Accepted Article

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

Elba Montes[a], Fred Kraus[b], Brahim Chergui[c], Juan M. Pleguezuelos[d]

[a]Department of Zoology, Faculty of Biological Sciences, University of Valencia, c/ Dr. Moliner, 50, Burjassot, E-46100, Valencia, Spain; [b]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor 48109, Michigan, USA; [3]Equipe de Recherche Ecologie, Systématique, Conservation de la Biodiversité, Faculté des Sciences de Tétouan, Université Abdelmalek Essaâdi, BP 2121 El M'Hannech, Tétouan, Morocco ; [d]Department of Zoology, Faculty of Sciences, Granada University, E-18071 Granada, Spain.

*Address correspondence to Elba Montes. Email: elbamontesv@gmail.com

Handling editor: Xiang Ji

Received on 31 October 2020; accepted on 7 March 2021

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 nine 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 offshore 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 amongst 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 Moorleghem 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*, *Atelerix 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 seven 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, thirty 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 ten records—including videos and pictures—of *H. hippocrepis* swimming in the sea within a distance of 10 to 1,000 m off the coast of Ibiza (Supplementary Materials, Figures S1, S2 and 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 (Salvador 2015; Cirer and Serapio 2015: 13). 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 vs. 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 km^2 and a maximum elevation of 486 m. The mean annual temperature is 18.3 ºC (mean monthly range 11.9 ºC [January] to 26.3 ºC [August]), and the average yearly rainfall is 413 mm (mean monthly range from 5 mm [July] to 58 mm [October]; standard meteorological averages for the Ibiza Airport weather station, 38.8728º N, 1.3730º 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, Pantellaria 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 2010-2018, 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 onwards, 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 (Quantum Gis 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 Figure 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 2010-2017, 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 (Fig. 1). All the transects went through natural areas, which have a very similar vegetative structure across the island. Lizards were widespread and rather equally common across the island before expansion of the invasive snake (Cirer and Serapio 2015: 13; R. García, pers. comm.; E. Montes, unpubl. 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 (EM). We surveyed on foot, moving at a speed of 2 km/h along an almost straight transect 500 m long; surveys consistently lasted 15 minutes. We also checked stones, logs and debris where lizards could take refuge by turning over such items of appropriate size within 2 meters of the transect line. We performed the surveys during June and July 2018, on clear days without wind (23.0–33.0 ºC, 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 meters 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 meters), shrub (height below 2 meters), 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 one 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

(Suppl. Mat. Figure S1, 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) (Fig. 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 EM) recorded the number of lizards seen within two meters from the progression line, during various (depending on the size of the islet) spans of 30 minutes 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, 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 to 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 (Bartón 2018) to generated 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, whilst 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 (Figs. 1, 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.

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, 3 models had Δ AICc < 2 (Suppl. Mat., 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 (Suppl. Mat., Figure S3). Tree cover was also a relevant predictor, as lizard abundance increased with greater tree cover, both in plots with and without snakes (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 (Suppl. Mat., 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 meters away from the islet in April of 2018 (Supplementary Materials, 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, pers. comm.; Suppl. Mat., Video S1). Moreover, during the last five 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 (Fig. 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, pers. comm.). With respect to *F. silvestris*, the hunting grounds where most cats are captured are located in the southwestern half of the island (Suppl. Mat., Table 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); 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 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., Gaubert et al. 2015, Birdlife International 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 (Fig. 1). However, the presence of several snake outliers beyond its core range on Ibiza (Fig. 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; EM, pers. obs.). Our census results strongly support the hypothesis that the snake extirpated the native lizard wherever snake populations are well established (Table 1, Suppl. Mat., Table S1), and we expect this process to continue apace. Following existing trends (Figs. 2, 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 2003). 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 (Suppl. Mat. 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 Grossa 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 Grossa (August 3 2019) is evident: we found the lowest lizard density on any offshore islet (Suppl. Mat. 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 m^2), 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, pers. comm.) 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 towards *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).

Acknowledgments

Federico Rey assisted with census and habitat measurement tasks and accompanied E. Montes to several islets, Xavier Santos advised with the data analysis, and Mónica Feriche critically read the manuscript. The environmental officers Service and especially Rocío García provided most of the geographical records for the invasive snake. The Balearic Government and the COFIB, especially Víctor Colomar, provided data of captured snakes and the shed of S'Espartar. Jordi Arilla (RIP) helped selflessly with the GIS and the map figure. Antònia Cirer helped in determining the disappearance of lizards on S'Ora islet, and provided with valuable information. The Balearic Government issued the authorizations (numbers SEN-758/19, CAP 19-19, and SEN-991/19) and provided transportation to the islets in the Marine Reserves. The Hunting Service of the Ibiza Island Council provided data on cat captures.

References

AHE, 2015. *Asociación Herpetológica Española. Proyecto piloto de control de ofidios en Ibiza 2015*. Consell Insular d'Eivissa. 48 pp.

Alcover JA, Seguí B, Bover P, 1999. *Extinctions and Local Disappearances of Vertebrates in the Western Mediterranean Islands: Extinctions in Near Time.* Boston: Springer, 165–188.

Álvarez C, Mateo JA, Oliver J, Mayol J, 2010. Los ofidios ibéricos de introducción reciente en las Islas Baleares. *Bolet Asoc Herpetol Españ* **21:**126–131.

Andersen MC, Adams H, Hope B, Powell M, 2004. Risk analysis for invasive species: general framework & research needs. *Risk Anal* **24:**893-900.

Ballouard JM, Gayraud R, Rozec F, Besnard A, Caron S et al., 2019. Excellent performances of dogs to detect cryptic tortoises in Mediterranean scrublands. *Biodivers Conserv* **28:**4027–4045.

Bartoń K, 2018. *Multi-Model Inference*. R package version 1.42.1. https://CRAN.R- project.org/package=MuMI.

Bates D, Maechler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* **67:**1–48.

Bellard C, Cassey P, Blackburn TM, 2016. Alien species as a driver of recent extinctions. *Biol Letters* **12:**20150623.

BirdLife International, 2015. *Tyto alba*. *The IUCN Red List of Threatened Species* 2015: e.T22688504A59994105. Downloaded on 11 January 2021

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ, 2004. Avian extinction & mammalian introductions on oceanic islands. *Science* **305(5692):**1955-1958.

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM et al., 2014. A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biol* **12:**e1001850.

Burnham KP, Anderson DR, 2002. *Model Selection & Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd edn. New York: Springer-Verlag.

Burnham KP, 2015. *Multimodel Inference: Understanding AIC Relative Variable Importance Values.* https://sites.warnercnr.colostate.edu/kenburnham/wpcontent/uploads/sites/25/2016/08/VARIMP.pdf [accessed 6 January 2021].

Cabrera-Pérez MÁ, Gallo-Barneto R, Esteve I, Patiño-Martínez C, López-Jurado LF, 2012. The management & control of the California kingsnake in Gran Canaria (Canary Islands): project LIFE+ *Lampropeltis*. *Aliens: The Invas Species B* **32:**20-28.

Carranza S, Arnold EN, Pleguezuelos JM, 2006. Phylogeny, biogeography, and evolution of two Mediterranean snakes, *Malpolon Monspessulanus* and *Hemorrhois Hippocrepis* (Squamata, Colubridae), using MtDNA sequences. *Molecular Phylogenetics and Evolution* **40(2):**532–546.

Cheke AS, Hume J, 2008. *Lost land of the Dodo: An Ecological History of Mauritius, Réunion & Rodrigues*. London: T & AD Poyser.

Cirer AM, Serapio J, 2015. *Eivissa i Formentera, sargantanes i illes*. 13. Eivissa: Balàfia Postals.

Clark PU, Dyke AS, Shakun JD, Carlson AE, Clark J et al. 2009. The last glacial maximum. *Science* **325(5941):**710-714.

Clark L, Savarie PJ, Shivik JA, Breckck SW, Dorr BS, 2012. Efficacy, effort, and cost comparisons of trapping and acetaminophen-baiting for control of brown treesnakes on Guam. *Human-Wildlife Interactions* **6(2):**222-236.

Clark L, Clark C, Siers S, 2017. Brown tree snakes: methods and approaches for control. In: Pitt WC, Beasley J, Witmer GW eds. *Ecology & Management of Terrestrial Vertebrate Invasive Species in the United States.* Boca Raton: CRC Press, 107–134.

COFIB, 2016. Consorci de Recuperació de Fauna de les Illes Balears. Informe del control de colúbridos invasores, Pitiusas 2016, SCF-COFIB 2016. Conselleria Medi Ambient i Territori, Balearic Government. 32 pp.

COFIB, 2017. Consorci de Recuperació de Fauna de les Illes Balears. Informe control d'ofidis a Pitiüses, SCF-COFIB 2017. Conselleria Medi Ambient i Territori, Balearic Government. 23 pp.

COFIB, 2018. Consorci de Recuperació de Fauna de les Illes Balears. Resumen de la campaña de control de ofidios en las Islas Baleares. Conselleria Medi Ambient i Territori, Balearic Government. 16 pp.

Cohen AN, 2002. Success factors in the establishment of human-dispersed organisms. In: Bullock JM, Kenward RE, Hails RS eds. *Dispersal Ecology*. London: Blackwell, 374–394.

Consell Insular d'Eivissa, 2018. Diagnòstic de la revisió del Pla territorial insular – Fase 1. Consell Insular d'Eivissa. http://www.conselldeivissa.es/portal/RecursosWeb/DOCUMENTOS/1/1_14857_2.PDF Accessed 24 June 2020.

Cooper Jr WE, Pérez-Mellado V, 2012. Historical influence of predation pressure on escape by *Podarcis* lizards in the Balearic Islands. *Biol J Linn Soc* **107:**254-268.

Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E et al., 2017. Invasion biology: specific problems & possible solutions. *TREE* **32:**13–22.

Crawley MJ, 1993. *GLIM for Ecologists*. Oxford: Blackwell.

Deso G, Probst JM, 2007. *Lycodon aulicus* Linnaeus, 1758 et son impact sur l'herpétofaune insulaire à La Réunion (*Ophidia: Colubridae: Lycodontinae*). *Bull Phaethon* **25:**29–36.

Durso AM, Willson JD, Winne CT, 2011. Needles in haystacks: estimating detection probability & occupancy of rare & cryptic snakes. *Biol Conserv* **144:**1508–1515.

Engeman RM, Vice DS, 2002. Objectives & integrated approaches for the control of brown tree snakes. *J Integr Pest Manag* **6:**59-76.

ESRI, 2017. *ArcGIS Desktop: ArcMap*: Release 10.4.1. Redlands, CA Environ. Syst. 654 Res. I.

Feriche M, 2017. Culebra de herradura – *Hemorrhois hippocrepis*. *Enciclopedia Virtual de los Vertebrados Españoles*. Sanz JJ, Martínez-Freiría F (Eds.), Madrid: MNCN. http://www.vertebradosibericos.org/ Accesed 21 January 2020.

Fisher SR, Fisher RN, Alcaraz SE, Gallo-Barneto R, Patino-Martinez C et al., 2019. Life-history comparisons between the native range and an invasive island population of a colubrid snake. *Island Invasives: Scaling up to Meet the Challenge*, no. **62:** 326.

Fox J, Weisberg S, Price B, Adler D, Bates D et al. 2017. *Package 'car'*. Retrieved from https://cran.rproject.org/web/packages/car/car.pdf.

Fritts TH, Rodda GH, 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu Rev Ecol Evol S* **29:**113–140.

Gaubert P, Carvalho F, Camps D, Do Linh San E, 2015. *Genetta genetta*. The IUCN Red List of Threatened Species 2015: e.T41698A45218536. https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T41698A45218636.en. Downloaded on 17 October 2020.

Global Forest Watch, 2019. https://www.globalforestwatch.org/map?map=eyJjZW50ZXIiOnsibGF0IjozOS4wMDkzNjEwNzI0NDExNCwibG5nIjoxLjMxNTEwMTEyNjI1ODY2OTZ9LCJiZWFyaW5nIjowLCJwaXRjaCI6MCwiem9vbSI6OS45OTEwNjI3Mjk3NTc5MjN9&mapPrompts=eyJvcGVuIjp0cnVlLCJzdGVwc0tleSI6InJlY2VudEltYWdlcnkiLCJzdGVwSW5kZXgiOjB9 Accessed 24 June 2020.

Griffiths RA, Schley L, Sharp PE, Dennis JL, Román A, 1998. Behavioural responses of Mallorcan midwife toad tadpoles to natural & unnatural snake predators. *Anim Behav* **55:**207–214.

Hawkins CL, Bacher S, Essl F, Hulme PE, Jeschke JM et al., 2015. Framework & Guidelines for Implementing the Proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). *Divers Distrib* **21:**1360–1363.

Hedrick PW, 1992. Genetic conservation in captive populations & endangered species. *Applied Population Biology*. **67:**45-68.

Hinckley A, Montes E, Ayllón E, Pleguezuelos JM, 2017. The fall of a symbol? A high predation rate by the introduced horseshoe whip snake *Hemorrhois hippocrepis* paints a bleak future for the endemic Ibiza wall lizard *Podarcis pityusensis*. *Europ J Wild Res* **63:**1–8.

Hu F, Zhao Y, Wang W, Huang X, 2013. *Discrete Point Cloud Filtering & Searching Based On VGSO Algorithm. Ecms* **4:**850-856.

IUCN, 2012. *IUCN Red List Categories and Criteria: Version 3.1*. 2nd edn. Gland, Switzerland and Cambridge, UK: IUCN.

IUCN, 2019. *Consultation Document: Proposed IUCN Standard Classification of the Impact of Invasive Alien Taxa*. Version 2.3. Gland, Switzerland and Cambridge, UK: IUCN.

Jaffe M, 1994. *And No Birds Sing: The Story of an Ecological Disaster in a Tropical Paradise*. New York: Simon & Schuster.

Jones HP, Holmes ND, Butchart SH, Tershy BR, Kappes PJ et al., 2016. Invasive mammal eradication on islands results in substantial conservation gains. *PNAS* **113:**4033–4038.

Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL et al., 2009. A global assessment of endemism & species richness across island & mainland regions. *PNAS* **106:**9322–9327.

Kraus F, 2009. *Alien Reptiles & Amphibians: A Scientific Compendium & Analysis*. Dordrecht: Springer.

Kraus F, 2015. Impacts from invasive reptiles & amphibians. *Annu Rev Ecol Evol S* **46:**75–97.

Kraus F, Stahl R, Pitt W, 2015. Thermal fumigation provides a simple & effective solution for sanitizing cargo from invasive snakes. *J Pest Sci* **88:**331–341.

Lovich RE, Hayes WK, Mushinsky H, Rodda GH, 2012. Transect surveys, including line distance. In: McDiarmid RW, Foster MS, Guyer C, Chernoff N, Gibbons JW eds. *Reptile Biodiversity, Standard Methods for Inventory & Monitoring*. Berkeley: Univ. California Press, 227–233.

Mayol J, 2004. A conservation proposal for most endangered insular lizards in the Balearics. In: Pérez-Mellado V, Riera N, Perera A eds. *The Biology of Lacertid lizards: Evolutionary and Ecological Perspectives.* Recerca, 8. Maó: Institut Menorquí d'Estudis: 231–238.

Mehring M, Stoll-Kleeman S, 2008. Evaluation of major threats to forest biosphere reserves: a global view. *GAIA* **17:**125–133.

Montes E, Estarellas J, Ayllón E, Carretero MA, Feriche M et al., 2015. Dades preliminars del projecte pilot de control de serps a l'illa d'Eivissa. *Monogr SHNB* ***20*****:**455–464.

Montes E, Feriche M, Ruiz-Sueiro L, Alaminos E, Pleguezuelos JM, 2020. Reproduction ecology of the recently invasive snake *Hemorrhois hippocrepis* on the island of Ibiza. *Curr Zool* **66(4):**363–371.

Ortega Z, Mencía A, Pérez-Mellado V, 2017. Rapid acquisition of antipredatory responses to new predators by an insular lizard. *Behav Ecol Sociobiol* **71:**1.

Palmer M, Pons GX, Cambefort I, Alcover JA, 1999. Historical processes & environmental factors as determinants of inter-island differences in endemic faunas: the case of the Balearic Islands. *J Biogeogr* **26:**813–823.

Pérez-Mellado V, 2002. *Podarcis pityusensis* (Boscá, 1883). Lagartija de las Pitiusas. *Atlas y libro rojo de los anfibios y reptiles de España*. 254-256. Pleguezuelos JM, Márquez R, Lizana M (Eds.). Madrid: DGCN, AHE.

Pérez-Mellado V, Martínez-Solano I, 2009. *Podarcis pityusensis*. The IUCN Red List of Threatened Species 2009. http://dx.doi.org/10.2305/IUCN.UK.2009.RLTS.T17800A7482971.enDownloaded on 13 August 2019.

Perry G, Campbell III EW, Rodda GH, Fritts TH, 1998. Managing island biotas: brown tree snake control using barrier technology. *Proceedings of the 18th Vertebrate Pest Conference*. 138–143. Davis: University of California Press.

Pinto T, Moreira B, Freitas H, Santos X, 2018. The role of fire history, land-use, and vegetation structure on the response of Mediterranean lizards to fire. *Forest Ecol Manag* **419:**139–145.

Pinya S, Carretero MÁ, 2011. The Balearic herpetofauna: a species update & a review on the evidence. *Acta Herpetol* **6:**59–80.

R Development Core Team, 2017. *R: A Language & Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Reaser JK, Meyerson LA, Cronk Q, De Poorter M, Eldredge LG et al., 2007. Ecological & socioeconomic impacts of invasive alien species in island ecosystems. *Environ Conserv* **34:**98–111.

Reed RN, Hart KM, Rodda GH, Mazzotti FJ, Snow RW et al., 2011. A field test of attractant traps for invasive Burmese pythons *Python molurus bivittatus* in southern Florida. *Wildlife Res* **38:**114–121.

Reed RN, Todd BD, Miano OJ, Canfield M, Fisher RN et al., 2016. Ecology & control of an introduced population of Southern Watersnakes *Nerodia fasciata* in southern California. *Herpetol* **72:**130–136.

Rodda GH, Fritts TH, Clark CS, Gotte SW, Chiszar D, 1999. A state-of-the-art trap for the brown treesnake. In: Rodda GH, Sawai Y, Chiszar D, Tanaka H eds. *Problem Snake Management: the Habu & Brown Treesnake*. Ithaca: Comstock Publ, 268–284.

Rodda GH, Savidge JA, 2007. Biology & impacts of Pacific island invasive species. 2. *Boiga irregularis*, the brown tree snake (*Reptilia: Colubridae*) 1. *Pac Sci* **61:**307–325.

Rodda GH, Farley JL, Bischof R, Reed RN, 2007. New developments in snake barrier technology: fly-ash covered wall offers a feasible alternative for permanent barriers to brown treesnakes *Boiga irregularis*. *Herpetol Conserv Biol* **2:**157–163.

Rodríguez V, Brown RP, Terrasa B, Pérez-Mellado V, Castro JA et al., 2013. Multilocus genetic diversity & historical biogeography of the endemic wall lizard from Ibiza & Formentera *Podarcis pityusensis* (Squamata: Lacertidae). *Mol Ecol* **22:**4829–4841.

Ruiz S, Pascual A, Garau B, Faugère Y, Alvarez A et al., 2009. Mesoscale dynamics of the Balearic Front, integrating glider, ship & satellite data. *J Marine Syst* **78:**3–16.

Salvador A, 2015. Lagartija de las Pitiusas. In: Salvador A, Marco A eds. *Podarcis pityusensis*. *Enciclopedia Virtual de los Vertebrados Españoles*. Madrid: MNCN. http://www.vertebradosibericos.org/

Santoleri R, Böhm E, Schiano ME, 1994. The sea surface temperature of the Western Mediterranean Sea: historical satellite thermal data. *Coastal Estuar Stud* **46:**155–155.

Sax DF, Gaines SD, 2008. Species invasions & extinction: the future of native biodiversity on islands. PNAS 105: 11490–11497.

Schätti B, 1993. *Coluber hippocrepis* (Linnaeus, 1758) - Hufeisennattern. *Handbuch der Reptilien und Amphibien Europas.* Band 3/I. *Schlangen (Serpentes) I (Typhlopidae, Boidae, Colubridae 1: Colubrinae).* 115-130. Böhme W (ed.). Wiesbaden: Aula-Verlag.

Schley L, Griffiths RA, 1998. Midwife toads *Alytes muletensis* avoid chemical cues from snakes *Natrix maura*. *J Herpetol* **32:**572–574.

Servei d'Agents de Medi Ambient, 2003. Report "*Aparició de serps en llibertat a l'illa d'Eivissa*". Conselleria de Medi Ambient i Territori, Balearic Government. 4 pp.

Servei d'Agents de Medi Ambient, 2014. Report "*Informe resumen del registro de serpientes recogido por los Agentes de Medio Ambiente en Ibiza*". Conselleria de Medi Ambient i Territori, Balearic Government. 8 pp.

Silva-Rocha I, Montes E, Salvi D, Sillero N, Mateo JA et al., 2018. Herpetological history of the Balearic Islands: when aliens conquered these islands & what to do next. In: Queiroz AI, Pooley SP eds. *Histories of Bioinvasions in the Mediterranean*. Cham: Springer, 105–131.

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA et al., 2013. Impacts of biological invasions: what's what & the way forward. *TREE* **28:**58.

Smith MJ, Cogger H, Tiernan B, Maple D, Boland C et al., 2012. An oceanic island reptile community under threat: the decline of reptiles on Christmas Island, Indian Ocean. *Herpetol Conserv Bio* **7:**206–218.

Sommer R, Zoller H, Kock D, Böhme W, Griesau A, 2005. Feeding of the barn owl, *Tyto alba* with first record of the European free-tailed bat *Tadarida teniotis* on the island of Ibiza (Spain, Balearics). *Folia Zoologica* **54(4):**364–370.

Stanford JW, Rodda GH, 2007. The brown treesnake rapid response team. In: Witmer GW, Pitt WC, Fagerstone KA eds. *Managing Vertebrate Invasive Species: Proceedings of an International Symposium*. Fort Collins: United States Department of Agriculture/Animal & Plant Health Inspection Service/Wildlife Services, 175–187.

Strauss SY, Lau JA, Carroll SP, 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol Letters* **9:**357–374.

Torres-Roig E, Mitchell KJ, Alcover JA, Martínez-Freiría F, Bailón S et al., 2020. Origin, extinction and ancient DNA of a new fossil insular viper: molecular clues of overseas immigration. *Zool J Linn Soc* in press.

Van Moorleghem C, Huyghe K, Van Damme R, 2020. Chemosensory deficiency may render island-dwelling lizards more vulnerable to invasive predators. *Biol J Linn Soc* **129:**128–142

Whittaker RJ, Fernández-Palacios JM, 2006. *Island Biogeography*. 2nd edn. Oxford: Oxford Univ. Press.

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E, 1998. Quantifying threats to imperiled species in the United States. *BioScience* **48:**607–615.

Table 1. Transect details and number of lizards (*Podarcis pityusensis*) on the island of Ibiza according to the presence/absence of invasive snakes. All surveys were carried out in 2018.

Invasive snakes	Transect number	Elevation (m	Coordinates	1st Survey		2nd Survey		3rd Survey	
				Date	No. of lizards	Date	No. of lizards	Date	No. 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

Figure 1. Map of Ibiza in the context of the Western Mediterranean (inset), showing: (1) records of the invasive *Hemorrhois 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).

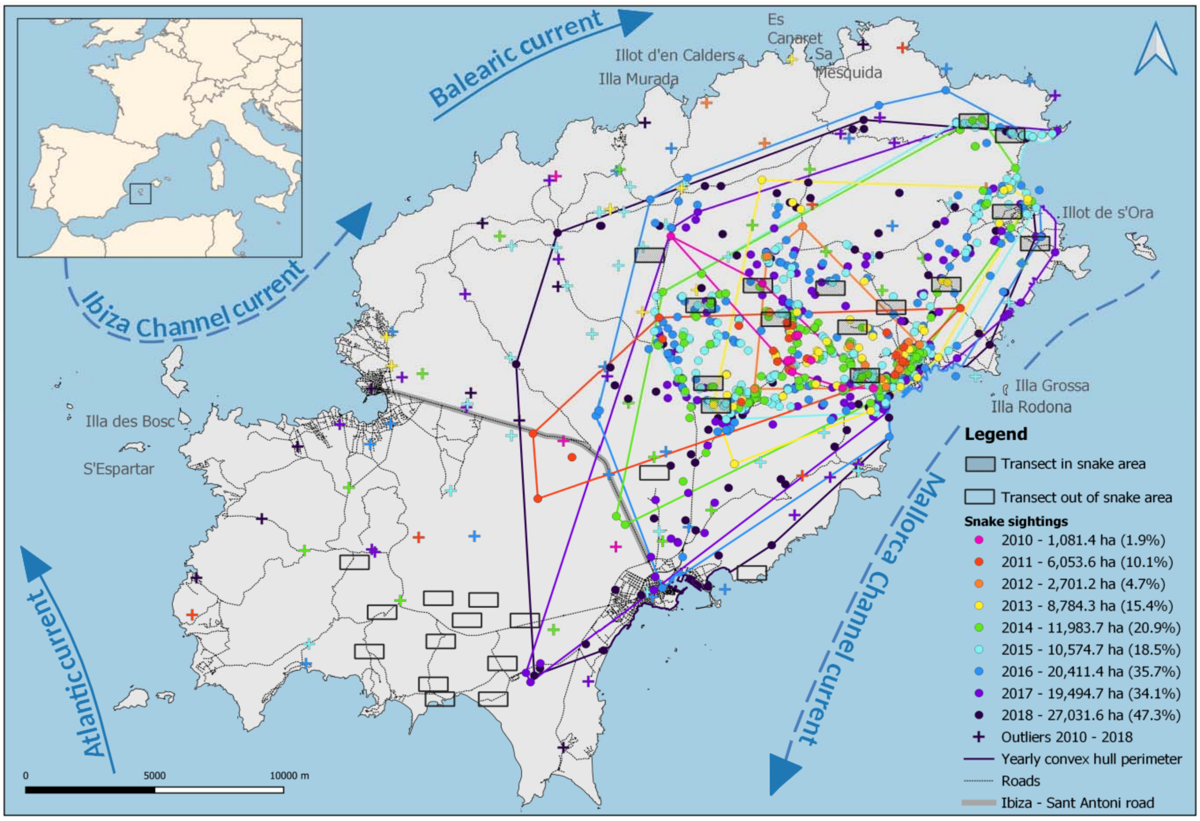

FIGURE IN COLOR (ONLINE ONLY)

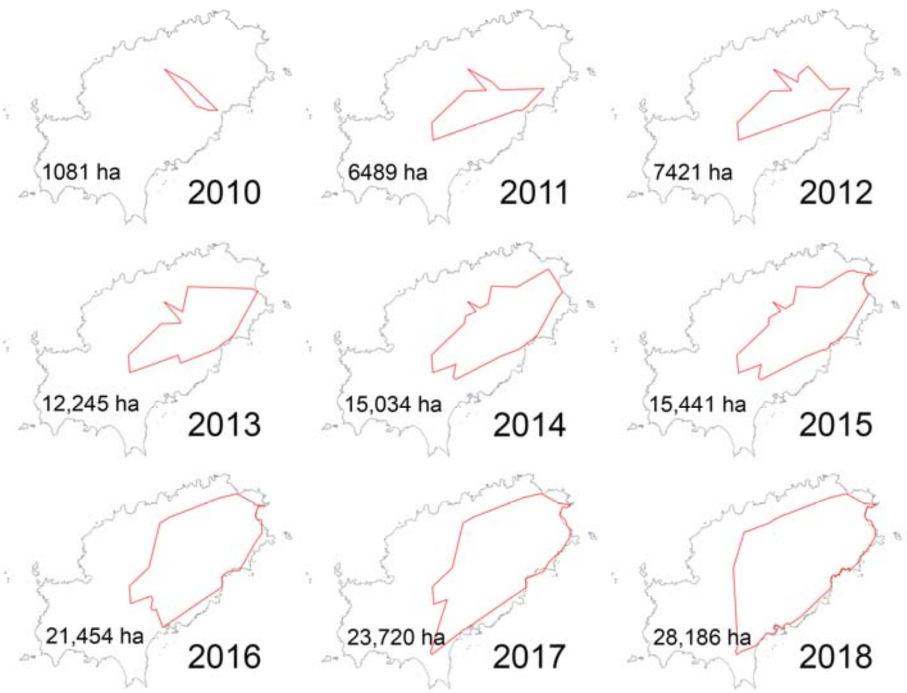

Figure 2. Yearly cumulative range expansion of *Hemorrhois hippocrepis* on Ibiza.

FIGURE IN COLOR (ONLINE ONLY)

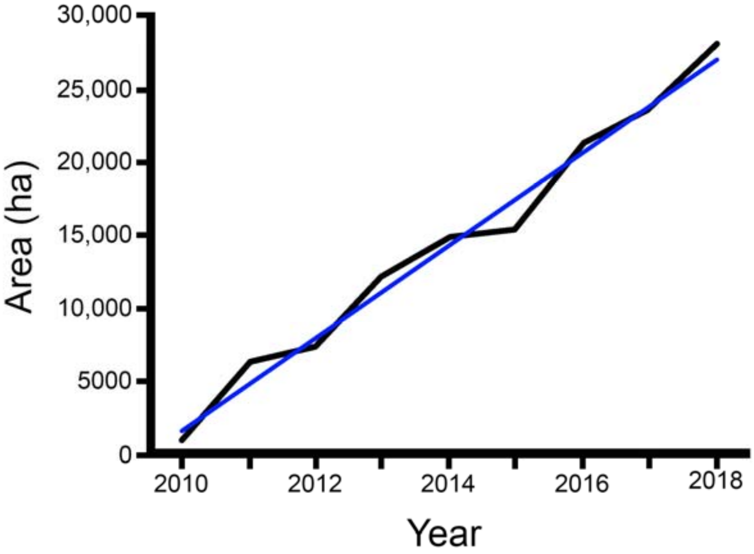

Figure 3. Growth in areal extent of the range of *Hemorrhois hippocrepis* on Ibiza from 2010-2018 (black line), and linear regression (blue line) explaining those data. For the regression, Area = 3189.5year – 1384.3, adjusted R^2 = 0.9800, $F_{1,7}$ = 394.14, $P < 0.0000$, standard error of estimate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

FIGURE IN COLOR (ONLINE ONLY)

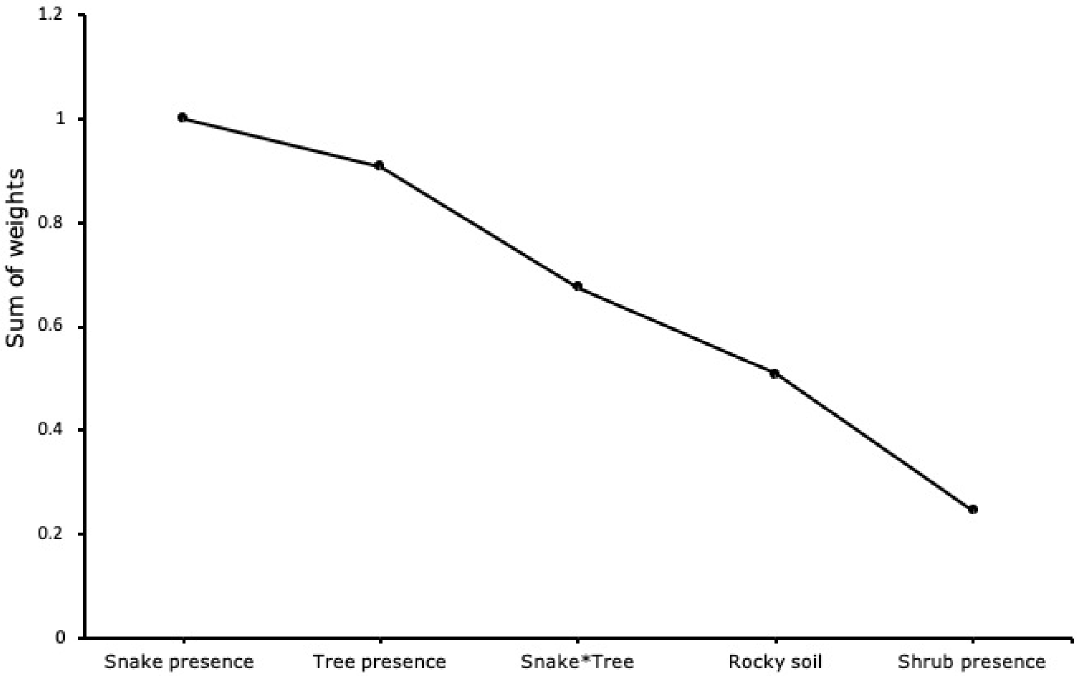

Figure 4. Ranking of the most explanatory variables for lizard abundance on Ibiza, based on the average modeling values of the GLMM. Snake presence and tree presence are the most explanatory variables for lizard abundance.

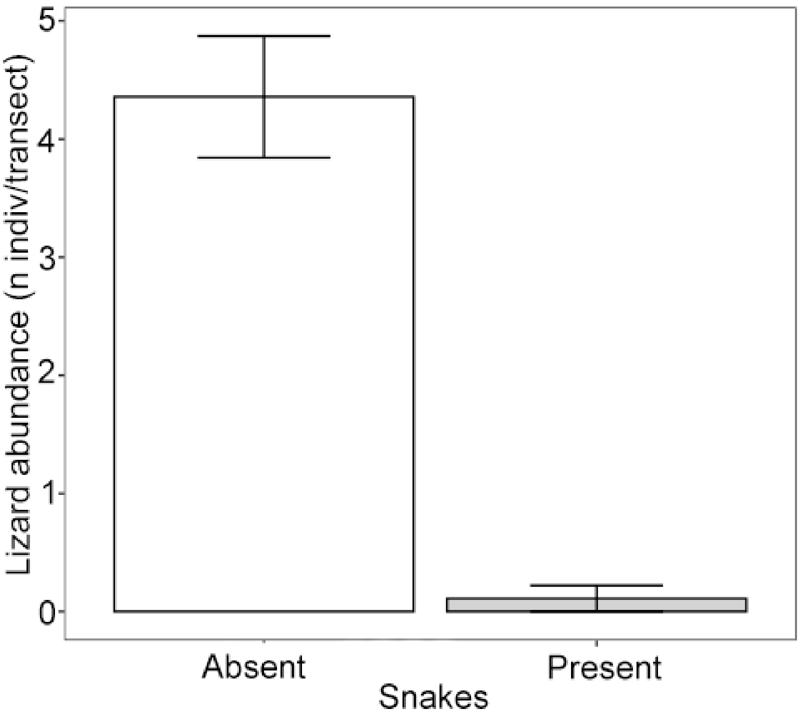

Figure 5. Generalized linear mixed model scores of lizard *Podarcis pityusensis* abundance per transect in relation to snake *Hemorrhois hippocrepis* presence. Boxplots indicate the error in the measurement of the average value for lizard abundance. Whiskers are ± 1 SE.