an area of 572 km² and a maximum elevation of 486 m. The mean annual temperature is 18.3°C (mean monthly range 11.9°C [January]–26.3°C [August]), and the average yearly rainfall is 413 mm (mean monthly range from 5 [July] to 58 mm [October]; standard meteorological averages for the Ibiza Airport weather station, 38.8728° N, 1.3730° E; www.aemet.es). The landscape consists of native pine and juniper forests (*Pinus halepensis* and *Juniperus phoenicea*), cultivated lands, and native shrubland. There are ca. 150,000 human inhabitants and approximately 30,000 houses scattered across the island (Consell Insular d'Eivissa 2018), with stone walls frequently delimiting gardens and croplands.

Study species

Hemorrhois hippocrepis is a thermophilic snake that ranges across two-thirds of the Iberian Peninsula and from Morocco to Tunisia in northern Africa. It is present on the islands of Zembra, Pantelleria, and Sardinia due to human introduction (Feriche 2017); in addition, it has been recently introduced to the Balearic Islands of Mallorca, Ibiza, and Formentera, currently maintaining established populations on Mallorca and Ibiza (Silva-Rocha et al. 2018). It preys almost exclusively on vertebrates, is rupicolous, and anthropic structures on Ibiza form favorable habitats for this snake (Feriche 2017).

Podarcis pityusensis is endemic to the islands of Ibiza, Formentera, and 38 of their surrounding islets, which hold 22 subspecies (Salvador 2015). It also is rupicolous and dwells in rocky landscapes, buildings, and on the traditional rock walls that are widespread on the Pityusic islands (Pérez-Mellado 2002).

Mapping spread of the invasive snake

In order to depict yearly range expansion of *H. hippocrepis* on Ibiza, we mapped 1,326 georeferenced records (± 10 m) of opportunistic snake sightings from 2010 to 2018, obtained from the Balearic Islands Government Environmental Service surveys across the entire island (Servei d'Agents de Medi Ambient 2014). We only used data from 2010 onward, as data from previous years were mainly confined to nurseries. We estimated the area of the core snake population by creating polygons that excluded isolated sightings using a

statistical outlier-removal algorithm. This consisted of creating yearly series with the mean distance of each point to its three closest neighbors, and classifying as outliers all points whose mean distance was higher than one standard deviation of the distribution (method used to remove outliers from 3D data works, see Hu et al. 2013). We ran this proximity analysis on a distance matrix using QGIS v. 3.8.1 (QGIS Development Team, 2019), and we created the yearly polygons using the tool Minimum Bounding Geometry (Convex Hull option), also in QGIS v. 3.8.1., calculating the area for each, and subtracting areas covered by sea. The map uses the geographic coordinate system and was built using ArcGIS v.10.4.1 (ESRI 2017). We calculated the cumulative area of the snake's range each year by adding each year's new range expansion to those of previous years, as the snake consistently maintained previous range (see Figures 1 and 2). We estimated areal expansion rate of the snake population by regressing these cumulative areas against year.

Lizard censuses on Ibiza

We assessed lizard abundance in both snake-present and snake-absent areas by dividing Ibiza into two areas: that with established snake populations (approximately the northeastern half of the island) and that without (approximately the southwestern half; Figure 1). We identified these two areas based on georeferenced data of snake sightings from citizens and environmental officers (850

records) obtained from 2010 to 2017, in anticipation of our 2018 surveys. In helping to identify high-density snake areas, as opposed to snake-free areas, we also considered the results of yearly eradication efforts carried out by the Balearic Government (an average of 200 traps maintained per year during 2016–2017; COFIB 2016, 2017). Capture rates of individual traps ranged from 0 to 1.34/100 days in 2017. We identified those traps with the highest capture rates (from 0.41 to 1.34, i.e., the four highest capture rate classes according to COFIB 2017), and we established our “snake-present” transects near those traps.

We used line transects to census lizards (Lovich et al. 2012), with 15 transects in areas with snake populations and 14 in the snake-free area, for a total of 29 transects arrayed from 4 to 185 m asl (Figure 1). All the transects went through natural areas, which have a very similar vegetative structure across the island before expansion of the invasive snake (Cirer and Serapio 2015: 13; R. García, personal communication; E. Montes, unpublished data); moreover, we always placed transects in sites with lizard populations in the previous decade, confirmed by our experience and by inquiry with local residents. We conducted three surveys along each transect, mostly by the same researcher (E.M.). We surveyed on foot, moving at a speed of 2 km/h along an almost straight transect 500 m long; surveys consistently lasted 15 min. We also checked

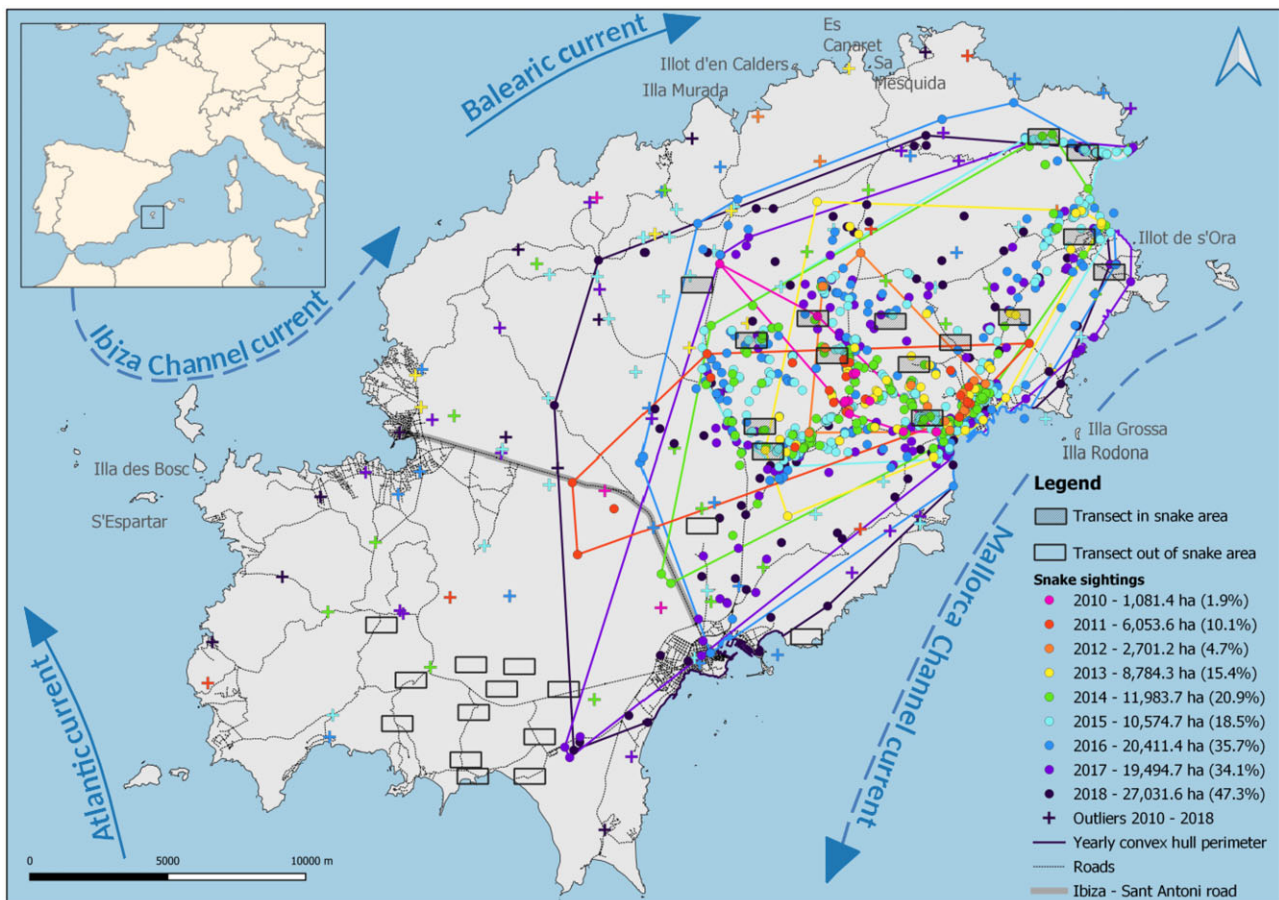


Figure 1. Map of Ibiza in the context of the Western Mediterranean (inset), showing: (1) records of the invasive *Hemorrhoids hippocrepis* by year (2010–2018), where crosses are outliers, for the calculation of the range area of each year (depicted by the polygons); (2) distribution of transects for lizard censuses in the invaded (filled rectangles) and snake-free (empty rectangles) parts of the island; (3) islets surveyed by us; and (4) main sea currents, including dominant currents (solid arrows) and mesoscale currents (dashed arrows).

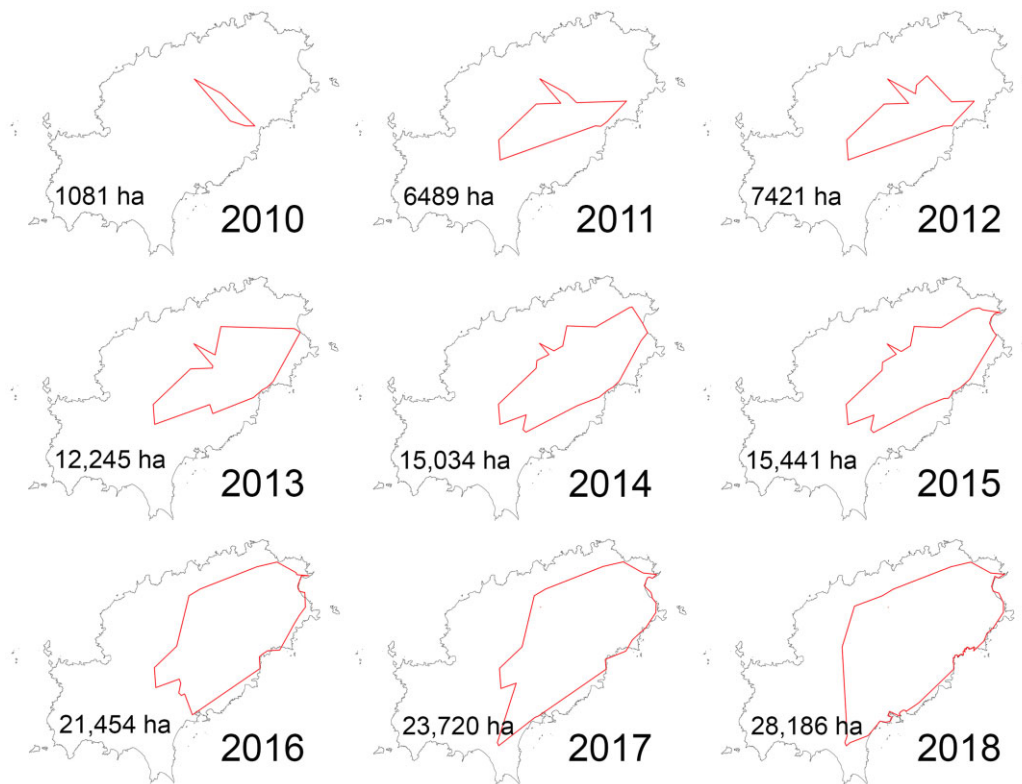


Figure 2. Yearly cumulative range expansion of *Hemorrhhois hippocrepis* on Ibiza.

stones, logs, and debris where lizards could take refuge by turning over such items of appropriate size within 2 m of the transect line. We performed the surveys during June and July 2018, on clear days without wind (23.0–33.0°C, ambient temperature), avoiding mid-day hours, arbitrarily mixing surveys among transects in areas with or without snake populations, and varying the time of each visit to a specific transect to avoid any temporal bias in the results. We assessed relative density of lizards as number of individuals/census. We placed transects at least 750 m away from one another, far enough to avoid double counts of moving lizards, considering their low vagility.

We assessed habitat cover every 20 m along each transect, alternating between the right and left sides of the transect, and 2 m away from the progression line (the average distance from the progression line at which lizards were observed); thus, we had 26 habitat-sampling points per transect. At each habitat point, we recorded which of four structural traits dominated the habitat: tree (height above 2 m), shrub (height below 2 m), earthy soil cover, or rocky soil cover. These habitat categories depict the structure of the habitat used by *P. pityusensis* (see Pérez-Mellado 2002). One of the transects chosen in 2018 as representing a snake-free area (#16) proved, with later data, to be inside some of the polygons with snakes (Figure 1); however, at the time the transects were selected (early 2018), there were no snake sightings in that vicinity.

Lizard populations on islets

The island of Ibiza is surrounded by 30 islets that hold a *P. pityusensis* population assigned to 1 of 22 subspecies (Salvador 2015). Considering the distribution of snakes on the main island (in the northeast), that the main marine currents circle Ibiza clockwise (Ruiz et al. 2009; Figure 1), and the locations of snake sightings in

the sea around Ibiza (Supplementary Figures S1 and S2), we selected a sample of nine islets to check for the presence of snakes and confirm the current status of their lizard populations: S'Espartar (19.8 ha), Es Bosc (16.4 ha), Murada (1.3 ha), En Calders (2.3 ha), Canaret (0.2 ha), Sa Mesquida (0.4 ha), S'Ora (0.4 ha), Grossa (4.5 ha), and Rodona (0.7 ha) (Figure 1). S'Espartar and Es Bosc are not close to the invaded area; however, the interest in surveying them was in their belonging to a nature reserve.

We visited the islets during the spring, summer, and fall of 2018 and 2019, always under sunny and calm conditions. We (always E.M.) recorded the number of lizards seen within 2 m from the progression line, during various (depending on the size of the islet) spans of 30 min while slowly walking (2 km/h) around the islet (0.4 ha plots). We also inspected each islet specifically for signs of snake presence (e.g., sheds and scat).

Other factors

Further, we considered the potential impacts of other native and introduced predators on Ibiza in leading to the decline of the native lizards (reviewed in Salvador 2015).

Statistical analysis

We treated lizard numbers on each transect survey as the response variable and used generalized linear mixed models (GLMMs) to determine the effect of snake presence, the four structural habitat variables (tree, shrub, earthy soil, and rocky soil), and the interaction snake presence * tree presence, on lizard abundance. We included that interaction because, from the habitat variables, the most critical is tree cover, since it influences reptile abundances in Mediterranean habitats (Pinto et al. 2018). We treated snake presence, the structural habitat variables, and the interaction of two variables, as fixed

effects, and survey unit (1–3) as a random effect. Thus, we used the lizard survey as the sampling unit (29 transects * 3 surveys per transect = 87 sampling units). We modeled lizard abundance with a zero-inflated negative-binomial distribution and a log-link function, using the lmer function implemented in the R package lme4 (Bates et al. 2015); this method has been suggested for data with many zeros in the data matrix and is appropriate for count data (Crawley 1993). We used a model-averaging approach and ordered all models according to AIC values (Burnham and Anderson 2002), identifying models with $\Delta AIC < 2$ as the best (Burnham and Anderson 2002). We used the dredge function within the MuMIn package (Bartoń 2018) to generate model sets for the analysis. We obtained relative importance values for each predictor variable (the sum of the Akaike weights in models where each predictor variable was included) using the Importance function (MuMIn). The predictor variable with the largest weight is estimated to be the most important of the predictors, while the variable with the smallest sum is estimated to be of least or no importance (Burnham 2015). We handled possible multicollinearity among effects by calculation of the variance inflation factor (VIF; car package: Fox et al. 2017). We found high VIF values indicating multicollinearity between the variables earthy soil and rocky soil in some models; thus, we discarded the first of these and retained only rocky soil as being more directly relevant for the mainly rupicolous *P. pityusensis*. We performed all analyses using the R software packages (R Development Core Team 2017).

Results

Spread of the invasive snake

Sightings of the invasive snake showed an increase in numbers and distribution during the 2010–2018 period, spreading to occupy 49.31% of the island area and 43.04% of the lizard’s entire range area (islands of Ibiza, Formentera, and 38 offshore islets) by December 2018 (Figures 1 and 2). The areal distribution of the snakes on Ibiza has grown dramatically (Figure 2) and linearly (Figure 3) during the 2010–2018 period. Under our regression model (Figure 3), the snakes are projected to inhabit 33,700 ha of Ibiza (more than 50% of the global range of *P. pityusensis*) by the end of 2020 and totally cover Ibiza by 2027–2028.

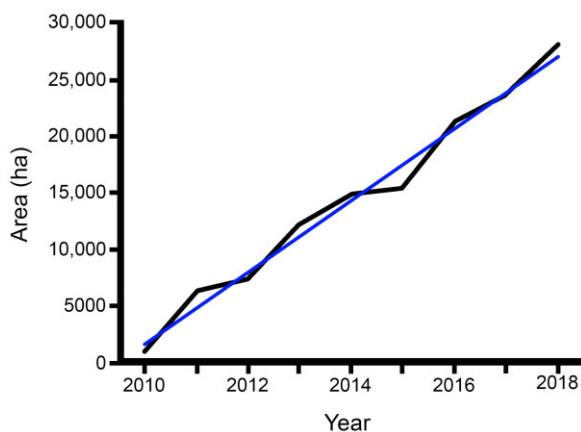


Figure 3. Growth in areal extent of the range of *H. hippocrepis* on Ibiza from 2010 to 2018 (black line), and linear regression (blue line) explaining those data. For the regression, Area = 3189.5 year—1384.3, adjusted $R^2 = 0.9800$, $F_{1,7} = 394.14$, $P < 0.0000$, standard error of estimate 1244.5.

Lizard censuses on Ibiza

Across the 29 census transects, we recorded 188 individual lizards (Table 1); the mean number of lizards in snake-absent areas was 4.36 per census (± 3.34 , range = 0–13, $n = 42$) but 0.11 lizards per census (± 0.75 , range = 0–5, $n = 45$) in snake-present areas. Based on AIC scores of the GLMM, three models had $\Delta AICc < 2$ (Supplementary Table S1). For the 20 models computed, presence of snakes and trees were the variables that best explained lizard abundance (Figure 4). GLMM results revealed highly significant variation in lizard abundance between transects according to snake presence/absence (Figure 5), with lizard abundance decreasing to extinction in the presence of snakes (Supplementary Figure S3). Tree cover was also a relevant predictor, as lizard abundance increased with greater tree cover, both in plots with and without snakes (Supplementary Figure S3).

Lizard populations on islets

Lizard numbers on the surveyed islets varied between 9 and 54 per survey on those islets maintaining lizards, with S’Espartar, Es Bosc, Murada, Sa Mesquida, and Rodona showing many individuals, and En Calders, Canaret, and Grossa very low densities (Supplementary Table S2). On S’Ora islet, no lizards were found during three visits (23 June and 8 July 2018, and 18 June 2019), nor were any lizard feces or shedding seen; this extinction happened in a maximum of 10 months (after the last record in 2017), coinciding with the sighting of a snake swimming 20 m away from the islet in April of 2018 (Supplementary Figure S1).

Among the sightings of swimming snakes near islets, one was recorded 1.1 km away from Sa Murada islet, on 12 June 2020 (C. Braun, personal communication; Supplementary Video S1). Moreover, during the last 5 years snake potential for islet colonization has been confirmed by two shed snake skins found on S’Espartar (where we presume there is at least one individual snake), one shed on Pou de Lleó (Supplementary Figure S4), and another snake seen during our visit to Grossa.

Discussion

Our results make clear that the invasive snake *H. hippocrepis* is driving a rapid decline in distribution and abundance of the endemic lizard *P. pityusensis* on Ibiza and its surrounding islets, to the point of extirpation within the invaded range. Transects in areas with snake populations all lack any evidence of remaining lizards, with the exception of a single (1 of 45) transect on 7 June 2018 (Table 1). Despite rapid acquisition by these lizards of antipredatory responses to *H. hippocrepis* as a novel predator—such as slow-motion movements and tail waving (Ortega et al. 2017)—the high predation pressure on this naïve prey (Hinckley et al. 2017) is leading populations of Ibiza’s only remaining endemic vertebrate to collapse. The same happened to the congeneric *P. lilfordi* on the larger Balearic Islands of Mallorca and Menorca, also partially attributed to invasive snakes, especially *M. mauritanicus* (Pinya and Carretero 2011). On Ibiza, the disappearance of lizards on the northeastern part of the island cannot be explained by other factors, like differences in the presence of other lizard predators. Five other lizard predators have been identified on the island: feral cats *Felis silvestris*, gulls *Larus cachinnans*, Genets *Genetta genetta*, barn owls *Tyto alba* (reviewed in Salvador 2015), and Kestrels (*Falco tinnunculus*; Servei d’Agents de Medi Ambient, personal communication). With respect to *F. silvestris*, the hunting grounds where most cats are captured are located in the southwestern half of the island (Supplementary Table

Table 1. Transect details and number of lizards (*P. pityusensis*) on the island of Ibiza according to the presence/absence of invasive snakes

| Invasive snakes | Transect number | Elevation (m) | Coordinates | First survey | | Second survey | | Third survey | |
|-----------------|-----------------|---------------|-----------------|--------------|-------------------|---------------|-------------------|--------------|-------------------|
| | | | | Date | Number of lizards | Date | Number of lizards | Date | Number of lizards |
| Present | 1 | 92 | 38.9851, 1.4501 | 10 June | 0 | 5 July | 0 | 8 July | 0 |
| Present | 2 | 18 | 39.0764, 1.5835 | 7 June | 0 | 2 July | 0 | 5 July | 0 |
| Present | 3 | 40 | 38.9888, 1.5202 | 6 June | 0 | 3 July | 0 | 8 July | 0 |
| Present | 4 | 158 | 39.0310, 1.4228 | 10 June | 0 | 4 July | 0 | 5 July | 0 |
| Present | 5 | 71 | 39.0086, 1.4799 | 6 June | 0 | 27 June | 0 | 5 July | 0 |
| Present | 6 | 39 | 39.0488, 1.5826 | 5 June | 0 | 7 June | 0 | 3 July | 0 |
| Present | 7 | 102 | 39.0207, 1.4716 | 6 June | 0 | 27 June | 0 | 5 July | 0 |
| Present | 8 | 49 | 39.0062, 1.5142 | 5 June | 0 | 4 July | 0 | 8 July | 0 |
| Present | 9 | 87 | 38.9771, 1.4537 | 10 June | 0 | 27 June | 0 | 5 July | 0 |
| Present | 10 | 125 | 39.0132, 1.4460 | 10 June | 0 | 5 July | 0 | 8 July | 0 |
| Present | 11 | 57 | 39.0375, 1.5954 | 5 June | 0 | 3 July | 0 | 5 July | 0 |
| Present | 12 | 51 | 39.0222, 1.5559 | 5 June | 0 | 7 June | 5 | 3 July | 0 |
| Present | 13 | 66 | 39.0202, 1.5041 | 5 June | 0 | 4 July | 0 | 8 July | 0 |
| Present | 14 | 61 | 39.0136, 1.5314 | 6 June | 0 | 10 June | 0 | 8 July | 0 |
| Present | 15 | 33 | 39.0814, 1.5671 | 7 June | 0 | 2 July | 0 | 5 July | 0 |
| Absent | 16 | 37 | 38.9520, 1.4271 | 5 June | 2 | 9 July | 4 | 12 July | 1 |
| Absent | 17 | 4 | 38.8821, 1.3611 | 5 July | 2 | 7 July | 4 | 11 July | 7 |
| Absent | 18 | 23 | 38.8691, 1.3572 | 5 July | 1 | 7 July | 0 | 11 July | 2 |
| Absent | 19 | 8 | 38.8688, 1.3334 | 6 June | 1 | 7 July | 13 | 9 July | 2 |
| Absent | 20 | 37 | 38.8741, 1.3304 | 6 June | 0 | 7 July | 1 | 9 July | 6 |
| Absent | 21 | 103 | 38.8897, 1.3333 | 6 June | 1 | 7 July | 1 | 9 July | 1 |
| Absent | 22 | 109 | 38.8975, 1.3449 | 28 June | 3 | 7 July | 6 | 11 July | 4 |
| Absent | 23 | 90 | 38.8998, 1.3068 | 28 June | 4 | 7 July | 5 | 9 July | 6 |
| Absent | 24 | 51 | 38.8977, 1.3707 | 28 June | 2 | 10 July | 8 | 11 July | 10 |
| Absent | 25 | 75 | 38.8855, 1.3015 | 7 July | 1 | 9 July | 9 | 12 July | 11 |
| Absent | 26 | 32 | 38.9163, 1.4715 | 7 July | 3 | 8 July | 3 | 12 July | 3 |
| Absent | 27 | 124 | 38.9049, 1.3521 | 7 July | 1 | 11 July | 9 | 12 July | 6 |
| Absent | 28 | 128 | 38.9053, 1.3318 | 11 July | 3 | 12 July | 7 | 15 July | 8 |
| Absent | 29 | 185 | 38.9177, 1.2941 | 9 July | 5 | 11 July | 9 | 15 July | 8 |

All surveys were carried out in 2018.

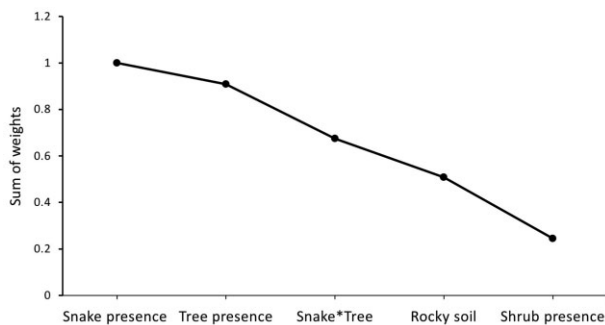


Figure 4. Ranking of the most explanatory variables for lizard abundance on Ibiza, based on the average modeling values of the GLMM. Snake presence and tree presence are the most explanatory variables for lizard abundance.

S3) where lizards remain common. For other lizard predators, *L. cachinnans* predation on lizards is limited to shoreline populations (Mayol 2004), the population of *G. genetta* is scarce and declining on the island (Gaubert et al. 2015), *P. pityusensis* represents just 0.5% of *T. alba* diet (Sommer et al. 2005), and there is no quantitative data on *F. tinnunculus* diet on Ibiza, although it is only occasionally observed to prey upon lizards. Furthermore, each of these predators is either native (*L. cachinnans*, *F. tinnunculus*, *T. alba*) or have been established on Ibiza for four millennia (*F. silvestris*, *G. genetta*; Cooper and Pérez-Mellado 2012), and their population

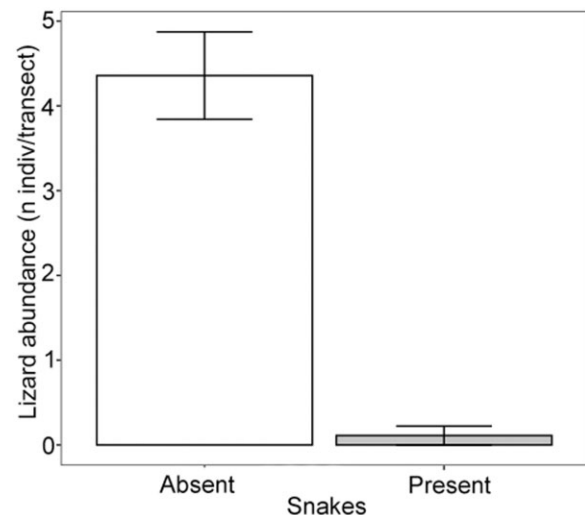


Figure 5. GLMM scores of lizard *P. pityusensis* abundance per transect in relation to snake *Hemorrhois hippocrepis* presence. Boxplots indicate the error in the measurement of the average value for lizard abundance. Whiskers are ± 1 SE.

numbers and distribution are not correlated to the rapid disappearance of lizards over the past decade across the northeastern part of the island yet not the southwestern portion (e.g., Birdlife

International 2015; Gaubert et al. 2015). Nor does habitat change explain lizard absence: Urban development increased by 5.5% from 2008 to 2015, yet maps show greater human development during this time in southwestern Ibiza (Consell Insular d'Eivissa 2018), where lizards are still common (this lizard frequently dwells in human structures; Pérez-Mellado 2002). In addition, forest extent has changed minimally in the last 20 years so can hardly be viewed as causative in the decline (Global Forest Watch 2019). Lastly, the subspecies on S'Ora islet has become extinct in the absence of habitat change in less than a year.

The distribution of *H. hippocrepis* has expanded, in less than 10 years (2010–2018), to occupy the northeastern half of the island and 43% of the lizard's global range (Figure 1). However, the presence of several snake outliers beyond its core range on Ibiza (Figure 1) suggests that this estimate may be too conservative inasmuch as these outliers could represent incipient populations instead of waif individuals. Moreover, snake sightings are becoming common in new areas of Ibiza, which have been snake-free until recently (Figure 1; E. Montes, personal observation). Our census results strongly support the hypothesis that the snake extirpated the native lizard wherever snake populations are well established (Table 1 and Supplementary Table S1), and we expect this process to continue apace. Following existing trends (Figures 2 and 3), we predict *P. pityusensis* to become extinct on Ibiza before 2030.

The importance of snake predation as an extinction factor for island vertebrates was originally dismissed when first presented in the 1980s (Jaffe 1994), but it has been compellingly demonstrated in loss of native bird, bat, and lizard species on Guam due to the invasive brown treesnake, *Boiga irregularis* (Fritts and Rodda 1998; Rodda and Savidge 2007). Snake predation is also likely to be at least in part responsible for losses of lizard species on Christmas Island (Smith et al. 2012), on the Mascarene Islands (Deso and Probst 2007; Cheke and Hume 2008), in the Canary Islands (Cabrera-Pérez et al. 2012), and elsewhere in the Balearic Islands (Mayol 2004). There are other examples in which invasive snakes have proven themselves to be a threat to populations of native vertebrates (reviewed in Kraus 2009, 2015), so it can hardly be viewed as surprising that an endemic lizard on the small island of Ibiza should also be so threatened.

Among the islets visited during this study, the lizard population on S'Espartar *P. pityusensis kameriana* is apparently healthy (Supplementary Table S2), despite at least one individual snake inhabiting the islet. This is probably due to the large size of the islet and the small number of snakes. On the smaller Gossa and Rodona islets—which share the subspecies *P. pityusensis redonae*—the effect of a medium-sized (approx. 800 mm snout–vent length) *H. hippocrepis* spotted on Gossa (3 August 2019) is evident: we found the lowest lizard density on any offshore islet (Supplementary Table S2). We also found low lizard numbers on En Calders *P. pityusensis pityusensis* and Es Canaret *P. pityusensis canaretensis*. En Calders has always had small numbers of lizards (Salvador 2015), and Es Canaret has a very small vegetated area (about 500 m²), so small lizard populations on those islets are not surprising. Our most disturbing finding is that the population of the small S'Ora islet vanished in at most 10 months, after living isolated from conspecific populations since the last Glacial Maximum (~26,500–19,000 years BP; Clark et al. 2009). During August 2017, lizards were common on S'Ora (P. dell'Agnolo, personal communication) but were absent during our surveys. This was the sole population for the subspecies *P. pityusensis hortae* (Salvador 2015), and we can presume that the extinction of this islet population was snake driven in very short time.

Finally, persistence of the population of Sa Murada *P. pityusensis muradae* is of concern due to the swimming snake observed nearby.

Colonization of these islets from Ibiza comprise the first contemporary trans-marine dispersals documented for *H. hippocrepis* (see Schätti 1993; Feriche 2017). However, this possibility was expected, given that these snakes colonized the Iberian Peninsula from North Africa around 90,000 years ago (Carranza et al. 2006). During that period both continents had been separated for more than 5 MY, so the only means of colonization was trans-marine migration, either rafting or swimming, across the Strait of Gibraltar (now 14 km wide). This facility for trans-marine dispersal serves as a behavioral threat for virtually all populations of *P. pityusensis*.

Given the results reported herein, so long as snakes are thriving on Ibiza, the spread of *H. hippocrepis* entails a serious threat not only to the main Ibizan population of *P. pityusensis*, but also to Formentera, which is 7 km from Ibiza and transportation of goods is continuous between both islands, and the 22 additional subspecies that inhabit 38 islets surrounding Ibiza and Formentera (Salvador 2015). These islet populations are at severe risk given their small sizes, lack of efficient lizard antipredatory responses toward *H. hippocrepis* (Ortega et al. 2017), and accessibility to *H. hippocrepis* dispersal, given several observations of snakes swimming in the sea (some only a few meters away from those islets) and along the coast of the main island. Most importantly, one of the islet populations of *P. pityusensis* vanished in a matter of months. Independent of anticipate lizard extinction on Ibiza within the next decade, it seems likely that many (maybe most) populations on offshore islets could also be lost during this time. Both are expected to greatly reduce the total genetic, phenotypic, and taxonomic diversity of this lizard lineage. Preventing snakes from dispersing to the islets is infeasible; therefore, our findings strongly support the urgent need to reinforce control efforts on Ibiza.

We have numerically demonstrated the virtual extinction of the sole remaining endemic vertebrate on Ibiza, *P. pityusensis*, from half of its former range and from an offshore islet within less than 10 years (2010–2018), mediated by the invasive snake *H. hippocrepis*. In light of our disturbing findings, a reassessment of this lizard's conservation status needs to be done, and managers now have an urgent duty to improve snake management to avert its extinction (Smith et al. 2012).

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Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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