VNIVERSITAT DE VALÈNCIA

Doctoral Programme in Biodiversity and Evolutionary Biology

DOCTORAL DISSERTATION

Natural History and impacts of an invasive snake: the horseshoe whip snake, *Hemorrhois hippocrepis* (Linnaeus, 1758), on Ibiza

Elba María Montes Vadillo

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Cover image: watercolor of a horseshoe whip snake (*Hemorrhois hippocrepis*), by Elba Montes.

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CERTIFICAN que la presente Tesis Doctoral, titulada "**Natural history and impacts of an invasive snake: the horseshoe whip snake, *Hemorrhois hippocrepis* (Linnaeus, 1758), on Ibiza**", realizada por la licenciada en Ciencias Ambientales **Elba María Montes Vadillo**, ha sido realizada bajo la dirección de Juan M. Pleguezuelos y Mónica Feriche y la tutela de Pilar Navarro, y autorizan su presentación para optar al título de Doctora en Biodiversidad y Biología Evolutiva por la Universitat de València.

Y para que así conste a los efectos oportunos y en cumplimiento de la legislación vigente, firman el presente certificado en Valencia, a 21 de mayo de 2021.

Director: Juan M. Pleguezuelos   Directora: Mónica Feriche   Tutora: Pilar Navarro

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Abstract

The island of Ibiza, located in the Balearic Islands (Western Mediterranean), has remained free of introduced snakes for millennia, unlike the majority of Mediterranean islands. But in 2003, with the Mediterranean garden fad, the entrance of old olive trees to the island became common, and three snake species appeared on Ibiza, traveling as stowaways inside the trunks of the olive trees. The most successful invader was the horseshoe whip snake (*Hemorrhois hippocrepis*). This PhD dissertation studies the natural history of the invasive population and compares it to the source population's, in the southern Iberian Peninsula, in order to acquire knowledge that helps fighting against the invasion. It also analyzes the impact on the native fauna, particularly on the endemic Ibiza wall lizard (*Podarcis pityusensis*), the only native terrestrial vertebrate of the island.

The 1st chapter focuses on the snake's trophic ecology, finding a critical result: more than half of the diet (55.4 %) consists of lizards, whereas on the source population, lizards constitute a 24.2 % of the snake's menu. We also observed that the length and weight was the highest recorded for the snake species throughout its range. In sight of the results, in the 2nd chapter we analyzed the historic spread of the snake's population (period 2009-2018) and how the presence of *H. hippocrepis* affects the abundance of *P. pityusensis*, through censuses on the island and the islets inhabited by the lizard's subspecies. The results were conclusive: the invasive population occupied the northeastern half of Ibiza by 2018, where none of the 45 censuses in snake areas had lizards except for one, while the opposite happened in snake-free areas (all 42 censuses found lizards, except for two). In addition, one of the islets' lizard populations, *P. pityusensis hortae,* has vanished some months after a snake was spotted swimming 20 meters away, and therefore, the subspecies has gone extinct. The rate at which the invasive population is spreading allows us to predict that the lizard will be extinct from the island of Ibiza before 2030.

In order to understand the causes of invasion success of *H. hippocrepis*, after checking that its main prey is a low-energetic animal, we studied its reproduction ecology (3rd chapter), under the hypotheses of an increased fertility and productivity in the invasive population. However, the findings pointed otherwise: despite a widening of the reproductive season and an earlier sexual maturity for females, the number of eggs and body condition of neonates was the same than for the source population, and the reproduction frequency reduced to 50 % of the adult females, i.e., females are reproducing every two years on Ibiza.

All these findings led us to the Enemy Release Hypothesis (ERH) supporting the success of the invasive population. The ERH states that the natural enemies of a species (predators, parasites and competitors) are no longer present in the invaded range, facilitating the invasion process. In order to test the ERH, we studied the predation pressure on the snakes (4th chapter) in an indirect way: by comparing tail breakage for both populations. In fact, the results supported the ERH, consistent with the fact that only two of the seven predators for the snake are present on the island, being able to predate only on small individuals. The study of parasites in the 5th chapter showed that, despite the higher prevalence on Ibiza, all of the parasites were larval innocuous forms, conversely to what was found in the source population, which harbored a higher number of parasite species and some adult and harmful forms. In addition, competitors of the invasive snake are inexistent on the island. Thus, the ERH is likely explaining the invasion success of the horseshoe whip snake.

Finally, in the light of the results from these studies, we propose in the 6th chapter an upgrade in the IUCN Red List category of the lizard from Near Threatened to Endangered. In addition, and given that the absence of natural enemies is behind the snake's invasive success, we propose some management proposals, such as controlling the entrance of olive trees and reinforcing the existing trapping campaigns, in order to artificially act as the missing predators for the snake and protect the lizard.

Resumen amplio

Introducción y objetivos

Con la globalización, el transporte de personas y mercancías alrededor del mundo ha aumentado enormemente (Hulme, 2009), y uno de los impactos derivados de este incremento en el transporte es la mayor introducción de organismos vivos fuera de sus rangos nativos, ya sea intencionadamente o no (Kraus, 2009). Muchas de estas introducciones acaban derivando en invasiones biológicas, cuando el organismo introducido es capaz de establecerse en el nuevo hábitat y además, causa un impacto sobre la biodiversidad y/o sobre la economía (Lockwood et al., 2013). De hecho, las invasiones biológicas son, actualmente, una de las mayores causas de pérdida de biodiversidad (Simberloff et al., 2013), perpetuando la tendencia hacia la homogeneización de las comunidades de organismos asociada a la globalización en un proceso llamado *McDonaldización de la biosfera* (Alonso y Castro-Díez, 2015). Las islas son especialmente vulnerables a las invasiones, ya que suelen hospedar un mayor número de endemismos (Kier et al., 2009) que han evolucionado en condiciones únicas, y a menudo en ausencia de depredadores; consecuentemente, con menos mecanismos de defensa frente a nuevos depredadores (Whittaker y Fernández-Palacios, 2006).

La isla de Ibiza, situada en el Mediterráneo Occidental, se mantuvo libre de serpientes introducidas por el ser humano durante toda su historia, a diferencia del resto de islas mediterráneas, incluidas Mallorca y Menorca, en las que hubo diversas introducciones de ofidios (Silva-Rocha et al., 2018). El único vertebrado terrestre que se ha mantenido en la isla, a pesar de la llegada del ser humano y de las introducciones asociadas, es la lagartija de las Pitiusas (*Podarcis pityusensis*). Este reptil es endémico de Ibiza y Formentera, y cuenta con 23 subespecies que habitan las dos islas principales y 38 de los islotes que las rodean (Salvador, 2015). Además, se ha convertido, con el paso de los años, en el símbolo de las islas Pitiusas (Silva-Rocha et al., 2018).

Sin embargo, en el año 2003 la historia de Ibiza cambió de forma crucial: aparecieron las primeras serpientes, asociadas al transporte de olivos de gran porte para uso ornamental en jardines mediterráneos procedentes del sur de la Península Ibérica. La culebra bastarda (*Malpolon monspessulanus*), que dejó de verse en 2010, la culebra de escalera (*Zamenis scalaris*), que mantiene una población pequeña pero estable en Ibiza (y es la única que se mantiene en Formentera) y la culebra de herradura (*Hemorrhois hippocrepis*), que es la más extendida en Ibiza, fueron las tres especies introducidas (Montes et al., 2015). A partir de 2010, la expansión de *H. hippocrepis* en Ibiza se hizo evidente, observándose en más lugares de la isla, nadando en el mar e incluso en los islotes cercanos. En 2014 y 2015, el Consell Insular d'Eivissa llevó a cabo un proyecto piloto de control de ofidios y a partir de 2016, el Govern de les Illes Balears tomó el relevo y ejecuta campañas de control cada año.

Los objetivos de esta tesis doctoral son, por un lado, estudiar la historia natural de la población invasora de *H. hippocrepis* en Ibiza y su comparación con la de la población fuente, para encontrar las causas de su éxito invasor, así como información útil para la lucha contra ella. Y por otro lado, analizar cuantitativamente los impactos sobre la lagartija endémica *P. pityusensis*, para proteger sus poblaciones. Los objetivos concretos son los siguientes:

- Estudiar la **ecología trófica** de la población invasora de serpientes, para comprobar si estaba depredando sobre la lagartija endémica: Capítulo 1. Ecología trófica.
- Evaluar la afección de la depredación de la culebra sobre la **distribución y abundancia de la lagartija** y la rapidez con que la población de **culebras se expande**: Capítulo 2. Impactos en las lagartijas nativas.
- Conocer el porqué del éxito invasor de la culebra, a pesar de estar alimentándose de una presa poco energética, con el análisis de la ecología de la reproducción de la culebra y comprobando si se está **reproduciendo más frecuentemente**, si ha extendido la **época de reproducción**, **pone más huevos,** o los **neonatos** tienen una mejor

condición corporal que en la población fuente: Capítulo 3. Ecología de la reproducción.

- Testear la Hipótesis de la Liberación del Enemigo (ERH, por sus siglas en inglés), midiendo la **presión por depredación** soportada por las culebras en ambas poblaciones, ya que la ecología de la reproducción no aportaba respuestas para el éxito invasor: Capítulo 4. Presión por depredación en las culebras invasoras.
- Estudiar y comparar la **presencia de parásitos** en ambas poblaciones del ofidio (la fuente y la invasora) para acabar de comprobar todos los aspectos de la ERH. También analizamos la ERH bajo el punto de vista de los competidores: Capítulo 5. Parasitismo.
- Evaluar el **riesgo de extinción** de la lagartija bajo el protocolo de la Lista Roja de la UICN y la propuesta de **medidas de conservación** adecuadas a la vista de los dramáticos resultados obtenidos: Capítulo 6. Medidas de conservación.

Ecología trófica

Las culebras estudiadas procedían de campañas de erradicación de las administraciones (detalles en Montes et al., 2015), y de ejemplares atropellados, y preservados en etanol en la colección de la Universidad de Granada. En 293 ejemplares (142 machos, 118 hembras y 33 inmaduros), medimos la longitud hocico-cloaca (LHC) (± 1 mm), la biomasa (± 0.1 g), comprobamos el contenido del aparato digestivo mediante una incisión medio-ventral, e identificamos las presas hasta el nivel de especie. Determinamos algunos micromamíferos por los restos de pelo siguiendo a Teerink (2004) bajo aumento (×400). Sólo medimos y pesamos las presas en buen estado. Comparamos la dieta con la del resto de poblaciones usando los datos de Pleguezuelos y Moreno (1990) (Sur de España), Pleguezuelos y Fahd (2004) (norte de Marruecos), Luiselli et al. (2012) (sur de Cerdeña) y Cattaneo (2015) (Pantelaria). Para el análisis estadístico, clasificamos las presas en cuatro tipos: (i) lagartijas, (ii) pequeños micromamíferos, (iii) grandes micromamíferos y (iv) otras presas. Estimamos la condición corporal mediante la medida de los cuerpos grasos en cinco categorías visuales (Pleguezuelos y Feriche, 1999).

Tan sólo siete especies aparecieron en la dieta de *H. hippocrepis*, 63.4 % eran reptiles (55.4 % *P. pityusensis*, 6.7 % *Tarentola mauritanica*, 1.3 % *Hemidactylus turcicus*), 35.1 % eran micromamíferos (16.2 % *Apodemus sylvaticus*, 10.8 % *Mus* sp., 2.7 % *Rattus rattus*, 5.4 % micromamíferos no identificados), y una presa era un ave (1.3 % pollos de *Turdus merula*). Al considerar la masa de las presas, la importancia de los mamíferos más aves se incrementaba (74.4 %). Encontramos una diferencia geográfica en la dieta, había mayor cantidad de lagartijas en la dieta de la población de Ibiza que en la de las demás poblaciones de *H. hippocrepis*, a excepción de la de Pantelaria (donde la lagartija es una especie introducida). Además, la diversidad trófica de la población de Ibiza fue la más baja, a pesar del mayor tamaño de muestra. El tamaño relativo de las presas era similar al del sur de la península, pero la pequeña *P. pityusensis* formaba parte de la dieta de ejemplares de todos los tamaños. La frecuencia de alimentación de las culebras de Ibiza resultó ser la más baja entre todas las poblaciones. Finalmente, el tamaño corporal en LHC y en peso era superior al de la población fuente, así como la condición corporal.

El análisis de la dieta de la serpiente confirmó una elevada tasa de depredación sobre la lagartija endémica *P. pityusensis*, un resultado muy preocupante para la integridad de sus poblaciones, dado que su especie hermana, *P. lilfordi*, desapareció de las dos islas Baleares más grandes (Mallorca y Menorca) por depredación de otras introduciones (Bover et al., 2008). Que los individuos de *H. hippocrepis* de Ibiza fueran más grandes que los de la población fuente, fue una manifestación de plasticidad fenotípica sorprendentemente rápida, pues fue observada en menos de 13 años desde el inicio de la invasión. El nivel de cuerpos grasos también fue mayor para la población invasora, a pesar de encontrar una baja frecuencia de presas.

Los resultados encontrados son, por lo tanto, confusos: encontramos culebras más grandes y con mejor condición corporal en la isla, pero con frecuencia de alimentación baja y con su principal presa, pequeña en biomasa. Este resultado nos empujó a seguir buscando la causa del éxito invasor de la culebra en otros factores, como la ecología de la reproducción (capítulos 3, 4 y 5), y a comprobar si las lagartijas, a pesar de estar siendo depredadas, estaban siendo capaces de mantener sus poblaciones, o bien si estaban sufriendo a nivel poblacional o de rango.

Impactos en las lagartijas nativas

Para representar la expansión anual de *H. hippocrepis* en Ibiza, mapeamos 1,362 registros georreferenciados de avistamientos de 2010 a 2018, obtenidos del Servicio de Agentes de Medio Ambiente del Govern de les Illes Balears (Servei d'Agents de Medi Ambient, 2014). Estimamos el área del núcleo de población de culebras creando polígonos que excluían avistamientos aislados, usando un algoritmo estadístico de eliminación de puntos aislados. Calculamos el área acumulada del rango de la culebra anual sumando el área de cada nuevo año a las anteriores (la culebra mantenía el área ocupada en años anteriores), y estimamos la ratio de expansión haciendo una regresión de estas áreas acumuladas contra los años durante el periodo estudiado.

También evaluamos la abundancia de lagartijas en áreas con y sin serpientes, dividiendo Ibiza en dos áreas, la que tiene poblaciones establecidas (aproximadamente la mitad nordeste) y la que no tiene culebras (aproximadamente la mitad suroeste). Asimismo, tuvimos en cuenta los resultados de las campañas anuales de erradicación realizadas por el Govern de les Illes Balears, (COFIB, 2017), situando nuestros transectos en áreas con serpientes cerca de aquellas trampas con el mayor rendimiento de captura. Usamos transectos lineales para censar las lagartijas (Lovich et al., 2012), 15 en zonas con serpientes y 14 en zonas sin serpientes. Todos ellos tenían una longitud de 500 m y transcurrían por paisajes naturales o escasamente antropizados. Repetimos cada uno de ellos tres veces (réplicas) a una velocidad de 2 km/h, buscando lagartijas activamente, durante los meses de junio y julio, evitando las horas centrales del día y variando las horas de cada repetición aleatoriamente. Los transectos estaban separados un mínimo de 750 m entre ellos para evitar doble conteo de individuos. Asimismo, también evaluamos la estructura del hábitat cada 20 m en cada transecto, alternando entre lado derecho e izquierdo, y la clasificamos en cuatro tipos: árbol, arbusto, tierra o roca. Además, visitamos una muestra de nueve islotes de entre los que rodean a la isla de Ibiza, en función de las corrientes marinas predominantes, los avistamientos de culebras nadando y su protección ambiental: S'Espartar, Es Bosc, Murada, En Calders, Canaret, Sa Mesquida, S'Ora, Grossa y Rodona. Censamos las lagartijas avistadas en bandas entre 0-2 m desde la línea de progresión durante lapsos de 30 minutos, a una velocidad de 2 km/h (abarcando un área de 0,4 ha).

Tratamos los números de lagartijas en cada censo como la variable respuesta, y utilizamos GLMMs para determinar el efecto de la presencia de serpientes, las cuatro variables de estructura del hábitat, y la interacción de las variables presencia de serpientes * presencia de árboles, en la abundancia de lagartijas. Tratamos la presencia de serpientes, las variables de la estructura del hábitat y la interacción de las dos variables, como efecto fijo, y los tres censos en cada transecto (1 – 3) como efecto aleatorio. Por tanto, utilizamos cada repetición como la unidad de muestreo (29 transectos * 3 repeticiones = 87 unidades de muestreo). Modelizamos la abundancia de lagartijas con una distribución binomial negativa *zero inflated* y una función *log-link*, usando la función lmer implementada en el paquete R lme4 (Bates et al., 2015). Utilizamos un enfoque de promediado de modelos acorde a los valores de AIC, identificando los modelos con ΔAIC <2 como los mejores (Burnham y Anderson, 2002).

Los avistamientos de *H. hippocrepis* mostraron un incremento en número y distribución durante el período 2010-2018, llegando al 49,31 % del área de la isla y al 43,04 % del total del rango de la lagartija en diciembre de 2018. La distribución de las culebras en Ibiza ha crecido drásticamente de forma lineal, y, de no cambiar las circunstancias, bajo nuestro modelo de regresión se prevé que ocupen toda la isla para 2027–2028. En los 29 transectos, registramos 188 ejemplares de *P. pityusensis*, siendo la media de lagartijas 4,36 por censo en zonas sin serpientes, y 0,11 por censo en zonas con serpientes. En los 20 modelos seleccionados en el GLMM, la presencia de serpientes y de árboles eran las variables que mejor explicaban la abundancia de lagartijas entre transectos, disminuyendo la abundancia de *P. pityusensis* hasta el punto de la extinción en presencia de culebras.

Las lagartijas avistadas en los islotes variaron entre 9 y 54 individuos por censo en aquellos islotes que aún mantienen poblaciones. S'Espartar, Es Bosc, Murada, Sa Mesquida y Rodona mostraron elevada densidad de individuos, y En Calders, Canaret y Grossa muy bajas densidades. En S'Ora no se encontraron lagartijas, heces o mudas en ninguna de las tres visitas realizadas (en junio y julio de 2018 y junio de 2019); esta extinción se ha producido en un máximo de 10 meses después del último registro en 2017, coincidiendo con el avistamiento de una culebra nadando a 20 m del islote en abril de 2018. Además, se encontraron dos mudas de culebra en S'Espartar y se avistó una culebra durante nuestra visita a Grossa.

Nuestros resultados dejan claro que la serpiente invasora *H. hippocrepis* está provocando un rápido declive en la distribución y abundancia de la lagartija endémica *P. pityusensis* en Ibiza y sus islotes circundantes, hasta el punto de la extirpación del área invadida. Todos los transectos en zonas con culebras están exentos de lagartijas excepto una de las repeticiones en uno de los transectos (1 de 45). A pesar de la rápida adquisición de respuestas antipredatorias por parte de las lagartijas frente a *H. hippocrepis*, la alta presión por depredación sobre esta presa naíf está llevando a la población del único vertebrado terrestre endémico de Ibiza al colapso. Respecto a los islotes visitados, cabe resaltar que, a pesar de la presencia de al menos una gran serpiente, la población de lagartijas de S'Espartar se mantiene aparentemente saludable (probablemente debido al gran tamaño del islote); el efecto de una culebra en la población de Grossa parece evidente, con la densidad más baja de lagartijas encontrada para cualquiera de los islotes; y por último, la población de S'Ora ha desaparecido, tras vivir aislada desde el Último Máximo Glacial (~26,500–19,000 años BP; Clark et al. 2009); sugerimos que la extinción de la única población de *P. pityusensis hortae* (Salvador, 2015) fue provocada por la presencia de serpientes. Los resultados encontrados confirman la necesidad de seguir ahondando en las causas de éxito de la población de culebra invasora que puedan dar pistas sobre la mejor forma de plantear su control y erradicación (capítulos 3, 4 y 5), de re-evaluar el estado de conservación de la lagartija, y la puesta en marcha de medidas de conservación inaplazables (capítulo 6).

Ecología de la reproducción

Los individuos para este estudio fueron obtenidos, procesados y examinados con el mismo protocolodescrito en el apartado de ecología trófica. Se examinaron un total de 545 especímenes (224 hembras, 261 machos y 60 inmaduros). Comparamos los datos de la ecología de la reproducción en la población invasora del ofidio con los obtenidos por Pleguezuelos y Feriche (1999), que complementamos con otros ejemplares de la colección de la Universidad de Granada del sur de la Península Ibérica (en total 477 culebras, 167 hembras, 182 machos y 128 inmaduros). En cada ejemplar medimos las siguientes variables: sexo (macho, hembra o indeterminado), en hembras número de folículos ováricos o huevos oviductales en cada lado, el mayor diámetro para cada folículo o huevo (± 0,1mm) y la presencia de oviductos con cámaras de incubación vacías pero visibles; en machos, los ejes sagital, transversal y longitudinal del testículo derecho (±0,1mm). Calculamos el volumen testicular usando la fórmula para un elipsoide aplanado (Mayhew, 1963).

Estimamos gráficamente el tamaño de adquisición de madurez sexual: en hembras ploteando la longitud del folículo o huevo más largo contra el tamaño corporal de la madre (LHC), o bien por la presencia de huevos oviductales u oviductos laxos; en machos ploteando el volumen testicular relativo (RTV) (Seigel y Ford, 1987) contra el tamaño corporal, y por la presencia del conducto deferente engrosado. Dedujimos el ciclo reproductivo ploteando la longitud del folículo o huevo mayor y del RTV, respectivamente en hembras y machos, contra los días del año, para individuos sexualmente maduros. Estas tres deducciones se basan en el brusco aumento del diámetro de los folículos o del RTV, lo cual indica el inicio de la actividad reproductiva (madurez sexual o período reproductor). También registramos los niveles de cuerpos grasos de la forma ya descrita en el apartado de ecología trófica (capítulo 1). Para los neonatos, estimamos el índice de condición corporal (BCI) (como los residuales del log de la masa corporal [g] sobre el log de la longitud corporal [SVL en mm]; Whittier y Crews, 1990), considerando aquellos capturados dentro de los 15 días anteriores y posteriores a la fecha media de eclosión (10 de septiembre), que mantenían una cicatriz vitelogénica fresca y sin contenido en el aparato digestivo.

Las hembras de Ibiza adquieren la madurez sexual a partir de los 628 mm LHC, al 48 % de la longitud máxima, mientras que en la población fuente, la madurez sexual se produce al 63 % (665 mm LHC). Los machos de las dos poblaciones son maduros sexualmente a la misma LHC (500 mm), lo que supone un 33 % en Ibiza debido a su mayor tamaño en la isla (mientras que en la población fuente es un 39 %). Encontramos hembras con folículos muy grandes (≥ 14 mm) o huevos oviductales desde finales de abril hasta finales de Julio, y con huevos oviductales totalmente desarrollados (≥ 38 mm) y marcas de oviposición reciente desde finales de mayo hasta finales de julio, por lo que dedujimos que la puesta ocurre durante junio y julio. La recrudescencia testicular de los machos maduros empezaba a mitad de marzo, con el mayor pico de RTV en junio, disminuyendo en julio. Algunos individuos mostraban una pequeña recrudescencia testicular entre el final de septiembre y octubre, sugiriendo un período de espermatogénesis secundaria.

Tan sólo el 50 % de las hembras se reproducen cada año, muy por debajo de lo observado para las hembras de la población fuente (82,6 %), encajando en una reproducción bienal. El 59.3 % de los machos maduros se reproducen cada año en Ibiza (frente a un 70 % en la Península Ibérica), sin diferencias significativas entre ambas poblaciones. Los cuerpos grasos se mantienen homogéneamente elevados a lo largo del año para las hembras adultas no reproductoras, y disminuyen durante el verano (consistente con el coste reproductivo), mientras que para los machos los niveles son heterogéneos a lo largo del año. Registramos el mayor tamaño de puesta para la especie en Ibiza (13 huevos), pero la media (6,9) no difiere de la población fuente (6,5). Por último, no encontramos diferencias significativas en la LHC, en la masa corporal ni en el BCI entre los neonatos de Ibiza y los ibéricos.

La población invasora muestra algunas diferencias en los rasgos reproductivos respecto a la población fuente: la madurez sexual es alcanzada a una longitud menor en las hembras, el período reproductor es más amplio y los cuerpos grasos son más altos en ambos sexos. Estos datos pueden hacer pensar que, gracias a la gran plasticidad fenotípica que *H. hippocrepis* ya ha demostrado, existe una ventaja derivada de la ecología de la reproducción que puede facilitar la invasión de Ibiza. Sin embargo, aquellos rasgos vitales para el *fitness* de la población sugieren justo lo contrario: la frecuencia de reproducción en hembras es menor, y no hay diferencias en el tamaño de adquisición de madurez en machos, el tamaño de puesta, ni el tamaño o condición corporal de neonatos. Estos resultados resaltan la necesidad de seguir buscando las causas de la invasión, quizás en factores extrínsecos, tales como la ausencia de enemigos naturales (ERH).

Presión por depredación en las serpientes invasoras

La Hipótesis de la Liberación del Enemigo (ERH) predice que una especie introducida en un nuevo ambiente encontrará menos enemigos naturales de los que encuentra en su área fuente, tales como depredadores, competidores y parásitos (Blumenthal, 2006; Lockwood et al., 2013). Tras los resultados de los capítulos anteriores, esta hipótesis ha cobrado más relevancia al intentar comprender las causas del éxito que *H. hippocrepis* está teniendo en Ibiza.

La presión por depredación en las serpientes es difícil de cuantificar, requiriendo de largos estudios de campo sobre la dinámica poblacional (Parker y Plummer, 1987). También puede ser estudiada por la dieta de sus depredadores, pero es una tarea ardua debido a la baja frecuencia con la que las serpientes aparecen en su dieta, especialmente en depredadores generalistas (Greene, 1997). Alternativamente, se puede evaluar por la ratio de heridas corporales causadas por depredadores (Pianka, 1970). La culebra de herradura tiene la habilidad de moverse y rotar longitudinalmente de forma vigorosa cuando es sujetada por la cola, causando su rotura, como otros ofidios (Savage y Slowinski, 1996; Marco, 2002). En otra serpiente mediterránea, *Natrix maura*, se demostró cómo la ratio de colas rotas era una función de la variación en la riqueza de depredadores del ambiente, un *proxy* de la presión por depredación, y varios autores interpretan el daño corporal en poblaciones naturales como prueba indirecta de la presión por depredación, especialmente en reptiles (Vidal-García et al., 2011). Para este estudio, medimos la tasa de colas rotas en la población invasora de *H. hippocrepis* en la isla de Ibiza.

La muestra para este estudio tiene el mismo origen que el descrito para los apartados de ecología trófica y de la reproducción, y se siguió el mismo protocolo. Examinamos 490 especímenes (233 machos, 199 hembras y 58 indeterminados), y registramos la LHC, el sexo y la integridad de la cola (rota o no), excluyendo aquellos ejemplares con colas recién rotas, y aquellos a los que únicamente les faltaba la escama apical (ya que también puede romperse al mudar la piel [Harkewiz, 2002]). La comparación se hizo con los datos de Pleguezuelos et al., (2018). Debido a que la frecuencia de la rotura de la cola varía ontogénicamente (Pleguezuelos et al., 2010), dividimos la población en 10 clases de LHC con iguales *n* y ajustamos a la mejor función, para evaluar la relación entre el tamaño corporal de las culebras y la frecuencia de colas rotas.

La tasa de colas rotas de la población invasora era significativamente menor que la población fuente, tanto considerando la totalidad de la población como por sexos. Al dividir la población en 10 clases por tamaño, la frecuencia de colas rotas se incrementó con el tamaño corporal ajustándose a una función cuadrática (mostrando colas rotas un 12,4 % de los individuos más largos, mientras que los 9 deciles inferiores mostraban un 3,85 %). Aun así, la ratio de colas rotas de las serpientes más grandes era considerablemente menor al mismo grupo de la población fuente.

La menor tasa de colas rotas en la población de Ibiza comparada con la población de la Península Ibérica sugiere una menor presión por depredación sobre la población invasora (Burghardt y Placyk, 2005; Vidal-García et al., 2011). En la población fuente, *H. hippocrepis* es depredada por al menos tres reptiles, tres aves de presa diurnas y un mamífero (Pleguezuelos y Feriche, 2014), mientras que en Ibiza, tan sólo hay dos depredadores potenciales de serpientes, y su habilidad para cazarlas está limitada a individuos pequeños y medianos.Por lo tanto, la ERH se cumple para los depredadores de la población invasora, tanto por el menor número de especies, como empíricamente, por la menor tasa de colas rotas, lo cual es cierto para la totalidad de la población y para los diferentes sexos o clases de longitud corporal por separado. En el siguiente capítulo (5), se analizan los otros dos enemigos de los organismos invasores (competidores y parásitos).

Competidores

Considerando esas pocas especies (filogenéticamente relacionadas o no) que depredan sobre las dos presas principales (lagartijas y micromamíferos) de *H. hippocrepis* en la isla de Ibiza, hay que tener en cuenta las siguientes, como posibles competidores: la otra serpiente introducida (*Z. scalaris*), la gineta (*Genetta genetta*), la lechuza (*Tyto alba*) y los gatos cimarrones (*Felis silvestris*). *Zamenis scalaris*, está demasiado localizada y es demasiado escasa como para ser considerada un competidor para *H. hippocrepis* (Silva-Rocha et al., 2018). La dieta de *G. genetta* y de *T. alba* se superpone ligeramente con la de *H. hippocrepis* en Ibiza (Clevenger, 1995; Sommer et al., 2005), pero ambas especies son nocturnas y la culebra es diurna, por lo que la competencia trófica es improbable. Además, ambas especies están en declive en Ibiza (Sommer et al., 2005; Gaubert et al., 2015). Por último, *F. silvestris* se alimenta principalmente de la segunda presa más importante de la serpiente (micromamíferos) (Bonnaud et al, 2011), pero las densidades más altas en la isla de Ibiza no se superponen con la distribución de la serpiente (capítulo 2). Por lo tanto, mientras que las serpientes tienen docenas de potenciales competidores tróficos en el área fuente (Salvador, 2014), tan sólo una puede actuar como competidor parcial en la isla. En conclusión, la ERH se cumple también para los competidores.

Parasitismo

Las muestras examinadas provienen del mismo origen y siguieron el mismo protocolo descrito en los apartados anteriores (capítulos 1, 3 y 4). Examinamos dos muestras de 30 ejemplares cada una, formadas por 10 individuos obtenidos antes de la hibernación (octubre y noviembre), 10 obtenidos inmediatamente después de la hibernación (de febrero a abril) y 10 de la mitad del verano (julio y agosto), para maximizar las probabilidades de encontrar parásitos y diferenciar los períodos del año críticos para los ciclos parasitarios. Dentro de cada sub-grupo, la mitad eran hembras y la mitad machos, para evitar sesgo por sexo, y todos los especímenes medían entre 560 – 930 mm LHC, por lo que únicamente se consideraron adultos y no excesivamente grandes en tamaño corporal. Tras la incisión ventral, extrajimos todo el tubo digestivo y examinamos la cara interna y externa bajo una lupa (x 10, rango de aumento 6,5 – 40). Sumergimos los órganos por separado en agua destilada para evitar que se secaran, y aislamos los parásitos y los preparamos para observación. Identificamos y contamos todos los helmintos; fijamos los acantocéfalos en Bouin acuoso y los conservamos en etanol al 70 %. Procesamos los helmintos siguiendo técnicas estándar (Pantin, 1968). Tintamos los acantocéfalos y los nematodos con carmín aluminio, los deshidratamos y los fijamos en bálsamo de Canadá.

No encontramos diferencias significativas en la prevalencia de parásitos entre períodos del año ni entre sexos. La comparación de la carga parasitaria tampoco era significativa entre períodos del año para ninguna de las poblaciones, ni juntando ambas poblaciones; por tanto, comparamos ambas poblaciones juntando los tres períodos del año y ambos sexos. La prevalencia de parásitos era significativamente mayor en la población invasora (66,7 %) que en la población fuente (36,7 %), y encontramos 438 parásitos en las serpientes de Ibiza, frente a 309 en las de la Península Ibérica, incluyendo un acantocéfalo (*Centrorhynchus* sp.) y un cestodo (*Diplopylidium acanthotethra*) en ambas poblaciones, más un ascaridoidea (Ascaridoidea gen. sp.) y un segundo cestodo (*Spirometra* sp.) en la Península Ibérica. La diferencia en la carga parasitaria media no era significativa, y todos los parásitos estaban presentes en su forma larvaria, excepto los cuatro ascaridoidea.

Este estudio, que por primera vez ofrece datos sobre los parásitos internos de *H. hippocrepis*, muestra que la población invasora presenta más individuos con parásitos que la población fuente, apoyando en principio la hipótesis nula. Sin embargo, la totalidad de los parásitos de la población invasora estaban presentes como formas larvarias, siendo el papel de las culebras el de meros hospedadores paraténicos. De hecho, el efecto de los parásitos en el *fitness* de la población invasora de ofidios es imperceptible, a juzgar por el gigantismo y su excelente condición corporal. Además, el hecho de que los dos únicos depredadores sean capaces de depredar culebras más bien pequeñas (un estadio ontogénico habitualmente menos parasitado que el adulto [Esch et al., 1990]), puede eventualmente suponer una dificultad para que los parásitos completen su ciclo vital, algo que actualmente ocurre gracias a *P. pityusensis*, y que podría dejar de ocurrir si ésta se extinguiera. Por otro lado, la riqueza de especies de parásitos es mayor en la Península Ibérica (cuatro especies, incluyendo formas adultas y dañinas) que en Ibiza (dos especies, sólo larvas inocuas). Por todo lo anterior, la mayor prevalencia y carga parasitaria tiene poco significado biológico, lo que nos lleva al cumplimiento de la ERH *de facto*.

Hay que tener en cuenta, asimismo, el riesgo asociado a que sigan entrando ejemplares de *H. hippocrepis* en la isla de Ibiza, por la posibilidad de la introducción de una nueva especie de parásito que pueda afectar a la lagartija, filogenéticamente relacionada con la especie invasora, con consecuencias impredecibles (Foster, 2019; Verneau et al., 2011).

A la vista de los resultados de este estudio y de los anteriores, concluimos que la ERH se cumple para todos los enemigos de *H. hippocrepis* en la isla de Ibiza, por lo que recomendamos que los gestores se metan en el papel de enemigos, actuando como depredadores mediante el trampeo (capítulo 6).

Medidas de conservación

Aplicamos la metodología estándar de evaluación del riesgo a la extinción en el proceso de las listas rojas (IUCN, 2012) para actualizar el estado de *P. pityusensis*, y utilizamos los criterios de Blackburn et al. (2014) y IUCN (2019) para evaluar el impacto de la serpiente invasora. Estos hallazgos nos llevaron a proponer varias acciones de conservación para asegurar el futuro de la lagartija endémica.

Actualmente, la lagartija *P. pityusensis* está considerada como Casi Amenazada (NT, por sus siglas en inglés) en la Lista Roja de Especies Amenazadas de la IUCN (Pérez-Mellado y Martínez-Solano, 2009). Sin embargo, esta evaluación se realizó en 2008, antes de que *H. hippocrepis* se expandiera por la isla de Ibiza. Extrapolando de la tasa de pérdida de rango de la lagartija (capítulo 2), se predecía que ésta hubiera perdido más del 50 % de su rango global al final de 2020, un período de 17 años desde la introducción de las culebras, pero tan solo de diez años desde su dispersión en la isla (ver capítulo 2). Por lo tanto, *P. pityusensis* debería ser clasificada como globalmente En Peligro, EN (por sus siglas en inglés) según el criterio A4 y los subcriterios (bce), ya que la causa de la reducción de la población continúa y, de hecho, se expande.

Respecto a la Clasificación del impacto Ambiental para Taxones Alóctonos de la IUCN (EICAT, por sus siglas en inglés), reconocemos a *H. hippocrepis* como productora de un Impacto Masivo (MV), debido a que la extinción local de poblaciones nativas se ha extendido, incluyendo la subespecie endémica del islote de S'Ora, un impacto dañino e irreversible (IUCN, 2019).

No puede ignorarse el hecho de que la lagartija endémica ha sido virtualmente extirpada de aproximadamente la mitad de su rango en menos de una década (capítulo 2); esta velocidad exige que se emprendan actuaciones de conservación de forma inmediata para salvarla de la extinción. Sugerimos, por lo tanto, 6 medidas necesarias si es que existe alguna esperanza de conservar la especie:

i. Establecer colonias de *P. pityusensis* en cautividad para asegurar la perdurabilidad de la especie.
ii. Controlar la vía de entrada de *H. hippocrepis*, mediante la restricción en el transporte de olivos a los meses de primavera y guardando una cuarentena en un recinto cerrado con trampas.
iii. Reforzar las campañas de erradicación existentes, con un mayor número de trampas.
iv. Desarrollar un protocolo de respuesta rápida para nuevos avistamientos de serpientes en zonas aún no invadidas por ellas.

v. Promover la investigación científica para hacer lo más eficientes posible las acciones de gestión.
vi. Desarrollar programas de educación ambiental.

Conclusiones

En esta tesis doctoral demuestro cómo la culebra invasora *H. hippocrepis* está depredando sobre la lagartija endémica *P. pityusensis*, el único vertebrado terrestre nativo de la isla de Ibiza, y está acabando con su población velozmente, siendo la causa del éxito invasor del ofidio la ausencia de enemigos naturales en la isla. Las conclusiones principales de este estudio son las siguientes:

1. Los ejemplares de culebra *H. hippocrepis* son más grandes y tienen mejor condición corporal en la isla de Ibiza que en la población fuente.
2. La culebra invasora *H. hippocrepis* está depredando sobre lagartijas (la lagartija endémica de Ibiza, *P. pityusensis*) con una tasa mucho mayor que en la población fuente, probablemente debido a la ingenuidad de esta lagartija.
3. En aquellas zonas en las que la culebra es abundante, la lagartija es extirpada.
4. La serpiente invasora ha ocupado ya la mitad de la isla y estimamos que ocupe toda susuperficie antes de 2030.
5. La serpiente invasora ya ha llegado a algunos de los islotes, con efectos devastadores sobre las poblaciones de lagartijas, y es cuestión de tiempo que llegue a más islotes y a Formentera.
6. La ecología de la reproducción de *H. hippocrepis* no explica el éxito invasor de la culebra en la isla de Ibiza, mostrando rasgos reproductivos lentos.
7. El éxito invasor de *H. hippocrepis* en Ibiza es explicado por la ausencia de enemigos naturales, tanto de depredadores, como de competidores y parásitos.
8. Es urgente cambiar la clasificación del riesgo a la extinción de *P. pityusensis* a En Peligro (EN) en la Lista Roja de Especies Amenazadas de la IUCN.

9. Es urgente emprender medidas de conservación que garanticen la supervivencia de *P. pityusensis*, entre ellas, detener la entrada de culebras a la isla y que los gestores actúen como depredadores de *H. hippocrepis* mediante el trampeo.

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Introduction

A little bit of history

The Balearic Islands are located in the Western Mediterranean Sea, and belong to Spain. The archipelago consists of four big islands, Mallorca and Menorca (called the Gimnesic Islands) and Ibiza and Formentera (called the Pityusic Islands), as well as numerous islets surrounding them. Humans have introduced several animal species to all of them, including a high number of reptiles (Silva-Rocha et al., 2018). As it happened frequently on Mediterranean islands, snakes were historically introduced to the Balearic Islands, with the peculiarity that the Pityusic Islands remained snake-free until the present times (Pinya and Carretero, 2011), when 3 snakes were introduced in this archipelago as well, one of them successfully.

In this PhD dissertation, I study the natural history of a snake (*Hemorrhois hippocrepis*) that has recently invaded the island of Ibiza, dramatically threatening the only endemic terrestrial vertebrate on this island, the Ibiza wall lizard (*Podarcis pityusensis*).

Globalization and biological invasions

With globalization, transportation of people and goods all around our planet has increased enormously (Hulme, 2009). This fact has expedited a high level of comfort –at least for rich countries–, allowing anyone to have nearly anything, independent of where it comes from, or to travel anywhere, in just a few hours. This immediacy has brought some associated impacts, like a growth in greenhouse effect gases emission, due to a massive transportation based on carbon fuels (Hansen et al., 1981). Another less evident consequence is an increasing trend towards a homogenization of everything: as an example, some types of food can be found everywhere, there is a well-known fast food restaurant that can be found in any country, or a Parisian food boutique whose motto is “everything, from anywhere, anytime”; artisan and local business are disappearing and being substituted by famous stores that can be found anywhere; in summary, the genuine and the unique is disappearing in favor of the globally-known items, associated to a dehumanization, in something called the *McDonaldization of society* (Ritzer, 1992).

Going back to global change, global warming is one of three main impacts on our planet. Habitat alteration and loss is the second one (Mantyka-Pringle et al., 2012), and there is one more impact caused by the unstoppable movements of goods and people across the world, which is the introduction of organisms to new environments with the highest rate in the history of humanity (Kraus, 2009). Intentional introduction takes place when the organisms are valued for some reason (as pets, as food, for horticulture or biocontrol of pests), whereas unintentional occurs when organisms travel as inadvertent stowaways in cargo or vehicles. Due to the variety of terms used related to biological invasions, from now on, I will use the broadly accepted terminology from Lockwood (2013), more detailed in *The invasion process* subsection.

Once a population establishes and the introduced species becomes an invader, it breaks the ecosystem’s former equilibrium, and the conditions at which the invaded ecosystem achieves a stationary state again are often adverse for one or more of the native species and usually for humans. Ecological impacts include genetic effects (like hybridization or introgression) (Krueger and May, 1991), individual impacts in morphology, behavior or demographic rates of natives (Parker et al., 1999), population impacts due to competition, predation or physic inhibition of the growth or reproduction of native species (Parker et al., 1999), changes in community composition which can ultimately lead to mass extinctions, and alteration of ecosystem processes, especially capturing resources where native species cannot, changing resource availability. Under a bigger scope, biological invasions cause landscape, regional, and global impacts, and economic loss (Perrings et al., 2000; Lockwood et al., 2013), currently being one of the most serious threats to biodiversity (Simberloff et al., 2013; Bellard et al., 2016; Courchamp et al., 2017).

Biological invasions are, therefore, perpetuating the trend towards homogenization mentioned before, but in this case, it is a homogenization of living organisms: more generalist and adaptable species are thriving, whereas vulnerable and rare endemics are disappearing, being substituted by the invaders, in a process called *biotic homogenization* (McKinney and Lockwood, 1999; Olden et al., 2004). Following the analogy with the fast-food restaurants, some authors have referred to this part of the global change as a *McDonaldization of the biosphere* (Alonso and Castro-Díez, 2015).

The invasion process

I am describing here the terms and process of biological invasions following Lockwood et al. (2013) (see Fig. 1):

- **Transport:** human-assisted movement of a species to a different geographical area, either within the range of the species (**translocation**) or out of the range of the species (see *introduction*).
- **Introduction:** human-assisted movement of a species from its native range to a different geographical area, beyond physical barriers that the species would not overcome by itself. This new location can be human-imposed confined (captivity or cultivation).
- **Establishment:** the stage at which an introduced species is able to survive and reproduce. If one of these two tasks fails, then it will eventually vanish.
- **Spread:** the ability of an established introduced species to disperse and overcome environmental barriers. This is the stage in which boom and bust cycles can take place.
- **Naturalized species:** a non-native species that has overcome the establishment stage.
- **Invasive species:** a non-native species that causes negative impacts on biodiversity or economy.
- **Alien:** a species that is non-native. It is a synonymous of *exotic*.
- **Native:** a species that naturally belongs to the location where it is found.

For a species to become a successful invader in a novel environment needs to overcome several barriers: it first has to survive transportation and introduction from its geographic origin, then it has to become established, and finally spread across the territory, dispersing and adapting to the new environment. Once it has accomplished the so-called naturalization, if the species causes an ecological or economic impact (or if it spreads aggressively, according to some authors [Daehler, 2001]), then it is considered an invader (Fig. 1). One example that can illustrate this process is the slider turtle (*Trachemys scripta*) introduced to Italy, where only some populations have become invaders, and others have remained just established, depending on the bioclimatic conditions (Ficetola et al., 2009).

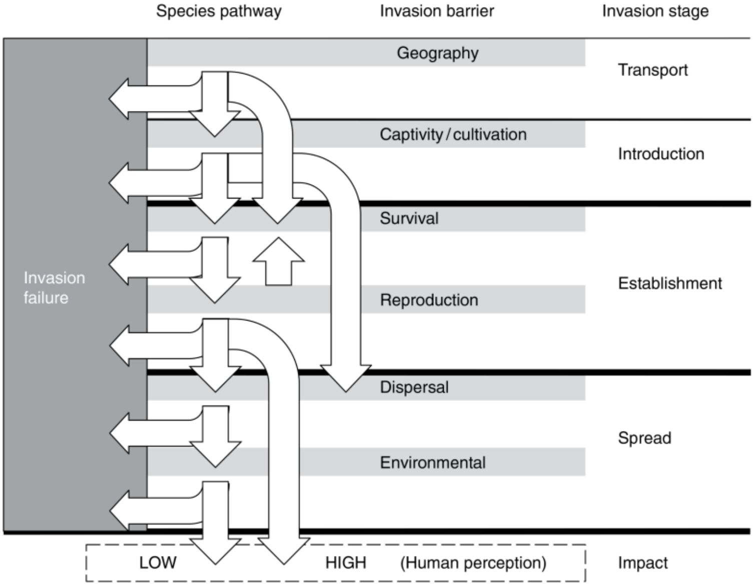

Fig. 1. Edited version of unified framework model by Blackburn et al. (2011), which combines stages, barriers, and species pathways. This version of the unified framework model differs from Blackburn et al. (2011) in that Lockwood et al. explicitly include an impact stage in the invasion process. Reproduced with permission of Wiley, from Lockwood et al. (2013), *Invasion Ecology*. John Wiley & Sons (Order License ID: 1122308-1).

Fighting against invasions and the Enemy Release Hypothesis

I already mentioned that biological invasions are one of the main threats to biodiversity, and the problem posed by an invasive species on the island of Ibiza was the incentive to carry out the study that the reader holds in their hands. Due to their extensive negative effects, fighting against biological invasions is becoming more important each day, and being able to predict and then prevent invasions is the most efficient and economic way to do so (Kraus, 2009). What factors will make a species a good invader is a key question first raised by Drake et al. (1989), encouraging many scientists to quantitatively analyse invader traits, in search for an answer (Lockwood et al., 2013). The problem to that question is that the response is complex: different traits are determinant at different stages of the invasion process, even varying among taxa (Kolar and Lodge, 2001). Jeschke and Strayer (2006) established that propagule pressure (understood as the sum of number of individuals plus release events) and human affiliation (whether the organism lives in close association with humans) were major determinants in vertebrate invaders in Europe and North America from 20 studied factors, but variability in decisive factors among invasion steps was common.

Biotic interactions have been studied as causing facilitation or resistance to invasion: competition with organisms that already occupy the existing niches in the novel environment (Elton, 1958), predation by native organisms and the lack of a necessary mutualist partner act as repellents of newly arrived species. Conversely, the same phenomena can mitigate the effects of an ecological stressor, facilitating the invasion process (Lockwood et al., 2013). For instance, Simberloff et al. (2002) found competitive resistance in Patagonian forests, where invasive conifers where almost inexistent in intact native forests, but very abundant elsewhere; the globally invasive European green crab (*Carcinus maenas*) failed to establish in locations overlapping with the native red rock crab (*Cancer productus*), which predates on the invasive one (Hunt and Yamada, 2003); and non-native plants usually form associations with mycorrhizae and bacteria in the newly invaded environment (Richardson et al., 2000).

One of the theories that aims at explaining invasive species' success is the Enemy Release Hypothesis (ERH); it states that the natural enemies that a species faces on its native range are absent on the invaded range, where its predators, competitors and parasites are missing (Wolfe, 2002; Blumenthal, 2006; Lockwood et al., 2013). Some authors argue that there is not enough evidence supporting a cause-effect relationship between the lack of enemies and invasion success, especially in ecologically complex environments (Roy et al., 2011). Other authors have come to contradictory conclusions depending on the study scale –biogeographical or community level (Colautti et al., 2004). But there are indeed numerous studies supporting the ERH, on invasive plants (Liu and Stiling, 2006; Jeschke et al., 2012) and animals (Prenter et al., 2004; Shwartz et al., 2009; Jeschke et al., 2012).

Invasive organisms that do not find predators in their new environment are more likely to survive (Liu and Stiling, 2006) and the same happens with competitors (Lucero et al., 2020). Lastly, the absence or decrease of parasites has been extensively studied as one of the keys for invasive species' success (Torchin et al., 2003; Dunn et al., 2012).

Introduced reptiles

Reptile introductions have increased exponentially since 1850, with snakes being no exception; their main pathway is pet trade, followed by cargo, and when considering entrance of alien snakes, nursery trade covers the same importance than cargo and pet trade (Kraus, 2009). These three pathways are a logical transportation for reptiles: pet trade for obvious reasons (there has been an increase in the taste for reptiles as pets since the 1950's), and cargo and nursery trade demand the organism to be secretive and able to survive for long periods of time without food or water, which fits perfectly with reptile's characteristics (Kraus, 2009).

The ecological impacts of invasive reptiles include:

i) Removal of native prey species, like the famous case of the brown treesnake (*Boiga irregularis*), that eradicated 13 bird, 1 to 3 bat and six lizard species from the island of Guam (Rodda and Savidge, 2007);
ii) Changes in ecosystem dynamics, like the ones caused by the extirpation of insectivores and frugivores on Guam, which led to an abnormal increase of spiders and a decrease in pollination and seed-dispersal of native plants (thus, leading to changes in floral composition and difficulties in plant regeneration), among others (Savidge, 1987; Fritts and Rodda, 1998; Perry and Morton, 1999; Rogers et al., 2012);
iii) Competition with native species, something that happens, for instance, with several alien lizards able to competitively displace native species (Case et al., 1994);
iv) Vectoring for novel parasites, for example the invasive American red-eared slider (*Trachemys scripta elegans*) has transmitted several parasites to the Mediterranean and European pond turtles (*Mauremys leprosa* and *Emys orbicularis*) (Meyer et al., 2015);
v) Community homogenization, like it is happening in Florida to herpetological communities attending alien introductions (Smith, 2006).

In addition, impacts of invasive reptiles include evolutionary effects (like genetic, morphological, physiological and behavioral changes) and social effects (economic, health, scientific loss) (Kraus, 2009). At the same time, whilst reptile invasions are more common every day, biodiversity and particularly reptiles are declining globally due to habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use and global climate change (Gibbons et al., 2000; Böhm et al., 2013), consistent with the process of biotic homogenization cited above.

About islands and invasions

Amongst geographic sites, islands are special biodiversity spots. Their isolation from mainland –sometimes since their origins –usually leads insular organisms to evolve in unique conditions with singular adaptations; for instance the absence of predators can make some birds lose their ability to fly (McNab, 1994). Accordingly, the consequences of biological invasions are particularly damaging on islands (Jones et al., 2016) due to their usually high endemism rate (Kier et al., 2009), and the few defense mechanisms of the insular organisms (Whittaker & Fernández-Palacios, 2006), two factors that make insular organisms highly vulnerable to newcomers. Furthermore, islands have been identified as invasive species hotspots (Dawson et al., 2017), in which the majority of endemics' extinctions are associated with invasive species (Bellard et al., 2016).

Some of the numerous examples of devastating invasions on islands are the brown treesnake above mentioned, the introduction of predatory mammals to the Mascarenes during the 17th century that caused the extinction of all of their flightless birds (Wood et al., 2017), the introduction of Pacific rats (*Rattus exulanus*) to Polynesian islands causing extinctions of several birds and invertebrates (Steadman, 2006; Hunt, 2007; Liebherr and Porch, 2015), or the predatory rose-wolf snail *Euglandina rosea*, introduced to the Society Islands to control another invasive snail (*Lissachatina fulica*), causing the extinction of 28 tree snail species (Gerlach, 2016). When biological invasions interact synergistically on islands, they usually cause invasional meltdowns, facilitating their spread or multiplying their impacts (Simberloff and Von Holle, 1999). The introduction of birds to Hawai'i that act as seed dispersers for invasive plants exemplifies this phenomenon (Vizentin-Bugoni et al., 2021).

The Balearic Islands are no exception. After being isolated for 5.3 MY from the Iberian Peninsula, the arrival of the Neolithic people was disastrous to the endemic organisms (Alcover and McMinn, 1993). Some of the fauna that the first humans found on the Gimnesic Islands included a dwarf goat (*Myotragus* sp.), a giant dormouse (*Hypnomys* sp.) and a shrew (*Nesiotites* sp.) (Alcover and

Mc Minn, 1993). Fossil records show as well several reptiles: a giant lizard (*Maioricalacerta refelensis*), a skink (*Chalcides* sp.), a glass lizard (*Dopasia* sp.), a giant tortoise, three snakes, and a small lizard, probably an ancestor of the extant Lilfordi's wall lizard (*Podarcis lilfordi*), among others (Bate, 1914; Bailon, 2004; Bailon et al., 2014; Bover et al., 2014). Regarding the smaller Pityusic Islands, 4000 years ago, the first colonizers found a very different faunistic scene, where birds, a dwarf viper (*Vipera latastei ebusitana* that arrived in Ibiza via transmarine dispersal, between 1.31 MY and 30,000 years ago) and a lizard (Ibiza wall lizard, *Podarcis pityusensis*) were the only vertebrates on the islands (Torres-Roig et al., 2020). This singular and scarce biodiversity can only be explained by an abrupt catastrophic event that likely took place about 2.5 MY ago, erasing from the Pityusic islands the giant dormouse, the giant tortoise, a bovid, a dwarf antelope and the other vertebrates that inhabited Ibiza and Formentera (Alcover and McMinn, 1993). One possibility is a volcanic occurrence, which could have taken place on the Columbretes archipelago, located 100 km away from Ibiza, that had volcanic activity until 300,000 years ago (Silva-Rocha et al., 2018).

With the arrival of humans and their associated introductions, soon most of these endemisms became extinct, leaving Mallorca and Menorca with only their Lilfordi's lizard –relegated to the islets surrounding the main islands– and Ibiza and Formentera with their Ibiza wall lizard (Mayol, 2004). The herpetological introductions that took place before 5th Century were two geckos (*Tarentola mauritanica* and *Hemydactilus turcicus*), a toad (*Bufo balearicus*), a tortoise (*Testudo hermanni*), a pond turtle (*Emys orbicularis*), and a snake (*Zamenis scalaris*) (Silva-Rocha et al., 2018). From 5th to 18th Century, two frogs (*Hyla meridionalis* and *Pelophylax perezi*), another tortoise (*Testudo graeca*), two lizards (*Scelaris perspicillata* and *Podarcis sicula*) and two snakes (*Macroprotodon cucullatus* and *Natrix maura*) were introduced to some of the islands. More recently (from 19th Century), another toad (*Alytes obstetricians*), three more pond turtles (*Chrysemys picta*, *Mauremys leprosa* and *Trachemys scripta*), and four lizards (*Chamaleo chameleon*, *Timon lepidus*, *Podarcis pityusensis* and *Psammodromus algirus*) have been introduced as well to some of the islands. Despite the high number of species listed here, only the two geckos and one of the frogs were introduced to Ibiza and Formentera, were the endemic *P. pityusensis* was able to survive and coexist with the new fauna (Silva-Rocha et al., 2018).

Ebusus, terra serpentes fugat

When the first human inhabitants of Ibiza arrived by the end of the third millennium BCE, they found a Polynesian-type fauna: birds, snails, lizards and vipers (the latter being quickly eradicated; Torres-Roig et al., 2020); thus, their dietary options were quite restricted (Alcover and McMinn, 1993), and introduction of animals as a food resource was a matter of survival. Later, the entire island was ruled by the Phoenician newcomers, who worshiped the Canaanite god Bes, represented grabbing a snake with one hand and a knife with the other (Mateo and Ayllón, 2012); it was believed to protect the house and the family from venomous snakes and most of the coins minted on Ibiza during this Punic period showed the image of the snake-killer god (Guirand, 1960; Fernández, 1975; Fig. 2). Consequently, Ibiza became the Bes' Island, its name probably coming from there (Ebusus - Ibiza; Mateo, 2015).

This aversion towards snakes and their absence on the island was adopted as an identity symbol by the Ibizan inhabitants. In contrast, on those Mediterranean locations where snakes were common and therefore considered as beneficial or neutral, their peoples worshiped gods related to snakes (e.g., Aesculapius, Astarté, Isis, Mitra; Fernández, 1975; Velázquez Brieva, 2007). Transport of snakes among those places was something usual and a high number of establishments and some naturalizations took place, some of them lasting until our days in most of the large and medium sized Mediterranean islands (Mateo et al., 2011). In the 2nd century BCE, when Carthage was defeated, the Ibizan population surrendered to the Romans. They were able to keep the Canaanite dialect Punic, and the worship of the god Bes. Later, in the first century CE, when Phoenicians and Romans still coexisted unmixed on Ibiza, two Latin authors wrote about the island and the mysterious lack of snakes. The geographer Pomponius Mela, in his work *De Chorographia* (Mela, around 43 D.A.), stated:

> *(…) (Ebusus) lacks harmful or wild animals, to the point that it does not breed them nor tolerate those brought there. In front of it there is the Colubraria, that comes to my mind because, being very abundant in many malefic genus of snakes, it is completely uninhabitable; however, if someone enters a place previously surrounded by Ebusitan soil, it becomes a pleasant place without danger, because those same snakes that otherwise attack all they find so often, they flee away frightened by the appearance of the dust.*

Thirty years later, Pliny the Elder, naturalist and historian, probably copying the previous author, included a similar reference in his work Naturalis Historia (Plinius the Elder, 77):

> *The soil of Ebusus banishes snakes, that from Colubraria begets them and it is very harmful for everyone, unless one brings with himself Ebusitan soil; …*

Both Latin authors assigned a magical character to the unusual absence of ophidians, as the Pityusic Islands were the largest Mediterranean Islands without snakes. By saying this, they were indirectly suggesting the existence of Ibizan soil trade to the city of Rome, as an element with occulted properties (Salazar de Mendonza, 1770). Obviously, there are no data supporting the magic properties of the Ibizan soil, but if we compare the number of established species on Ibiza and Formentera before 1975 with other Mediterranean Islands, such as Mallorca or Menorca, the Pityusic Islands have suffered much less historical introductions than the rest (Mateo et al., 2011).

Fig. 2. Coins and Bas-relief with god Bes holding the snake and the knife. Clapboard from the Ptolemaic necropolis of Saqqara (3rd century BCE). Source Allard Pierson Museum, Amsterdam. Reproduced with permission of Springer Nature (License number: 5093180599386).

In the meanwhile, the conspicuous Ibizan wall lizard became the symbol of the island (Dappen et al., 2013). Ibizan and Formenteran people are proud of their lizards and their images are present everywhere: on clothes, jewelry, lizard-shaped stickers on the cars, in decorative elements such as lamps, wall figures, mirrors, etc; magazines and pamphlets frequently exhibit the lizard, and several companies use it in their logos. It is used as a tourist attraction too, and any tourist information about the island will have the symbol on it (Silva-Rocha et al., 2018). Maybe because it was the sole terrestrial vertebrate that the first humans found on the Pityusic Islands that was conspicuous and harmless at the same time (Alcover and McMinn, 1993). In a way, the lizard symbolizes the purity of the original Ibiza and Formentera, as well as the harmless and innocuous fauna to humans that every visitor would find there, something worth using as advertising for an idyllic place like the Pityusic Islands (Silva-Rocha et al., 2018).

It was only at the beginning of the 21st century that three snake species were introduced to Ibiza and Formentera. The change in agricultural practices occurred during this period in mainland Spain may have indirectly prepared the ground for such introductions. After Spain became a member of the European Union, in 1986, the more competitive market forced Spanish farmers to transform their traditional agriculture into a mechanized one. Hence, between 1996 and 2005, more than 900,000 olive trees were ripped out ending up as firewood or used for gardening (Fortuny, 2002) in order to gain more agricultural fields. The massive trade of these olive trees between the south of the Iberian Peninsula and the Pityusic Islands, where the Mediterranean garden had became a fad, provoked the first introduction of snakes in these islands. The Montpellier snake (*Malpolon monspessulanus*) was introduced to Ibiza, but it has not been sighted since 2010, and we therefore presume it did not establish and disappeared from the island. The Ladder snake (*Z. scalaris*) has a low capture rate on Ibiza, but is the most abundant snake on Formentera. The Horseshoe whip snake (*Hemorrhois hippocrepis*) was introduced to Ibiza and to Formentera, but seems to have disappeared from the latter, given that not a single specimen was captured since 2016. It is, however, the most widespread on Ibiza (Montes et al., 2015).

Actions and snake control

Eleven years after the first report of snake introduction, the snakes had proliferated and there was an intense social alarm. Hence, during 2014 and 2015, the Ibiza Island Council (island government) carried out a pilot project to control snake populations under the scientific advice and participation of the Spanish Herpetological Society (AHE). This first approach gave useful information about the snake's distribution and the methods that best worked to eradicate the snakes. The main goals of this project consisted of promoting public awareness and testing methods to capture snakes. Pamphlets in three different languages were distributed among the community; informative meetings were held for neighbors, as well as formative sessions for authority agents who had to deal with emergency calls related to snakes. A unified protocol was agreed among all the authority agents (Silva-Rocha et al., 2018).

Several capture methods were tested in 2014 (plywood cover boards, PVC double funnel traps, and box-traps—baited and unbaited), resulting in lab mice baited box-traps giving the best results. Therefore, in the second year of the project, the Ibiza Island Council arranged the manufacturing of wooden box-traps, according to their guidance, with the Arts School (Secondary Level) of Ibiza. A total of 121 snakes were captured in 2015 by 200 box traps (Fig. 3A). Trained dogs were also used and proved quite effective in detecting snakes, but not very practical in the study area, which is covered by hundreds of kilometers of stone fences where the snakes were difficult to catch (Silva-Rocha et al., 2018).

From 2016 to the present day, the Balearic Government has been carrying out yearly campaigns in order to control the snakes' population, using an improved version of the wooden box trap (Fig. 3B), capturing hundreds of snakes each year (COFIB, 2016; 2017; 2018).

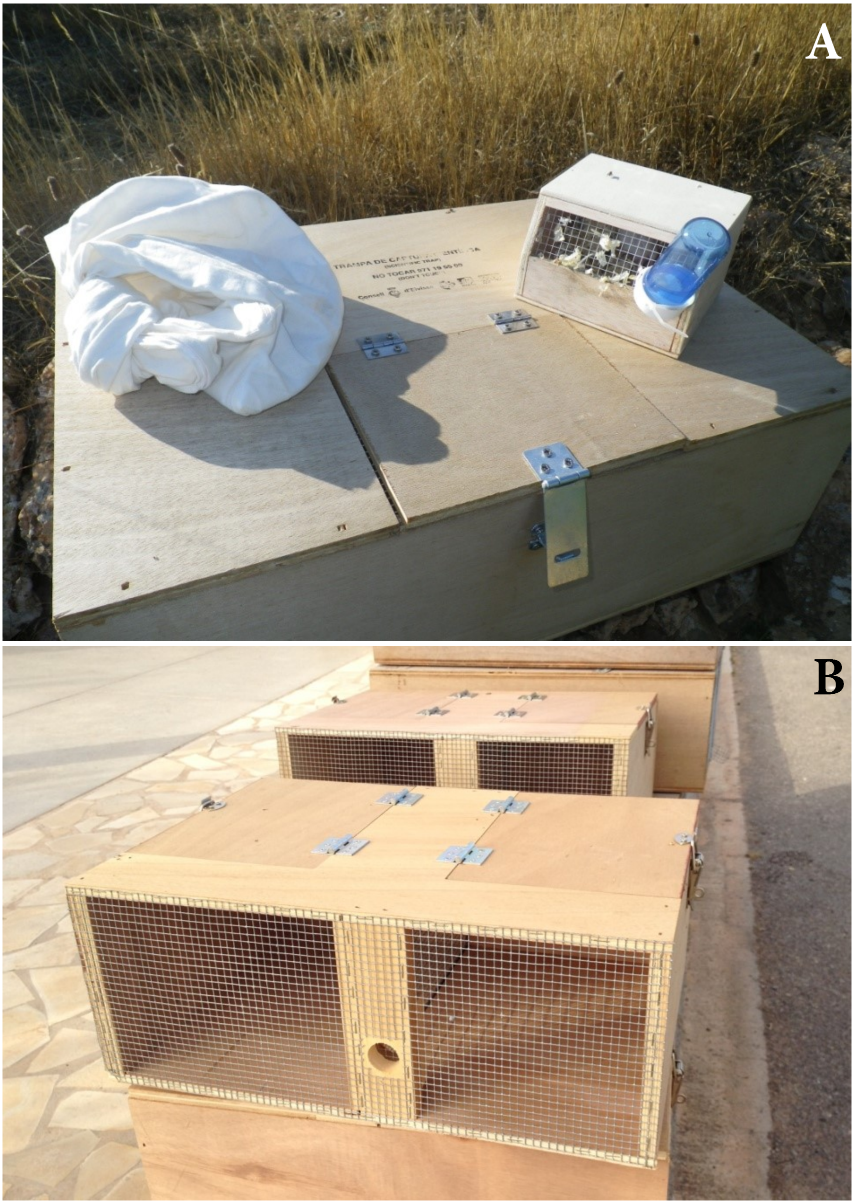

Fig. 3. Wooden box traps for capturing snakes on Ibiza. (A) First version, with an access hatch on the top, a funnel in each side, and the small cage for restraining the lab mouse within the snake trap. (B) Improved version without funnels, a small door instead, and two different compartments, one for the mouse and one for the snakes. Photos by E. Ayllón and E. Montes.

The invasive species: the horseshoe whip snake

The horseshoe whip snake, *H. hippocrepis*, is a thermophylic snake whose origin is Northern Africa, colonizing the Iberian Peninsula 90,000 years ago by transmarine dispersal (rafting or swimming) (Carranza et al., 2006). Today, the native distribution of *H. hippocrepis* comprises the two southernmost thirds of the Iberian Peninsula, and from Morocco to Tunisia (Feriche, 2017); and it has been introduced to the islands of Zembra, Pantelleria, Sardinia, Gran Canaria, Mallorca and Ibiza (Feriche, 2017; Montes et al., in press, annex I). There was also an introduction to Lugo, in the Northern Iberian Peninsula (Cabana, 2017). All recent introductions (all except for the islands of Zembra, Pantelleria and Sardinia, where the introduction pathway is unknown) were linked to olive trees transportation, for nursery trade (Feriche, 2017; Montes et al., in press, annex I). As mentioned before, nursery trade is a common pathway for reptile (and more specifically snake) introductions. On the same island of Ibiza, several examples can be found: Iberian worm lizards (*Blanus cinereus*) were detected in a tree nursery (Mateo and Ayllón, 2012); a *Natrix astreptophora* and two *Anguis fragilis* specimens were found, likely introduced via nursery trade and in an *Erica multiflora* cargo, respectively (Montes and Ruiz, in press; annex II).

It is a slender snake, with a mean total length of 705.7 mm (range: 256 – 1,749 mm, n = 260) a mean snout-vent length of 641.8 mm (range: 235 – 1,292 mm, n = 371) and a mean weight of 116.3 g (range: 4.5 – 675 g, n = 232) in its native range. Its tail is relatively long to the body, representing an average of 22.97 % of its total length, and the variation of this percentage is indicative of sexual dimorphism, with males having relatively longer tails than females. Sexual dimorphism is also present in the number of ventral scales, with females having more than males. It is the only Iberian colubrid with a row of subocular scales between the eyes and the supralabial scales. The color pattern consists of a light background (olive, yellowish or pinkish tone) with dark spots (brown, grey or black), shaped like a horseshoe on the top of the head and like circles or diamonds along the body. Ventral scales are often orange but they also appear whitish, yellowish or pinkish. Young individuals tend to have lighter and more contrasted colors, whereas older specimens tend to get darker to the point of melanism (Pleguezuelos and Feriche, 2014; Fig. 4).

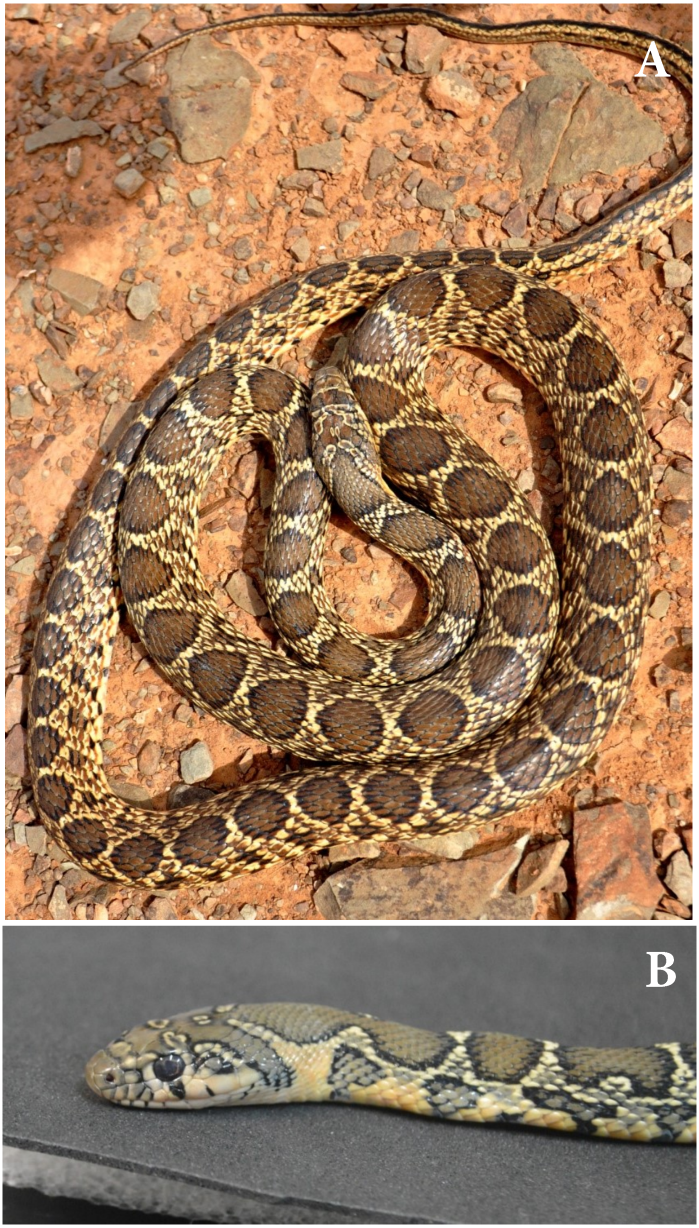

Fig. 4. Dorsal (A) and lateral (B) aspect of *Hemorrhois hippocrepis.* Photos: Mónica Feriche and Marta Gómez.

It is a rupiculous snake, frequently using rock walls, mines and garrets as a shelter, and inhabiting open and sunny locations, rocks, low shrublands, river galleries or croplands, especially near ruins or human buildings. It easily climbs vertical surfaces (natural or artificial) thanks to its slim and long body, their presence being common in urban areas (Feriche, 2017).

The horseshoe whip snake feeds almost exclusively on vertebrates, mainly mammals, but reptiles, birds and invertebrates are also prey in decreasing importance (Pleguezuelos and Moreno, 1990). It can occasionally eat amphibians, carrion and bats (Feriche, 2017). There is an ontogenic shift in diet, predating invertebrates and reptiles in early ages and birds and mammals when the snakes attain maturity (Pleguezuelos and Moreno, 1990). Regarding its reproduction ecology, males attain sexual maturity at 500 mm snout-vent length (SVL) and females at 680 mm SVL; males have a spring spermatogenesis, being sexually active from the end of March until the end of June. This type of cycle prevents the species from colonizing colder locations, given the need for long and warm springs. Females present a prenuptial vitellogenesis and reproduce each year, with a mean clutch size of 6.8 eggs (range: 3 – 10, n = 10) and a positive relationship between the mother SVL and clutch size. Offspring size ranges from 237 to 308 mm SVL (mean = 267.8 mm, n = 16), and their weight ranges from 6.1 to 9.0 g (mean 7.5 g, n = 13) (Pleguezuelos and Feriche, 1999).

Regarding its behavior, it remains active from March to November in general terms, but this pattern varies depending on the temperatures (Feriche, 2017). There are sporadic sightings during winter months, especially in warmer zones, but observations concentrate in certain times of the year, coinciding with two cycles: unimodal for males, with a late-spring maximum (mating period), and bimodal for females, with the first peak synchronized with males and the second one in early autumn, probably used to recover from the reproductive effort. Some individuals of both sexes tend to avoid the highest summer temperatures by going into summer latency (Pleguezuelos and Feriche, 1999; Pleguezuelos and Fahd, 2004). The horseshoe whip snake is mainly diurnal, but it can be active during twilight and even nocturnal if temperatures are very high (Franco et al., 1980; González de la Vega, 1988).

It is listed as Least Concern at global scale (Mateo-Miras et al., 2009), and in Spain (Pleguezuelos and Feriche, 2002). The Bern Convention and the Habitats Directive (92/43/EEC) protect this species. It is listed as invasive in the Spanish Exotic Species List (RD 1628/2011) only for the Canary Islands, Ibiza and Formentera, despite its recent introduction to the island of Mallorca and its well-known invasive potential (Ayllón, 2015).

The endemic species: the Ibiza wall lizard

It is a robust lizard, with a high head, and a green or brown color pattern, although it is rather variable in color and body size among populations. Males are bigger than females, but they show a high variability among populations, with a trend towards gigantism, more dorsal scales and higher degree of melanism in populations isolated for a longer period. It is an omnivorous lizard, eating several types of invertebrates (arthropods and gastropods), plants (including nectar, pollen, flowers, leaves, fruits and seeds), carrion and sea crustaceans, and different studies show that *P. pityusensis* is an opportunistic feeder that varies its diet depending on food availability (Salvador, 1986; 2015; Pérez-Mellado and Corti, 1993).

It inhabits the Pitiusic Islands and 38 of the surrounding islets, which hold 23 endemic subspecies of the lizard. It has been introduced to the city of Barcelona, to two peninsulas in the Basque Country, and to specific locations of Mallorca (Salvador, 2015). Its habitat rarely includes pine forests, being more common in open areas, especially in shrub areas and in the omnipresent rock walls characteristic of the Pityusic Islands (Salvador and Pérez-Mellado, 1984). It remains active throughout the year, as long as temperatures are high enough, and it is an opportunistic omnivorous reptile that acts, at the same time, as a pollinator and seed disperser (Pérez-Mellado and Traveset, 1999; Salvador, 2015). Before the arrival of snakes to Ibiza, *P. pityusensis* was common across the islands of Ibiza and Formentera (chapter 2), and the IUCN Red List considers it as Near Threatened (Pérez-Mellado and Martínez-Solano, 2009).

The main island population of *P. pityusensis* has shown anti-predatory responses towards *H. hippocrepis* (a saurophagus snake), the one that is thriving on Ibiza, whereas the islet populations are missing those defense mechanisms (Ortega et al., 2016). The same happens to the remaining populations of the endemic Lilfordi's lizard, present only on the islets close to Mallorca and Menorca, which lack anti-snake response (Mencía et al., 2017); this loss is related to geographic isolation (Durand et al., 2012). The cause for recovery of anti-snake defense mechanisms on Ibiza's main island is not yet clear whether it is an evolutionary or a learned response (Ortega et al., 2016).

Approach and objectives

In summary, the only native terrestrial vertebrate on the island of Ibiza is the lizard *P. pityusensis*, which maintained a healthy population on the island despite the introduction of numerous alien species. The first snakes arrived to the island in 2003, and they started to be seen around nurseries. From 2010, the spread of the snake's population became evident, and during the following years, a shed was spotted on an islet (S'Espartar), and the Ibiza Island Council carried out a pilot project in order to test the effectiveness of different kinds of traps and the viability of eradication campaigns (Montes et al., 2015). In 2015, the first of many snakes was seen swimming, and the suspicion that the snakes were eating lizards was present among managers. I started this PhD during that year.

The goals of this dissertation are, on one hand, to study the natural history of the invasive population of *H. hippocrepis* on Ibiza and compare it to the source population, hoping to find the causes to their invasion success and useful information in order to defeat the invasion; and on the other hand, to numerically and scientifically analyze the impacts on the endemic *P. pityusensis*, in order to improve the chances of protecting their populations. The study of natural history is broadly used in herpetology, as a way to better know the species with a conservation goal (Lovich et al., 2012). In addition, invasive species have shown greater phenotypic plasticity (Davidson et al., 2011) and faster history traits are frequent in invasive reptiles (Allen et al., 2017).

I organized the dissertation in chapters fitting the concrete objectives here raised (Fig. 5):

- In 2015, the most urgent topic to study was the **trophic ecology** on the invasive snakes' population, in order to test if the endemic lizard was being predated by the invasive snake, a typically saurophagous snake through its native range. This goal is addressed in *Chapter 1. Trophic Ecology*.

- Once I knew that lizards constituted more than half of the snake's diet, the next goal was to assess how the predation by snakes **affects lizard distribution and abundance**, how quickly the **snake population spreads**, and to analyze the lizard populations from the **islets** of Ibiza. This is addressed in *Chapter 2. Impacts on native lizards*.

- In order to know why the invasive snakes are being successful, despite mostly eating a low-energetic prey (the lizard), I analyzed their reproductive ecology, in order to see whether the snakes on Ibiza are **reproducing more frequently**, have expanded their **reproductive periods**, **lay more eggs,** or **neonates have a better body condition** than in the source population. This is analyzed in *Chapter 3. Reproduction ecology*.

- Since the reproduction ecology did not provide answers regarding the invasion success of the snakes, I wanted to test one aspect of the Enemy Release Hypothesis (ERH), measuring if the **predation pressure** supported by the snake's invasive population is lower than the source population, as a partial explanation of their success. This is addressed in *Chapter 4. Predation pressure on invasive snakes*.

- In order to completely test the ERH, I studied the **presence of parasites** in both populations and compared them. I also analyzed the ERH under the competitors' standpoint. This is done in *Chapter 5. Parasitism*.

- In view of the results of the study in which I analyzed snake's affection to lizards, I assessed the **extinction risk** of the lizard under the rules of the IUCN Red List procedure. Moreover, as a corollary of the dramatic results obtained in relation to the survival of the endemic Ibiza wall lizard, I propose adequate **conservation measures**. This is addressed in *Chapter 6. Conservation measures*.

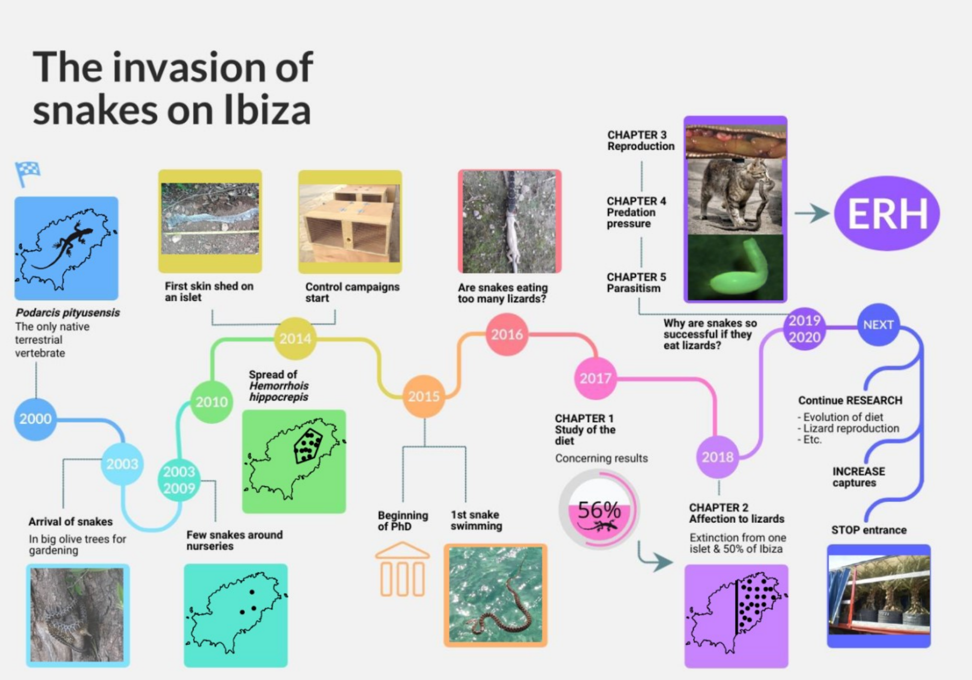

Fig. 5. Explanatory diagram of events regarding the snake invasion on Ibiza and the steps of this PhD dissertation. Source: E. Montes.

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Chapter 1. TROPHIC ECOLOGY

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*

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Abstract

Invasive species currently account for a major threat to global biodiversity, and island ecosystems are among the most vulnerable, because of the frequency and success of species introductions on islands. Within Mediterranean islands, reptiles not only are frequently introduced species but are also among the most threatened because of these introductions. The Balearic archipelago is a good example of this, since only two of its current 16 species of reptiles are native. Thirteen years ago, the snake *Hemorrhois hippocrepis* was introduced by cargo in Ibiza island, and it is in expansion. Individuals obtained from an early eradication campaign showed a fast expression of phenotypic plasticity and acquired larger sizes than those of the source population, probably due to a high prey availability and predator scarcity. The species is thriving at the expense of a small variety of native and non-native prey, but the predation pressure on the endemic *Podarcis pityusensis*, the only native reptile in the island, is very high, as this lizard represents 56% of the prey in frequency, which might threaten its survival on the long term. Our results on the feeding ecology of the snake are of sufficient concern to justify the maintenance of actions to eradicate this invader.

Keywords: Balearic islands, *Hemorrhois hippocrepis*, Invasive species, Snake, Lizard

Introduction

Introduction and establishment of alien invasive species is one of the major threats to biodiversity on a global scale (Brooks et al. 2006). Island ecosystems are among the most vulnerable to invasive species, mainly due to the intrinsic traits of their native biota. Species that have evolved for a long time in islands are usually unsuccessful competing and avoiding being predated by newcomers and are also more vulnerable to parasites brought by invaders (Whittaker and Fernández- Palacios 2007; Simberloff et al. 2013). The Balearics have been isolated from the continent for 5.33 million of years, and its biota has evolved to adapt to these insularity conditions and experienced natural extinction processes during the Plio- Pleistocene (Bover et al. 2008) and human-mediated ones by the end of the third millennium BCE, when humans colonized the islands, and alien species introductions started (Pinya and Carretero 2011). Some of these introductions, like that accomplished by two mammals, *Martes martes* and *Mustela nivalis*, together with an introduced snake, *Macroprotodon cucullatus*, have been considered responsible for the extinction of the native lizard *Podarcis lilfordi* in the main islands (Mallorca and Menorca; Alcover et al. 1981). The ability of reptiles as invaders is due in part to their biological characteristics: as ectotherms, a low metabolic rate allows them to survive in the absence of trophic resources during transportation; their secretive behavior makes them undetected during the first stages of the introductions; and they are able to show a rapid ecological niche shift when facing a new environment (Carretero 2004; Kraus 2009).

Within reptiles, snakes are a good example of harmful invasive species in islands, often having devastating impacts on native fauna (Martínez-Morales and Cuaron 1999; Guicking et al. 2006; Monzón-Argüello et al. 2015). Until quite recently, all except two of the 63 Mediterranean islands larger than 75 km2 harbored at least one snake species, in most cases introduced; the exception were the westernmost Balearic islands, also called the Pityusic islands, Ibiza, and Formentera, which were never colonized by snakes (J.A. Mateo, com. per.), offering for these reptiles an empty niche scenario. Pliny the Elder realized this, when two thousand years ago he wrote "Ebusi, terra serpentes fugat", stating that Ibiza was free of snakes and that these could not thrive there; nowadays, it can be stated that he was wrong. In between 12 and 13 years, three species of snakes (*Hemorrhois hippocrepis*, *Rhinechis scalaris*, and *Malpolon monspessulanus*) were introduced in Ibiza by accident, transported from southern Iberian Peninsula within old ornamental olive trees, and apparently in high numbers (Mateo et al. 2011). However, there have not been any records of *M. monspessulanus* in Ibiza during the last 6 years, and *R. scalaris* has been captured in a low rate which might mean that the first species failed in establishing and disappeared, while the second does not seem to have adapted well. But this is not the case of *H. hippocrepis*, which is expanding in Ibiza (Montes et al. 2015).

H. hippocrepis is a rather large-sized, slender-bodied, and long-tailed colubrid; it is distributed throughout the Western Mediterranean, being present in the southern two thirds of the Iberian Peninsula, northwestern Africa, and islands of Pantelleria, Sardinia, and Zembra, where it was also introduced (Pleguezuelos and Feriche 2014). In 2003, the species was reported for the first time in Ibiza, a rather topographical homogeneous island, where climate matches that of the source areas of the species, and where since then it has been repeatedly introduced by human assistance (Mateo et al. 2011), being these all the circumstances that predict a high spread rate of alien herpetofauna (Liu et al. 2014). It is thermophilic, rupicolous, and a frequent species in the thermomediterranean and mesomediterranean bioclimatic regions, where it thrives in open and sunny spaces with bare rocks and scrub formations, besides human constructions, which are often used as habitat and shelter. It is an active forager that feeds almost exclusively on vertebrates (Pleguezuelos and Moreno 1990), thus representing a main threat to the native island vertebrates. Ibiza's ecosystems host some unique endemisms that could be suitable preys for the newcomer, like pulls of the Balearic shearwater (*Puffinus mauritanicus*), the Balearic warbler (*Sylvia balearica*), and the most iconic one, the Ibiza wall lizard, *Podarcis pityusensis*. This lizard ranges through the main island and 39 of the islets surrounding it, most of them housing distinct subspecies, and have introduced populations in another Balearic island and in the Iberian Peninsula (Salvador 2014). Aside its intrinsic, biological value, this endemism has an economic and social value for the island. Being the only native reptile, it is very popular and became a symbol that appears contoured in any signal or pamphlet referring to the biodiversity of the island. Besides this, it is also highly present in its tourism, the main income for the island (on clothing, jewelry, restaurants, hotels, paintings, sculptures …), and in its culture (Pérez-Mellado 2009).

Ecological niche models show current low habitat suitability in the Balearics for H. hippocrepis, with predictions for high suitability in Ibiza, in most climate change scenarios, by 2080 (Silva-Rocha et al. 2015); however, the species is perfectly thriving currently in Ibiza, and preliminary data show a fast spreading and large body size of individuals (Montes et al. 2015). These are signs of a good feeding and low mortality rate in Ibiza, given the absence of almost any natural predators, the latter being named the enemy release hypothesis (Liu and Stiling 2006). Because of evidences on the rapid range expansion of the introduced snake and the potential risk posed for the native fauna, in 2014, the Island Administration begun an eradication program mostly based on trapping (Montes et al. 2015).

Improved understanding of the characteristics of successful invaders is necessary in order to counteract invasions and their negative impacts on ecosystems and develop management strategies (Liu et al. 2014). Diet studies on invasive species can shed light not only on applied aspects of its invasion success and effects on the native biota but also on evolutionary issues like local adaption and plasticity (Almeida et al. 2012; Riofrío-Lazo and Paez-Rosas 2015). We use the specimens afforded by the eradication program to analyze the diet habits of the *H. hippocrepis* introduced in the Ibiza island and compare these and other ecological traits of this population with conspecifics from the source population (southern Iberian Peninsula), with another native population (northwestern Africa), and with two populations introduced in other Mediterranean islands (Sardinia, Pantelleria). The main goal is to seek for the negative impact on Ibiza's biota, particularly on some endemic species like the lizard *P. pityusensis.* As comparisons of prey composition between the Ibiza population of *H. hippocrepis* and other native or introduced populations will simply reflect variation in prey availability (Monzón-Argüello et al. 2015), we also seek for the variation of other measures commonly used in feeding ecology, indicators of the success of this species as alien invader in the island. Thus, we also investigated (i) the trophic diversity, under the hypothesis that in this introduced population it must be low considering the usual reduced richness of potential preys in islands (Whittaker and Fernández-Palacios 2007); (ii) the snake and prey size, under the hypothesis that the large body size of introduced snakes (Montes et al. 2015) is favored by feeding on larger preys (Boback 2003), based on the rule that relates predator and prey size in ophidians (Arnold 1993); and (iii) the feeding rate and body condition, under the hypothesis that introduced individuals feed more frequently and are in better body condition than the ones in their native areas, given the naïve prey presence (Paolucci et al. 2013).

Methods

Ibiza, with 572 km$_2$ of area and 475 m asl of maximum altitude, is the largest of the Pityusic islands and exhibits a mean annual temperature of 17.9 °C, and the average yearly rainfall is 413mm(IbizaAirport weather station, 38° 52′ 22″ N, 1° 22′ 23″ E; www.aemet.es). The landscape is characterized by a mosaic of two habitats, pine forests (*Pinus halepensis*) and cultivated land (orchards, cereal crops), with scattered patches of garrigue (*Quercus coccifera*, *Juniperus phoenicea*).

The individuals for this study come from the entire area invaded by the species, an area of 148 km^2 in the northeastern quarter of the Ibiza island (38° 58′ –39° 05′ N, 39° 2′ –39° 4′ E; range in Ayllón 2015), and were captured during the 2013– 2015 period by the Island Administration staff during eradication campaigns (details in Montes et al. 2015). Specimens were sacrificed in a veterinary facility within the island (except 18 roadkills) and preserved in ethanol in the collection of the Granada University. In total, 293 specimens (142 males, 118 females, 33 immature) were examined. Before fixation and preservation, snout-vent length (SVL) was measured to the nearest millimeter and biomass to the nearest 0.1 g. Gut contents were checked by making a mid-ventral incision and prey items were identified to the species level. Some micromammals were identified by their hair remains according to Teerink (2004), under magnification (×400). Only prey in good conditions were measured (SVL, ±1 mm) and weighed (±0.1 g), after draining them on paper towel.Weight of partially digested prey was estimated by comparison with conspecifics from the study area and from the bibliography (Gosàlbez 1987), considering this trait at the time of ingestion. While most prey remains were accurately measured for body length, body weight had to be inferred for many of them; for this reason, prey body length was used in comparisons.

The diet of *H. hippocrepis* is rather well known through its range, both for native (southern Spain and northern Morocco; details in Pleguezuelos and Moreno 1990; Pleguezuelos and Fahd 2004) and island-introduced populations (southern Sardinia and Pantelleria; details in Luiselli et al. 2012; Cattaneo 2015), favoring comparisons. To test if there was a difference in feeding frequency (the frequency of individuals having gut content) between pairs of locations, we used the Pearson chi-squared test. Prey frequency of the snakes was compared among all regions and between pairs of regions by the same test, using only animals with gut content. To compare the diet of *H. hippocrepis* among the five regions with quantitative data, and because of statistical constraints, we reduced the number of prey types to four: (i) lizards, (ii) small micrommamals (below *Rattus* size), (iii) large micromammals (*Rattus* size and above), and (iv) other prey (other reptiles, amphibians, birds, invertebrates; Table 1). Food-niche breadth was calculated according to Shannon's index; to calculate this index, specimens without gut contents or with unidentified prey were not considered. Absolute snake and prey size (SVL, weight) were compared between populations (the source one in southern Spain and the introduced one in Ibiza) by t test and M-WU test and prey size relative to snake size by ANCOVA, after testing for the homocedasticity of variances.

Body condition (the relationship between body mass and body length) is considered as an accurate indicator of foraging success in snakes (Bonnet et al. 2001). The body mass variability is influenced by fat-body reserve (Bonnet et al. 2003); thus, we estimated body condition according to the importance of fat bodies (Waye and Mason 2008). Because we were not able to accurately weigh fat bodies from some road-killed specimens, we scored fat body level of the *H. hippocrepis* from Ibiza in five visual categories: zero, no traces of fat; one, small traces of fat among intestine loops; two, fat bodies covering less than half of the intestinal surface; three, fat bodies covering more than half of the intestinal surface; and four, a continuous fat layer in the ventral zone of the abdominal cavity. This procedure was already followed for the source population (Pleguezuelos and Feriche 1999) thus, enabling direct comparisons. Fat-body reserves in snakes tend to exhibit ontogenetic, sexual, and seasonal shifts (Santos and Llorente 2004); we minimize the variability of data by comparing this trait according to sex, only for adult specimens (SVL > 500 mm in males and SVL > 680 mm in females; Pleguezuelos and Feriche 1999), and only for the spring-summer seasons. Since body size in reptiles can vary with altitude, introduced source area comparisons have only considered data (SVL, body weight, fat-body level) from source area (S Spain) specimens collected below 475 m asl, the maximum altitude of the Ibiza island. However, because of the little sexual size dimorphism and the lack of sexual differences in diet for the source population (Pleguezuelos and Feriche 2014), we did not take into account the sex of the individuals in the diet analysis. Correlation between snake body length and prey body length was fitted to the best regression type. Distributions of data were checked for normality prior to analyses, and in this article, mean values are followed by ± one standard deviation with alpha set at 0.05. All comparisons in multiple tests were significant after the Bonferroni correction.

Results

Only seven prey species appeared in the diet of *H. hippocrepis* in Ibiza, 63.4% were reptiles (55.4% *P. pityusensis*, 6.7% *Tarentola mauritanica*, 1.3% *Hemidactylus turcicus*), 35.1% were mammals (16.2% *Apodemus sylvaticus*, 10.8% *Mus* sp., 2.7% *Rattus rattus*, 5.4% unidentified micromammals), and one prey was a bird (1.3% *Turdus merula* pulls; Table 1); thus, 56.7% of prey were native to Ibiza (*P. pityusensis* and *T. merula*). When prey mass was considered, the importance of mammals plus birds as prey increased (74.4%).

There was a geographic shift in diet (4 × 5 table, $\chi_2 = 134.26$, $p < 0.0001$; Table 1); the composition of the diet of the Ibiza population differed from that of all other populations (2 × 4 table, χ_2 test, $p < 0.0001$ in all comparisons between Ibiza and other regions), particularly in that there was an excess of lizards with respect to the continental plus Sardinian populations (2 × 2 table, χ_2 test, $p < 0.0001$ in the three comparisons), and only the Pantelleria population did not significantly differ from the Ibiza population in the rate of lizard consumption (2 × 2 table, $\chi_2 = 1.78$, $p = 0.18$). As a consequence of the dominance of *P. pityusensis* in the diet, trophic diversity for the Ibiza population was the lowest, despite the sample size for this island was much larger than for the other regions (Table 1). For the Sardinian population, prey-type number and diversity index were probably infrascored, because 13 prey items were determined at the coarse level of "bird" prey type. In general, trophic diversity was lower in island populations with respect to mainland ones (Table 1).

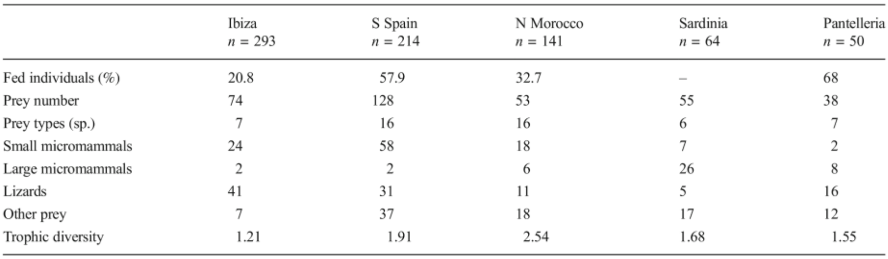
Prey size of *H. hippocrepis* from Ibiza, as measured by prey SVL, averaged 62.6 ± 23.0 mm (n = 47) and ranged from 22.8 mm (*H. turcicus*) to 150.0 mm (*R. rattus*). It was larger than the prey size of the native population of southern Spain (from the raw data in Pleguezuelos and Moreno [1990]; = 3.33, d.f. = 136, p = 0.0017). However, Ibiza individuals did not predate significantly on relatively larger prey (ANCOVA, with prey SVL as dependent variable, snake SVL as covariate and region as grouping factor; $F_{1,134} = 2.80$, $p = 0.09$; Levene's test for homogeneity of variances, $p = 0.147$). There was a positive relationship between snake body length and prey body length for the Ibiza's population ($r = 0.630$, $n = 47$, $p < 0.0001$), although an ontogenetic shift in prey type hardly appeared, as the main prey, *P. pityusensis*, was preyed by snakes of a wide spectrum of body size; the biggest prey, *R. rattus*, was preyed by the largest snakes (Fig. 1).

Body size of individuals of *H. hippocrepis* from Ibiza was larger than that of individuals from the source region (southern Spain) as measured by SVL (mean = 712.8 ± 238.8 mm, n = 290, vs mean = 640.5 ± 261.3 mm, n = 144; t = 2.87, d.f. = 432, p = 0.004) and as measured by body weight (mean = 143.8 ± 165.7 g, n = 262, vs 103.7 ± 165.7 g, n = 69; M-WU test, Z = 2.16, p = 0.030).

Feeding frequency of Ibiza individuals was rather low, and below that showed by other populations of the species, either native and introduced (2 × 2 table, χ_2 test, $p < 0.007$ in all paired comparisons including Ibiza population; Table 1).

Body condition of adult Ibiza individuals, measured by fat body level, was higher than in individuals from southern Spain (from the raw data in Pleguezuelos and Feriche [1999]), either in males (mean = 3.49 ± 0.79, n = 119 vs mean = 2.22 ± 1.24, n = 59; M-WU test, Z = 6.41, p = 0.0001) or females (mean = 2.93 ± 1.21, n = 49 vs mean = 2.11 ± 1.25, n = 36; M-WU test, Z = 2.85, p = 0.003).

Table 1. Data on feeding ecology of five populations of *Hemorrhois hippocrepis* from the Western Mediterranean. Prey types have been reduced to four operational groups to avoid zero cases. In the Ibiza population, small micromammals were 12 *Apodemus sylvaticus*, eight *Mus* sp., and four undetermined micromammals; all large micromammals were *Rattus rattus*; all lizards were *Podarcis pityusensis*; other prey were five *Tarentola mauritanica*, one *Hemidactylus turcicus*, and one *Turdus merula* nestlings. For a detailed composition of the diet of the other populations view the sources (Pleguezuelos & Moreno, 1990; Pleguezuelos & Fahd, 2004; Luiselli et al., 2012; Cattaneo, 2015). Trophic diversity (Shannon index) was computed from prey identified at the species level.



	Ibiza *n* = 293	S Spain *n* = 214	N Morocco *n* = 141	Sardinia *n* = 64	Pantelleria *n* = 50
Fed individuals (%)	20.8	57.9	32.7	–	68
Prey number	74	128	53	55	38
Prey types (sp.)	7	16	16	6	7
Small micromammals	24	58	18	7	2
Large micromammals	2	2	6	26	8
Lizards	41	31	11	5	16
Other prey	7	37	18	17	12
Trophic diversity	1.21	1.91	2.54	1.68	1.55

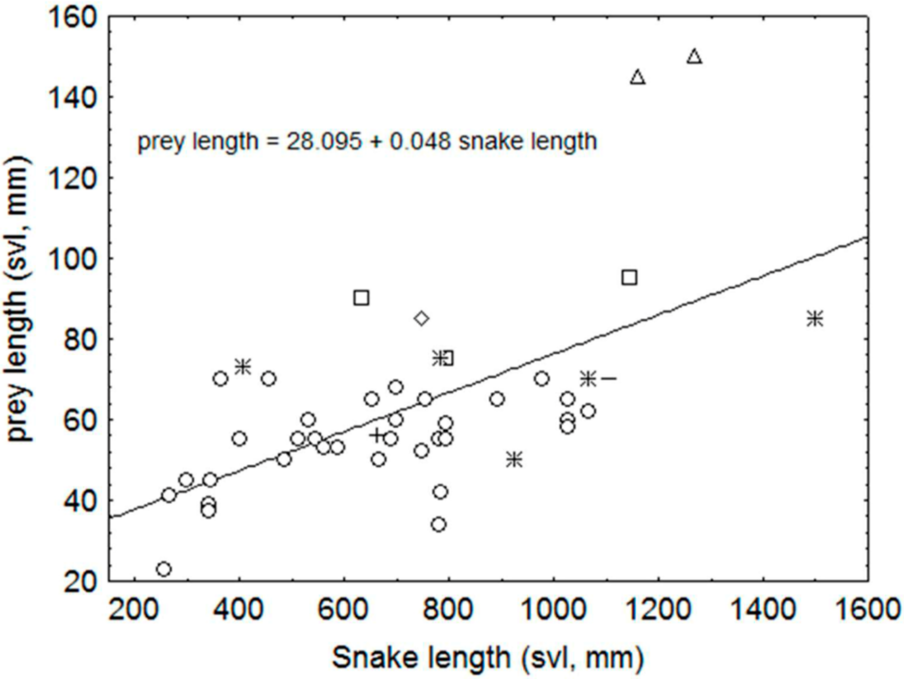


Fig. 1. Prey size relative to snake size (expressed as snout-vent length in both variables) for the population of *Hemorrhois hippocrepis* introduced in the Ibiza island. The best fitting for the data was to an exponential regression. Different symbols correspond to different prey types: *Podarcis pityusensis* (circle), *Hemidactylus turcicus* (cross), *Tarentola mauritanica* (star), *Mus* sp. (diamond), *Apodemus sylvaticus* (square), *Turdus merula* pulls (dash), *Rattus rattus* (triangle).

Discussion

The most commonly considered ecological impact from alien species is predation on sensitive native species (Kraus 2009). Analysis of the dietary habits of *H. hippocrepis* in Ibiza has confirmed a strong predation on the endemic lizard *P. pityusensis*, which makes up the largest proportion of prey. This is a concerning result for the integrity of the native and endemic fauna of the rather small Ibiza island. *P. pityusensis* is the only endemic vertebrate in Ibiza, and its sibling species, *P. lilfordi*, disappeared from the two largest Balearic islands (Mallorca and Menorca) by predation of other introduced species (Bover et al.

2008; Pinya and Carretero 2011). Indeed, reptiles are not only among the most introduced vertebrate group in Mediterranean islands but also among the most affected by introduction of other reptiles (Kraus 2009). The secondary prey for *H. hippocrepis* in Ibiza in frequency, but primary in biomass, are micromammals (*A. sylvaticus*, *Mus* sp., *R. rattus*), aliens in Ibiza, thus, of no conservation concern. However, these aliens, of early arrival and high reproductive rate, are providing food resources for later aliens, like *H. hippocrepis*, in a process named invasional meltdown (Simberloff and Vonn Holle 1999), probably with synergic and badly effects on the native prey, in this case, *P. pityusensis.*

H. hippocrepis is a rather generalist in diet where the species is native (Pleguezuelos and Fahd 2004). The low diet diversity showed by the Ibiza newcomer individuals would be the consequence of the low prey-type richness for this snake in that island. Although this might seem obvious at first hand, and in accordance with MacArthur's theory of island biogeography (where diet diversity is expected to be lower on islands than on mainland), the present literature provides both according (Alivizatos et al. 2005) and conflicting cases (Clevenger 1993) with it. However, its diet in the study area was not only reduced in terms of prey type but was also more dependent on lizards than any mainland native population (Pleguezuelos and Moreno 1990; Pleguezuelos and Fahd 2004) and other island-introduced populations, like Sardinia (Corti et al. 2000; Luiselli et al. 2012). Only conspecifics from another small island, Pantelleria, included many lizards in their diet (Cattaneo 2015), although the case in that island is not much comparable, since there the snake is feeding on an alien and invasive lizard, *Podarcis sicula* (Capula 1994). We confirm our hypothesis on the low trophic diversity of that population and suggest that the feeding habits of *H. hippocrepis* from Ibiza reflect the high availability for this snake of a yet abundant and naïve prey: the endemic lizard *P. pityusensis* that evolved in a snake-free island during the Pleistocene (Bover et al. 2008). The fall of this symbol would not only mean a huge loss for the island's natural and cultural heritage but could also trigger negative cascading effects on some plant populations/species that depend on it (Pérez- Méndez et al. 2016), as the lizard provides an important role as seed disperser (Riera et al. 2002). As in many other cases (Close et al. 2002; Garibaldi and Turner 2004), the embracement of this symbol by the local communities might be the key to its conservation and the control/eradication of the aliens.

We also confirmed that *H. hippocrepis* individuals from Ibiza are larger than the native ones from southern Spain, the source population. Contrasted body size has been widely recorded between conspecific snake populations in mainland and islands (Shine 1987; Boback 2003; Aubret et al. 2004). Nearby to our study area, R. scalaris introduced in the islands of the Mediterranean coast of France showed large body size (Cheylan and Guillaume 1993), just like *M. cucullatus* introduced in the other Balearic Islands (Salvador 2014), or *H. hippocrepis* in Pantelleria (Cattaneo 2015). Large body size (in some cases gigantism) is one type of island syndrome (Pafilis et al. 2011). But the most striking fact of this case study is that in Ibiza's *H. hippocrepis*, this phenotypic change has occurred in a very short period, as the species was introduced in the island only 13 years ago, providing an impressive example of the fast rate at which phenotypic plasticity can take place after the invasion of a novel habitat (within ecological time scale; Herrel et al. 2008). Certainly, islands provide unusual environmental conditions that trigger rapid phenotypic (and evolutionary) changes in snakes (Aubret 2015; Luiselli et al. 2015).

Variation in snake body size between mainland and island populations has been interpreted as a consequence of differences in prey abundance and/or prey size between both environments (Boback 2003). Higher prey abundance in the islands would be translated in a higher feeding success of snakes, and their concomitant effect on the body condition of individuals (Bonnet et al. 2001), and the same applies when aliens ingest larger prey (Boback 2003). Indeed, individuals from Ibiza showed a higher body size and level of abdominal fat bodies when compared to the mainland populations (Pleguezuelos and Feriche 1999; Montes et al. 2015). However, conflicting results were also found, as in Ibiza there were few individuals with gut content. Moreover, although there was a difference in prey size between Ibiza alien and southern Spain native snakes, this difference was rather the result of larger body size of Ibiza snakes, as there was no difference in relative prey size between both populations. The average prey size for the Ibiza snakes is mediated by the high frequency on the diet of a rather small prey, the lizard *P. pityusensis*. Accordingly, our results do not support the hypothesis that the large body size of introduced *H. hippocrepis* is the consequence of the availability of largest prey in the island (Boback 2003).

Thus, if the large body size and good body condition of Ibiza's *H. hippocrepis* do not rely on the largest size of their prey, we suggest that our results on the feeding frequency are misleading. In ectotherms, the physiological response to feeding varies dramatically among organisms due mainly to the effects of meal size and body temperature (Secor 2003,Wang et al. 2003). Smaller meals are digested faster than larger ones (Secor and Diamond 1997), and we suggest that we found relatively few fed snakes in Ibiza because they ingest rather small and slender-bodied prey, like *P. pityusensis*, of fast digestion. In ectotherms, higher body temperatures elevate metabolic rates and shorten the time of the passage of ingesta through the gut (Lillywhite et al. 2002), probably the case of *H. hippocrepis* in Ibiza, distributed in lowlands, where the temperature is warm (Guijarro 2002), providing a suitable thermal envelope for this thermophylous snake. Moreover, among snakes, gracile species are also characterized by short time of passage of the ingesta (Lillywhite et al. 2002), and *H. hippocrepis* is a slender-bodied snake. To support this statement, three anecdotal records have been obtained of only 55–60 h for the gut passage of a lab mouse, in two average sized snakes kept in an outdoor enclosure in Ibiza (unpublished results).

There is an alternative hypothesis behind the larger body size and high abdominal fat level of individuals from Ibiza. Despite the lack of quantitative data on predation pressure on this snake in the island, only two of the seven predators identified for the species in southern Spain are in the island (*Falco tinnunculus* and feral *Felis silvestris*; Pleguezuelos and Feriche 2014). Moreover, almost all the individuals from Ibiza have shown tail integrity and are devoid of other body scars, these circumstances being proposed as parameters for measuring predation risk in snakes (Santos et al. 2011). Suitability of the host region for aliens may be increased by the absence of predators (Kraus 2009). The paucity of the predator community and the scarcity of signals of (failed) predation events, suggest a scenario of predation release (Liu and Stiling 2006), which would favor longevity and large body size of *H. hippocrepis*, turning the snake into a nutrient sink in the island (Greenlees et al. 2006).

After the analysis of diet habits, body size, and body condition, we conclude that the population of *H. hippocrepis* recently introduced in the Ibiza island threatens its biodiversity. The snake relies on the abundance and/or easy predation of the island, naïve, primary prey (*P. pityusensis*), threatening the conservation of this endemic lizard. Moreover, the threat would be much more acute for the lizard subspecies in the surrounding islets, all nearby the main island (within 5 km from coastline, 1.17 km on average), and most maintaining a small population of lizards (29 ssp. have been described; Salvador 2014); if the alien snake arrives to any of them, it would lead to the extinction of a unique evolutionary unit, because of the lack of alternative prey. This possibility is real, as the snake has been observed in the sea swimming at least five times, and a shed has been obtained from one islet (unpublished results). Our results warrant the current eradication measures as well as the improvement of resources invested in these (Montes et al. 2015). Because of evidences here afforded, we also suggest a regular census of the lizard, as an alternative method to monitor the impact of predation (Monzón-Argüello et al. 2015).

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Chapter 2: IMPACTS ON NATIVE LIZARDS

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 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

Introduction

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 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 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 (1.17km average distance from the coast, and a maximum of 5km 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 10–1,000m 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 572km2 and a maximum elevation of 486 m. The mean annual temperature is 18.3 ºC (mean monthly range 11.9 ºC [January]–26.3 ºC [August]), and the average yearly rainfall is 413mm (mean monthly range from 5 [July] to 58mm [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, 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 (610 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. Lizards were widespread and rather equally common 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 500m long;

surveys consistently lasted 15 min. We also checked 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 ºC, ambient temperature), avoiding midday 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 20m along each transect, alternating between the right and left sides of the transect, and 2m 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.

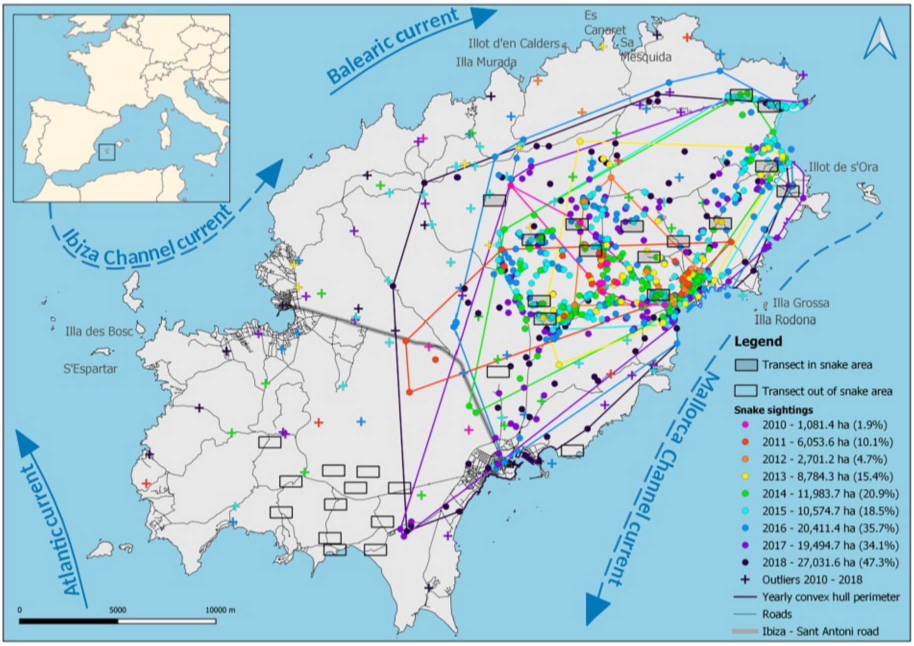


Figure 1. Map of Ibiza in the context of the Western Mediterranean (inset), showing: (1) records of the invasive *Hemorrhois hippocrepis* by year (2010–2018), where crosses are outliers, for the calculation of the range area of each year (depicted by the polygons); (2) distribution of transects for lizard 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).

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 (63.34, range = 0–13, n = 42) but 0.11 lizards per census (60.75, range = 0–5, n = 45) in snake-present areas. Based on AIC scores of the GLMM, three models had ΔAICc < 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

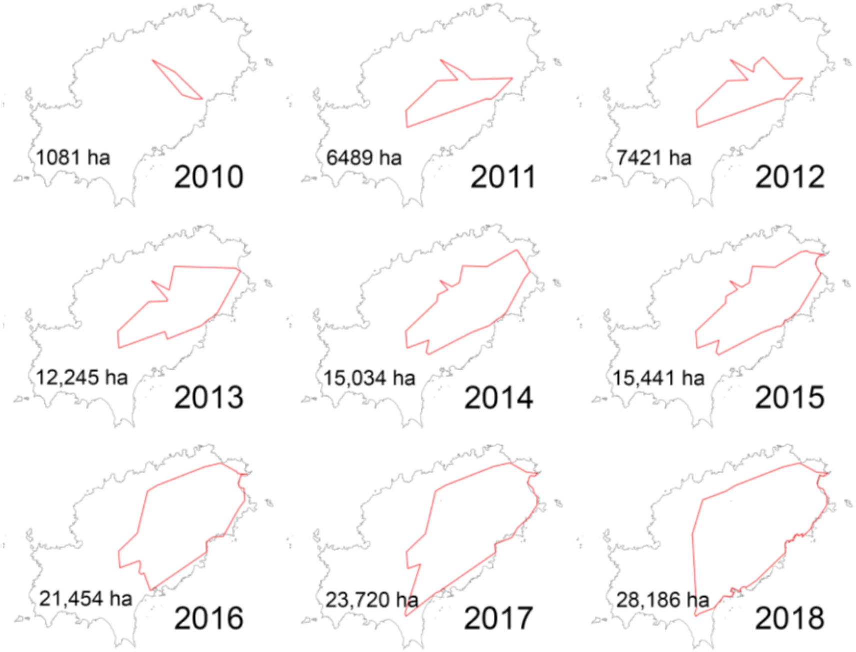


Figure 2. Yearly cumulative range expansion of *Hemorrhois hippocrepis* on Ibiza.

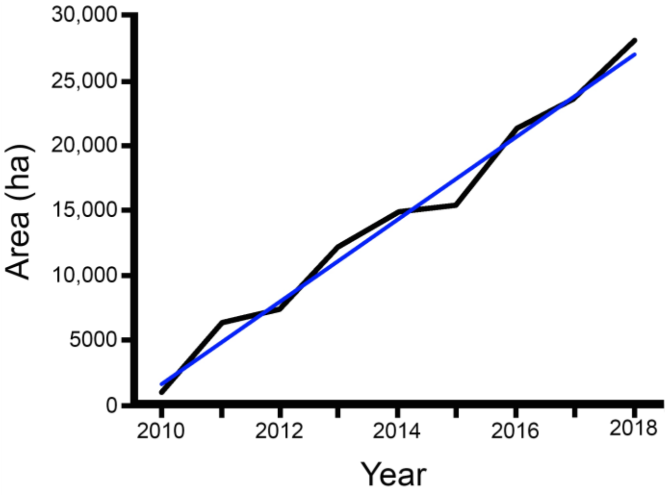
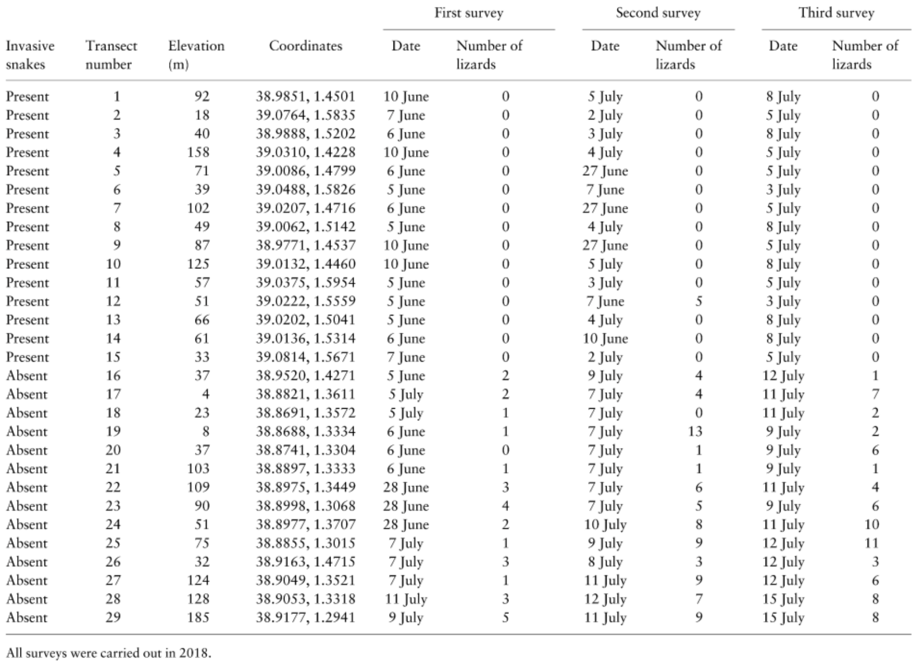


Figure 3. Growth in areal extent of the range of *H. hippocrepis* on Ibiza from 2010 to 2018 (black line), and linear regression (blue line) explaining those data. For the regression, Area = 3189.5 year—1384.3, adjusted $R^2 = 0.9800$, $F_{1,7} = 394.14$, $P<0.0000$, standard error of estimate 1244.5.

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



				First survey		Second survey		Third survey	
Invasive snakes	Transect number	Elevation (m)	Coordinates	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.

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).

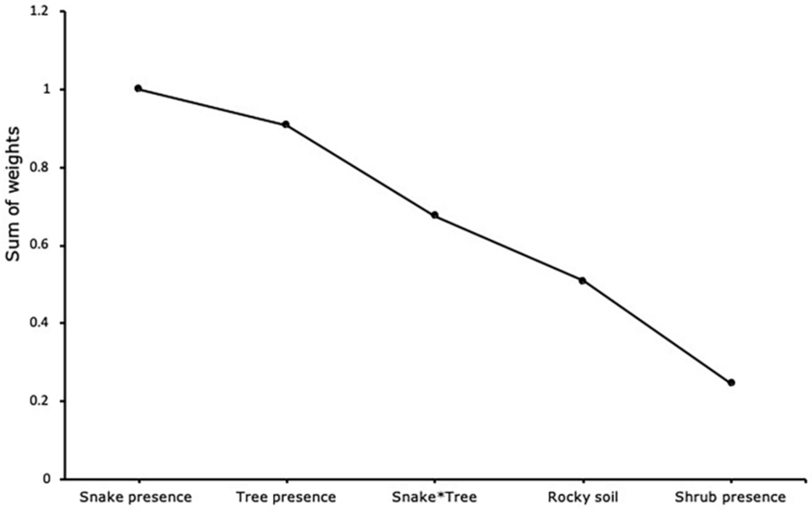


Figure 4. Ranking of the most explanatory variables for lizard abundance on Ibiza, based on the average modeling values of the GLMM. Snake presence and tree presence are the most explanatory variables for lizard abundance.

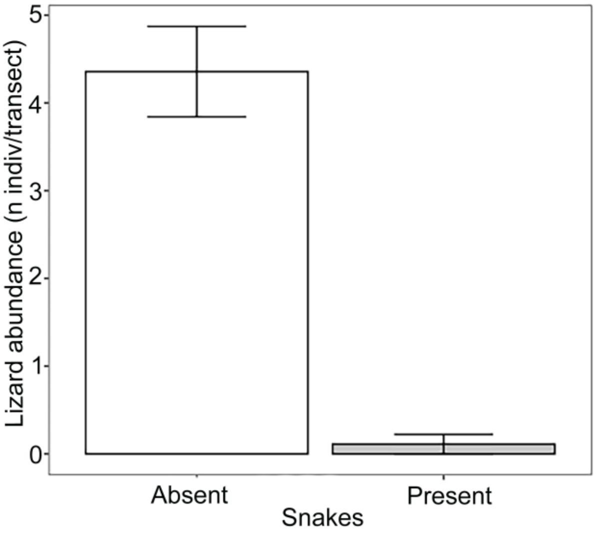


Figure 5. GLMM scores of lizard *P. pityusensis* abundance per transect in relation to snake *Hemorrhois hippocrepis* presence. Boxplots indicate the error in the measurement of the average value for lizard abundance. Whiskers are ±1 SE.

Among the sightings of swimming snakes near islets, one was recorded 1.1km 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 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 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 Grossa and Rodona islets—which share the subspecies *P. pityusensis redonae*—the effect of a medium-sized (approx. 800mm snout–vent length) *H. hippocrepis* spotted on Grossa (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 500m_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, 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

Table S1. Model-selection results for generalized linear mixed models explaining the effect of snake presence, habitat structural variables, and the interaction snake presence*tree presence, on lizard abundance. Presence of a variable or interaction in a model is indicated by the + symbol. Degrees of freedom (df), Akaike information criterion with a correction for small sample sizes (AICc), increase of the AIC (ΔAIC), Akaike weights (ω) and model deviance explained (R2) are presented for each model. Models are ranked by AIC values, and those with ΔAIC < 2 (in bold) are considered good models. All models had negative-binomial error distributions and log link, with survey unit as a random factor.

Model	Intercept	snake	rocky soil	shrubs	trees	snake*tree	df	log Lik	AICc	ΔAIC	ω	R^2
1	**0,7707**	**+**			**0,05239**	**+**	**6**	**-115,932**	**244,9**	**0**	**0,263**	**0.7902**
2	**0,9898**	**+**	**-0,03979**		**0,0818**	**+**	**7**	**-114,787**	**245**	**0,08**	**0,253**	**0.7957**
3	**0,5292**	**+**	**-0,04613**		**0,129**		**6**	**-116,827**	**246,7**	**1,79**	**0,107**	**0.7859**
4	0,7867	+		-0,001049	0,05277	+	7	-115,932	247,3	2,37	0,081	0.7902
5	1,276	+	-0,04096	-0,0182	0,08903	+	8	-114,751	247,3	2,43	0,078	0.7958
6	0,2011	+			0,1012		5	-118,394	247,5	2,61	0,071	0.778
7	1,387	+					4	-120,188	248,9	3,95	0,037	0.7687
8	0,6947	+	-0,04679	-0,01083	0,1337		7	-116,814	249	4,13	0,033	0.7859
9	1,821	+	-0,03047				5	-119,434	249,6	4,69	0,025	0.7726
10	0,09959	+		0,006814	0,09853		6	-118,389	249,8	4,91	0,023	0.778
11	0,3592	+		0,05284			5	-119,789	250,3	5,4	0,018	0.7708
12	0,8084	+	-0,03003	0,0517			6	-119,058	251,2	6,25	0,012	0.7746
13	-2,139			0,2302	-0,1238		5	-165,602	341,9	97,03	0	0.3429
14	-2,285		0,01324	0,2293	-0,1254		6	-165,422	343,9	98,98	0	0.3456
15	-2,814			0,1853			4	-170,172	348,8	103,92	0	0.2701
16	-2,919		0,009116	0,1843			5	-170,084	350,9	105,99	0	0.2716
17	0,685						3	-180,391	367,1	122,16	0	0.0768
18	1,361				-0,05486		4	-179,321	367,1	122,21	0	0.09924
19	1,154		0,01752		-0,05731		5	-178,98	368,7	123,79	0	0.1063
20	0,4828		0,01497				4	-180,139	368,8	123,85	0	0.08212

Table S2. Lizard numbers observed on each of the visited islets surrounding Ibiza (see Figure 1). N is the number of 30-minute time periods invested on each islet; for S'Ora islet three visits were made on three different days.

Islet	Number of lizards		N
	Mean	Range	
S'Ora	0	-	3
Illa Rodona	51	-	1
Illa Grossa	9	-	1
S'Espartar	54	42-77	4
Es Bosc	47	39-55	2
Sa Murada	34	-	1
En Calders	14	-	1
Sa Mesquida	41	-	1
Es Canaret	10	-	1

Table S3. Cats captured on Ibiza hunting grounds by season during the last decade. The location of each hunting ground can be obtained from the IDEIB viewer (https://portalideib.caib.es/portal/home/webscene/viewer.html?layers=656853d6e4944e3bb111798e0c593682). Only hunting grounds with data are included. (Data provided by the Hunting Service of the Ibiza Island Council).

Hunting Ground	Number of cats by season									
	2010 - 11	2011 - 12	2012 - 13	2013 - 14	2014 -15	2015 - 16	2016 - 17	2017 - 18	2018 - 19	2019 - 20
PM-10.559 Salinas	9	12		17	12	12	20	16	18	14
PM-11.029 Portinatx	3									
PM-11.259 San José		76	93		83	112	136	179	220	250
PM-11.438 Balanzat		30								
PM-11.481 Ses Caderneras			19	19	48	68	56	65	104	118
PM-11.485 Portmany	10	20	20	32	20	27	33	50		30
PM-11.652 Es Puig de Baix	9	12	17	17	18	12	22	23	24	20
PM-11.710 Corona										52
PM-11.819 St. Rafel de sa Creu	6	10	16	16	19	12	14	20	20	9
PM-11.877 Es Perdigot	4	8			17	8	14	16	16	9
PM-12.031 Cas Felius	5			8	5	5	4	4		2
PM-12.057 Sa Gravera		14	25	25	22	15	22	30	30	25
PM-12.063 Es Rafal Trobat	5	12			7	14	16	18		
PM-12.086 Cas Puig			3	3	3	3	3	2		
Total	51	194	193	137	254	288	340	423	432	529

Figure S1. The intercepted *Hemorrhois hippocrepis* individual swimming towards S'Ora Islet, Ibiza, on 17 April 2018 (photo: Lauren R. Young).

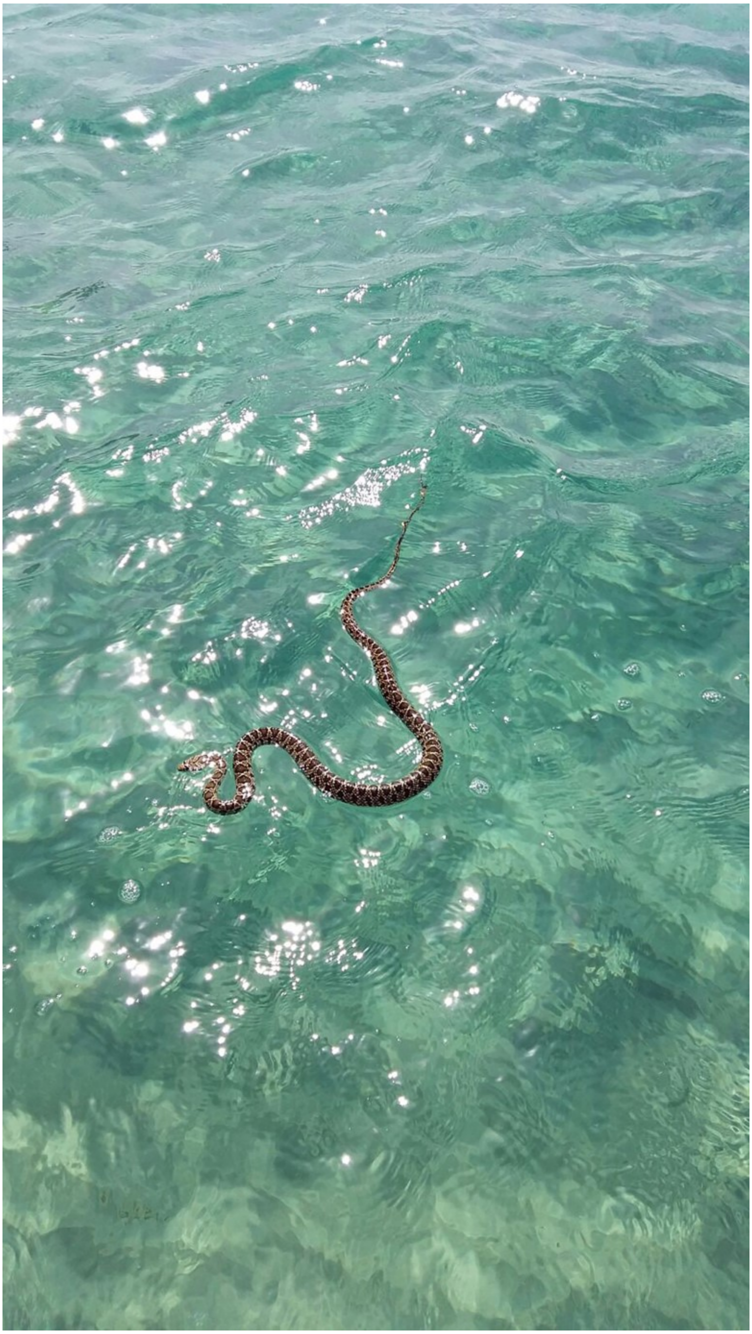

Figure S2. An individual *Hemorrhois hippocrepis* swimming off the coast of Cala de Sant Vicent, Ibiza, on 12 April 2016 (photo: Daniel Ferrer).

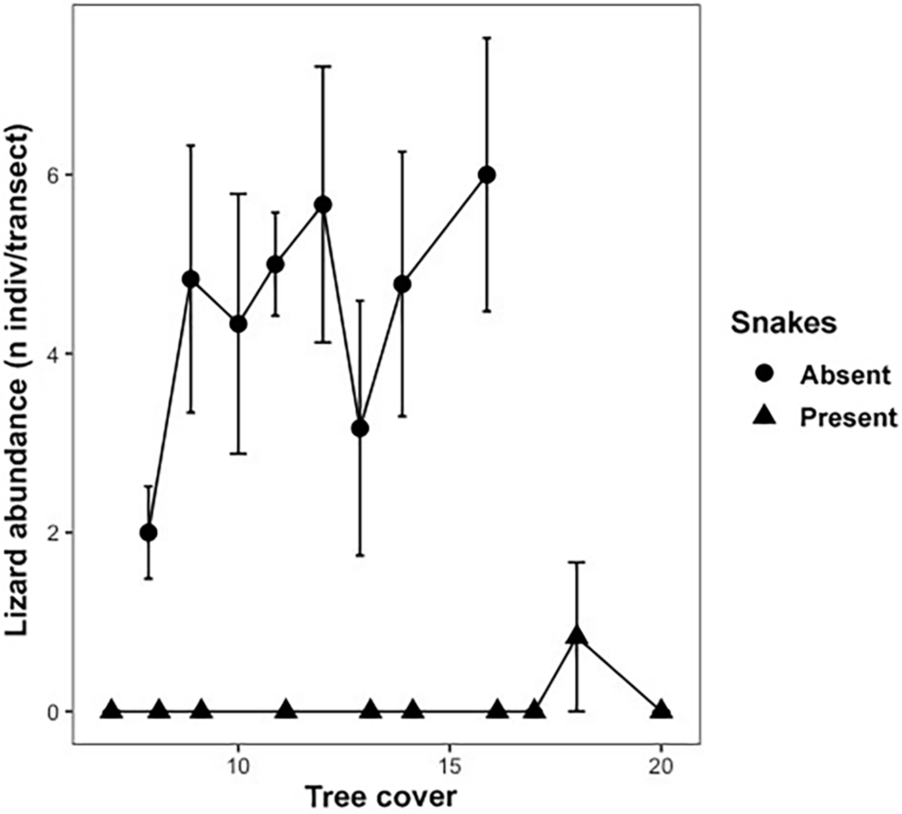

Figure S3. Generalized Linear Mixed Model plots of the interaction between snakes and tree cover for lizard (*Podarcis pityusensis*) abundance from Ibiza. Circles stand for snake absence; triangles stand for snake presence. Symbols refer to mean values and whiskers are ± 1 standard error.

Figure S4. A *Hemorrhois hippocrepis* shed found on 15 September 2019 along the coast of Pou des Lleó, near S'Ora Islet, Ibiza (photo: A. Cirer).

Video S1. An individual *Hemorrhois hippocrepis* swimming off the coast of Port de Sant Miquel beach, 1.1 km away from Sa Murada islet, Ibiza, on 12 June 2020 (video: Christian Braun).

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

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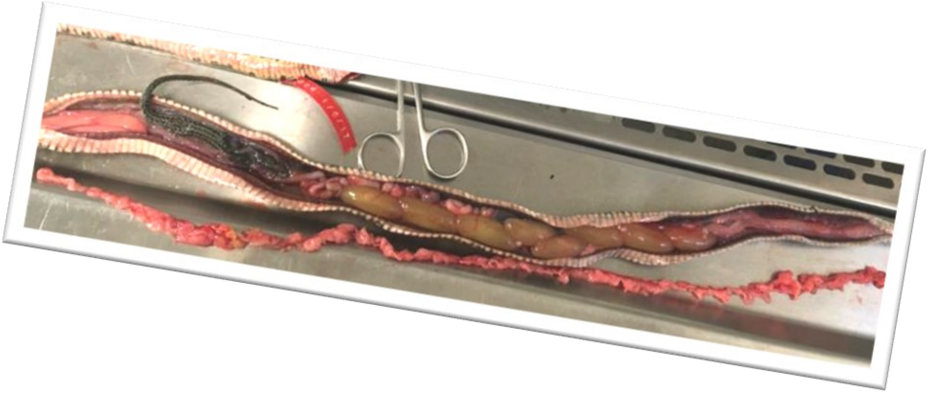
Chapter 3: REPRODUCTION ECOLOGY



Reproduction ecology of the recently invasive snake *Hemorrhois hippocrepis* on the island of Ibiza

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Abstract

Knowing the causes of biological invasion success can be relevant to combat future invasive processes. The recent invasion of the horseshoe whip snake *Hemorrhois hippocrepis* on the island of Ibiza provides the opportunity to compare natural history traits between invasive and source populations, and to unravel what makes this snake a successful invader that is threatening the only endemic vertebrate of the island, *Podarcis pityusensis*. This study compares the basic reproductive traits of mainland native and invasive populations of the snake. Our results revealed that invasive populations were characterized by female maturity at a smaller size, extended reproductive period, and much lower reproduction frequency compared to the native population. In contrast, some major reproductive traits—the abdominal fat body cycle, clutch size, hatchling body size, and hatchling body condition, did not differ between the two populations. Some of these results must reflect the environmental differences in the recently invaded island with respect to the source area, and overall plasticity of reproductive traits. Plasticity is evolutionarily interesting, and may aid the successful growth of this species in their invasiveness of Mediterranean islands like Ibiza. The most significant finding is that this expression of phenotypic plasticity occurred rapidly in this invasive population, within a period of 14 years maximum. Our results on the reproduction ecology of the invasive population were not conclusive regarding the factors determining the invasiveness of the snake and pointed to alternative causes.

Key words: Ibiza, invasion success, islands, reproduction frequency, snakes

Introduction

Invasive species affect ecosystems around the planet, mostly threatening island species (Jones et al. 2016), which are particularly vulnerable due to their inherent characteristics. Island species have evolved in relatively isolated conditions, and are adapted to fit the typically innocuous insularity of their environment; newcomers to islands, however, are usually more efficient than native species (Cohen 2002; Simberloff et al. 2013). Therefore, knowing the possible causes of success regarding biological invasions would give us accurate predictions for invasive processes as well as efficient control and eradication mechanisms for non-indigenous species (Jeschke and Strayer 2006; Hayes and Barry 2008; Rödder et al. 2009; Mahoney et al. 2015).

Diverse factors have been tested in order to determine a causal effect with invasion success, like the reproductive traits of invader species (Cohen 2002): early sexual maturity has been reported as a facilitator of establishment for the invader turtle *Trachemys scripta* in Southern Europe (Pérez-Santigosa et al. 2008). Evidence for the expansion of the reproduction period or disappearance of reproduction seasonality has been described in the invasive population of the snake *Boiga irregularis* in Guam (Savidge et al. 2007). A greater portion of the population reproducing every year, which implies an increase in reproductive frequency, also happens in the case of *T. scripta* (Pérez-Santigosa et al. 2008). Fecundity rise is also an observed feature in invaders that contributes to their success (Mahoney et al. 2015), as demonstrated with the case of *Lithobates catesbeianus* (Kaefer et al. 2007) along with other aquatic invasive animals in North America (McMahon 2002). Lastly, the neonate size of the invasive snake *B. irregularis* is larger in the invasive population in Guam than in the native population (Rodda and Savidge 2007).

The aforementioned cited shifts on reproductive traits can im- prove the fitness of organisms, and some of them are expected to be displayed by invasive populations when compared to the source populations of the same species. However, it is not the general rule, and none of the invasive species presented all the shifts at the same time (Parker et al. 2013). For instance, sexual maturity is delayed in the populations of the invasive treefrog *Osteopilus septentrionalis* in the South-eastern United States (McGarrity and Johnson 2009), and females of *B. irregularis* do not appear to increase reproduction frequency in the invasive population of Guam (Rodda and

Savidge 2007). With respect to productivity, the *Coccinella septempunctata* beetle lays larger clutches with smaller eggs in the invasive populations of North America (Kajita and Evans 2010), and the invasive *Lampropeltis californiae* in the Canary Islands showed low levels of juvenile recruitment (Fisher et al. 2019).

Therefore, there is an accelerating need to study to what extent reproductive traits can aid invasive population success; understanding the mechanisms of a particular invasion can help managers take actions against it. The recent invasion of the island of Ibiza (Balearic Islands) by the Horseshoe whip snake *Hemorrhois hippocrepis* from the southern Iberian Peninsula yields a good opportunity to study and determine whether reproduction ecology is behind the quick expansion of the invasive population (Fisher et al. 2019). Snakes as invaders frequently cause drastic impacts on the environment (Willson 2017). Moreover, they exhibit such a broad diversity in their intraspecific reproductive strategies (Shine 2003), that this group is considered a model taxa for studies of reproductive ecology (Shine and Bonnet 2000). In parallel, the study of invasive populations offers the opportunity to understand basic processes in natural history (like reproduction), thanks to the velocity of the changes exhibited by invasive organisms (Sakai et al. 2001).

The Balearic archipelago, in the Mediterranean Sea, has been isolated from the mainland for 5.33 million years. Later, it suffered severe climatic oscillations that influenced species range and extinctions (Bover et al. 2008). In Ibiza, the westernmost of the Balearic Islands, a sudden mass extinction occurred during the Pleistocene that is yet to be explained (Alcover and McMinn 1993). Consequently, the only non-flying vertebrates found in the fossil records right after this event are two reptiles: an undescribed dwarf viper (Alcover JA, personal communication) and the Ibiza wall lizard *Podarcis pityusensis*, the latter being the only extant endemic reptile to Ibiza Island.

During the end of the 3rd millennium BCE, humans colonized the islands and the introduction of alien species began; human-mediated extinctions started taking place (Pinya and Carretero 2011), among them, the case of the dwarf viper. By the beginning of the third millennium CE, there were consistent importations of big and old olive trees from the south of the Iberian Peninsula, which inadvertently caused a surge of stowaway snakes, in a process of multiple introductions at a rather high propagule pressure during several years (Silva-Rocha et al. 2018): *Malpolon monspessulanus*—the Montpellier snake, *Zamenis scalaris*—the ladder snake, and *H. hippocrepis* (Álvarez et al. 2010). *Malpolon monspessulanus* first disappeared from the island of Ibiza a few years after the intro- duction, *Z. scalaris* maintains a small and stable population, and *H. hippocrepis* is thriving well and spreading quickly throughout the lowlands of the island (Silva-Rocha et al. 2018), occupying an empty functional niche.

Hemorrhois hippocrepis is a slender-bodied, medium to large-sized colubrid, native to north-western Africa and southern Iberian Peninsula, also present in some Mediterranean islands, where it was probably introduced (Pleguezuelos and Feriche 2014). It is a rupicolous snake that usually prowls human dwellings and masonry stone walls, which are used for shelter and foraging (Pleguezuelos and Feriche 2014), man-made and rather simplified habitats that may be favorable for the invasive population (Sakai et al. 2001). The importance of controlling the fast spread of *H. hippocrepis* on Ibiza island lies in the major impact it poses for the only Ibizan endemic vertebrate, *P. pityusensis*, the most consumed prey of the invasive snake on the island (57% in frequency; Hinckley et al. 2017). Indeed, reptiles are not only among the most introduced vertebrate species in Mediterranean islands, but also among the most affected by the introduction of other reptile species (Kraus 2009). However, when studying the feeding ecology of the invasive Ibizan *H. hippocrepis*, we found puzzling results that hardly account for the success of the Ibiza invasive population; despite a rather low percentage of individuals with gut content while maintaining a high body condition

(Hinckley et al. 2017). Hence, we searched for other aspects of the snake's natural history, such as its reproductive ecology, that could help us in our understanding of its invasion success as well as in the management of these populations.

The reproduction ecology of *H. hippocrepis* is well known in its native area, including the region where the invaders come from (Pleguezuelos and Feriche 1999). These circumstances offer an excellent opportunity to investigate the degree of potential plasticity of the reproductive traits (Ajtić et al. 2013), and whether the reproductive ecology of the snake is an alternate explanation of its invasion success on the island of Ibiza. In invasive reptiles reproduction is a natural history aspect scarcely ever addressed (Kraus 2015). In addition, just a decade after the first reference to the invasion, some expressions of phenotypic plasticity were observed, like an increase of the maximum body size and the level of fat reserves (Montes et al. 2015; Hinckley et al. 2017). In snakes colonizing islands, body size shifts at a fast pace with respect to the source population (Aubret 2015), and populations with easy access to prey exhibit fast growth and high fecundity (Bronikowski and Arnold 1999). Thus, it is likely that the reproductive ecology of *H. hippocrepis* is already being affected to complement the new phenotypes on the island of Ibiza.

The main goal of this study was to assess whether any trait of the reproductive ecology of the invasive population of *H. hippocrepis* in Ibiza has changed with respect to the source population in the southern Iberian Peninsula. For both sexes, we compared the body size at sexual maturity, the timing of the reproductive cycle, the monthly variation of fat bodies in relation to the reproductive cycle, reproductive frequency and clutch size in females, and newborn size, that is, traits whose variation can also modify fitness in invasive populations (Parker et al. 2013). Our hypotheses are the following: 1) in females, maturity will be reached at the same body size in the invasive and in the source populations, given that in snakes the mother needs a minimum abdominal space to allocate the eggs

(Seigel and Ford 1987); 2) we expect an extension of its reproductive season, favored by warmer thermal envelopes, compared to the mainland population (Shine 2003; Mathies 2016). This is due to the fact that the invasive snake is spreading exclusively on the warm lowlands of the island, whose thermal conditions are different with respect to the southern Iberian Peninsula, and that the reproductive traits of ectothermal organisms may change due to variation in the thermal environment (Huey 1982); 3) we expect that mature snakes on the island do not skip opportunities to reproduce and do so on a yearly basis (Seigel and Ford 1987), due to the excellent body condition of most mature females (Hinckley et al. 2017) and being that reproduction frequency in temperate snakes relies upon this parameter (Bonnet et al. 2001); 4) since we are observing gigantism in the insular population (Hinckley et al. 2017) and fecundity is related to the mother's size (Shine 1992), particularly in *H. hippocrepis* (Pleguezuelos and Feriche 1999; Pleguezuelos and Fahd 2004), we expect larger clutch sizes for the invasive than for the mainland population (topic reviewed in Parker and Plummer 1987); 5) in an alternative but not exclusive way, invasive females, because of their excellent body condition, will produce larger hatchlings and/or in better body condition (Ford 2011; Tuttle and Gregory 2014). These changes refer to the acquisition of fast reproductive traits (Tuttle and Gregory 2014; Allen et al. 2017) and would provide evidence on the success of the invasion process (Sax et al. 2007), a topic that has been scarcely addressed previously in snakes between source and introduced populations (Fisher et al. 2019; but see Reed 2005; Rodda and Savidge 2007).

Materials and Methods

The island of Ibiza is within the Balearic archipelago, in the Western Mediterranean Sea. It has an area of 572 km^2, and is rather flat, with a maximum altitude of 486 m asl. The mean annual temperature is 17.9°C and the average yearly rainfall 413 mm (Ibiza Airport weather station, 38° 52' 22" N, 1° 22' 23" E; www.aemet.es). The landscape is shaped by pine forests and cultivated land, with alternating scrubland. Thousands of houses are scattered throughout the island, with stone walls frequently delimiting gardens and crops, both landscape traits favorable for *H. hippocrepis*.

Individuals for this study come from eradication campaigns of *H. hippocrepis* on the island (2014–2017 period), fostered by the Regional Administration, together with road kills and specimens collected by the locals. Specimens were euthanized in the field, right after the capture, with a pentobarbital injection in the heart, and preserved in ethanol in the collection of the Granada University (DBAG). In total, 545 specimens from Ibiza (224 females, 261 males, and 60 immature of undetermined sex) were examined. Comparisons with the characteristics of the source population were made by using raw data from Pleguezuelos and Feriche (1999), updated with other specimens from the DGAB collection, from the same area of the Southern Iberian Peninsula, and processed by the same protocol here explained (477 specimens: 167 females, 182 males, and 128 immature). Before fixation and preservation, snout- vent length (SVL; ±1 mm) and body mass (±0.1 g) were measured. Gonads were examined by making a ventral incision and the following variables were measured after fixation: sex (male, female, or un- determined). In females, we recorded the number of ovarian follicles or oviductal eggs on each side, the biggest diameter of each follicle or oviductal egg (±0.1 mm) and the presence of oviducts with emptied but distinct, incubation chambers (indicative of postpartum condition; Almeida-Santos et al. 2014); in males, sagittal, transverse, and longitudinal axis of the right testis (±0.1 mm), anterior in the body and larger than the left one. Measurements were only taken from well-preserved specimens and organs, which resulted in some variability in the sample size of the traits. Testicular volume (TV) was obtained using the formula for a flattened ellipsoid (Mayhew 1963). In females, size at maturity was graphically estimated by plotting the length of the largest vitellogenic follicle/oviductal egg against maternal body size (SVL; Figure 1A), and by the presence of oviductal eggs or folded oviducts; in males maturity was graphically deduced by plotting Relative testicular volume (RTV; residuals of the correlation between log TV on SVL) to the male body size (Seigel and Ford 1987; Figure 1B), and by the presence of convoluted ductus deferens. The reproductive cycle was deduced by plotting the length of the largest follicle/oviductal egg, and the RTV against the days of the year (Julian calendar), for sexually mature females and males, respectively (Figure 2). These three deductions were made based on the point at which follicle diameter or RTV suddenly increases, which indicates the beginning of the reproduction activity (sexual maturity or reproductive period). We also recorded when the oviducts were glandular and folded or the ductus deferens thickened. In both sexes, we recorded fat body reserves by scoring abdominal fat body level in five visual categories according to Pleguezuelos and Feriche (1999): zero, no traces of fat; one, small traces of fat among intestine loops; two, fat bodies covering less than half of the intestinal surface; three, fat bodies covering more than half of the intestinal surface; and four, a continuous fat layer on the ventral zone of the abdominal cavity. Body condition index (BCI) is a good estimator of body reserves in snakes (Santos and Llorente 2004), and in general, individuals with better BCI usually increase future survival (Giesel 1976). We estimated the BCI (residuals of log body mass [g] on log body length [SVL in mm]; Whittier and Crews 1990) in hatchlings (individuals not damaged by traffic casualty) from the source and the invasive populations. We considered hatchlings only those individuals within 15 days before and after the average hatching date (10 September), maintaining a fresh vitellogenic scar and without gut content.

Sexual dimorphism in body size (SVL) was assessed by using a Mann–Whitney U test, because of differences between groups in the variances. Student *t*-test was used to compare SVL between the group of mature females within each population that reproduced and the group that did not, as well as between the group of mature males that accomplished spermatogenesis and the group that did not. The clutch size was compared between groups by ANCOVA (maternal SVL as a covariate). Homogeneity of fat bodies among months was tested by the Kruskal–Wallis test. The percentage of reproductive females (gravid and with oviductal scars indicating recent oviposition) in the appropriate period was taken as a measure of the reproduction frequency and was compared between study areas and to biennial theoretical reproduction by a 2 x 2 contingency table. Mean values are followed by ±1 SD, with alpha set at 0.05. Statistical analyses were carried out by the program STATISTICA version 8.

Results

Size at maturity

The mean SVL of the Ibizan *H. hippocrepis* was 723.4 mm (±216.5 mm, range = 239–1499 mm, n = 485), females being on average shorter than males (661.4 ± 177.1 mm, range = 239–1305, n = 224 versus 776.6 ± 232.7 mm, range = 283–1499, n = 261; U = 21004.0, $P < 0.0001$; all individuals considered). The young females of any month and all adult females from late June to late April (out of the vitellogenesis period) exhibited follicles <8 mm maximum diameter (primary vitellogenic follicles). A female with oviductal eggs was 628 mm SVL, and several females just above this size showed secondary vitellogenic follicles or oviductal eggs (Figure 1A). Thus, we consider that maturity is reached at approximately 628 mm SVL in females. Female sexual maturity was reached at 48% of the maximum SVL on Ibiza, whilst at 63% in the source population (the smallest mature Iberian female was 665 mm SVL).

Males from Ibiza strongly increased RTV at 500 mm SVL (Figure 1B), at which we estimated sexual maturity is achieved. Even though a male with 431 mm SVL (DBAG HEMO-670) had relatively big and turgid testis, we considered this specimen as an exception. Sexual maturity was reached at

33% of maximum SVL and on the south of the Iberian Peninsula it was reached at the same SVL (500 mm), but at 39% of the maximum body size (SVL).

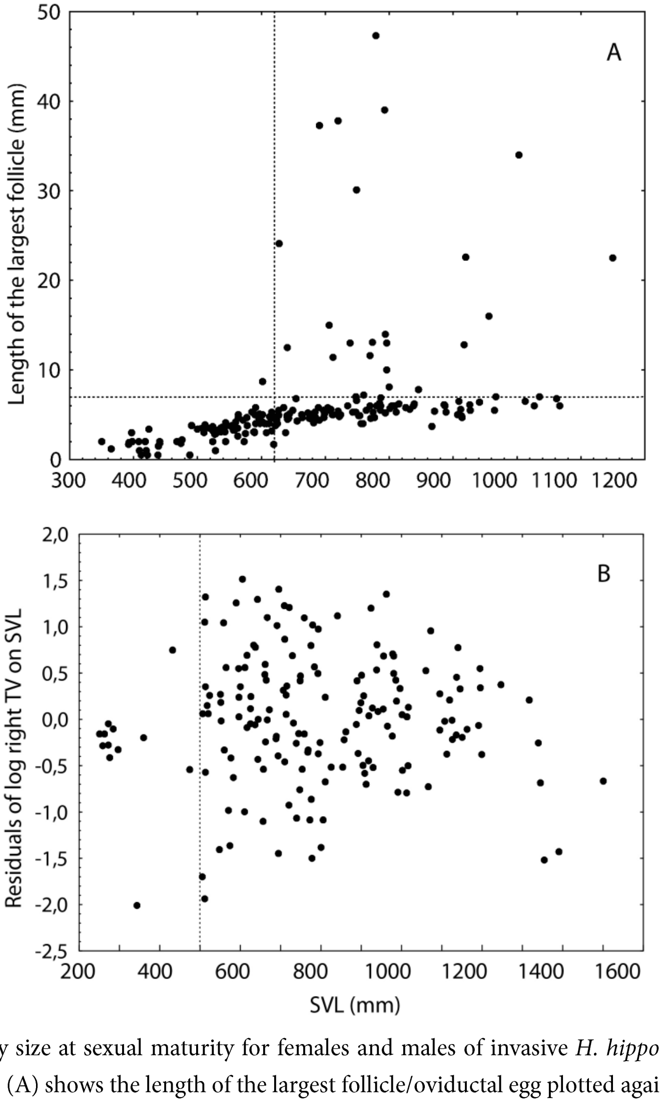

Figure 1. Body size at sexual maturity for females and males of invasive *H. hippocrepis* on the island of Ibiza. (A) shows the length of the largest follicle/oviductal egg plotted against body size (SVL; *n*=204). Dashed horizontal line tentatively separates between primary and secondary vitellogenic follicles or oviductal eggs; dashed vertical line tentatively separates between immature (on the left) and adult females. (B) shows residual scores of the right testis volume (log-transformed) on SVL plotted against body size (SVL; *n*=171). The vertical dashed line tentatively separates immature (on the left) from mature males. Each point represents one individual.

Reproductive cycles

Females with enlarged follicles (≥8 mm) and expanded and/or folded gonoducts were found throughout the year, with very large follicles (≥14 mm) or oviductal eggs from late April to late July, and with fully developed oviductal eggs (≥38 mm) and oviductal marks of recent oviposition from late May to late July (Figure 2A); thus, we deduced oviposition occurred during June and July.

Testicular recrudescence of mature males (SVL >500 mm) started in mid-March, with the highest peak of RTV in June, and declined through July. Some individuals showed a small testicular recrudescence between the end of September and October, suggesting a secondary spermatogenesis period (Figure 2B). From that plot, we also calculate that every year, 59.3% (70 out of 118 individuals in the plot) of males from Ibiza island with body size large enough to be adults did accomplish spermatogenesis; there were no significant differences in body length between those which accomplished spermatogenesis and those which did not ($t = 1.36$, $P = 0.18$). The frequency of mature males in spermatogenesis was not significantly different in the south of the Iberian Peninsula either (70%, $n = 46$; 2 x 2 table, $\chi^2 = 1.48$, $P = 0.22$).

Female reproductive frequency

Among the 58 adult females from the period of mid-April to mid-August, 29 showed enlarged follicles (>10 mm), oviductal eggs, or clear signs of recent oviposition, meaning that 50% of adult females reproduce every year. Some females with SVL slightly larger than 628 mm but with very small follicles and low-fat body levels were considered still immature and not included in this calculation. SVL of these reproductive females (812.3 ± 122.7 mm, $n = 29$) did not differ from that of the subsample of non-reproductive females in the same period (763.2 ± 89.8 mm, $n = 29$; $t = 1.74$, $P = 0.09$), indicating that this result was not affected for the different size of the specimens in the two subsamples. This frequency of reproduction is below that observed for the south of the Iberian Peninsula (82.6%, $n = 23$; in a comparison between regions of the frequency of reproductive females; 2 × 2 table, $\chi^2 = 5.97$, $P = 0.01$), and fits to a biennial reproduction frequency (2 × 2 table, $\chi^2 = 0.00$, $P = 1$).

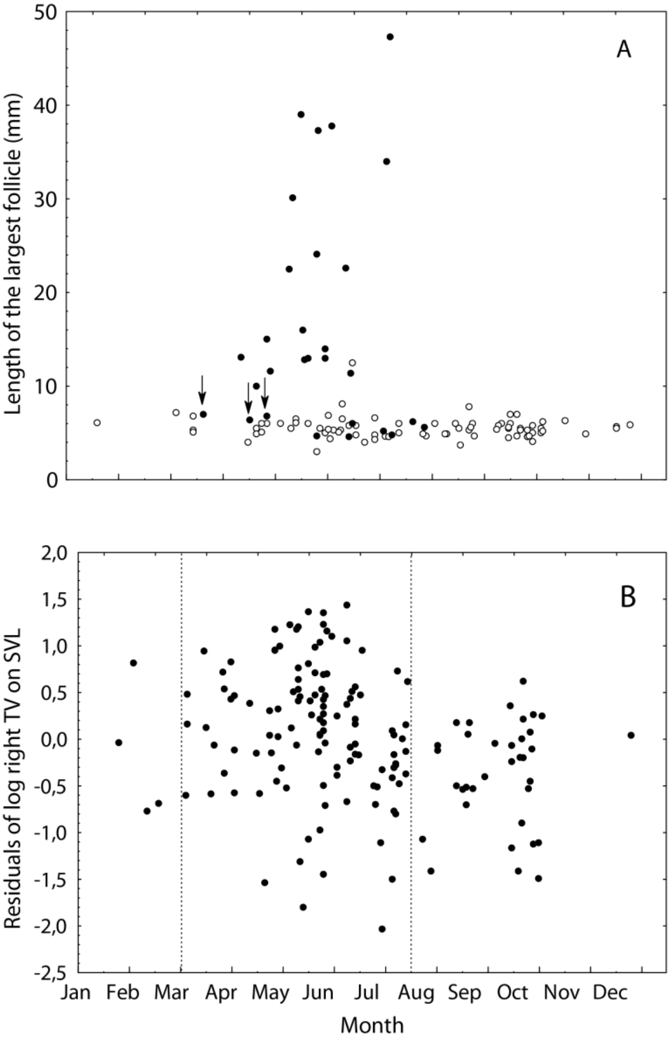

Figure 2. Reproductive cycles of invasive *H. hippocrepis* on the island of Ibiza. (A) shows the length of the largest follicle or oviductal egg in females plotted against the day of the year (only potentially adult individuals, SVL>628mm; *n*=110); empty circles represent non-reproductive females whereas full circles show reproductive females. Three specimens from spring, with no

developed follicles, were considered as reproductive females because of maximum fat-body levels and the presence of folded oviducts (indicated by arrows). Full circle cases within the cloud of empty circles correspond to individuals with oviductal scars and/or folded oviducts. (B) shows residual scores of the right testis volume (log-transformed) on SVL plotted against the day of the year (only potentially adult individuals, SVL>500mm; *n*=157). Vertical dashed lines are intended to mark the beginning and end of spermatogenesis. Each point represents one individual.

Abdominal fat bodies

Sexually mature females showed a mean fat body level of 2.77 ± 1.14 (N = 116), and sexually mature males 3.24 ± 0.95 (n = 231). Mature but non-reproductive females reached maximum fat-body levels throughout the spring, explained by the fact that they do not invest their fat reserves on vitellogenesis, whereas reproductive ones attained elevated fat-body levels at the beginning of the spring, decreased during June and were minimum in July and August, showing that vitellogenesis does have a cost on fat reserves (Figure 3A). In an inter-monthly comparison, fat-body levels were homogeneous in mature but non-reproductive females (Kruskal–Wallis test, $H_{8,\ 87} = 8.60$, $P = 0.34$), different in reproductive females (Kruskal–Wallis test, $H_{4,\ 29} = 18.04$, $P = 0.0012$), and heterogeneous in males (Kruskal–Wallis test, $H_{8,\ 231} = 26.79$, $P = 0.008$), with maximum level during the period May–July (Figure 3B).

Clutch size

The maximum clutch size for the Ibiza population was 13 (Figure 4), larger than in the source population (11), and the mean clutch size was 6.9 ± 2.9 (n = 9), but did not differ from the same parameter in the source population (6.5 ± 2.4, n = 13). These results hold in absolute ($t = 0.309$, $P = 0.75$) and relative terms (ANCOVA, with clutch size as dependent variable, maternal SVL as covariate, and region as grouping factor, F = 0.41, $P = 0.53$; homoskedasticity of the variances, $P < 0.401$; slope of the regression lines, $P = 0.853$; Figure 4).

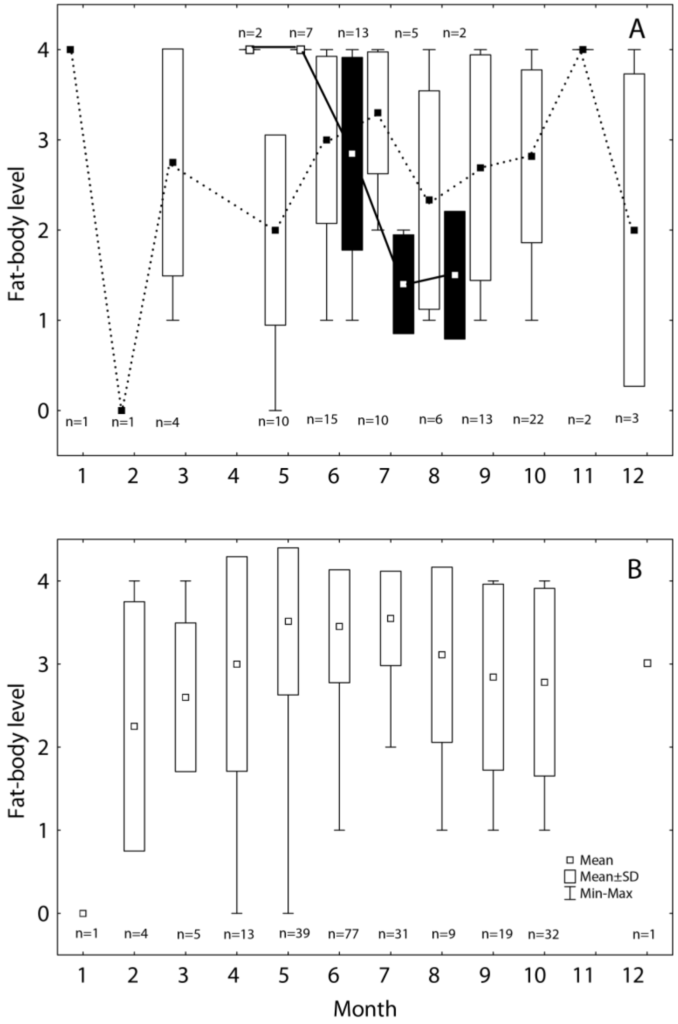

Figure 3. Abdominal fat-body level of sexually mature female (A) and sexually mature male (B) *H. hippocrepis* on the island of Ibiza. For the period April- August we differentiate between reproductive and non-reproductive females, black box-plots represent reproductive females and empty box-plots show non-reproductive females. Fat-body level is scored in five categories, from zero to four (see “Material and Methods” section for more details). Females *n*=116, males *n*=231. In both sexes, successive winter months pooled because of a small sample size.

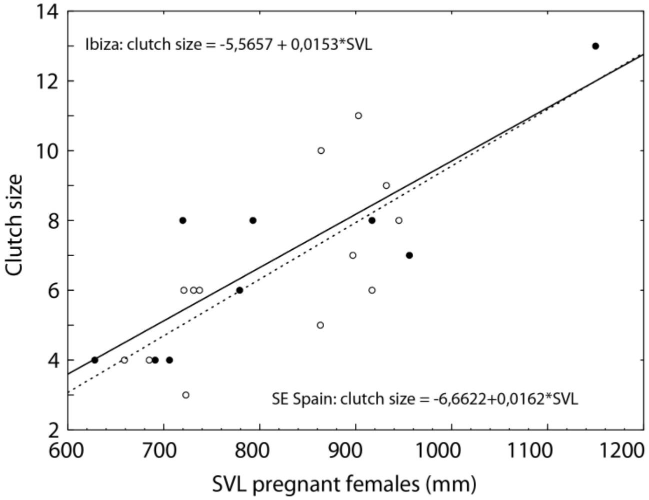

Figure 4. Linear regression between clutch size and maternal SVL of *H. hippocrepis* for the invasive population on the island of Ibiza (solid circles and continuous line, *r*=0.866; *P*=0.002) compared to the source and native population from the south of the Iberian peninsula (empty circles and dashed line, *r*=0.708; *P*=0.006).

Hatching period and offspring size

On the island of Ibiza hatchlings were found in the field from the end of August, with mean SVL of 282.9 ± 27.8 mm (range 250–325 mm; *n* = 13) and mean body mass of 6.9 ± 2.4 g (range = 4.2–10.8 g; *n* = 13). There was no difference in SVL neither in body mass from hatchlings from the source population (277.9 ± 24.3 mm, *n* = 11, *t* = 0.46, *P* = 0.64; and 5.7 ± 1.5 g, *n* = 10, *t* = 1.37, *P* = 0.18, respectively for SVL and body mass). There was no significant difference in BCI between Ibizan and Iberian hatchlings (0.051 ± 0.11, *n* = 13 versus −0.067 ± 0.20, *n* = 10; *t* = 1.82, *P* = 0.08).

Discussion

The invasive population in Ibiza shows some differences in reproductive traits with respect to the source population: maturity is attained at smaller body size in females, the reproductive season is longer, and fat body levels are higher in both sexes (see Pleguezuelos and Feriche (1999) for data of the source population). However, female reproductive frequency is lower, and there are no differences in body size at maturity in males, absolute or relative clutch size, hatchling body size, or hatchling body condition. Whilst the results for the first set of reproductive traits could be supporting the invasion success, some of the latter, vital for population fitness, suggest slow reproductive traits that do not help to explain invasion success.

Size at maturity

Regarding the female body size at which sexual maturity is acquired, our hypothesis is not met. Reproduction represents a risk for female survival regardless of their offspring productivity (Aldridge and Duvall 2002); hence, natural selection forces females to attain a minimum body length to reproduce, which implies a minimum clutch size that overcomes the risks of their first reproductive period (Seigel and Ford 1987). For this reason, we expected females from both populations to become sexually active at the same body length. However, we found smaller reproductive females in Ibiza than in the source population. This suggests a shorter time from hatchling to the age at which reproduction occurs, although we have no data on the growing rate of the individuals. Ford and Seigel (1994) found in the oviparous *Elaphe guttata* that neither age nor size of first reproduction was fixed; Cardozo and Chiaraviglio (2011) found in *Boa constrictor* that females from healthy environments mature at smaller body sizes than those from poor environments; the population of the Lake Erie Water Snake *Nerodia sipedon insularum* accelerated its sexual maturity and raised its offspring production after starting to feed almost exclusively on a newly arrived and abundant, invasive prey, proving that an improvement in diet can actually enhance the reproductive characteristics of a population only in a one or two-generation lapse (King et al. 2006). Something similar may have happened in Ibiza (at least in body size, as we do not have data on age), since the invasive population of *H. hippocrepis* has shifted its diet toward naïve and abundant prey, especially the endemic *P. pityusensis*; the excellent body condition showed by snakes of this population (Hinckley et al. 2017; body condition data in this study) supports this interpretation. In males, the lack of differences in body size at maturity would be just a consequence of less important trade-offs between sexual maturity and other natural history traits, compared to females (Cardozo and Chiaraviglio 2011).

Reproductive cycles

As we hypothesized, the reproductive period expanded in both sexes in the invasive population compared to the source one, representing a fast manifestation of phenotypic plasticity in one of the reproductive traits. Vitellogenesis advanced 1 month and oviductal eggs got delayed by one week compared to populations on southern Iberian Peninsula (Pleguezuelos and Feriche 1999), meaning that the invasive population has expanded the laying period. In temperate reptiles, reproduction seasonality is forced by the thermal requirements of embryogenesis (Vitt and Vangilder 1983), besides, *H. hippocrepis* is a very thermophilic snake. The species shows quite high thermal needs in order to perform its peculiar vernal spermatogenesis, a typical cycle on the warm southern belt of the Mediterranean Basin (Saint Girons 1982), where the species originated (Carranza et al. 2006). The invasive population's use of a wider reproductive window may be explained by Ibiza's favorable climate and habitat. This may allow the population to be less strict regarding their original reproduction boundaries. The same has been observed in the round goby *Neogobius melanostomus* in the Upper Detroit River (MacInnis and Corkum 2000), in the introduced population of *Anolis sagrei* in Taiwan (Norval et al. 2012), and in the well-known invasive *B. irregularis* in Guam (Rodda and Savidge

2007), whose males switch between synchronized seasonal reproduction and asynchronous continuous reproduction (Mathies et al. 2010); this generally occurs in snakes of tropical environments (Mathies 2016). Future eradication campaigns on *H. hippocrepis* in the island of Ibiza can take advantage of the precise knowledge of its reproductive seasonality in the invaded area.

Reproductive frequency

Given the optimal environmental conditions (Seigel and Ford 1987) and since most adult females showed high-fat body level at the start of the breeding season on Ibiza (Figure 3A), we hypothesized that all adult female individuals of the invasive population would reproduce every year. However, reproductive frequency is significantly lower than on the source population in the Iberian Peninsula (Pleguezuelos and Feriche 1999; this study), to the point of being biennial. The male gametal production on the island population, as measured by the frequency of mature males in spermatogenesis, is statistically similar, but with a high portion of males not accomplishing spermatogenesis on Ibiza (40.7%, reproductive cycles "Results" section). Nonetheless, the absence of spermatogenesis is not determinant to dismiss sexual activity, as the sperm might be stored in the ductus and males would fecundate females by sperm produced in the previous season or year (Saint Girons 1982). In addition, mature males might not accomplish spermatogenesis in sequential years because females usually store sperm from from previous matings in their ovi- ducts (Almeida-Santos et al. 2004), as recorded for this species in captivity (Cattaneo 2015). These possibilities can only be tested out by histological examination.

Regarding the rather small amount of reproductive females found in Ibiza, female snakes carrying eggs tend to decrease their locomotory capacity and perform a secretive behavior (Shine 1980; Gregory et al. 1999) that makes them less vulnerable to being captured, producing a bias toward non-pregnant females in field surveys (Fitch 1987); Bonnet and Naulleau (1996) found the opposite in a viper, with a higher catchability in pregnant females. However, these biases, if they occur in *H. hippocrepis*, must happen on both populations, the source and the invasive one, and therefore, it does not explain the results here obtained. Low reproduction frequency has been described for the invasion-front population of cane toads *Rhinella marina* in Australia, suggesting a trade-off where the costs of reproduction are too elevated to achieve an effective dispersal (Hudson et al. 2015). Indeed, scarcity of pregnant females seems to be a common and not well-understood characteristic of invasive organisms, particularly snakes (Savidge et al. 2007), as it happens with *B. irregularis* on Guam (Rodda and Savidge 2007), although in the reptiles there is a clear advantage of frequent clutches for the success of introduced species (Allen et al. 2017).

Fat bodies and clutch size

We knew that fat reserves on the invasive population were much higher than on the source population of *H. hippocrepis* (Hinckley et al. 2017), a circumstance opposite to that observed for invasive *B. irregularis* in Guam (Rodda and Savidge 2007). In this study, we expected to find fat reserves vary, according to the reproduction phases, as usual in temperate snakes (Seigel and Ford 1987). In our study this variation was only evident when differentiating non- reproductive females from reproductive females of the invasive population, the former group showing rather homogeneous and high abdominal fat body levels, indicating an absence of investment on vitellogenesis; furthermore, this fact proves that the choice of not reproducing is not linked to the lack of feeding resources, opposite to what happens for other Eurasian snake species (Pleguezuelos et al. 2007). The group of reproductive females does show a variation that perfectly matches the vitellogenic processes: maximum levels at the beginning of spring and, as follicles are developing during May and June, fat reserves decrease until July and August, when eggs have been laid. The high level of abdominal fat bodies at the beginning of spring suggests a capital strategy (*sensu* Drent and Daan 2002) to fuel vitellogenesis and oogenesis in the invasive females; however, the presence of prey in the gut content during pregnancy (Hinckley et al. 2017) also suggests an income strategy, in which snakes produced better body condition and higher survivorship of females after reproduction (Feriche et al. 2016). For invasive males, there is indeed a variation on fat reserves, but spermatogenesis does not have an impact on their lipid stores (see Mathies et al. 2010 for similar results in the introduced *B. irregularis*); conversely, the fat body levels increase as the spermatogenesis does, and do not seem to be affected by the males actively searching for females in late spring (Pleguezuelos and Feriche 2014). In brief, the results from the study of fat body levels do not support that energetic constraints are be- hind the low reproduction frequency in both sexes of the invasive population. The increased weight in the invasive snake population of *L. californiae* on the Canary Islands, has been also suggested to be tied to their predation success on naïve prey (Fisher et al. 2019), the same that could be occurring for *H. hippocrepis* on the island of Ibiza.

Despite the good body condition of mature females from the invasive population, the results do not meet our hypothesis on the clutch size; the important accumulation of fat reserves in the invasive population seems to not be diverted into energy for reproduction, and the clutch size failed to differentiate from the same trait on the source population. Although a very large invasive female had the largest clutch recorded for the species in the wild, the female size to clutch size relationship was maintained in the comparison between populations, suggesting that this trait is somewhat genetically fixed for this rather slender bodied snake. In Florida, the invasive potential of *Python bivittatus* is determined by its large size and high reproductive potential (Reed et al. 2012; see Allen et al. 2017 for an interspecific analysis of this topic), but the invasive population of *B. irregularis* on Guam showed smaller values of clutch size than in the native populations, even though invasive snakes were larger (Savidge et al. 2007).

Apparently, the invasive success of *H. hippocrepis* on the island of Ibiza does not rely on a larger clutch size for females with very fine body condition, and this rather low reproduction rate suggests also a low population turnover.

Hatchlings

We hypothesized that invasive females would produce bigger hatchlings. Data show no significant differences between invasive hatchlings and native ones in length, weight or body condition, therefore, the hypothesis is not met. In agreement with our findings, in other snake's intraspecific comparisons, egg/hatchling size tend to be less variable than clutch size, as occurred in the Chinese *Naja atra* (Ji and Wang 2005), and in *Thamnophis marcianus*, for which differences in food availability for reproductive females affected both clutch size and clutch mass, whilst offspring size remained unaffected (Ford and Seigel 1989); however, in the congeneric *T. elegans*, females of different populations, under different environmental conditions, produced neonates of different body size (Bronikowski and Arnold 1999), and hatchling mass of *Tropidonophis mairii* is influenced by maternal phenotype (Mayer et al. 2016). Once more, this reproductive trait does not explain the success of the invasive population of *H. hippocrepis*.

We conclude that the reproductive ecology scarcely explains the invasion success that *H. hippocrepis* is showing in Ibiza (similarly to the case of the famous and invasive *B. irregularis* in Guam; Rodda and Savidge 2007). But this study on the reproductive ecology of the invasive population discovered a fast expression of phenotypic plasticity, something that occurs under new environmental conditions such as insularity (Ajtić et al. 2013), and it uncovered too that the degree of plasticity differs among the various life-history traits (Seigel and Ford 2001). This expression of phenotypic plasticity arising from environmental factors (thermal envelope and naïve prey) is interesting because of the rapidity of the process (Sakai et al. 2001). The changes observed in this study, together with the increase in body size (Hinckley et al. 2017), occurred within a period that lasted a maximum of 14 years or 3–4 generations (unpublished data of the authors), whilst reproduction traits of the introduced *A. sagrei* in Hawaii did not change after 20 years (Goldberg et al. 2002). In looking for the reasons for the success of this invasive snake through the analysis of intrinsic factors of the population, like its feeding and reproduction ecology (Hinckley et al. 2017; this study), we obtained rather inconclusive results. However, the reasons for the success could be extrinsic, like the almost absolute lack of threats faced (predators and competitors) in the new and insular environment of Ibiza (Silva-Rocha et al. 2018), favoring high survivorship for this recently invasive snake.

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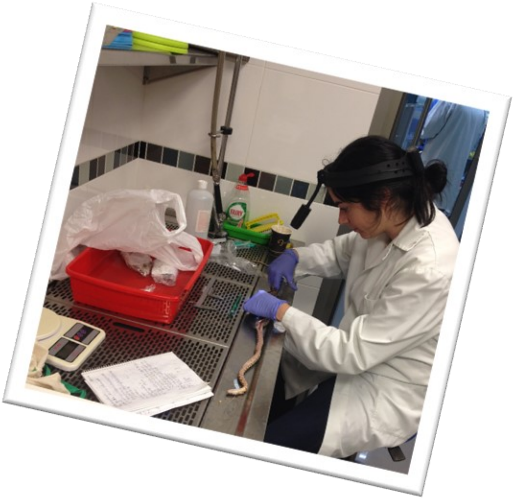
Chapter 4: PREDATION PRESSURE ON INVASIVE SNAKES



The Horseshoe whip snake (*Hemorrhois hippocrepis*) on Ibiza: predator release in an invasive population

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Abstract

The key to fighting a biological invasion may lie in understanding every variable that can explain its success. The Enemy Release Hypothesis (ERH) states that when an invader arrives to a new environment, the absence of its common enemies (predators, parasites and competitors) facilitates the invasion success. The Horseshoe whip snake (*Hemorrhois hippocrepis*) has been recently introduced from the Iberian Peninsula to the island of Ibiza, and it is currently threatening the only endemic vertebrate, the Ibiza wall lizard (*Podarcis pityusensis*). We hypothesized that the snake invasion success is caused by the absence of natural predators, and we checked the ERH by relating the tail breakage rate to predation pressure. The invasive population showed a much lower incidence of tail breakage than the source population, which is in agreement with the almost absence of snake predators among the Ibizan reduced and naïve native vertebrate community. These results confirm the ERH, and support the prolongation of invasive snake trapping campaigns.

Key words: islands, invasive snakes, tail breakage, enemy release hypothesis

Article

The success of biological invasions is often claimed to be ruled by the Enemy Release Hypothesis (ERH). This hypothesis predicts that a non-native species introduced to a new environment will have fewer natural enemies compared to their source range, like predators, parasites or competitors (Wolfe, 2002; Blumenthal, 2006; Lockwood, Hoopes and Marchetti, 2013). Some authors, however, criticize the lack of empirical evidence when stating the causality between invasive species success and ERH, given that the target invasive species can be affected by other predators, native to the invaded ecosystem (Roy et al., 2011); Colautti et al. (2004) described contradictory conclusions depending whether the study scale was at a biogeographical or community level. The majority of studies supporting the ERH focus on invasive plants (Liu and Stiling, 2006; Jeschke et al., 2012). But it has also been found in animals with this cause-effect relationship (Prenter et al., 2004; Shwartz et al., 2009; Jeschke et al., 2012). Here we analyzed the ERH through the study of a snake that recently invaded an island almost devoid of wild predators for these reptiles.

The Balearic Islands, like many other islands around the world, suffer the especially severe effects of one of the major threats to biodiversity: invasive species (Whittaker and Fernández-Palacios, 2007; Silva-Rocha et al., 2018). Located in the western Mediterranean Sea, these islands have been isolated from the continent for 5.33 million of years, developing a specific biota which has suffered natural extinction processes during the Plio-Pleistocene, and anthropogenic extinctions from the end of the third millennium BCE, coinciding with human colonization of the islands (Bover, Quintana and Alcover, 2008). Snakes, particularly, have been historically introduced to the Balearic Islands, except for the two smallest islands of the archipelago, Ibiza and Formentera (the Pitiusic Islands; Silva-Rocha et al., 2018). However, since 2003, the horseshoe whip snake (*Hemorrhois hippocrepis*) has been introduced to Ibiza by cargo, within the holes of old olive trees coming from southern Iberian Peninsula and used for ornamental gardening (Silva-Rocha et al., 2018). It has spread to more than half of the island area and is threatening the only endemic terrestrial vertebrate, the Ibiza wall lizard (*Podarcis pityusensis*; unpubl. data of the authors).

The invasiveness of an alien species depends on both species-specific traits and the environmental conditions in the region invaded (Sakai et al., 2001). The invasive population of *H. hippocrepis* on Ibiza is exhibiting a fast process of phenotypic plasticity; in only 13 years, some island individuals have become larger (105% of body length and 213% of body weight) than individuals from the source population (Montes et al., 2015). However, the study of its feeding and reproduction ecology failed in supporting the extraordinary body condition of individuals and the invasiveness of the population (Hinckley et al., 2017; Silva-Rocha et al., 2018; Montes et al., 2020). Thus, we suggest that their success in terms of body condition and range spread may be favored by one of the environmental conditions of Ibiza, that is the low predation pressure on *H.*

hippocrepis on this island (Hinkley et al., 2017), given that most of its predators in the source area are absent on the invaded island.

Predation rate on snakes is difficult to quantify, since they are usually secretive or scarce animals, requiring long field studies of the population dynamics (Parker and Plummer, 1987). It can be studied by the diet of its predators, but this is a hard task due to the low frequency in which snakes appear in predators' diet – especially in generalist predators (Greene, 1997). Alternatively, it can be assessed by the rate of body injuries caused by predators (Pianka, 1970). Snakes, when grasped by the tail by a predator, will often thrash vigorously and rotate their body longitudinally in one direction, causing tail brakeage (Savage and Slowinski, 1996), and *H. hippocrepis* has this ability (Marco, 2002).

In a strict consideration of the meaning of tail breakage, those injuries inform us on the rate of inefficient predation (Schoener, 1979). Inefficient predators frequently inflict injuries upon their prey, but prey tend to survive (Seligmann, Beiles and Werner, 1996), and this consideration would be a drawback for using tail breakage as a measure for the intensity of predation pressure. However, we found in another Mediterranean snake, *Natrix maura*, that the rate of tail breakage was a function of the variation in the richness of predators in the environment, a proxy of predation pressure (Vidal-García et al., 2011; see also Burghardt and Placyk, 2005); and several authors interpret body damage in natural populations as indirect proof of predation pressure, especially in reptiles (Vidal-García et al., 2011).

Under the last consideration, the goal of this study is to test if the ERH can account for the success of the invasive *H. hippocrepis* on Ibiza, measured by the rate of damaged specimens, and comparing it to those in their source population. If the ERH applies for the invasive *H. hippocrepis*, we should find on Ibiza fewer wounded individuals (broken tails) than in the source population. The key to fight a biological invasion may lie in understanding every variable that can explain its success (Shwartz et al., 2009), and here we focus on one of those aspects.

Snake samples for this study come from the whole area recently invaded by the species (the northeastern half of the island; Silva-Rocha et al., 2018). This island, with 572 km^2 of area, exhibits a mean annual temperature of 17.9°C, and the average yearly rainfall is 413 mm (Ibiza Airport weather station; www.aemet.es), which is climatically similar to the alien source region. The landscape is characterized by a mosaic of pine forests (*Pinus halepensis*) and cultivated land (orchards, cereal crops), with scattered patches of garrigue (*Quercus coccifera*, *Juniperus phoenicea*). On the island there are only two of the seven predators described for the species in Iberia (*Falco tinnunculus*, and domestic *Felis silvestris*; Pleguezuelos and Feriche, 2014), although occasional predation by *Larus michaellis* on small individuals, and by feral dogs on medium sized ones, have been observed (E. Cardona and B. Brosius, pers. comm.). The snakes from Ibiza were captured in between 2014-2017, during eradication campaigns by trapping (Montes et al., 2015). Specimens were sacrificed in a veterinarian facility, and 490 specimens (233 males, 199 females and 58 undetermined) were examined.

For all individuals we recorded body size, measured as snout–vent length (SVL, to the nearest mm), sex, determined upon dissection, and integrity of the tail (broken or not), excluding those specimens with freshly broken tails. Non-predator factors can lead to damaged tail, such as incomplete skin shedding, which can seclude the tip of the tail followed by necrosis (Harkewicz, 2002). To minimize bias derived from these circumstances, we did not consider individuals with the tip of the tail (the unique apical scale) missing as cases of tail breakage (Burghardt and Placyk, 2005). In snakes, predation pressure can also be inferred by body scarring (Sparkman et al., 2013). However, considering that the snakes from Ibiza were captured in traps that could injure them (pers. obs. of the authors), and taking into account that the traps were checked every 10 to 14 days, leaving enough time to form scar tissue, we did not include the scarring ratios in this study. We compared rates in tail breakage of the island population to the source population by using the raw data in Pleguezuelos, Alaminos and Feriche (2018) by the Pearson's Chi-squared test. Tail breakage frequency can vary ontogenetically (Pleguezuelos et al., 2010); for this reason, in order to assess the relationship between snake body size and tail breakage frequency, we divided the invasive population in 10 classes of SVL with equal *n* and fitted the best function (among linear, exponential and polynomial, according to the goodness of fit). Alpha was set at 0.05. For graphical comparative purposes between both populations, frequency of tail breakage in the Ibiza population was adjusted to a theoretical sample size of 31 individuals within each size class, i.e. the sample size within each body size class from the Iberian population (Pleguezuelos et al., 2018).

Tail breakage rate of the invasive population of *H. hippocrepis* on Ibiza was significantly lower than the native population in southern Iberian Peninsula, either considering the whole population or the subsamples according to sexes (all χ^2 tests, $P < 0.05$, Table 1; see also Figure 1). When we divided the Ibiza population in 10 groups by body size, the frequency of tail breakage increased with the increase of body size, fitting a quadratic function; in fact, 12.4 % of individuals from the largest body size class exhibited tail breakage, whereas the individuals from the lower deciles, including juveniles, exhibited very low or none tail breakage frequency (3.85 % for the 9 lower deciles; Figure 1). Despite the ontogenetic variation and the larger classes suffering more tail breakage, the rate of tail breakage of the largest snakes from Ibiza was much lower than the same trait of the largest snakes from the source population (Table 1).

Table 1. Rates of tail breakage in *Hemorrhois hippocrepis* from the invasive population of Ibiza island considering the complete population, adult females and males, and the upper decile of body size (absolute frequency, total sample, relative frequency). For comparison purposes, we included the same figures for the native population from the southern Iberian Peninsula (from the data in Pleguezuelos, Alaminos and Feriche, 2018).

	Ibiza	SE Iberian Peninsula	χ^2	*P*
All population	23/490, 4.7 %	43/328, 13.1 %	18.76	0.0000
Upper decile of body size	6/49, 12.2 %	12/31, 38.7 %	7.63	0.0058
Adult females	6/101, 5.9 %	12/74, 16.2 %	4.89	0.0271
Adult males	11/219, 5.0 %	27/99, 27.3 %	32.08	0.0000

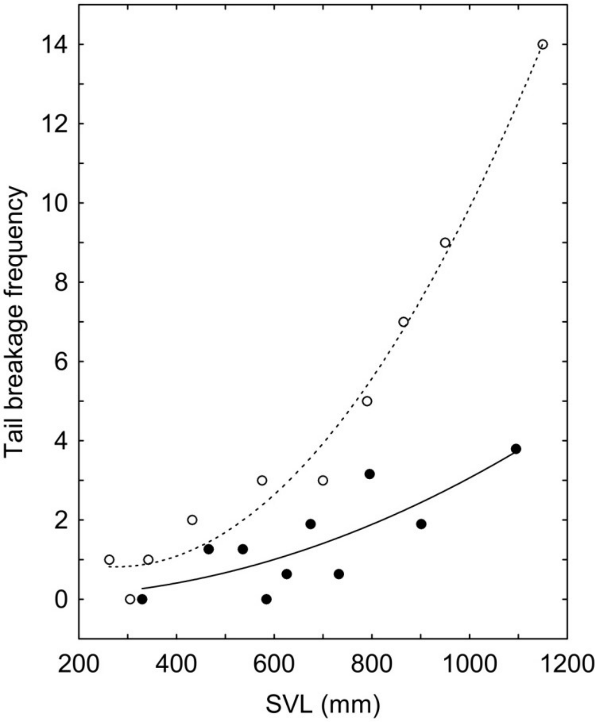

Fig. 1. Fit of tail-breakage frequency to medians of 10 deciles of snout-vent length (SVL) in *Hemorrhois hippocrepis* from the Iberian population (each body size class n = 31, empty dots and dashed line; from the data in Pleguezuelos et al. 2018) and theoretical tail-breakage frequency from Ibiza (each body size class *n* = 49, solid dots and line), adjusting the sample size for each body size class to the same than in the source population. The solid line represents the quadratic function estimated ($y = 5.7165\ e^{-6}\ x^2 - 0.001x + 0.1366$; $r^2 = 0.6206$, $P = 0.0068$ for the Ibiza population).

The lower tail breakage frequency of snakes from Ibiza compared to those from Iberia suggests lesser predation pressure on the invasive population (Burghardt and Placyk, 2005; Vidal-García et al., 2011). In the source area, *H. hippocrepis* is preyed upon by at least three reptiles, three diurnal raptors, and one mammal (Pleguezuelos and Feriche, 2014), whereas there are only two potential snake predators on Ibiza, and their ability to prey upon snakes is limited to small and medium sized individuals. Therefore, the Ibizan snakes met the ERH by both a lower number of predator species (Shwartz et al., 2009) as well as empirically, by the low tail breakage rate (Vidal-García et al., 2011), which is true for the whole population and for the different sexes or body length classes, separately. This small rate is showed graphically when plotting tail breakage frequency against snake body size classes, as the curve was more flattened than the one for the source population (Figure 1; see also Pleguezuelos, Alaminos and Feriche, 2018). We discard alternative causes of tail breakage for the Ibiza snake population, like tail cut by large and dangerous prey as rats being subdued (*Rattus* sp.; Gregory and Isaac, 2005), because of the low frequency of this prey in its diet (only two of 293 individuals were found with that prey in their guts; Hinckley et al., 2017).

Furthermore, the trophic and reproduction ecology of *H. hippocrepis* failed to explain the success of that invasive population on Ibiza; the low rate of feeding frequency (20.8% of fed individuals) and the small size for the main prey (a small lizard, 4 g of body weight on average), poorly supports the high body condition of alien individuals (Hinckley et al., 2017); and their much lower female reproduction frequency compared to the native population (biennial *vs* annual) was not conclusive in determining the invasiveness of the snake (Montes et al., 2020).

Inasmuch as the invasion success of *H. hippocrepis* seems to be scarcely linked to their natural history traits (such as resource acquisition, productivity; see above), we suggest the key for the success of the invaded population relies on the characteristics of the invaded community (see Roy et al., 2011); the lack of natural snake enemies has been proved here (except for parasites), and the climate matches between source and invaded area. As it happens for other invasive animals, like the fish *Cephalopholis argus,* in the Hawaiian Islands (Vignon, Sasal and Galzin, 2009), the toad *Rhinella marina*, in Australia (Phillips et al., 2010), the bird *Psittacula krameri*, in Israel and the UK (Shwartz et al., 2009), and in many plants (see review in Liu and Stiling, 2006), the enemy release poses an advantage to the abundance and expansion of alien species (Roy et al., 2011); particularly on an island like Ibiza, populated by a naïve and reduced native community of vertebrates.

In this scenario, the endemic lizard *P. pityusensis* is our first concern, representing more than half of the snake diet (Hinckley et al., 2017), while steeply disappearing from the invaded area (unpubl. data of the authors). Hence, in the lack or scarcity of native or alien predators for the invasive snake on the island, we propose that humans take on the role of efficient predators; thus, we highly recommend environmental managers to continue and increase in the use of traps in the current eradication campaigns as much as possible.

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Chapter 5: PARASITISM

Parasites and enemy release: the case of the invasive snake *Hemorrhois hippocrepis* on the island of Ibiza

Short Title.—Parasites and enemy release: the case of an invasive snake

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Abstract

The invasive Horseshoe Whip Snake (*Hemorrhois hippocrepis*) is spreading on the Mediterranean island of Ibiza, threatening the endemic Ibiza wall Lizard (*Podarcis pityusensis*). In order to understand the mechanisms of the invasion, we studied if the Enemy Release Hypothesis (ERH) is behind its success. After proving that the ERH is met for the snake's predators in previous studies, here we analyzed the parasites of both populations –source and invasive, and then compared them. We found that despite Ibizan snakes having higher parasitic prevalence (the proportion of infested hosts), all parasites were present in innocuous larval forms that did not affect their fitness, whereas the source population also harbored harmful adult forms, and a greater number of species. In conclusion, the ERH is valid for parasites as well, and therefore, it is subservient to the invasion process. Managers must increase the efforts on the already functioning snake trapping campaigns on the island where, in the absence of natural enemies (parasites included), perform as artificial enemies against the invasive *H. hippocrepis*.

Key words: acanthocephalans; ascaridoidea; Balearic Islands; cestodes; *Podarcis pityusensis*.

Resumen

La invasora culebra de herradura (*Hemorrhois hippocrepis*) se está expandiendo en la isla mediterránea de Ibiza, donde amenaza a la endémica lagartija de las Pitiusas (*Podarcis pityusensis*). Con el objeto de comprender el mecanismo de esta invasión, estudiamos si la Hipótesis de la Relajación de los Enemigos (HRE) está detrás del éxito de la invasión. Después de comprobar en estudios previos que la HRE se cumple para los depredadores del ofidio, aquí analizamos los

parásitos del ofidio en las dos poblaciones, la fuente y la invasora, y las comparamos. Encontramos que, a pesar que los ofidios de la isla de Ibiza mostraban una prevalencia parasitaria (proporción de huéspedes infestados) más elevada, todos los parásitos estaban presentes en una inocua forma larvaria, que no afectaban su condición física, mientras que la población fuente, albergaba formas adultas patógenas y un mayor número de especies de parásitos. Concluimos que la HRE también se cumple para los parásitos del ofidio invasor y está ligada al proceso de esta invasión biológica. Los gestores deben aumentar el esfuerzo de las campañas de trampeo de ofidios que ya están funcionando en la isla, donde en la ausencia de enemigos naturales (parásitos incluidos), actúan como enemigos artificiales contra la invasora *H. hippocrepis*.

Introduction

Biological invasions are currently among the most important causes of biodiversity loss in global terms (Simberloff et al. 2013; Bellard et al. 2016; Courchamp et al. 2017), and this threat is especially serious on islands, where natives have evolved in isolation lacking defense and competitive mechanisms to survive the arrival of newcomers (Cohen 2002; Simberloff et al. 2013). Understanding the causes of invasive species success in their new habitats can be the key to prevent and fight off biological invasions (Hayes and Barry 2008; Mahoney et al. 2015). One of the possible explanations for invasion success is the Enemy Release Hypothesis (ERH), which states that invasive organisms thrive in new environments because they do not face their natural enemies, like predators, parasites or competitors (Wolfe 2002; Blumenthal 2006; Lockwood et al. 2013). Although it is not easy to establish a cause-effect relationship supporting this hypothesis in ecologically complex environments (Roy et al. 2011), some authors found a direct relationship between the absence of enemies and the success of biological invasions (Prenter et al. 2004; Shwartz et al. 2009; Jeschke et al. 2012). Parasites, for instance, are extensively considered as missing enemies in biological invasions. Both the number of parasite species and the number of invasive individuals infected by these parasites, have shown to be much lower than in the source populations (Torchin et al. 2003). Thus, the absence or reduction of parasites can be one of the keys for invasive species success (Dunn et al. 2012).

The population of the Horseshoe Whip Snake (*Hemorrhois hippocrepis*) on the Mediterranean island of Ibiza has been thriving since their arrival in 2003, when they arrived inadvertently inside the holes of old olive trees, imported from the southern Iberian Peninsula for gardening purposes (thereafter the snake source population; Silva-Rocha et al. 2018). This population is highly invasive on the island (Montes et al. 2021) and its study has resulted in concerning findings: i) individuals of the invasive population are reaching the largest body size in terms of body length and weight, as well as the best body condition across its range (Montes et al. 2019); ii) it is predating at high rates on the only native terrestrial vertebrate, the endemic Ibiza wall Lizard *Podarcis pityusensis* (56 % of their diet in frequency; Hinckley et al. 2017); and iii) censuses show that within the island, where the invasive snake is present, the lizard has become absent (Montes et al. 2021).

In looking for causes for the success of *H. hippocrepis* invasive population, on one hand, its trophic ecology did not shed any light, given the low intake of food and that the most frequent prey is a small and low-energetic animal, *P. pityusensis.* In addition, the study of their reproduction ecology gave poor answers to the same question, showing that only half of the adult females reproduce every year, whereas the reproduction is annual in the source population (Montes et al. 2019). The analysis of predation pressure on the snakes, on the other hand, revealed a hint of a plausible explanation: the absence of predators on the island is relieving the invasive population from one stressor that the source population faces; there are only two potential snake predators on the island, whose predation ability is restricted to small individuals, whilst the source population is controlled by seven predators, most of which do prey upon adult snakes (Montes et al. 2020). In summary, these data strongly support the ERH acting in our study system in respect to the predators.

However, in order to reinforce whether the ERH is behind the success of the invasive population, it is necessary to test the absence of the other enemies that the species is facing. Regarding competitors, we considered those few species, either phylogenetically related or not, which also prey upon the two main preys of *H. hippocrepis* on the island, i.e., the lizard *P. pityusensis* and micromammals (mainly mice, *Apodemus sylvaticus* and *Mus* sp.) (Hinckley et al. 2017). There are no native snakes on the island, since a dwarf viper went extinct coinciding with human colonization, three thousand years ago (Torres-Roig et al. 2020). There is another introduced snake, the Ladder Snake (*Zamenis scalaris*), but it is too localized and scarce on the island to be considered a competitor of *H. hippocrepis* (Silva-Rocha et al. 2018). The diet of genets (*Genetta genetta*) and barn owls (*Tyto alba*) slightly overlap with that of *H. hippocrepis* on Ibiza (Clevenger 1995; Sommer et al. 2005), but being that these two species are nocturnal and *H. hippocrepis* diurnal, thus, trophic competence is unlikely; moreover, both species are declining on the island (Sommer et al. 2005; Gaubert et al. 2015). Finally, feral cats (*Felis silvestris*) mainly feed on the snake's second most important prey (micromammals) (Bonnaud et al. 2011), but their highest densities within Ibiza do not overlap with the snake distribution (Montes et al. 2021). Therefore, whereas the snakes have dozens of potential trophic competitors in the source population (see review in Salvador 2014), only one may act as a partial competitor on the island. Hence, the ERH also seems to meet for competitors.

Finally, there is one more enemy left to study: parasites. Multiple studies support the ERH in invasive animals with respect to parasites, including a lower prevalence of parasitic nematodes in several invasive slugs in the USA (Ross et al. 2010), the decrease of metazoan parasites in round and tubenose gobies (*Apollonia melanostoma* and *Proterorhinus semilunaris*) in the Great Lakes (Kvach and Stepien 2008), metazoan parasite global loss in the invasive populations of the African clawed frog (*Xenopus laevis*; Schoeman et al. 2019), an important decline of helminths and hematozoans in lizards (*Podarcis muralis* and *P. sicula*) introduced to North America (Burke et al. 2007), a lower diversity and prevalence of haemosporidian parasites in house sparrows (*Passer* *domesticus*) around the globe (Marzal et al. 2011), a reduction of parasites in a sciurid (*Callosciurus erythraeus*) in Argentina (Gozzi et al. 2020), and the list goes on.

The aim of this study is to analyze the presence of parasites in two populations of *H. hippocrepis*, the introduced and highly successful invasive population of Ibiza island, and the native one from the south of the Iberian Peninsula, source for the former population, so that the comparison between them allows us to test the ERH for parasites as stressors. Our hypothesis is that there will be differences in the diversity and prevalence of parasites, with lower values in the invasive population; this would prove there has been a release of parasites in addition to the other enemies (predators, competitors), and making the ERH a generalized cause for the invasion success of *H. hippocrepis* on Ibiza. Our results would contribute to understanding the mechanisms behind the success of the invasive snake population, and to design effective management proposals to combat this highly island invasive, that is threatening the only endemic vertebrate on Ibiza, *P. pityusensis*. Furthermore, this is the first study that provides information about internal parasites for this species (Ribas et al. 2010).

Materials and Methods

We collected the sample of the source population from an area of approximately 20,000 km^2 in the south-eastern Iberian Peninsula (coordinates 38º45'-37º15'N; 5º45'-2º30'W), where the climate is typically Mediterranean, with an average yearly rainfall of 412.1 mm, and a mean annual temperature of 16.4º C (data from the Cartuja weather station, representative of the study area; www.aemet.es). The landscape is mainly composed of cultivation (olive orchards and cereal crops), forest and scrubland (*Quercus ilex*), and pine plantations (*Pinus* sp.). We obtained Specimens from road kills or among those killed by local people during the period of 2000-2020, and then preserved in ethanol in the collection at Granada University. The island of Ibiza, where the invasive population thrives, is 572 km^2 in area and is located in the Western

Mediterranean Sea. It is a similar environment to that of the source population, with an average yearly rainfall of 413 mm, and a mean annual temperature of 17.9° C (Ibiza Airport weather station; www.aemet.es). The landscape is a mixture of pine forests (*Pinus halepensis*), cultivated lands (orchards and cereal crops) and garrigue (*Quercus coccifera* and *Juniperus phoenicea*). The invasive snake sample comes from eradication campaigns, carried out by the Regional Administration from 2014 to 2017. Managers euthanized snakes with a pentobarbital injection in the heart right after their capture, and then frozen and deposited as vouchers in the collection at the University of Valencia, with parasite defaunation being virtually non-existent.

We studied two snake samples of 30 individuals each to compare both populations. Each sample was integrated with 10 specimens obtained before hibernation (October through November), 10 specimens from immediately after hibernation (February through April) and 10 individuals from mid-summer (July and August). This was done to maximize the chances of finding parasites and differentiate the periods of the year critical for parasite cycles. Within sub-groups, half of the individuals were females and half males, to avoid sex bias, and all specimens were between 560–930 mm snout-vent length (SVL), therefore only adults and not excessively large snakes were studied (Montes et al. 2019).

We performed full-body necropsies of the hosts. We looked for parasites along the digestive tract by making a ventral incision, removing the esophagus, stomach, small and large intestines, and examining the external and internal surface under a dissecting magnification (10x, magnification range 6.5–40); we submerged the organs separately in distilled water to avoid desiccation during examination. We isolated spotted parasites and prepared them for observation. We identified and counted all helminthes. We fixed acanthocephalans in aqueous Bouin and conserved them in 70 % ethanol. Later, we processed helminthes according to standard techniques (Pantin 1968). We stained acanthocephalans and tapeworms with aluminic carmine, then dehydrated them and permanently mounted them in Canada balsam. We studied nematodes using Amann-lactophenol wet mounts. We have used the terms prevalence, mean intensity and range relative to the parasite populations as defined by Bush et al. (1997). We identified parasites from classic references (López-Neyra and Muñoz-Medina 1921; Petrochenko 1956; Yamaguti 1959, 1961, 1963; Chabaud 1974; Sharpilo 1976; Vojtkova 1979; Roca et al. 1987, 2012; Cordero del Campillo et al. 1994; Yildirimhan et al. 2007).

Mean values are followed by ± 1 SD, we compared prevalence of parasitism between sexes and between populations by 2 x 2 contingency tables, and we set alpha at 0.05. We compared parasitic load among times of the year by the Kruskal-Wallis test and among populations by using a Mann-Whitney U test. We carried out statistical analyses by the program STATISTICA version 8.

Results

There were no significant differences in parasites prevalence among periods of the year (2 x 3 table, $\chi^2 = 1.19$, $P > 0.05$; because of statistical constraints, source and invasive populations pooled); nor between sexes on Ibiza or in the south-eastern Iberian Peninsula (2 x 2 table, Yates corrected $\chi^2 \leq 1.34$, $P > 0.05$ in both cases). The comparison of parasitic load among periods of the year was not significant for neither population (Kruskal-Wallis test, $H_{2, 30} < 2.30$, $P > 0.31$), nor pooling both populations (Kruskal-Wallis test, $H_{2, 60} = 3.04$, $P = 0.22$). Therefore, we compared the source and invasive populations pooling the three periods of the year and both sexes. Prevalence of parasites differed between the source (36.7 %, 11 hosts infected, n = 30) and the invasive population (66.7 %, 20 hosts infected, n = 30; 2 x 2 table, $\chi^2 = 5.41$, $P = 0.02$). We found a total of 309 parasites in the snakes from the source population, versus 438 in the snakes from the invasive population, including an acanthocephalan and two cestodes in both populations plus an ascaridoidea in the source population (Table 1); the difference in the mean parasitic load for each individual was not statistically significant (10.3 ± 19.3 parasites in the source population, range = 0–68, n = 30 versus 14.6 ± 20.3 parasites on Ibiza, range = 0–73, n = 30; $U = 341$, $P = 0.11$).

All parasites presented in their larval form, in cysts, except for four ascaridoidea found in snakes from the south Iberian Peninsula. The snakes harbored the following species:

(1) *Diplopylidium acanthotethra*, larvae (Parona, 1886) (Fig. 1A)

Source population

Prevalence, mean intensity and range: hosts infected, four of 30 (13.3 %, 35.0 ± 19.6, range 16–62).

Yearly distribution: before hibernation, two hosts with 27 and 16 individuals, respectively; after hibernation, none; during summer, two hosts with 62 and 35 individuals, respectively.

Site of infection: cysticercoid cysts attached to the external wall of the intestine.

Invasive population

Prevalence, mean intensity and range: hosts infected, seven of 30 (23.3 %, 26.3 ± 25.9, range 2–67).

Yearly distribution: before hibernation, two hosts with 67 and 17 individuals, respectively; after hibernation, two hosts with 46 and two individuals, respectively; during summer, three hosts with 44, six and two individuals, respectively.

Site of infection: cysticercoid cysts attached to the external wall of the intestine and the esophagus.

(2) *Spirometra* sp., larvae (Fig. 1B)

Source population

Prevalence, mean intensity and range: hosts infected, two of 30 (6.7 %, 1.0 ± 0.0, 1).

Yearly distribution: before hibernation, two hosts with one individual each; after hibernation, none; during summer, none.

Site of infection: plerocercoids in the body cavity, outside the intestine.

(3) Ascaridoidea gen. sp.

<u>Source population</u>

Prevalence, mean intensity and range: hosts infected, one of 30 (3.3 %, 4.0 ± 0.0, 4).

Yearly distribution: before hibernation, none; after hibernation, none; during summer, one host with four individuals.

Site of infection: inside the intestine.

(4) *Centrorhynchus* sp., larvae (Fig. 1C)

<u>Source population</u>

Prevalence, mean intensity and range: hosts infected, seven of 30 (23.3 %, 23.3 ± 25.8, range 1–68).

Yearly distribution: before hibernation, none; after hibernation, thre hosts with 68, 18 and 17 individuals, respectively; during summer, four hosts with 50, seven, two and one individuals, respectively.

Site of infection: cystacanth cysts attached to the external wall of the intestine.

<u>Invasive population</u>

Prevalence, mean intensity and range: hosts infected, 20 of 30 (66.7 %, 12.7 ± 14.5, range 1–67).

Yearly distribution: before hibernation, five hosts with 13, 12, seven, six and one individual, respectively; after hibernation, eight hosts with 18, 11, eight, seven,

seven, five, four and four individuals, respectively; during summer, seven hosts with 67, 29, 23, 12, 12, five and three individuals, respectively.

Site of infection: cystacanth cysts attached to the external wall of the intestine.

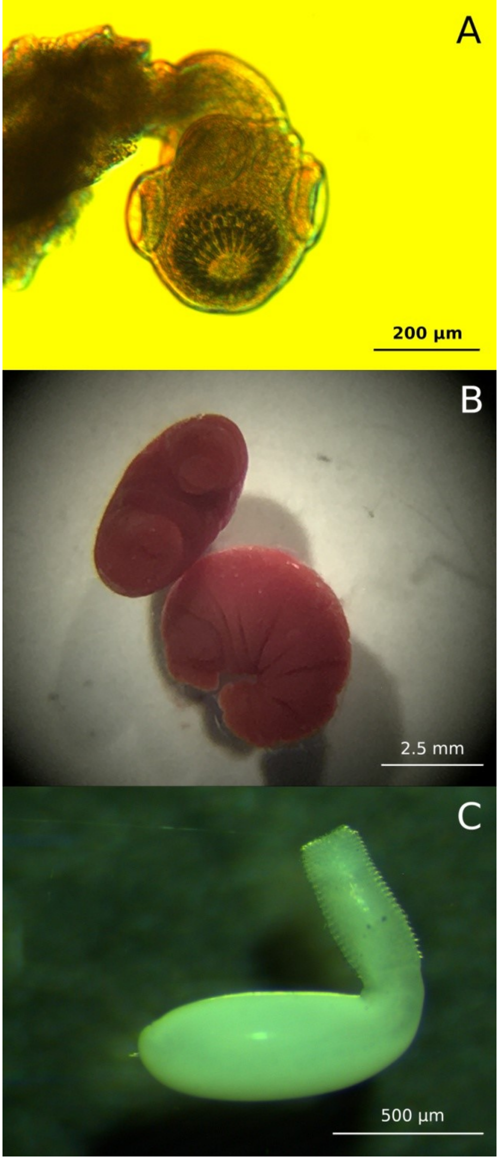

Figure 1. Parasites of *Hemorrhois hippocrepis*: cysticercoid larvae of *Diplopylidium acanthotethra* (A), plerocercoid larvae of *Spirometra* sp. (B), and cystacanth larva of *Centrorhynchus* sp. (C). (Photographed by Pilar Navarro and Elba Montes).

Table 1. Parasites and their numbers found in *Hemorrhois hippocrepis* individuals from the source and the invasive population, classified by time of the year and by sex. The species are *Diplopylidium acanthotethra* (*D. a.*), *Spirometra* sp. (*S.* sp.), *Ascaridoidea* gen. sp. (*A.* g. sp.) and *Centrorhynchus* sp. (*C.* sp.). All parasites were found in larval form (cysts), except for the *A.* g. sp.

	Source population (South Iberian Peninsula)		**Invasive population (Ibiza)**	
	Females	Males	Females	Males
Before hibernation	27 *D. a.*	16 *D. a.* 2 *S.* sp.	38 *C.* sp. 84 *D. a.*	1 *C.* sp.
Post hibernation	103 *C.* sp.	-	19 *C.* sp. 46 *D. a.*	45 *C.* sp. 2 *D. a.*
Mid-summer	3 *C.* sp. 97 *D. a.*	57 *C.* sp. 4 *A.* g. sp.	122 *C.* sp. 46 *D. a.*	29 *C.* sp. 6 *D. a.*
Total/sex	106 *C.* sp. 124 *D. a.*	57 *C.* sp. 18 *D. a.* 4 *A.* g. sp.	179 *C.* sp. 176 *D. a.*	75 *C.* sp. 8 *D. a.*
Total/class	140 *D. a.* 2 *S.* sp. 4 *A.* g. sp. 163 *C.* sp.		184 *D. a.* 254 *C.* sp.	

Discussion

This study gives information for the first time about internal parasites for the colubrid snake *H. hippocrepis*, showing that the invasive population on the island of Ibiza does have a significant difference in parasites prevalence, with more individuals harboring parasites than in the source population. Thus, this result supports the null hypothesis: the invasive population does not show fewer parasites than the native population, even the opposite. However, the totality of parasites from the invasive population was found in larval forms, being the role of the snakes mere paratenic hosts. In fact, the effects of parasites on the fitness of the Ibiza snake's population are imperceptible, as deduced by the gigantism and excellent body condition (as measured by their fat body level) of the individuals (Hinckley et al. 2017; Montes et al. 2019). Moreover, on Ibiza there are only two of the seven predators described for *H. hippocrepis* on the Iberian Peninsula, kestrels (*Falco tinnunculus*) and domestic cats (*Felis silvestris*), both only being able to prey on rather small snakes (Montes et al. 2021), a host ontogenetic stage often less parasitized than the adult stage (Esch et al.1990). This can ultimately pose a difficulty for most parasites to complete their life cycles when parasitizing the snakes in the invasive population's ecosystem, but their presence is ensured as long as their main prey, the lizards, are present on the island. If *P. pityusensis* were to become extinct, something that is not a mere speculation (Montes et al. 2021), the permanence of these parasite species on Ibiza might be doomed to failure. In addition, species richness is higher in the source population (four species, including more harmful adult forms) versus the invasive population (two species, only innocuous larvae), a common effect on islands due to the founder host harboring just a subset of the parasites, described for helminth species on Mediterranean islands (Roca et al. 2012). The higher parasitic prevalence and load on Ibiza's snake population has, overall, little biological meaning taking into account all the above, which leads to an accomplishment of the ERH *de facto*. We ignore the explanation for the high numbers of larval forms found on Ibiza; they are consistent with the insular effect described for larval cestodes in gekkonids from the Canary Islands, including *D. acanthotethra* (Roca et al. 1897); however, this phenomenon was observed after evolutionary adaptation, something that has not happened yet in our study system, only a few generations old. The simplest explanation is that the snakes probably take on these parasites from the lizards after consumption.

Regarding cestodes, the life cycle of *D. acanthotethra* relies on reptiles as second intermediate hosts, and mammals or birds that feed on reptiles are the definitive hosts in which adult forms develop (Bowman 2014), causing very little pathology even when adults (Richardson and Nickol 2008). The first intermediate host is unknown, although it is believed to be a coprophagous insect (Bowman 2014); if that were the case, it is virtually impossible that *H.*

hippocrepis would ingest such prey (Pleguezuelos and Feriche 2014), but the snakes do feed on *P. pityusensis* (Hinkley et al. 2017), that harbors this cestode (Roca et al. 2012). Cats acting as predators of both *P. pityusensis* and *H. hippocrepis* would allow *D. acanthotethra* to complete their life cycle (Bowman 2014). With respect to the other cestode species, the presence of *Spirometra* sp. in plerocercoid form has been cited in many snakes, which act as paratenic hosts (Yildirimhan et al. 2007); their first intermediate hosts are planktonic crustaceans, and amphibians, reptiles, birds and mammals serve as second intermediate hosts. Definitive hosts include carnivore mammals (felines and canids) and occasionally humans, and adult forms can cause sparganosis in their hosts (Kuchta et al. 2015). This cestode was present in the source population only, but it would be able to proliferate on Ibiza, since all the necessary hosts inhabit the island; human health issues might arise.

The bad condition of the adult Ascaridoidea specimens found made their adscription to an inferior taxon impossible. Nevertheless, it was possible to observe the morphology of their oral and esophagic regions, which allowed us to identify their superfamily (Chabaud 1974). Snakes are common final hosts for nematodes (Dea 2005; McAllister et al. 2019), and the effects on the snakes are often detrimental, due to nutrient plunder if the number of helminthes is high enough, and can ultimately cause their death (Dea 2005). This is the only parasite found in this study that can actually harm the snakes, and it was only found in the source population; its absence in the invasive population could suggest a release from this enemy.

Lastly, the life cycle of *Centrorhynchus* sp. includes arthropods as intermediate hosts and amphibians and reptiles as paratenic hosts, being flesh-eating birds their definitive hosts (Choi et al. 2010). Despite *H. hippocrepis* not being an arthropod consumer, Ibiza wall Lizard harbors cystacanths of *Centrorhynchus* sp. (Roca et al. 2012), and these lizards are the major prey for *H. hippocrepis* on Ibiza (Hinckley et al. 2017). Finally, kestrels are known for being final hosts for *Centrorhynchus globocaudatus* (Komorová et al. 2015), although only *C.aluconis* and *C. buteonis* are cited in the Balearic Islands (Cordero del

Campillo et al. 1994). Regardless of the particular species, it is clear that its life cycle is completed on Ibiza, via *P. pityusensis*.

Besides the enhancing effects that pathogenic parasite release can have on an invasive population, there are other possible consequences from parasites associated to invasion processes. It is common that new parasites trigger disastrous effects in invaded communities (Prenter et al. 2004; Dunn et al. 2012). Oftentimes, parasites brought by invasive hosts cause infections that diminish and threaten the survival of native populations, like the case of the invasive American red-eared slider (*Trachemys scripta elegans*), which has transmitted several parasites to the Mediterranean and European pond turtles (*Mauremys leprosa* and *Emys orbicularis*) (Meyer et al. 2015). There can also be indirect effects, like parasites affecting the interactions in the competition or consumer-resource processes, and these effects can spread through trophic levels of the community (Dunn et al. 2012). The invasive population of Brown Tree Snake (*Boiga irregularis*) on Guam harbors a parasitic flatworm whose origin is neither Guam nor the native range of the snake, and the consequences of this parasitization still remain unknown (Holldorf et al. 2015). Ibiza has a rather simple animal ecological community, making most of those complex processes unlikely; but the only endemic vertebrate (*P. pityusensis*) is phylogenetically related to the invader, both being reptiles. Therefore, there is a risk that snakes could introduce a novel species that might parasitize the lizards, with unpredictable consequences (Foster 2019; Verneau et al. 2011).

We conclude that the ERH does apply to the parasites as enemies in this case, since there are less parasite species in the invasive populations and they are present in innocuous larval forms, not affecting the body condition or fitness on Ibiza's snakes (Hinckley et al. 2017). Since the invasion began at most 20 years ago, which represents at best four ophidian generations –probably less-, we suggest that this study be repeated after two more decades to check if our current interpretation is still valid after some generations; assuming the snakes have not been eradicated. Knowing that the ERH does apply for predators (Montes et al. 2020), competitors and parasites (this study) in the invasive snakes on Ibiza, we also recommend managers to play the role of the invasion population's enemies by conservation managing. Humans cannot influence via competition or parasitism, and the only feasible chance to make this happen is acting as predators by capturing them. For that reason, we encourage the managers to increase the efforts on the already functioning snake trapping campaigns (Consorci de Recuperació de Fauna de les Illes Balears, unpubl. report). In addition, stopping the entrance of snakes to the island is vital to effectively and efficiently control of the invasive *H. hippocrepis*, and to ultimately avoid the arrival of parasites that could affect the endemic lizard of Ibiza (Silva-Rocha et al. 2018).

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Chapter 6: CONSERVATION MEASURES

Rapid endangerment of the lizard *Podarcis pityusensis* by an invasive snake demands immediate conservation response

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Abstract

Fifteen years after the arrival of the invasive snake *Hemorrhois hippocrepis* to the island of Ibiza (Balearic Islands, Spain), the only endemic vertebrate, the Ibiza wall lizard (*Podarcis pityusensis*), has disappeared across half of the island, a subspecies restricted to an offshore islet has vanished, and its extinction as a species is likely to happen in the next several years if managers do not implement conservation measures with alacrity and decisiveness. In light of these findings, our re-assessment of the IUCN extinction risk category for the lizard shows that its status has worsened by two levels since its last assessment in 2008, from Near Threatened to Endangered. We also classify the snake as producing a Massive (MV) impact under the Environmental Impact Classification for Alien Taxa. Lastly, we suggest six management measures to avoid extinction of the majority of this endemic lizard's genetic and taxonomic diversity on Ibiza, Formentera and its numerous surrounding islets.

Key words. Balearic Islands, conservation, extinction, Ibiza, invasive species, management

Introduction

The importance of invasive predators in leading to species extinction on islands is well known (e.g., Ebenhard 1988; Courchamp et al. 2003; Blackburn et al. 2004; Reaser et al. 2007). Most attention has, however, historically focused on impacts from mammalian predators. With respect to reptiles, the devastation of Guam's native species by the brown treesnake (*Boiga irregularis*) was admitted too late to save most of its bird and lizard species (Jaffe 1994), but the snake has since become famous for its wide-ranging ecological impacts (Fritts and Rodda 1998; Rodda and Savidge 2007; Rogers et al. 2012; Caves et al. 2013).

Subsequently, snake predation has been inferred as contributing to species losses on other islands (Deso and Probst 2007; Cheke and Hume 2008; Smith et al. 2012), though those invasions have been less intensively studied. Because impacts from invasive snakes on islands can develop quickly, it is imperative that introductions of snakes to islands be studied soon after establishment.

Ibiza is the largest of the Pityusic Islands, the southwestern portion of the Balearic Islands, a small archipelago in the western Mediterranean that is politically part of Spain. Ibiza has an area of 572 km^2, a maximum elevation of 486 m, mean annual temperature of 18.3 °C, and mean yearly rainfall of 413 mm. The island is covered by native pine and juniper forests (*Pinus halepensis* and *Juniperus phoenicea*), cultivated lands, and native shrubland. The Pityusic Islands have one endemic vertebrate—the lacertid lizard *Podarcis pityusensis*—though an endemic dwarf viper (*Vipera latastei ebusitana*) went extinct with human colonization of Ibiza 4000 years ago (Torres-Roig et al. 2020). This lizard occupies Ibiza, Formentera, and most of the surrounding rocks of the Pityusic Islands, a total land area of 656 km^2. Ibiza comprises the large majority of this lizard's native range. The species has been divided into 23–28 subspecies, most of which are restricted to single small rocks surrounding Ibiza and Formentera (Salvador 2015; Rodríguez et al. 2013).

In 2003, the colubrid snake *Hemorrhois hippocrepis* was introduced to Ibiza in imported olive trees and rapidly expanded in numbers and range (Silva-Rocha et al. 2018). Its primary diet on Ibiza consists of lizards (Hinckley et al. 2017). This is of concern because of the documented and inferred ability of invasive snakes to exterminate endemic insular vertebrates, including lizards (Fritts and Rodda 1998; Rodda and Savidge 2007; Cheke and Hume 2008; Smith et al. 2012). Consequently, in 2018, we conducted surveys for *P. pityusensis* along 29 500-meter line transects in areas with and without established snake populations (Montes et al. 2021). We found lizards to have disappeared in all but one of the transects with snakes, whereas they maintained healthy populations in areas without snakes. We found the snakes to be expanding their geographic range at a linear rate (Area = 3189.5 X – 1384.3, where X = year since 2010, adjusted $R^2 = 0.9800$, $F_{(1,7)} = 394.14$, $p < 0.0000$), conservatively occupying 28,200 ha (49.3% of Ibiza) by 2018 and projected to occur island-wide by 2027–2028. We also found snakes swimming far from shore, to have reached some of the offshore islets, and that the lizard subspecies *P. p. hortae*, restricted to S'Ora (0.4 ha) went extinct in the space of ten months (Montes et al. 2021).

Methods

Based on our demographic findings (Montes et al. 2021) we applied standard threat-assessment methodology (IUCN 2012) to update the red-list status of *P. pityusensis*, and we used the criteria of Blackburn et al. (2014) and IUCN (2019) to assess the impact of the invasive snake. These findings lead us to propose several conservation actions to secure the future of the endemic lizard.

Results

In the current IUCN Red List of Threatened Species *P. pityusensis* is considered Near Threatened (NT) due to hunting and trapping, human intrusions and disturbance, and invasive rats and feral cats (Pérez-Mellado and Martínez-Solano 2009). However, this species was last assessed in 2008, before *H. hippocrepis* became widespread on Ibiza (range < 1000 ha). Extrapolating from the rate of range loss in *P. pityusensis* discovered by Montes et al. (2021) –with data in that paper current to 2018– the lizard is expected to have lost more than 50% of its global range (33,700 ± 1244 Ha) by the end of 2020, a period of 17 years since the introduction of the snake and only ten years since the snake occupied only 1080 ha comprising tree-nurseries and surrounding agricultural and residential areas. Thus, we conclude that *P. pityusensis* should now be classified as globally Endangered, EN A4(bce) based on observed and projected population reduction, where the cause of reduction is ongoing and, indeed, expanding. This observed population reduction is based on our transect surveys (Montes et al. 2021), which constitute an index of abundance appropriate to the taxon (b), a quantified decline in extent of occurrence (c), and effects of introduced taxa (e) (IUCN 2012). It is remarkable that this species should have jumped two IUCN categories (NT to EN) in just a decade.

Using the IUCN Environmental Impact Classification for Alien Taxa (EICAT), we recognize *H. hippocrepis* as producing a Massive (MV) impact, given that local extinction of native populations is now widespread, including the endemic subspecies on S'Ora Islet, a harmful irreversible impact (IUCN 2019).

Discussion

In a review of the impacts from invasive herpetofauna Kraus (2015) noted that massive impacts were often caused by these species, but only rarely via the mechanism of predation. Indeed, only two species – a snake, *B. irregularis*, and a lizard, *Anolis carolinensis* – have been documented to exert these impacts via predation (Kraus, unpubl. data), though others have retrospectively been inferred to have done so (Cheke and Hume 2008; Smith et al. 2012). *H. hippocrepis* joins this small contingent of damaging reptiles, being only the third reptile documented during an ongoing invasion to impose massive predation impacts.

It is remarkable that the endemic Ibizan lizard has been virtually extirpated from roughly half its range in less than a decade (Montes et al. 2021). The brown tree snake (*B. irregularis*) required approximately 30-40 years to decimate the native vertebrates on the slightly smaller island of Guam (Fritts and Rodda 1998; Rodda and Savidge 2007), perhaps because there was a greater number of prey items to consume. The rapidity of decline in *P. pityusensis* and its clear relationship to the expansion of the invasive snake (Hinckley et al. 2017; Montes et al. 2021) demand that immediate conservation actions be taken to save this lizard from extinction. Clearly, the existing trapping and removal efforts implemented by the Balearic Government (COFIB 2017; 2018) are insufficient to protect the lizard. We suggest six necessary measures if there is to be a hope of preserving *P. pityusensis* from the invasive snake:

i. *Establish captive assurance colonies of* P. pityusensis. Our assessment is that *P. pityusensis* could be extinct on Ibiza within a decade, with further extinctions likely on Formentera and the offshore islets as the snake continues trans-marine dispersal. Therefore, it seems critical to develop captive populations of this species as assurance colonies in the event of its extinction in the wild. These should be designed to keep the species from extinction, conserve its genetic diversity, and possibly repopulate certain areas should future snake management allow for it (see Hedrick 1992). It is clearly questionable that all named subspecies can be conserved this way, so first priority should be given to the populations on Ibiza and its nearest islets.

ii. *Control the introduction pathway.* Ideally, trade in landscaping trees should be banned to defend against further invasions of snakes and other species. The European Union compels member countries to carry out mechanisms to prevent entrance of invasive species (EU Regulation 1143/2014 on prevention and management of introduction and spread of invasive alien species). However, simultaneously, the 1st article of the Council Regulation 2679/98 demands the contradictory goal of removing any obstacle to “free” trade throughout EU territory. This makes it virtually impossible to implement meaningful biosecurity that could prevent pest importation inasmuch as effective biosecurity necessarily imposes a cost to "free" trade. Given that this legal obstruction will not be immediately addressed, we suggest an alternative approach permitting importation of large trees only from 1 April to 15 June. This avoids movement of trees during the cold season (15 October to 15 March), when *H. hippocrepis* hibernates inside such trees (Feriche 2017), as well as during summer (July to September) when eggs are incubating in those same refuges (Pleguezuelos and Feriche 1999). We further suggest that during this 2.5-month period imported trees also pass quarantine for at least four weeks in an enclosure surrounded by a snake-proof fence (Rodda et al. 2007) holding baited traps (Engeman and Vice 2002). It is essential that the enclosure be located within facilities of the Ibiza entrance port, because trees can be sent from many different origins in mainland Spain. While in quarantine, trees should also be searched with detector dogs to minimize chances of further snake incursions (Clark et al. 2017).

iii. ***Reinforce existing eradication campaigns*** with a greater number of permanent traps, which are showing good results (COFIB 2018) compared to trapping studies in the literature (0.0825 snakes/trap-night in high-density locations, compared to 0.044 for aquatic snakes in south Carolina [Durso et al. 2011], 0.0005 for *Python molurus bivittatus* in the Everglades [Reed et al. 2011], 0.127 for *B. irregularis* on Guam [Clark et al. 2012], or 0.019 for *Nerodia fasciata* in Southern California [Reed et al. 2016]). This would aim to reduce snakes in their core area and, hopefully, reduce emigration pressure. Canine teams have demonstrated high detectability of individual snakes (see Ballouard et al. 2019); however, the rock walls used as shelter by snakes make capturing them virtually impossible. We suggest field testing canine-team effectiveness in concert with thermal fumigation (Kraus et al. 2015) to drive snakes from these shelters when detected.

iv. ***Develop a rapid-response protocol for snake sightings*** in new satellite localities across the southwestern part of Ibiza (where the invasive snake is not yet widespread) and on the islets. This is necessary because snakes can disperse discontinuously in transported nursery materials, construction materials, or by swimming. The protocol could follow methods developed for other snakes (Stanford and Rodda 2007). We suggest surrounding the area of any new record with baited traps separated at a maximum of 20 m from each other, maintained during four weeks (Engeman and Vice 2002).

v. ***Promote scientific research*** in concert with the above-mentioned actions to solve the problems impeding effective lizard conservation and snake control. Research is needed to optimize captive management procedures for the lizards, monitor their population trends and range shifts, deepen understanding of the snake's natural history, and identify biological weaknesses of the snake that may lead to development of more effective tools to manage it (Andersen et al. 2004). Topics in tool development that require study include determining optimal spacing among traps, optimal set time for maximizing capture probability per unit area, optimal use of canine teams, possible development of snake toxicants, and use of thermal fumigation to drive snakes from refuges in stone walls.

vi. *Develop public-education programs* to improve reporting of snake sightings and increase likelihood of snake removal. Immediate reporting of snakes is essential to their successful capture by management personnel, and improved public engagement is needed for this. The Balearic and Ibiza Island governments carry out different campaigns focused on trapping and educating the public by delivering traps and pamphlets to citizens. The conflicting system of authorities among the different national, regional, and local administrations—along with fluctuating political interests—make these efforts discontinuous, uncoordinated, and of uncertain duration. We recommend that already-functioning campaigns become unified and consistent so that Ibiza inhabitants and visitors are provided a unified message about the problem, the need for continued and immediate reporting, and their option to place traps around their homes.

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General discussion

The invasive horseshoe whip snake, *Hemorrhois hippocrepis*, was introduced to the island of Ibiza in 2003, transported as stowaway inside big olive trees used for Mediterranean gardens, an introduction pathway that still happens to the present day. During the first years, it established around tree nurseries and in 2010, the process of spreading began. The results of this study show that this invasive snake is seriously threatening the Ibizan endemic lizard, *Podarcis pityusensis*, to extinction. The snake is currently thriving, but what are the keys to its success? This dissertation is aimed to answer this question, in order to better manage this biological invasion. Apparently, the trophic and reproduction ecology analysis do not explain the snake's invasive success; but the low predation pressure that the horseshoe whip snake suffers and the innocuous parasites that they harbor on Ibiza, suggest that the Enemy Release Hypothesis (ERH) can explain it. The changes observed on the lizard distribution and abundance motivate an upgrade of its extinction risk category by two levels. Therefore, I finish this study proposing urgent conservation measures that need to be implemented to reduce the extinction risk of this island endemic and currently endangered species.

About the diet of the invasive snakes (Chapter 1)

Predation by invasive species is frequently the main factor driving negative impacts on autochthonous communities (Kraus, 2009). Therefore, I started analyzing the snake's diet in order to assess if *H. hippocrepis* entailed a predation threat to the native fauna of the island. The main finding of the trophic ecology analysis is that most of the diet in frequency of the invasive snake is composed by the endemic lizard *P. pityusensis*. Taking into account that this is the only native terrestrial vertebrate on Ibiza, this is the first concerning outcome that could possibly happen from this invasion. Its sibling species, *Podarcis lilfordi*, suffered a catastrophic impact caused by predation of other invasive predators from human introductions to Mallorca and Menorca (Pinya and Carretero, 2011), and this finding is too similar to ignore. If measured by biomass and not by frequency, micromammals are the primary source for the invasive snakes (chapter 1). Micromammals were introduced with the arrival of humans (Drake and Hunt, 2009), thus, they are not of concern under the scope of biodiversity conservation within the island; rather, they can contribute synergistically to the success of *H. hippocrepis*, providing additional food resources that favor the invasive species population in a process called invasional meltdown (Simberloff and Von Holle, 1999). This process has aggravated the negative effects of some biological invasions caused by vertebrates that included other non-natives in their diet, in addition to the native organisms (Relva et al., 2010).

The invasive *H. hippocrepis* is a generalist predator in its native range (Pleguezuelos and Fahd, 2004); however, the island of Ibiza harbors a reduced prey-type diversity that explains the low variety of prey that we found in the analysis of the snake diet, just seven different prey types in spite the large sample size. In addition, the percentage of lizard presence is the highest for any native or island-introduced population (Pleguezuelos and Moreno, 1990; Corti et al., 2000; Pleguezuelos and Fahd, 2004; Luiselli et al., 2012; Cattaneo, 2015). The explanation for this increased lizard consumption may lie on the availability and naïveté of *P. pityusensis*, given its evolution in isolation during the Pleistocene, without contact with other snakes (Bover et al., 2008) until a dwarf viper, *Vipera latastei ebusitana*, colonized the island via transmarine dispersal (between 1.31 MY and *c.* 30 000 years ago), and then went extinct with human arrival, 4000 years ago (Torres-Roig et al., 2020). However, the contact with *V. latastei ebusitana*, a sit-and-wait predator, seems that was not enough to make the lizard develop defense mechanisms against an active-forager predator like *H. hippocrepis* (Pleguezuelos and Moreno, 1990).

There is a second highlight from this study, which is that the invasive individuals are the largest recorded for the species. Contrasted body size between conspecific snake populations mainland and islands is broadly recorded (Shine, 1987; Cheylan and Guillaume, 1993; Boback, 2003; Salvador, 2014), including the species here considered, but on the island of Pantelleria (Cattaneo, 2015); certainly, gigantism is a type of island syndrome in reptiles (Pafilis et al., 2011). However, it is striking that this phenotypic change in the invasive population of *H. hippocrepis* took place in a maximum period of 13 years, providing an impressive example of the fast rate at which phenotypic plasticity can act when a species invades a novel habitat (ecological time scale; Herrel et al., 2008). This ability entails an added risk regarding the potential harmful impacts of this invader as a predator and as a competitor.

In addition to larger size, we also found a higher level of abdominal fat bodies than in the source population, something that is hardly explained by the few fed individuals and the high proportion of a small sized prey in the diet, lizards. The high rate of unfed individuals may be a consequence of the species long-shaped body and its thermophilia, something that might suggest even a higher percentage of lizard presence in their diet. A possible explanation for the success of the invasive snake, since the trophic ecology does not account for it, is the absence of enemies (chapters 4 and 5).

The disappearance of the lizard might trigger a cascade effect in the island's biodiversity decline, given that *P. pityusensis* is a seed disperser and pollinator to several plants of the island and islets (Traveset, 1995), and as a consequence, a proliferation of lizard's prey could take place, similarly to what happened on Guam, where spiders and insects are overly abundant due to the absence of birds (Rogers et al., 2012). The lizard populations on islets are of particular concern, given that several snakes have been seen swimming in the sea and the islets have endemic plant species and lizard subspecies (Castro and Rossello, 2005; Salvador, 2015). After the analysis of diet habits, body size, and body condition, the conclusion is that the population of *H. hippocrepis* recently introduced on Ibiza potentially threatens its biodiversity, particularly the survival of the endemic lizard *P. pityusensis.*

After results on the foraging ecology of the invasive snake on Ibiza, I suggest at least one research line that should be explored in the future:

i) If the lizard's densities decrease, the snake's diet will inevitably shift. Therefore, it would be interesting to analyze the trophic ecology along the past and the coming years and see how it changes. Will the snakes eat more micromammals, taking profit of the above mentioned invasional meltdown on Ibiza? Or will they focus on native birds, pushing up a further step on the impact of the invasive snakes on the island native biodiversity.

Snakes are eating them, but how are lizards doing? (Chapter 2)

After finding out that the snakes are eating many lizards (chapter 1), the natural question was: "are they eating enough of them to damage the lizard's population?" Given that *P. pityusensis* has developed defense responses towards the snakes on the main island of Ibiza (but not on the surrounding islets) (Ortega et al., 2016), the answer to this question was not a simple one, and it was necessary to census and to study the distribution of the lizards. The results show that the worst predictions are coming true: in the northeastern half of the island, the lizards are absent, conversely to what happens in the southwestern half of the island. The only factor that explains this phenomenon is the presence of snakes, whereas other factors, such as habitat structure or other predators, do not support lizard absence.

With respect to the island of Ibiza, by 2018, the snakes' population had spread to cover the northeastern half of the area (which means 43 % of the lizard's global range) in a conservative estimate with data from 2018, and the expansion rate allows to predict that the lizard will be extinct from Ibiza before 2030.

Among the nine islets visited, three of them deserve special attention:

- S'Espartar (19.8 ha) was visited because two shed skins had been found on the islet. Despite at least one big snake inhabiting the islet, it still maintains a stable lizard population, probably due to the big size of the islet and the *P. pityusensis* population.

- Grossa (4.5 ha) was visited because it is in front of the snake-area of Ibiza, and the main sea currents could eventually aid a snake swim towards the islet. It presented a poor lizard population, consistent with a snake living on the islet, sighted during the visit.
- Lastly, I confirmed that the population of S'Ora (0.4 ha) has disappeared, after some kayakers intercepted a snake swimming towards the islet, 20 meters away. Whilst there is not actual proof of the snakes causing the extinction of *P. pityusensis hortae*, the lizard population was healthy at least 10 months before my visit, after living isolated from its conspecifics since the last Glacial Maximum (~26,500 – 10,000 years BP, Clark et al., 2009).

Extirpation of native biota mediated or facilitated by introduced snakes has occurred on several islands, such as Guam (Rodda and Savidge, 2007), Christmas Island (Smith et al., 2012), or other Balearic Islands (Mayol, 2004), among others. These examples are illustrative of what the Ibiza wall lizard is relentlessly facing.

These dramatic results highlight the need for a reassessment of the lizard's conservation status, as well as urgent convincing control measures that cannot be postponed (approached in chapter 6). Trapping campaigns for the already present snakes on the islets are a priority. It is likely, however, that more unique islet subspecies end up vanishing, drastically reducing the total genetic, phenotypic and taxonomic diversity of this lizard lineage. These results also urged to continue this investigation, searching for an explanation of the invasive snake's success on Ibiza, and ultimately find the key factors to effectively fight against it. The reproduction ecology (chaper 3) and the lack of enemies (chapters 4 and 5) were the next logical steps.

In light of these concerning results, future research is much recommended in the following topics:

i) It is absolutely necessary to keep track of the population status of the main island as well as all islet populations, especially those with snake sightings on the islet or swimming close by.

ii) Possible cascading effects on Ibiza's and surrounding islets' biodiversity once the lizard disappears, including the survival of endemic plants or the proliferation of arthropods (Traveset, 1995).

iii) Reproduction ecology of *P. pityusensis* is still partially unknown, it would be interesting in order to design captivity breeding programs (chapter 6).

Is reproduction behind the snake's success? (Chapter 3)

The snake's feeding ecology showed that the main prey (*P. pityusensis*) contributes with little mass to the snakes' diet. This fact again opens a question that is key in this dissertation: why is the invasive snake thriving? How is it possible that Ibizan snakes are fatter and bigger than native snakes, and that they are spreading throughout the island, despite feeding rather scarcely and on a small prey? To answer this nuclear question, I studied the reproductive ecology. Surprisingly again, the results that are vital for the snake population fitness showed slow reproductive traits.

Females attain sexual maturity at a shorter body size than Iberian snakes, something that has been observed for the Lake Erie snake *Nerodia sipedon insularum* when started feeding almost exclusively on a newly arrived and abundant invasive prey (King et al., 2006). The invasive *H. hippocrepis*, on arrival to Ibiza, shifted its diet as well to a menu based on small lacertids, and this parallelism may explain the early maturity in females. The reproductive period also expanded on Ibiza, vitellogenesis advancing by one month and egg-laying delaying by one week, compared to the source population (Pleguezuelos and Feriche, 1999). This wider reproductive window may be explained by Ibiza's favorable climate and habitat, a phenomenon already observed for other invasive animals (MacInnis and Corkum, 2000; Rodda and Savidge, 2007; Norval et al., 2012). In addition, both sexes showed higher fat body levels than the source population, and this energetic availability facilitates female reproductive frequency and male spertmatogenesis (Pleguezuelos and Feriche, 1999). These three traits observed for both sexes, can be considered as supportive of the snake's invasion success.

However, reproductive frequency is significantly lower, to the point of being biennial on Ibiza, whereas females reproduce every year in the source population (Pleguezuelos and Feriche, 1999; see also Pleguezuelos and Fahd, 2004). This shift has been described for the invasive brown treesnake *Boiga irregularis* on Guam without a clear explanation (Rodda and Savidge, 2007), despite frequent clutches being an advantage for the success of introduced species (Allen et al., 2017). Fat body levels kept high values for non-reproductive females, showing that the "choice" of not reproducing is not conditioned by low food availability or poor body condition. Moreover, a very large Ibizan female harbored the largest clutch recorded for the species in the wild, female size to clutch size relationship being maintained in the comparison between populations, but the average clutch size was not statistically different for both populations. Hatchlings' length, weight or body condition, was not significantly different between source and invasive population either. This set of reproductive traits, which can initially be considered as crucial for the success of a species in a new habitat, do not support *H. hippocrepis* success on Ibiza. Therefore, I continued searching for the causing factors.

Research lines on the snake reproduction ecology that could provide with useful information are:

i) Search for the causes of low reproduction frequency: could it be a biological response of the population to a density-dependent situation? Or is it an individual conservative response, due to a low predation pressure on the snakes?

ii) Study the reproductive ecology along the years, in order to see if the parameters change and why (in relation to the change of other abiotic or biotic factors during the period after the invasion).

The Enemy Release Hypothesis as a plausible explanation (Chapters 4 and 5)

What if *H. hippocrepis*' success is not explained by changes in its phenotypic traits, but by extrinsic factors, such as the lack of natural enemies in the new environment? This hypothesis, called the Enemy Release Hypothesis (ERH) could be driving the snake's invasion, something that has happened for many invasion processes before (Prenter et al., 2004; Liu and Stiling, 2006; Shwartz et al., 2009; Jeschke et al., 2012). Natural enemies include predators, competitors and parasites.

Predation is rarely observed in nature; thus, snake predation pressure is a hardly measurable parameter. Tail breakage rate is related not only to an unefficient predation, but to the predators' density (Vidal-García et al., 2011). For this reason, I indirectly measured predation pressure on the snakes through the tail breakage rate, proving that it was lower on Ibiza's population than in the source population (Vidal-García et al., 2011; chapter 4). This is consistent with the presence of only two of the seven natural predators that *H. hippocrepis* faces in the Iberian Peninsula (Pleguezuelos and Feriche, 2014). Furthermore, these two predators' ability to predate upon *H. hippocrepis* is restricted to small snake individuals.

Regarding competitors, I considered the other invasive snake (*Zamenis scalaris*), genets (*Genetta genetta*), barn owls (*T. alba*), these two slightly overlapping their diets with *H. hippocrepis*'s, and cats (*Felis silvestris*). Regarding *Z. scalaris*, it is too scarce on Ibiza to be considered a competitor (Silva-Rocha et al., 2018). *Genetta genetta* and *T. alba* are nocturnal whereas the snake is diurnal; moreover, they are declining on the island (Clevenger, 1995; Sommer et al, 2005; Gaubert et al., 2015). Lastly, the highest densities of *F. silvestris*) within Ibiza do not overlap with the snake distribution (Montes et al., 2021).

The study of parasites resulted in a higher parasitic prevalence for the invasive individuals (chapter 5). However, the totality of parasites from the invasive population was found in larval forms, being the role of the snakes mere paratenic hosts. In fact, the negative effects of the presence of parasites in the invasive population fitness are nonexistent, as deduced by the gigantism and excellent body condition found in the trophic and reproductive ecology analyses (chapters 1 and 3, respectively). In addition, the absence of predators that feed on all sizes of snakes can pose a difficulty for completing the parasite's life cycles, especially if the lizard –currently the main paratenic host– goes extinct; something that can ultimately make these parasite species disappear from Ibiza. Finally, the source population harbored a higher species richness that included harmful adult forms.

Thus, the ERH is clearly met for all three enemies (predators, competitors and parasites) on the invasive population of *H. hippocrepis* on Ibiza, suggesting that it can be the cause of its invasion success.

I suggest a future research line that may be useful:

i) Study the predation rate upon the snakes along the years. It could maintain a stable value, as a result of the poor predator community, or it could increase over time due to the few predators eating more and more snakes, as *H. hippocrepis* becomes more abundant.

What can we do? Management and conservation proposals (Chapter 6)

The rupiculous and thermophylic invasive horseshoe whip snake has found a paradise on the island of Ibiza: the omnipresent rock walls that once belonged to the Ibiza wall lizard (Salvador and Pérez-Mellado, 1984) serve now as shelter for the snake (Montes et al., 2015, annex III), and the favorable weather and climate conditions of the island are proving to be perfect for the invasive snake: in its Iberian range, the average yearly rainfall ranges from 170 mm (Cabo de Gata, Almería) to 1800 mm (Grazalema, Cádiz), and the average yearly temperature ranges from 12.0 ºC to 18.5 ºC (Pleguezuelos and Feriche, 2014); whilst on Ibiza, the mean annual temperature is 18.3 ºC and the average yearly rainfall is 413 mm (standard meteorological averages for the Ibiza Airport weather station, 38.8728º N, 1.3730º E; www.aemet.es), making the island highly suitable for the snake. After finding that the ERH is favoring the invasion, the logical and most important conclusion is clear: humans need to act as the missing predators. In order to do that, there are some management actions that include, not only the control of the snake population, but also some measures to protect the lizard.

The endemic *P. pityusensis* must be now classified as globally Endangered, EN, in the IUCN Red List of Threatened Species; and the invasive *H. hippocrepis* should be recognized by the IUCN Environmental Impact Classification for Alien Taxa (EICAT) as producing a Massive (MV) impact, given that local extinction of native populations is now widespread, including the endemic subspecies on S'Ora Islet, a harmful irreversible impact (IUCN 2019). Specific measures include:

i. Establish captive assurance colonies of *P. pityusensis*. This should be aimed at protecting the lizard from extinction, prioritizing those populations that are more threatened (main island of Ibiza and the closest islets or those which already have a snake on them). This would conserve its genetic diversity and would allow to repopulate certain areas (Hedrick, 1992).
ii. Control the introduction pathway. Ideally, trade in landscaping trees should be banned to defend against further invasions of snakes and other species. There is an alternative approach that would allow the importation of large trees from 1 April to 15 June. This avoids movement of trees during the cold season (15 October to 15 March), when *H. hippocrepis* hibernates inside such trees (Feriche, 2017), as well as during summer (July to September) when eggs are incubating in those same refuges (Pleguezuelos and Feriche, 1999). We further suggest that during this 2.5-month period imported trees also pass quarantine for at least four weeks.

iii. Reinforce existing eradication campaigns with a greater number of permanent traps, which are showing good results (COFIB, 2018). This would aim to reduce snakes in their core area and, hopefully, reduce emigration pressure.
iv. Develop a rapid-response protocol for snake sightings in new satellite localities across the southwestern part of Ibiza (where the invasive snake is not yet widespread) and on the islets. We suggest surrounding the area of any new record with baited traps (Engeman and Vice, 2002).
v. Promote scientific research in concert with the above-mentioned actions to solve the problems impeding effective lizard conservation and snake control. Research is needed to optimize captive management procedures for the lizards, monitor their population trends and range shifts, deepen understanding of the snake's natural history, and identify biological weaknesses of the snake that may lead to development of more effective tools to manage it (Andersen et al., 2004).
vi. Develop public-education programs to improve reporting of snake sightings and increase likelihood of snake removal. We recommend that already-functioning campaigns become unified and consistent so that Ibiza inhabitants and visitors are provided a unified message about the problem, the need for continued and immediate reporting, and their option to place traps around their homes.

The current management actions can still be greatly improved, particularly controlling the entrance of big trees (without stopping the entrance, solving the problem is impossible) and increasing trapping effort (something that should have been done during the first years of the invasion). It is fundamental aiming at the eradication and not just the control of the invasive population, since the response of native reptiles to invasive predator’s eradication has proven to be positive in native populations (Krebs et al., 2015). With a number of traps high enough, this goal may be possible to achieve, given the good results observed for the current traps (COFIB, 2018).

The invasive *H. hippocrepis* is quickly spreading and its ability to travel as a stowaway and to swim to other islands or islets is indisputable. If there is no change in the current management measures, the endemic *P. pityusensis* will go extinct in less than 10 years (chapter 2), and it will be a matter of time that the species vanished from all its native range, losing the only endemic terrestrial vertebrate and symbol of the Pityusic Islands (Silva-Rocha et al., 2018).

Figure 6. *Podarcis pityusensis formenterae.* Formentera, 30 March 2019. Photo: Baravi Thaman

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Conclusions

1. Invasive *H. hippocrepis* individuals are larger and have a better body condition on Ibiza than in the source population, with the longest and heaviest snake recorded for the species.

2. The results of the trophic ecology analysis show that the invasive snake *H. hippocrepis* is massively predating on lizards (the endemic Ibiza wall lizard, *P. pityusensis*) with a much higher rate than in the source population, probably due to the naïveté of the only terrestrial vertebrate native to Ibiza. However, the high frequency of invasive snakes without gut content and the small body size of their most frequent prey, hardly explain the excellent body condition and success of the invasive population.

3. Censuses across the island of Ibiza show that in those areas where the snakes are present, the lizard is extirpated, whereas in snake-absent areas, *P. pityusensis* is abundant. The only variable that statistically explains that difference in the lizard population density is the presence of snakes.

4. The invasive snake has already spread and established throughout half of the island; the expansion rate allows us to predict that the entire island will have snakes, and therefore, *P. pityusensis* will be extinct from Ibiza by 2030.

5. The invasive *H. hippocrepis*is able to swim and has arrived to some of the islets that surround Ibiza, with devastating effects on the lizard populations, some of them unique subspecies of. The subspecies *P. pityusensis hortae* has already gone extinct, and it is a matter of time that the snakes arrive to other islets and to Formentera.

6. The reproduction ecology of *H. hippocrepis* also fails to explain the invasive success of the snake on the island of Ibiza, since the

comparison to the source population shows that Ibizan snakes present slow reproductive traits: lower reproduction frequency (biennial) and similar clutch size, hatchlings' length, weight and body condition.

7. The invasion success of *H. hippocrepis* on Ibiza seems to be better explained by the absence of natural enemies (Enemy Release Hypothesis, ERH), which include predators, competitors and parasites. On Ibiza, there are only two of the seven predators that the snake naturally encounters in the source population, and they are able to predate only upon small-medium individuals; with respect to competitors, only feral cats can potentially be enemies, but their highest densities do not overlap with the current distribution of the snake within the island; and lastly, with respect to parasites, Ibizan populations of snakes only harbor innocuous larval parasites, whilst Iberian snakes do have more parasite species which include adult harmful forms.

8. It is urgent to upgrade the category of extinction risk for *P. pityusensis* from Near Threatened (NT) to Endangered (EN) in the IUCN Red List of Threatened Species, according to criterion A and subcriteria A4 (abce), given that the lizard would have lost more than 50 % of its range in 10 years since the beginning of the snake expansion process. In addition, the invasive *H. hippocrepis* should be recognized by the IUCN Environmental Impact Classification for Alien Taxa (EICAT) as producing a Massive (MV) impact, the extinction of the subspecies *P. pityusensis hortae* from the islet of S'Ora.

9. It is urgent as well to implement management and conservation measures that guarantee *P. pityusensis* survival, such as establish captive assurance colonies, develop a rapid-response protocol for snake sightings, promote scientific research, and develop public-education programs. But most importantly, the main conclusion of this study is that *H. hippocrepis*'s invasion success likely relies on the lack of enemies; since it is not advisable to introduce snake competitors or

parasites, we suggest that managers focus their efforts to act as artificial snake predators by intense trapping campaigns. This effort is useless without closing or controlling the entrance pathway of this and other ophidians to the island.

ANNEXES

Annex I. Presence of the horseshoe whip snake (*Hemorrhois hippocrepis*) on Gran Canaria, Spain

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Resumen: Tras 12 años de invasión de la culebra de herradura (*Hemorrhois hippocrepis*) en la isla de Ibiza (Baleares), debido a su transporte en grandes olivos destinados a jardinería, en 2015 aparecieron dos ejemplares de esta especie en el norte de la isla de Gran Canaria, en las inmediaciones de un vivero en el barranco de Casa Ayala, límite entre los municipios de Las Palmas de Gran Canaria y Arucas. Aunque se trata de dos casos aislados, la introducción de esta especie podría tener consecuencias nefastas para su biodiversidad, que ya está amenazada por la invasión de la culebra real de California (*Lampropeltis californiae*).

Short Note

The horseshoe whip snake *Hemorrhois hippocrepis* (Linnaeus, 1758) is a native species to the western Mediterranean, ranging from the southern Iberian Peninsula to northwestern Africa, and has been introduced in historical times to the islands of Pantellaria, Sardinia and Zembra (Pleguezuelos & Feriche, 2014). It has recently been introduced to the Balearic Islands of Majorca, Ibiza and Formentera (Pinya & Carretero, 2011). These recent introductions are associated with unintentional transportation inside olive trees brought to the Balearic Islands in which snakes travelled as stowaways (Mateo *et al.*, 2011). The rate of the snake's spread from nursery gardens on Ibiza has been rapid, in 15 years it has invaded and occupied half of the island (Montes *et al.*, 2021). Invasive snakes have proven to be a harmful predator for native fauna on islands (Savidge, 1987; Reaser *et al.*, 2007; Jones *et al.*, 2016), and *H. hippocrepis* in particular increases the rate of reptiles in its diet when invading islands, such as Ibiza (Hinckley *et al.*, 2016).

On 15th June 2015, one specimen of *H. hippocrepis* was photographed in the Casa Ayala ravine (island of Gran Canaria, UTM coordinates X 452161,0031, Y 3112048,328; 25 masl), but not caught. From the picture (Figure 1) it can be deduced that it was an adult snake of around 150 cm total length. Later, on 6th August 2015, the invasive species control team of the Canary Islands Government captured a specimen in the same area (UTM coordinates X 452086,1678, Y 3111472,72; 46 masl). This snake was a male, 1350 mm from snout to vent and 1640 mm total length, although the last part of the tail was missing. At 724 g body mass, it surpassed the maximum weight (550 g) known from the native range in the Iberian Peninsula (Pleguezuelos & Feriche, 2014), but it was lower than the species record, an individual captured on Ibiza that weighed 1200 g. Both photographed individuals were not the same, as the latter exhibited melanism (Figure 2). There is a nursery in the same zone were these two snakes were found, but the owner claims not to have imported olive trees for over ten years.

Within its native range, the horseshoe whip snake feeds almost exclusively on vertebrates, mammals and reptiles, but also on birds and invertebrates (Pleguezuelos & Moreno, 1990). On Ibiza, the invasive horseshoe whip snake finds an auspicious environment to thrive (Hinckley *et al.*, 2017). Gran Canaria characteristics are not so different to Ibiza's in terms of landscape (numerous stone walls near human dwells), absence of snake predators and potential preys not used to snakes, that fit well with the diet of this snake (Pleguezuelos & Feriche, 2014); the climate of this island is also suitable for the species, as it inhabits the African Macaronesian region in front of Canary Islands (Bons & Geniez, 1996). The island of Gran Canaria has already suffered a colubrid invasion from a species with similar characteristics but very different origin (from pet keepers), the California kingsnake (*Lampropeltis californiae*) (Monzón-Argüello *et al.*, 2015). Its successful establishment suggests the impact on biodiversity that another invasive snake, like *H. hippocrepis,* would presumably have: the diet of the California kingsnake is based, in the invaded territory, on a 94% of reptiles, 81% being two endemic lizards (Monzón-Argüello *et al.*, 2015).

Figure 1: Individual of the horseshoe whip snake, *Hemorrhois hippocrepis*, seen on 15th June of 2015, in the Casa Ayala ravine. Photo anonymous (Early Warning System LIFE-Lampropeltis).

Figura 1: Individuo de culebra de herradura, *Hemorrhois hippocrepis*, vista el 15 de junio de 2015, en el barranco de Casa Ayala. Foto anónimo (Sistema Alerta Temprana LIFE-Lampropeltis).

Figure 2: Individual of the horseshoe whip snake, *Hemorrhois hippocrepis*, captured on 6th August 2015, in the Casa Ayala ravine. Photo J. Saavedra Bolaños (invasive species control team, Gesplan).

Figura 2: Individuo de culebra de herradura, *Hemorrhois hippocrepis*, capturado el 6 de agosto de 2015, en el barranco de Casa Ayala. Foto J. Saavedra Bolaños (equipo de control de especies invasoras, Gesplan).

The horseshoe whip snake is not a common species in the pet trade, being a protected species and its possession being forbidden, at least in Spain (Law 42/2007, of December 13, on Natural Heritage and Biodiversity). Therefore, we dismiss the possibility that these individuals were released as pets. The fact that it had been more than 10 years since the last importation of olive trees took place, and that it is the first time that this species has been seen, suggests that there were few entrances of *H. hippocrepis* to Gran Canaria. Nevertheless, these findings rather uncover concerns on the integrity of the native and endemic fauna of the island, as these individuals survived growing as much as possible, as they do on Ibiza, where gigantism has also been recorded (Montes *et al.*, 2015). The same Canarian nursery imported 42 more olive trees approximately a year after the findings, and there are other nurseries on the island currently importing olive trees from the Iberian Peninsula. Therefore, it is recommended that the environmental authorities take special care in avoiding new entrances (especially avoiding those of big olive trees during hibernation and egg laying seasons), given the successful settlement for a similar species in the same habitat, the invasive *L. californiae* (Monzón-Argüello *et al.*, 2015), and the invasiveness showed by *H. hippocrepis* on other islands (Ayllón, 2015; Montes *et al.*, 2021).

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Annex II. *Natrix astreptophora* and *Anguis fragilis* on the island of Ibiza

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Key words: alien species, snake, slow worm, biological control, Balearic Islands

Resumen

En esta nota se recogen las primeras observaciones de dos especies de reptiles continentales, culebra de collar mediterránea (*Natrix astreptophora*) y lución (*Anguis fragilis*) en los alrededores de Roca Llisa (Ibiza). Se valora el origen de su introducción y se pone de manifiesto la necesidad de llevar a cabo un control sobre los agentes importadores para evitar introducciones posteriores de estas u otras especies.

Short Note

The island of Ibiza, located in the Western Mediterranean Sea, was invaded by three different snake species in 2003: the Montpellier snake (*Malpolon monspessulanus*), last seen in 2010; the ladder snake (*Zamenis scalaris*), which maintains a small population on the island; and the horseshoe whip snake (*Hemorrhois hippocrepis*), which is quickly spreading and threatening the endemic Ibiza wall lizard (*Podarcis pityusensis*) (Montes*et al.*, 2021). These snakes continue to enter the island inside the holes of big olive trees used for gardening (Álvarez *et al.*, 2010), and the urgent need of controlling the entrance of snakes has been stated on different occasions, warning that the entrance of any other organism is a matter of time (Ayllón, 2015; Silva-Rocha *et al.*, 2018). Currently, the most thriving invader on Ibiza (*H. hippocrepis*) feeds on the only endemic terrestrial vertebrate (*P. pityusensis*), which conforms 56% of its diet (Hinckley *et al.*, 2017), and the lizard is disappearing from the areas where the snake has high density populations (Montes *et al.*, 2021). This is one of many unexpected impacts that the arrival of alien organisms may have on the native biota of islands, where the species are more naïve and less adapted to defend or compete than continental ones (Whittaker & Fernández-Palacios, 2006).

In the golf course of Roca Llisa (Santa Eulària des Riu, Ibiza; coordinates 38°56'45.8"N 1°29'37.5"E), on June 2018, a snake was spotted and killed. The snake was impossible to retrieve, and only some pictures were sent to E. M. (Fig. 1). Because of the color pattern, we identify it as *Natrix astreptophora*, but we were not able of taking measurements or other natural history traits from the specimen. Two years later, on 4 June 2020, on the waste treatment facility of Ca na Putxa (coordinates 38°56'30.7"N 1°28'48.7"E), very close to Roca Llisa, a worker found and killed a slow worm (*Anguis fragilis*; Fig. 2), and almost a year later, on 4th March 2021, M.R. found and killed another one. The first one was not kept and it was not possible to inspect the animal, but from the picture and video we identify it as an adult male; and the second one was 20.5 cm snout-vent length and 27 cm total length, and it was a male (identified upon dissection of the animal).

How the snake arrived in Ibiza remains unknown; it might have traveled as a stowaway in olive trees or other nursery trees, given that its preferred habitat includes the edge of crops and it is present across most of the Iberian Peninsula (Pleguezuelos, 2018). *Natrix astreptophora* prefers environments with elevated edafic humidity and close to marshes or river gallery formations (Pleguezuelos, 2018), making Ibiza suitable only in very specific areas of the island (like the golf course pond where it was captured, Fig. 1). The slow worms were likely introduced as stowaways in the large *Erica multiflora* cargo used as a biofilter to clean the air from the waste facility, imported from the southern region of France (between Cahors and Potier), within the slow worm range (Dely, 1981); given that the first one was seen during the *E. multiflora* unload in the waste facility, and the second one some meters away from the biofilter. There are multiple cases of species introductions with nursery trade (Hulme, 2009; Bergey *et al.*, 2014), and the closest example is the current snake invasion on this island (Silva-Rocha *et al.*, 2018). The presence of *A. fragilis* within its native range is closely linked to forests and scrublands with *E. multiflora* and other plant species, with a clear preference towards a mean annual rainfall higher than 600 mm, cold, cloudy and wet climatic conditions, and negatively correlated to annual sun hours and the mean temperature of the warmest month (Galán & Salvador, 2015); whereas the island of Ibiza has a typical Mediterranean warm climate, with an average yearly rainfall of 413 mm, high annual sun hours (a monthly mean ranging between 151 and 334 h) and the mean temperature of the warmest month is 26.3 ºC (August); standard meteorological averages for the Ibiza Airport weather station, 38º 52' 22" N, 1º 22' 23" E; www.aemet.es. This makes the island an unsuitable habitat for the slow worm. One of the biofilters from the waste facility started working on December 2021, increasing the environment temperature to 27 - 35 ºC with 100 % humidity. We suspect that due to the changes in environmental conditions, the second slow worm had to go out and was then captured.

Natrix astreptophora mainly feeds on anurans, amphibian larvae, earthworms, but also oligochaetes, insects and micromammals (Pleguezuelos, 2018). Snails and earthworms are frequent prey of *A. fragilis*, but it preys on arthropods as well (Galán & Salvador, 2015). There are some endemic arthropods and snails on Ibiza that might potentially become prey to these two species, like the endemic coleopteran *Geonemus palaui* or the endemic snails *Iberellus tanitianus*, *Xerocrassa caroli* and *X. ebusitana*, all of them listed as Vulnerable on the Spanish Red List, except for *I. tanitianus* (Verdú & Galante, 2009). There are also anurans (*Pelophylax perezi* and *Bufotes balearicus*, the latter is listed as extinction risk in the Balearic Endangered Species List [Decree 75/2005, of July 8]) and micromammals (*Rattus rattus*, *Mus* sp., *Apodemus sylvaticus* and *Crocidura ichnusae*) that would sustain *N. astreptophora* if more specimens were to arrive (Balearic Bioatlas; http://bioatles.caib.es/).

Figure 1. Specimen of *Natrix astreptophora* found in the golf course of Roca Llisa (Ibiza), from different angles. Photos P. Fernández.

Figura 1. Espécimen de *Natrix astreptophora* encontrado en el campo de golf de Roca Llisa (Ibiza), desde diferentes ángulos. Fotos P. Fernández.

Figure 2. Specimens of *Anguis fragilis* found in the waste facilities next to Roca Llisa (Ibiza). Photos M. Ruiz and Toni Roig, respectively.

Figura 2. Especímenes de *Anguis fragilis* encontrados en las instalaciones de residuos próximas a Roca Llisa (Ibiza). Fotos M. Ruiz y Toni Roig, respectivamente.

It is unlikely that any of them has established on the island forming reproductive populations, due to habitat low suitability and the lack of other conspecifics. The impossibility to make predictions about the outcomes of an unprecedented introduction should not be a motive to disdain these findings. Rather, they are a warning that these or any other species could enter the island and become a problem, in addition to the *H. hippocrepis* invasion (Ayllón, 2015; Montes *et al.*, 2021). As an example, some specimens of Iberian worm lizard (*Blanus cinereus*) were detected in a tree nursery in 2004 on Ibiza (Mateo & Ayllón, 2012). We urge policy makers with jurisdiction over invasive species management to control the entrance of organisms to the island as a priority.

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Annex III. MONOGRAPHIC ARTICLE

Dades preliminars del projecte pilot del control de serps a l'illa d'Eivissa

Montes, E. M, J. Estarellas, E. Ayllón, M. A. Carretero, M. Feriche, P. L. Hernández i J. M. Pleguezuelos. 2015. Dades preliminars del projecte pilot de control de serps a l'illa d'Eivissa

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Dades preliminars del projecte pilot de control de serps a l'illa d'Eivissa

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Resum

El Consell Insular d'Eivissa va iniciar a 2014 un programa pilot per avaluar la distribució, l'estat de les poblacions, conèixer aspectes sobre la seva biologia i controlar les poblacions d'ofidis a Eivissa. Les dades preliminars indiquen que dos espècies introduïdes a l'illa d'Eivissa estan naturalitzades i que són abundants a l'entorn de Santa Eulària des Riu, Sant Llorenç de Balàfia i Santa Gertrudis de Fruitera; predomina *Hemorrhois hippocrepis* i és més escassa *Rhinechis scalaris*; tanmateix, no hi ha dades de *Malpolon monspessulanus* des de 2010. Les dos espècies presents en l'actualitat realitzen festejos i còpules al mateix període que a les regions on són natives. Almenys *H. hippocrepis* realitza postes amb ous viables. La presència de nadons de les dos espècies en dates d'eclosió per la Península Ibèrica pareix constatar la reproducció efectiva. Almenys en *H. hippocrepis*, s'ha constatat la predació sobre *Podarcis pityusensis*. Des de la seua introducció en 2003, *H. hippocrepis* ha mostrat una resposta funcional cap al gigantisme, amb exemplars que mostraven el 213% de la biomassa màxima registrada a la seua àrea nativa de la península Ibèrica. La utilització de trampes pareix efectiva, sempre que el seu número sigui elevat. L'elecció del tipus de trampa, esquer i lloc de col·locació condiciona els resultats obtinguts. Tanmateix, la continuïtat d'aquest estudi al llarg de l'any 2015 es fa imprescindible per augmentar la mida de mostra. El proper any es pretén la utilització de nous mètodes de captura i especialment, la col·locació d'un major número de trampes tipus caixa.

Introducció

La introducció d'espècies en zones que no formen part de la seua àrea de distribució natural és una de les primeres amenaces per a la biodiversitat i un problema econòmic important. Les illes de la Mediterrània són molt vulnerables a les invasions biològiques i les seues comunitats presenten a l'actualitat un gran nombre d'espècies continentals. En aquest sentit, les comunitats presents a les Illes Balears posseeixen, per exemple, comunitats de rèptils en les quals el nombre d'espècies introduïdes és major que el de natives. Mallorca, Menorca, Eivissa i Formentera venien de patir els efectes de les glaciacions quaternàries, de tal manera que els primers humans que s'assentaren en elles només van trobar sargantanes com a rèptils locals (Mateo *et al*., 2011). Els dragons, els grans lacèrtids, els escínids, els testudínids, els anfisbènids i per descomptat, els ofidis que havien poblat les illes fins el Plistocé no varen sobreviure als grans vaivens climàtics de l'Holocé (Bover, 2008). Més tard, els humans durien, de forma voluntària o involuntària, la resta d'espècies que ara es poden trobar a les illes (Mateo *et al.*, 2011).

Al territori de l'illa d'Eivissa, com a la resta d'illes i illots de l'arxipèlag, no hi havia ofidis fa poc més de quatre mil anys (Álvarez *et al.*, 2010). Però, mentre que Mallorca i Menorca van ser ràpidament colonitzades durant el període Talaiòtic per algunes espècies introduïdes, les Pitiüses es van mantenir lliures de colobres fins els darrers anys del segon mil·lenni de la nostra era (Mateo *et al*., 2011). Aquesta tardança podria haver estat determinada per la vinculació de l'illa al culte a Bes, una deïtat protectora front als ofidis, que probablement determinà que en l'antiguitat no s'introduïssin colobres en aquestes dues illes com a símbol d'identitat (Mateo i Ayllón, 2012).

Així que, mentre que Mallorca i Menorca quedaren ràpidament despoblades de sargantanes (en l'actualitat només els illots que rodegen ambdues illes tenen poblacions de *Podarcis lilfordi*), degut a la predació per part del ofidis introduits, a les Pitiüses les sargantanes autòctones continuen essent comunes (Pleguezuelos *et al.*, 2002). En els primers anys del segle XXI es detectaren les primeres serps en diverses localitats de la Pitiüsa major (Mateo *et al.*, 2011). La presència de tres espècies d'ofidis a l'illa pareix estar associada a la importació d'oliveres i altres arbres ornamentals des de la Península Ibèrica (Mateo *et al.*, 2011), així com possiblement a la importació de materials vegetals tals com llenya o palla, també des de la Península Ibèrica. Es tracta de la serp blanca (*Rhinechis scalaris*), la serp de ferradura (*Hemorrhois hippocrepis*) i la serp verda (*Malpolon monspessulanus*) (Álvarez *et al.*, 2010; Mateo *et al.*, 2011). Totes elles presenten en la seua fase adulta mides mitjanes o grans- *M. monspessulanus* arriba a sobrepassar els dos metres de longitud total –, totes són depredadores de vertebrats i estan íntimament lligades als ecosistemes mediterranis ibèrics. Resulta previsible que la seua presència afecti de forma severa les espècies de vertebrats terrestres autòctons de l'illa, especialment a *P. pityusensis* i a aus de petita i mitjana mida, així com a totes les espècies d'interès cinegètic (Mateo y Ayllón, 2012). Les primeres cites de serps daten de l'any 2003, i des d'aleshores s'han vist cada vegada més exemplars (Mateo *et al*., 2011).

Actualment els nuclis establerts de poblacions de serps coincideixen amb les rodalies de determinats vivers de planta ornamental, a partir dels quals s'han expandit cap a altres zones. Així, les poblacions de serps existents a Eivissa presenten un model d'ocupació en el territori determinat per aquesta situació d'expansió des dels nuclis d'introducció cap a les zones agrícoles més o menys properes a aquests, que coincideixen amb l'entorn de Santa Eulària des Riu, Sant Llorenç de Balàfia i Santa Gertrudis de Fruitera. És a dir, l'assentament de les serps encara no ocupa una distribució uniforme en el territori de l'illa.

S'ha fet necessari iniciar un projecte pilot que té com a objectiu general el control i l'avaluació de la possibilitat d'eradicació de les poblacions de serps a l'illa d'Eivissa. El projecte té una durada de dos anys, i donat el nivell d'assentament actual de diferents espècies de serps a l'illa i l'entrada oberta al nostre territori d'aquests animals, és impossible aconseguir l'objectiu de l'eradicació total.

Els objectius concrets d'aquest projecte pilot, a més de treure informació per actuacions posteriors, són la minimització poblacional dels diferents nuclis presents a Eivissa i la fragmentació de les diferents poblacions per tal d'evitar la connexió espacial entre els esmentats nuclis, la qual cosa afavoriria un establiment definitiu. Aquesta actuació, en la qual se centra aquest article, s'executa mitjançant trampeig amb diversos tipus de trampes i una unitat canina de cerca.

Així mateix, el projecte inclou com a objectius concrets la millora d'una xarxa efectiva i unificada d'informació a Eivissa (mitjançant l'establiment d'un protocol d'informació per als serveis públics, la creació d'una xarxa d'informadors entre els serveis públics, mitjançant xerrades impartides entres aquests col·lectius, l'elaboració d'un tríptic informatiu, i una campanya informativa entre la població eivissenca, amb l'ajuda del tríptic); i la col·laboració en la creació d'una unitat de recolzament i recollida ràpida (mitjançant un protocol d'actuació detallat acordat entre les diverses administracions afectades i mitjançant l'entrenament de l'equip d'intervenció ràpida en la captura d'ofidis) (Ayllón *et al.*, 2014)

Material i mètodes

Des del començament del projecte es va simultaniejar la construcció de les trampes amb la seua col·locació i revisió, i es van anar provant, en base a l'experiència dels casos més semblants i propers al de l'illa d'Eivissa, que són la prova realitzada al viver Sa Porrasa (a Mallorca) i l'illa de Gran Canària, de manera que es van anar fent modificacions sobre allò proposat en un principi.

La campanya de 2014 tenia una durada de dos mesos i mig, durant el període primaveral – estival. Els mètodes emprats són els següents:

a. Mètodes de captura passiva:

-Trampes de doble embut amb ratolí viu (Fig. 1), amb i sense malla de desviament (Fig. 2): es tracta de tubs de PVC de 80 centímetres de longitud i 15 cm de diàmetre, amb dos embuts fixats en cada extrem pels quals la serp sap entrar però no sortir. Es col·loquen en àrees – font o de molt alta densitat.

Degut a la mortalitat massiva dels ratolins, després de la primera setmana es va deixar d'utilitzar l'animal viu com a esquer en aquest tipus de trampa, tanmateix es va mantenir el cadàver per provar-lo com a mètode d'esquer.

Fig. 1: Gàbia amb el ratolí viu, que es col·loca a l'interior de la trampa.

Fig. 2: Trampes de doble embut amb utilització de malles de desviament.

En setmanes posteriors es tornaren a instal·lar trampes de doble embut provant altres tipus d'esquers, com exemplars vius de *Tarentola mauritanica*, pell de ratolí, i fenc de cria de ratolí, finalment es va decidir utilitzar aquest últim com a únic esquer per a totes les trampes de doble embut, polvoritzant aigua sobre ell per mantenir l'olor amb la màxima intensitat possible.

-Taulers de xapa marina: consten d'un tauler contraxapat de 60 x 60 cm que es col·loca al terra per crear refugis artificials. S'usa en àrees amb pocs refugis amb densitat d'ofidis alta o mitjana, o en punts de baixa densitat amb observació molt recent. El problema d'aquest tipus de trampa és que l'ambient típic de l'illa d'Eivissa ofereix multitud de refugis que fan esperar molt poca efectivitat.

-Trampes tipus caixa (Fig. 3): es tracta d'una caixa de 50 x 50 cm (i 15 cm d'altura) amb un embut a cada paret; se'n van construir i instal·lar 5, utilitzant l'esquer de ratolí viu en gàbia en 4 d'elles, i femelles de serp en zel per atraure mascles sexualment actius, tot i que aquesta decisió es va prendre quan l'època de reproducció ja estava finalitzant, per la qual cosa no es pot valorar realment la seua efectivitat.

b.Mètodes de captura activa:

-Revisió de refugis potencials després d'un albirament molt recent (menys de 24 hores): a qualsevol àrea (àrea – font, àrea de densitat baixa, mitjana o alta), acompanyats de la unitat canina.

-Revisió de refugis potencials després d'albirament no molt recent (més de 24 hores): en qualsevol àrea (àrea – font, àrea de densitat baixa, mitjana o alta); recomanable l'ús de taulers de xapa marina com a refugi artificial. S'han realitzat visites aleatòries a aquestos punts, acompanyats de la unitat canina quan ha estat possible.

-Revisió de refugis potencials sense albirament previ: en àrees – font i àrees de densitat mitjana o alta. Es va fer revisió de refugis potencials al mateix temps que es revisaven les trampes durant tot el període de treball, també en zones perifèriques i límits de la distribució coneguda, amb l'objectiu de localitzar possibles tendències d'expansió .

-Ús de cans ensinistrats com a recolzament als mètodes de captura activa (Vice & Engemim, 2000): com que l'ensinistrament en recerca de serps dels cans de treball es va començar a realitzar poc temps abans de l'inici del projecte, els cans han estat en període d'aprenentatge durant tota aquesta campanya, però es pot dir que al final d'aquesta ja s'utilitzava la unitat canina per saber on valia la pena buscar manualment i on no, degut al seu èxit. La unitat està formada per 5 cans.

-Recorreguts nocturns en cotxe a poca velocitat, per a la detecció d'activitat crepuscular de *Rhinechis scalaris* en zones favorables i de presència coneguda per a l'espècie.

Les ubicacions de les trampes (Fig. 4) coincideixen normalment amb els vivers dels quals se sospita que poden ser les fonts d'entrada dels ofidis, a les rodalies de les zones abans esmentades, sempre seguint consells i recomanacions d'experts en quant a les condicions d'ombra / sol, humitat, vegetació, murs, etc.

Fig: 3. Trampa tipus caixa amb malles de desviament.

Fig 4: Ubicacions de les trampes a l'illa d'Eivissa.

Resultats

Captura passiva

A la taula següent es detallen les trampes col·locades a cada ubicació, així com les captures realitzades (que figuren entre parèntesi i que corresponen en tots els casos a exemplars d'*Hemorrhois hippocrepis*), i el total de captures amb cada tipus de trampa:

Com es pot veure, es van realitzar 8 captures mitjançant les trampes.

A la Taula 2 s'analitza la taxa de rendiment de cada tipus de trampa segons l'esquer utilitzat, és a dir, quantes trampes hi hauria col·locades en 1 dia si tenim en compte el número de trampes i el número de dies que han estat al camp. D'aquesta taxa "trampa/dia" podem extreure el rendiment de les trampes en les quals hem obtingut captures, això és, quantes trampes/dia necessitem per fer una captura:

Captura activa i altres

A més a més dels mètodes de captura activa esmentats a l'apartat "Material i mètodes", també s'han dut a terme captures mitjançant avisos de la població que ja els tenien capturats (vius o morts) i mitjançant captura directa d'animals morts per atropellament a la carretera. A la Taula 3 s'han recollit els resultats de captures per espècies d'ofidi amb cada mètode, incloent les trampes:

Com es pot observar, els mètodes més efectius amb diferència són els avisos de la població. És per això que, de cara a la propera campanya, es potenciarà aquesta part del projecte per treure-li el màxim partit. En segon terme, trobam els atropellaments i la captura manual i canina, que és difícil separar-los en dues categories degut a que pràcticament en tots els casos un no hauria estat possible sense l'altre. Cal dir que els cans han realitzat la campanya de 2014 mentre encara estaven aprenent, i tot i així han obtingut uns resultats sorprenents, motiu pel qual esperam de cara a l'any que ve un augment de captures per part de la unitat canina.

Localitats	Doble embut	Tauler de xapa	Trampes Caixa Ratolí	Trampes Caixa Femella sp
Noahs Garden	20 (1)	25 (2)	2(1)	1 *H. hippocrepis*
Pont de Can Font	5 (1)			
Can Marines	7			
Can Guash	5		1	
Finca Can Pol	22(3)		1	
Can Nadal				1 *R. scalaris*
Aigües Blanques				1 *H. hippocrepis*
Altres	2			
Total trampes	61	25	4	3
Total captures	5	2	1	0

Taula 1. Número i tipus de trampa per ubicació (les captures apareixen entre parèntesi).

Tipus trampa	Període	Esquer	Trampa/dia	Captura	Taxa de rendiment	Període captura
Doble embut	1/5/2014 12/06/2014	Cadàver ratolí	387	0	0	
Doble embut	15/05/2014 21/07/2014	Fenc de cria	2682	5	0,002(1/536)	10/06/2014 16/07/2014
Doble embut	28/05/2014 21/07/2014	Fenc de cria + Malla direc.	432	0	0	
Doble embut	15/05/2014 28/05/2014	Pèl de ratolí	26	0	0	
Doble embut	15/05/2014 28/05/2014	*T. mauritanica*	26	0	0	
Tauler	02/05/2014 21/07/2014	Sense	920	2	0,002(1/460)	26/05/2014 20/06/2014
Tauler	28/05/2014 21/07/2014	Tapant sortida embut	432	0	0	
Caixa	04/06/2014 21/07/2014	Ratolí viu	150	1	0,007(1/150)	10/06/2014
Caixa	04/06/2014 21/07/2014	Femella *H. hippocrepis*	40	0	0	
Caixa	06/06/2014 18/06/2014	Femella *R. scalaris*	12	0	0	

Taula 2. Taxes de rendiment per tipus de trampa i esquer, relacionat amb el període de permanència i període de resultats favorables.

	Avisos població	Captura manual + Unitat Canina	Trampes	Atropellament	Altres	Total
H. hippocrepis	44	17	8	18	2	89
R. scalaris	5	1	0	0	0	6
Sense identificar	3	0	0	0	0	3
Elaphe guttata	1	0	0	0	0	1
Total serps	53	18	8	18	2	99

Taula 3. Origen de la recollida i de les captures totals de serps, per espècie.

Distribució

Durant l'any 2014 s'han recollit 146 cites de colobres provinents de captures i d'observacions directes d'exemplars, mudes, restes i albiraments notificats al telèfon d'emergències 112. Les cites consten de 109 exemplars de *Hemorrhois hippocrepis*, 8 de *Rhinechis scalaris*, 1 d'*Elaphe guttata* i 28 cites d'albiraments sense identificar l'espècie. Cal tenir en compte que aquestes dades només contemplen el període de 2014 fin el 31 de juliol, però existeixen observacions posteriors no incloses en aquesta anàlisi.

A la Fig. 5 es mostra un mapa de distribució les cites a l'any 2014, que si es comparen amb les cites d'anys anteriors, són molt més abundants, la qual cosa indica no només un possible augment d'individus al territori, sinó també un major esforç en la seua localització.

L'espècie *Hemorrhois hippocrepis* pareix tenir una distribució ampla a la part oriental de l'illa, en la resta de l'illa les cites són ocasionals. Manté unes poblacions abundants i estables al municipi de Santa Eulària des Riu, i més esporàdicament al municipi de Sant Joan de Labritja. La major presència de l'espècie es dona al polígon format entre Sant Carles de Peralta, Sant Miquel de Balansat, Santa Gertrudis de Fruitera, Ca na Negreta i el casc urbà de Santa Eulària des Riu. Apareixen cites en menor escala al nord de l'illa, però amb una consistència que fa pensar que l'espècie està present a tot el municipi de Sant Joan de Labritja, però en densitats més baixes que al nucli principal. La distribució pareix presentar una continuïtat manifesta, no existint punts d'alta densitat voltejats per zones de baixa, com es pensava al començament del treball. Totes les cites sense identificar de les UTM CD61, CD62, CD71 i CD72 clarament pareixen pertànyer a aquesta espècie.

Les cites de *Rhinechis scalaris* són més escasses, i localitzades a l'entorn de Sant Llorenç de Balàfia i Sant Rafael de sa Creu, i per la quantitat de cites aportades any rere any, no pareix que les seues poblacions augmentin en efectius i en extensió a la mateixa velocitat que la serp de ferradura, tot i que les cites sense espècie identificada al municipi de Sant Josep de sa Talaia ens fa prendre aquests comentaris amb precaució, a més dels costums menys antropòfils que la serp de ferradura, cosa que li donaria menys visibilitat. La cita de l'espècie a la Cala de Sant Vicent és un albirament, i degut a que és una cita tan aïllada ens fa pensar en una possible errada d'identificació, tot i que no es descarta l'aparició d'algun exemplar de nova introducció per la jardineria o un altre mitjà, degut a la data de l'observació (21 de gener de 2014).

Pel que fa a *Malpolon monspessulanus*, no existeixen observacions des de juny de 2010, i no ha estat observada durant aquest any d'estudi. No pareix probable la seua existència actual a l'illa, però no es descarta la possible entrada d'exemplars per les vies d'introducció ja conegudes.

Per últim, la presència d'altres espècies d'ofidis en aquest període són esporàdiques i relacionades amb la terrariofília. La cita d'*Elaphe guttata* corresponia a un exemplar albí, clarament fugat d'un terrari o alliberat al medi deliberadament per part del propietari. Els censos realitzats als voltants del viver principal (Noah's Garden) tampoc han donat cap resultat positiu per a *Blanus cinereus*, espècie citada a la zona els anys 2004 i 2007, tot i que no és un ofidi.

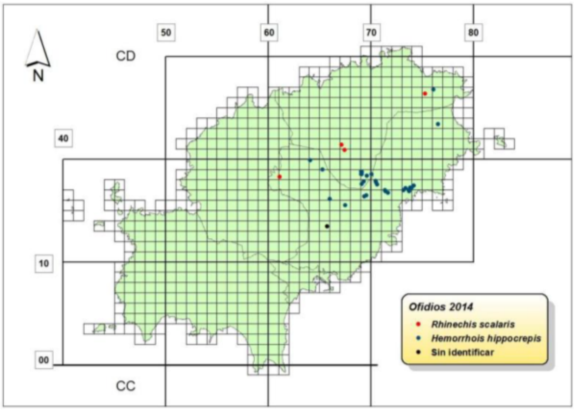

Fig. 5:. Mapa de distribució de cites d'ofidis per a l'any 2014.

Biologia i primeres valoracions de l'estatus de les colobres introduïdes a Eivissa

Hemorrhois hippocrepis

Analitzats els exemplars capturats durant 2014, aquesta colobra presenta a Eivissa longituds totals (LT) que comprenen entre els 29 cm de longitud mínima fins els 174 cm de longitud màxima (n = 54), essent la mitjana de 90,9 cm. Quant al pes corporal, va des dels 3 g de pes mínim fins els 1.200 g de pes màxim (n = 49), essent la mitjana de 216,4 g. En comparació a la Península Ibèrica (Feriche, 2004), la talla mitjana a l'illa supera en un 102,2 % la LT mitjana de la Península (89,1 cm), superant a l'illa en un 172 % el pes mitjà al detectat en la Península (125,8 g). A 2013 es trobà un exemplar de 183 cm de LT i 1.440 g de pes, la qual cosa representa un 105 % de la talla màxima i un 213 % de la biomassa màxima registrada històricament a la població ibèrica (Salvador, 2014). En el termini de tan sols 10 anys d'invasió, l'espècie pareix estar realitzant un canvi fenotípic cap al gigantisme, un procés comú a les illes, i un clar exemple de divergència adaptativa en una escala de temps ecològic. Com es desprèn dels valors anteriors, l'espècie no només creix en longitud, sinó que s'està fent molt més robusta a Eivissa.

Pel que fa a l'hàbitat, a la Península és una espècie molt termòfila i rupícola. Aquestes dos característiques ecològiques condicionen l'hàbitat que ocupa allí. Si traslladem aquest hàbitat definit per a la Península Ibèrica a l'existent a l'illa d'Eivissa, ens adonem que, pràcticament tota l'illa és hàbitat favorable per a l'espècie. Les nostres observacions a Eivissa la defineixen com una espècie clarament rupícola, que freqüenta espais oberts i assolellats, zones rocoses i torrents. Es troba sovint a terrenys agrícoles i cultius de garrovers, i utilitza freqüentment bancals de pedra seca tan comuns a tota l'illa. Es molt habitual als medis urbans rurals.

Quant a la dieta, a la Península Ibèrica s'alimenta quasi exclusivament de vertebrats (mamífers, rèptils, aus), encara que els exemplars més joves també consumeixen oligoquets i hexàpodes. Buscador actiu d'aliments, recorre de forma lenta però contínua el medi, inspeccionant escletxes i forats. Les observacions directes al medi natural a l'illa ens han donat dades de predació sobre *Tarentola mauritanica* en dos casos a més d'una altra dada d'un exemplar jove mantingut en captivitat per l'ensinistrament de cans que es va alimentar d'un cadàver de *T. mauritanica*. També sobre un poll de xoriguer (*Falco tinnunculus*), així com sobre dos pollades i un adult de canari (*Serinus canaria domestica*) en gàbies de cria situades a un corral.

Les dades obtingudes a l'any 2013 indicaven restes d'exemplars de rosegadors del gènere *Apodemus sp.*, així com restes de vèrtebres de *Podarcis pityusensis*, que pareixien ser assignades a vèrtebres caudals, confirmant al menys la predació de cues de l'espècie. Durant aquest projecte, es va obtenir un excrement d'un exemplar capturat; l'anàlisi d'aquest sota la lupa mostra escames caudals i ventrals de lacèrtid (Fig. 6), la qual cosa confirma definitivament la predació sobre exemplars de *Podarcis pityusensis*. S'ha de tenir en compte l'abundància de mudes al camp, en certes localitats s'han trobat entre 5 i 10 mudes en una hora de cerca sense cans. Aquesta dada, a més d'indicar l'abundància d'exemplars a la zona, mostra també l'existència d'una bona alimentació que pot provocar més d'una muda anual a la majoria dels exemplars.

A l'illa d'Eivissa no existeixen els predadors naturals que té aquesta espècie a la Península, exceptuant al gat domèstic. De fet, durant el projecte es va observar la predació d'un exemplar per un gat domèstic, que va ser retirat de la seua boca quan ja havia menjat al voltant del 50 % del seu cos (longitud de la resta = 29 cm, exemplar possiblement de 60 – 70 cm de LT). Hem estat informats de dos casos més, per la qual cosa podem pensar que la predació per gats domèstics és habitual.

Sobre la seua reproducció, hem observat dos comportaments de festeig i/o còpula. Les dates d'aquests comportaments foren el 19 de maig de 2014 i el 18 de juny de 2014. Es va trobar una posta en un aljub amb la femella atrapada, això ens fa pensar que no va tenir més remei que pondre els ous al seu interior; una altra atrapada en una trampa que es va descompondre i que portava ous; i per últim la femella que utilitzàvem com a esquer a la trampa va realitzar allí mateix una posta. Les mides de la posta eren de 8, 5 i 6 ous respectivament (mitjana = 6,33; n = 3), i les dates de la posta 29 de juny, 11 de juliol i 21 de juliol respectivament. La presència d'exemplars recentment eclosionats ha estat constatada durant l'època de la tardor, sense cap mena de dubte ja que es podia apreciar encara la sutura al sac vitel·lí.

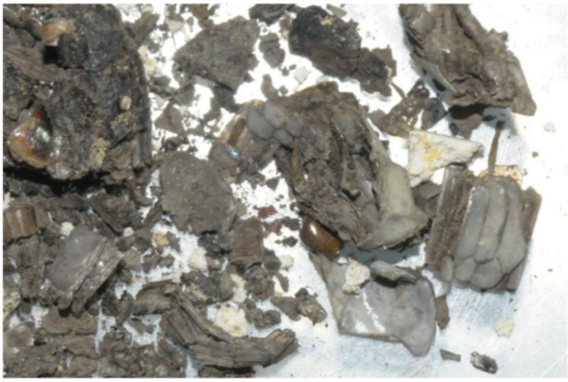

Fig. 6 :. Excrement d'*Hemorrhois hippocrepis* contenint escames caudals i ventrals de lacèrtid.

Rhinechis scalaris

Analitzats els pocs exemplars capturats durant 2014 i les dades de pes i LT d'alguns exemplars de 2013, aquesta colobra presenta a Eivissa LT que van des dels 29 cm fins els 120 cm (n = 13), essent la mitjana de 82,5 cm. Quant al pes corporal, comprèn entre els 16 g i els 665 g (n = 14), essent la mitjana de 239 g. Tot i que l'anàlisi es fa amb poques dades, tant la talla mitjana com el pes mitjà són similars als detectats per a la Península Ibèrica (82,5 cm *vs* 82,9 cm i 239 g *vs* 240 g).

A Eivissa ocupa les zones menys poblades utilitzant àrees del límit de pinars, i de cobertura vegetal mitjana. Tot i tenir hàbitats favorables, no pareix ser el més idoni per a l'espècie, que en zones del sud-est ibèric necessita llocs més ombrívols i humits que altres espècies de colúbrids.

S'han obtingut poques dades sobre la seua biologia, només es va observar una còpula el 5 de juny de 2014; la presència de nadons no ha estat constatada per aquest estudi, però la captura d'exemplars petits a dates lògiques d'eclosió en altres anys apunta a l'existència de reproducció efectiva (el 5 d'octubre de 2013 amb 16 g de pes i 29 cm de LT).

Discussió

La població de serps introduïdes a l'illa d'Eivissa pareix ben assentada i abundant a l'entorn de Santa Eulària, Sant Llorenç de Balàfia i Santa Gertrudis de Fruitera, predominant la serp de ferradura, essent més escassa la serp blanca i sense dades que confirmin la presència a l'illa de la serp verda des de fa més de 5 anys. Per poder intentar limitar les poblacions de serps, la primera actuació urgent és el control de l'entrada de nous espècimens: tot esforç per mantenir o disminuir els nuclis actuals no té cap sentit si no existeix un control exhaustiu de l'entrada que permeti evitar-la.

En aquest sentit, ja existia normativa que situava els ofidis a les illes Pitiüses com a espècies exòtiques invasores i instaven a executar mesures de control, però darrerament s'ha publicat nova normativa que parla específicament d'aquest problema. Concretament, el Real Decret 630/2013, de 2 d'agost, pel qual es regula el Catàleg espanyol d'espècies exòtiques invasores, estableix les mesures de control en ports i en el territori; i el Reglament núm. 1143/2014 del Parlament Europeu i del Consell, de 22 d'octubre de 2014, sobre la prevenció i la gestió de la introducció i propagació d'espècies exòtiques invasores, estableix obligacions i prohibicions específiques, incloent la prohibició d'introduir aquestes espècies fins i tot involuntàriament, i incloent l'obligació de l'administració competent a dur a terme mesures de gestió i de recuperació dels ecosistemes danyats, entre altres coses.

Independentment de l'obligació establerta per la normativa, existeix una obligació moral en favor de la biodiversitat, per tant, mantenir un control sobre les poblacions de serps per evitar el seu augment desaforat, és imprescindible tot i que no s'aconsegueixi la seua eradicació. La inacció permetria l'expansió de les poblacions per tota l'illa amb conseqüències nefastes per a les espècies autòctones i en particular les endèmiques, molt més sensibles.

La col·laboració ciutadana, tant en la localització d'exemplars com en la seua captura és molt important, per no dir imprescindible. Una bona difusió del problema i dels canals de comunicació (telèfon 112), així com una resposta eficient i ràpida dels grups de recollida (unitat canina pels albiraments i recollida ràpida pels exemplars vius) és molt necessària.

La utilització de trampes pot resultar efectiva, sempre que el volum de trampes col·locat sigui alt. L'elecció del tipus de trampa, tipus d'esquer i que el lloc concret de col·locació sigui l'idoni per a cada tipus d'ambient condiciona molt els resultats obtinguts. La continuïtat d'aquesta anàlisi al llarg de 2015 es fa imprescindible per poder determinar els millors resultats. El disseny de nous mètodes de captura com xarxes d'intercepció, adequació de les trampes de doble embut i la col·locació d'un major nombre de trampes tipus caixa, tant amb esquer viu com amb femella en zel, pareix primordial per augmentar el número de captures.

Concretament, pel que fa a les trampes, podem extreure que:

1. El rendiment de les trampes, tot i que no s'han col·locat de manera regular en el temps, ha estat l'esperat basant-nos en els resultats d'altres projectes, encara que una col·locació més regular i primerenca seria més efectiva per avaluar adequadament els distints mètodes.
2. La utilització d'esquer viu en trampes d'embut pareix inviable per l'alta mortalitat de ratolins.
3. la utilització d'esquer viu en trampes tipus caixa és molt viable i la mortalitat de ratolins és baixa, però el manteniment de l'esquer genera un volum gran de treball, en la revisió i manteniment de la trampa, sobre tot en el moment de més calor en el qual les visites han de ser més freqüents.
4. Segons les dades obtingudes, per a la captura de 100 exemplars en un període de 100 dies de trampes col·locades d'abril a juliol, es necessitarien 536 trampes de doble embut amb fenc de cria o 460 taulers o 150 tipus caixa amb ratolí viu. Les dades ens indiquen que si aquestes trampes se simultaniegessin, es podrien capturar fins 300 exemplars per campanya.
5. La ineficàcia de les trampes tipus caixa amb femella en zel és més deguda a l'època de col·locació, ja tardana per al zel, que a la ineficàcia real del mètode.
6. Consideram que tan important és el mètode utilitzat per trampejar com l'elecció d'un lloc i ubicació adequada.
7. Amb la prova realitzada aquest any no podem valorar quan seria convenient abandonar un lloc degut a que la majoria o el total d'exemplars de la zona han estat capturats. Aquesta dada seria molt interessant per poder rentabilitzar l'ús de les trampes.
8. La utilització de barreres direccionals no ha estat especialment efectiva al trampeig d'exemplars, però si aquestes barreres es posessin amb malla d'intercepció, potser serien molt més efectives.

Específicament, pel que respecta a les poblacions, la seua situació i la seua influència sobre la fauna existent a l'illa d'Eivissa, podem afirmar que:

1. Les poblacions de colobres introduïdes a l'illa d'Eivissa es troben actualment distribuïdes de forma generalitzada pel terme municipal de Santa Eulària des Riu, així com a l'entorn de Sant Llorenç de Balàfia i Santa Gertrudis de Fruitera.
2. *Hemorrhois hippocrepis* és l'espècie de major distribució, amb zones d'alta abundància i poblacions contínues en la seua àrea de distribució principal amb una tendència a l'expansió de la seua distribució espacial.
3. *Rhinechis scalaris* pareix mantenir poblacions estables i poc denses, així com una lenta capacitat d'expansió a l'illa.
4. La presència de *Malpolon monspessulanus* pareix rara o inexistent, ja que no ha estat localitzada des de 2010.
5. L'existència de cites d'exemplars (molts d'ells sense identificar) a zones de l'illa on, en principi pareixen lliures de serps, indica que els esmentats exemplars podrien estar apareixent per l'entrada de nous exemplars a l'illa o trasllats accidentals i puntuals dins de l'illa des de localitats font.
6. Les dos espècies presents a l'actualitat realitzen festejos i s'han observat còpules dins de l'època lògica de cria en zones mediterrànies.
7. Al menys, *Hemorrhois hippocrepis* realitza postes amb ous viables. La presència de nadons ha estat confirmada.
8. Al menys en *Hemorrhois hippocrepis* s'ha constatat la predació efectiva sobre l'endemisme *Podarcis pityusensis*. Altres dades d'alimentació podrien apuntar a possible predació sobre pollades d'aus endèmiques.
9. Les relacions de talla i pes confirmen una bona condició física i una línia que marca la seua tendència al gigantisme, al menys en *Hemorrhois hippocrepis*.

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Annex IV. BOOK CHAPTER

Herpetological History of the Balearic Islands: when aliens conquered these islands and what to do next

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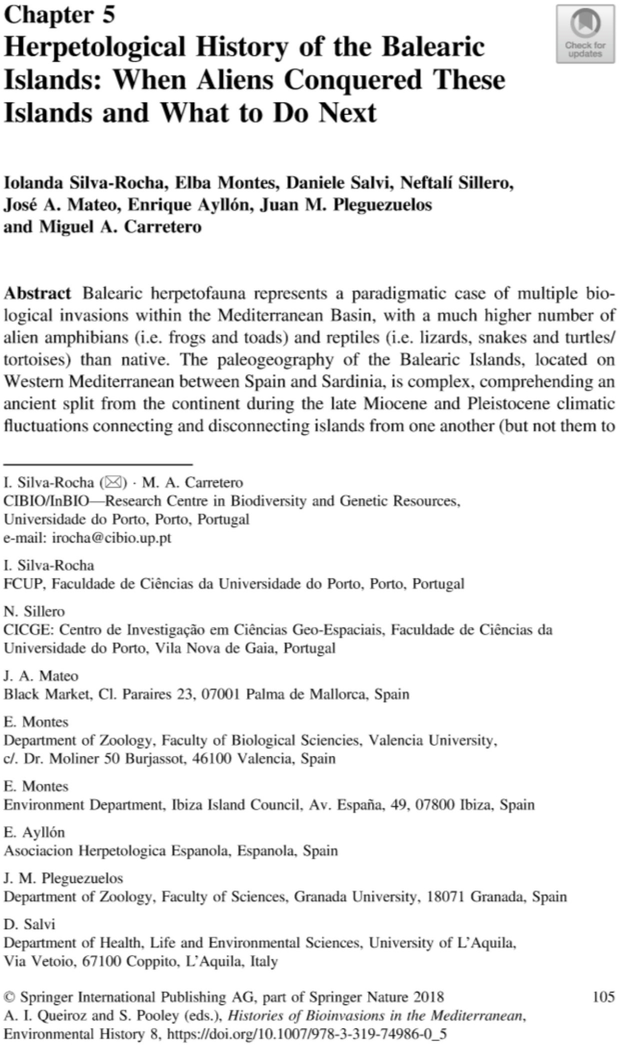

Chapter 5

Herpetological History of the Balearic Islands: When Aliens Conquered These Islands and What to Do Next

Iolanda Silva-Rocha, Elba Montes, Daniele Salvi, Neftalí Sillero, José A. Mateo, Enrique Ayllón, Juan M. Pleguezuelos and Miguel A. Carretero

Abstract Balearic herpetofauna represents a paradigmatic case of multiple biological invasions within the Mediterranean Basin, with a much higher number of alien amphibians (i.e. frogs and toads) and reptiles (i.e. lizards, snakes and turtles/tortoises) than native. The paleogeography of the Balearic Islands, located on Western Mediterranean between Spain and Sardinia, is complex, comprehending an ancient split from the continent during the late Miocene and Pleistocene climatic fluctuations connecting and disconnecting islands from one another (but not them to

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the continent) that eventually re-shaped the archipelago's biota. The archipelago has been also influenced by humans since the Neolithic, being a cross-road for alien biota between North Africa and Southern Europe, which caused range regressions and extinctions in the native herpetofauna, nowadays restricted to one amphibian and two reptiles. During the last century, tourism development, the pet trade, and cargo transport of ornamental plants have produced a new wave of biological invasions. Recently introduced snakes are of particular concern, since the effect of predation may seriously threaten the remaining native reptiles in the main islands and endemic subspecies in surrounding islets. Balearic people have a negative social perception of such snakes, mainly due to the lack of familiarity with snakes among islanders but also to the herpetophobic attitude of many Mediterranean cultures. Here we review the herpetological invasions in the Balearic Archipelago and their impacts. We further discuss the on-going management actions on alien reptiles in this archipelago, namely the control of invasive snakes in Ibiza involving monitoring, trapping, environmental education and promotion of social participation.

Keywords Alien reptiles · Balearic Archipelago · Cabrera · Formentera
Humans · Ibiza · Invasive species · Islands · Gimnesic Islands
Lizards · Mallorca · Menorca · Snakes · Nursery trade · Pityusic Islands
Tourism

5.1 The "Deep History" of the Balearics

The Mediterranean Basin is one of the richest and most complex regions on Earth on several facets, namely geological, biological and cultural. Nowadays, it is considered one of the global biodiversity hotspots (Myers et al. 2000). The region is the result of a complex history encompassing profound geological processes such as tectonic dynamics, climatic shifts, and biogeographical interchanges (Blondel et al. 2010). All these processes have contributed to the development of a particularly rich biota. The most influential geologic events were: (1) the Messinian Salinity Crisis (from 5.9 to 5.3 Myr ago) during which the Mediterranean Sea went into a nearly complete desiccation, which allowed substantial faunal interchanges between land masses; and (2) the Pleistocene climatic oscillations between glacial and interglacial episodes (especially in the last Myr), which played a key role in molding and shaping present-day biota, including species range shifts and extinctions (Blondel et al. 2010).

The Balearic Archipelago represents an ancient and isolated system within the Mediterranean. The last separation of this archipelago from the mainland dates back to the end of Messinian salinity crisis, about 5.3 Myr ago. At that time, two sub-archipelagos arose and never contacted each other again: the western group or Pityusic Islands comprising Ibiza, Formentera and nearly 60 smaller surrounding islets; and the eastern group or Gymnesic Islands comprising Mallorca, Menorca and about 30 medium and smaller surrounding islets.

The Messinian represented the last massive terrestrial exchange of fauna between Europe and Africa and among the Balearic Islands as a whole. Since then, faunal interchanges have only taken place within each sub-archipelago islands and islets. Thus, terrestrial species evolved there in isolation during the Pliocene under mild subtropical conditions (Bover et al. 2008). Subsequent climatic changes occurred in the Late Pliocene with a shift towards a Mediterranean climate regime characterized by long summer drought (Jiménez-Moreno et al. 2010), followed by substantial oscillations in temperature and humidity during the last 2.5 million years due to glaciations (Bover et al. 2008).

Pleistocene glaciations not only brought about radical changes in climate compared to the Pliocene, but also promoted temporary connections among islands within the same sub-archipelago. A number of vertebrate groups became extinct in that period (e.g. vipers; Bailon et al. 2010). The surviving fauna underwent separate evolutionary and ecological pathways to those of their continental relatives. In particular, there was a shift from a primarily insectivorous lizard fauna to a lizard fauna with a mainly plant-based diet (Pérez-Mellado and Corti 1993), while small species shifted to gigantism (Novosolov et al. 2013), namely many populations of *Podarcis lilfordi* present in small islets (Brown and Perez-Mellado 1994).

During glaciations, the Pityusic Islands (nowadays separated by a narrow and shallow channel) were connected, therefore sharing their fauna. In the Gimnesic Islands Mallorca and Menorca, a deeper sea channel prevented their connection during the Tertiary, but not during the Pleistocene glacial phase, when they were connected several times allowing interchanges of some faunal elements. Thus, current Mallorcan and Menorcan faunas are a mixture of shared and unique elements. Last but not least, the small islets that were connected to the main islands until the end of the glaciations became isolated due to the post-glacial marine transgression.

Nowadays, the Balearic Islands have a total area of 5040 km^2 and 1428 km of coastline, lying from 80 to 300 km east of the Iberian mainland (Fig. 5.1). Mallorca is the largest island, with very diverse ecosystems and landscapes, which can be divided into three distinct districts: the Serra Tramuntana, an elevated mountain range that shapes the northern coast of the island, with the highest peak at 1445 m; the Serres de Llevant, comprising small rounded hills that mark the landscape of white-sand coves and green pine forest; and a flatland area located between the two mountain ranges and characterized by rural landscapes.

Menorca Island is predominantly flat with subtle rolling hills, and is sheltered by a small mountain range along the northern coast (347 m above sea level). Therefore, in the north, the island is more rugged, with a jagged coastline, while the south is flatter with cliffs, water-carved gullies and white-sand coves nestled amid pine trees.

Cabrera is located south of Mallorca and it was officially declared a Marine and Land National Park in 1991. It is an area with a great wealth of biodiversity, featuring a multitude of endemic invertebrates, and 150 migratory bird species stop over on the island during both their spring and autumn migrations.

Ibiza has a uniform landscape and moderate relief, the highest point being Sa Talaiassa (486 m). Habitats include marshes, dunes, saltflats (*salines*), cliffs and

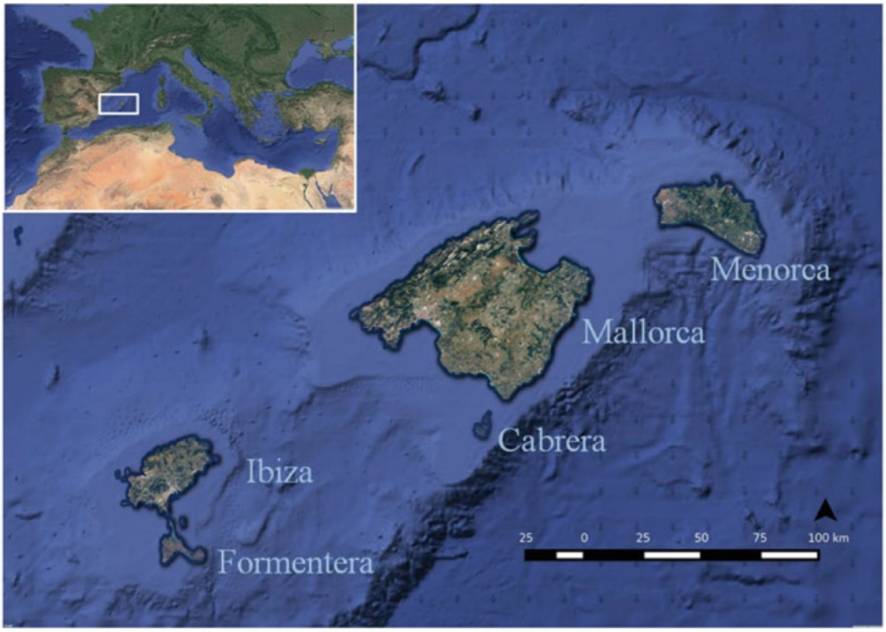

Fig. 5.1 The Balearic Archipelago and its geographical position in the Mediterranean Basin

beaches. The flat alluvial plain is formed by Quaternary calcareous deposits and two enclosing wooded hill ranges. This island is part of a Special Protection Area for Birds and The European Economic Community's Natura 2000 Network, and it is listed on the Ramsar List of Wetlands of International Importance.

Formentera is 19 km long and located 6 km south of Ibiza. It has a narrow shape that gives it a long stretch of coast (82 km) in proportion to its surface area (83 km^2). The landscape is composed of Mediterranean shrubs in dune areas as well as pine and savin (juniper) forests.

The general climate on the Balearic Islands is Mediterranean, with a hot and dry summer, mild winter and the scarce rains concentrated in autumn. During the winter the minimum temperature is 10 °C and in July temperatures can reach 35 °C (30-years standard meteorological averages; AEMET and IM 2011).

5.2 The Balearics and the Bioinvasions

5.2.1 *Invasions on Islands*

Islands harbour peculiar ecosystems, due to their isolation from the continents. The number and organismal taxa that can naturally reach and colonize island ecosystems is limited, the number of populations is fewer, and the total population size is smaller than in continents. Island communities are, therefore, impoverished and unbalanced in comparison with continental ones. They experience less biotic interactions and opportunities to evolve independently and differently compared to their mainland relatives, as a result of having less competitors, predators and parasites (Whittaker and Fernández-Palacios 2007). These factors create a higher sensitivity to disturbances and vulnerability to biodiversity extinction, compared to continental ecosystems (Vitousek et al. 1996; Reaser et al. 2007; Ficetola and Padoa-Schioppa 2009).

The theory of island biogeography states that species richness on islands results from the equilibrium between colonization (as a function of distance to continent or to other islands), speciation (as a function of time) and extinction (as a function of island size and habitat heterogeneity) (MacArthur and Wilson 1967). However, humans have shifted this balance on some insular ecosystems by increasing colonisation rates by alien (introduced) species; hence islands where human impact is very high may end up with more alien species.

Biological invasions on islands are even more dangerous when the presence of native predators is low, competitors are absent, and the native species are vulnerable to the aliens or to its parasites (Whittaker and Fernández-Palacios 2007; Álvarez et al. 2010). In addition to that, islands normally have a more benign environment (i.e. more stable abiotic conditions, such as milder temperatures) and lower habitat diversity, which facilitate the establishment of invasive species (Gimeno et al. 2006).

5.2.2 *A Long History of Successive Herpetoinvasions*

The Balearic Archipelago is one of the most isolated in the Mediterranean (i.e. farther from mainland) and because of that, its exploration and discovery by humans took place later than in other archipelagos. The first records of humans on the Balearics date from the last third of the third millennium BCE (Alcover et al. 2001; Ramis et al. 2001; Bover et al. 2008). The first settlers were hunters and farmers, also herding goats, cattle, sheep and pigs, brought from the mainland (Ayuso 2001).

A long history of migratory waves followed this period, as in other parts of the western Mediterranean with high demographic growth, the discovery of new uninhabited regions and the development of maritime contacts setting the Balearic Islands in the route of several civilizations (Iberians, Nuragics (from Sardinia), Phoenicians, Greeks, Carthaginians, Romans, Byzantines, Arabs and Berbers). All these civilizations introduced alien species passively (with cargo) or voluntarily (as food source or for religious purposes). The Romans may have introduced snakes to frighten their enemies, and—associated to Aesculapius cult—to give them good luck; tortoises were introduced by several civilizations (i.e. Phoenicians, Greeks and Arabs) to serve as food and pets. The Nuragics are thought to have introduced the Balearic green toad *Bufotes balearicus* for religious purposes (Lewthwaite 1985; Chapman 1990).

During the twentieth century, an intensification of human activity occurred in the Balearic Islands, especially on Mallorca, due to massive tourism development and to the pet trade and the nursery trade (trade of live plants for ornamental purposes). These activities have resulted in range retractions in the native herpetofauna, which is nowadays composed of only one toad, the Mallorcan midwife toad (*Alytes muletensis*) and two lizards, the Lilford's wall lizard and the Ibiza wall lizard (*P. lilfordi* and *P. pityusensis,* respectively) (Pinya and Carretero 2011).

The number of species introduced to the main islands increased strikingly, with Mallorca having the highest number of assumed aliens, with 21 species, followed by Menorca with 15, both Formentera and Ibiza with eight species, and Cabrera with two introduced species. The number of observations per year has been increasing for all the alien species in the Balearic Islands, suggesting they are expanding both in terms of range and population size.

5.2.2.1 Herpetofauna Before Invasions

On Mallorca, fossils dating from the Pliocene Epoch include a giant lacertid lizard (*Maioricalacerta refelensis*), a skink (*Chalcides* sp.), and a glass lizard (*Dopasia* sp.) (Bailon et al. 2014; Bover et al. 2014). In Menorca, two post-Messinian faunas occurred: one during the Early and Middle Pliocene (Quintana 1998; Alcover et al. 1999) and the other during the Late Pliocene or Early Pleistocene (Bover et al. 2008). The first one was composed of a giant tortoise (Bate 1914), a lizard (*Podarcis* sp., likely an ancestor of Lilfordi's wall lizard, Bailón 2004), geckos (Gekkota undetermined), an amphisbaenian (Blanidae, Garcia-Porta et al. 2002; Bailon et al. 2005), and three snakes including a colubrid and two viperids (*Vipera natientis* and *Vipera* sp., Bailon et al. 2005). The Late Pliocene/Early Pleistocene records report a lizard (*Podarcis* sp.) and two amphibians (Mallorca midwife toad *A. muletensis*, Barbadillo 1987, and *Discoglossus* sp., Alcover et al. 1981; Quintana 1998).

Regarding the Pityusic Islands, three different fossil assemblages have been recorded in three different periods: during the Late Miocene/Early Pliocene, a lizard and a tortoise (Moya-Solà et al. 1984, 1999), during the Late Pliocene, a middle sized tortoise (*Cheirogaster* sp., Bour 1985) and a lizard (*Podarcis* sp, Kotsakis 1981); and in the deposits of the Late Pleistocene, a lizard species (*P. pityusensis*, Boscá 1883).

5.2.2.2 Prehistoric and Ancient Introductions (Older Than 5th Century)

The lack of older fossils in the palaeontological record on the Balearic Islands suggests ancient introductions of one toad (Balearic green toad), two turtles (Hermann's tortoise, *Testudo hermanni*; and the European pond turtle, *Emys orbicularis*), two geckos (Mediterranean house gecko, *Hemidactylus turcicus*; and the Moorish gecko, *Tarentola mauritanica*) and one snake (Ladder snake, *Rhinechis*

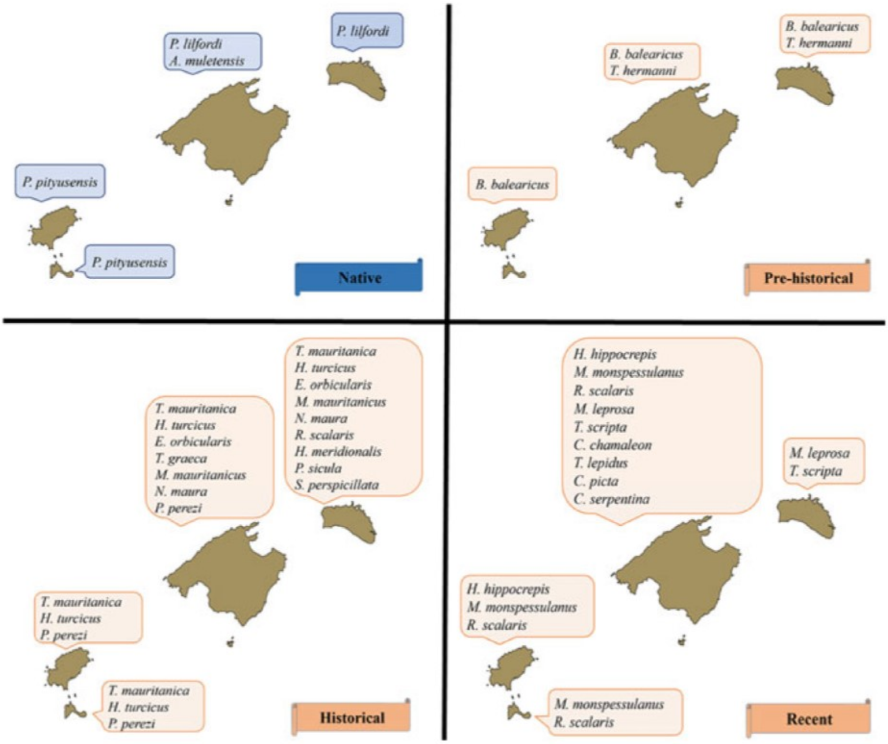

Fig. 5.2 Herpetoinvasions in the Balearic Archipelago, through time, by island

scalaris) (Fig. 5.2). The exact timing and the arrival pathway of the Balearic green toad is unknown. Both the Hermann's tortoise and the European pond turtle were introduced as a food source from the Western Mediterranean region (Fritz et al. 2006). Both gecko species were presumably introduced by passive transportation, with apparently no impact on native communities. No negative impacts on native species or ecosystems are known for these species, with the exception of the snake, which as a predator has a high risk of impact (see below).

5.2.2.3 Historical Introductions (5th Century–18th Century)

The lack of fossils combined with the low genetic differentiation observed, suggests the introduction of two frogs and nine reptiles (i.e. lizards, snakes and turtles) during historical times (Fig. 5.2): the Mediterranean tree frog *Hyla meridionalis* and Perez' frog *Pelophylax perezi*; two turtles, the European pond turtle *Emys orbicularis* and the spur-thighed tortoise *Testudo graeca*; two lizards, the Moroccan rock lizard *Scelarcis perspicillata* and the Italian wall lizard *Podarcis sicula*; and two snakes, the false smooth snake *Macroprotodon mauritanicus* and the viperine snake *Natrix maura*.

The Mediterranean tree frog could have been introduced from the south-western region of the Iberian Peninsula (Silva-Rocha 2012), either voluntarily or accidentally. It is suggested that this frog may have been unwittingly transported to the Canary Islands by the first settlers in cargos such as cattle and seeds (Recuero et al. 2007); this could also be the case in the Balearics. On the other hand, Perez's frog is suspected to have been introduced to control insects (Pinya and Carretero 2011). The latter could have had competitive interaction with the native Mallorcan midwife toad (Román 2004) and predated on this same species (Alcover et al. 1984).

Regarding the chelonians (turtles and tortoises), the pathway of introduction both for the spur-thighed tortoise and the European pond turtle is considered, similarly to pre-historical introductions, as a food resource (Velo-Antón et al. 2011; Cau et al. 2016). These two species have likely no impacts on native species, though the European pond turtle could have contributed to the decrease of Mallorcan midwife toad populations (Pleguezuelos 2004).

The Italian wall lizard arrived in Mallorca and Menorca from Sicily-Sardinia (Greca and Sacchi 1957; Silva-Rocha et al. 2012), probably involuntarily, as this species is known to live close to human populations, which increases the chances of it being introduced by passive transport. From our experience in other Mediterranean islands, this is an aggressive lizard, able to compete with native species (Silva-Rocha et al. 2012 and references within).

As to the two snakes introduced, their arrival pathways are not clear. A passive transportation could have happened in ships due to the maritime trade established between the Balearic Islands and the mainland, as may have occurred with European pond turtle in Corsica and Sardinia (Pedall et al. 2011). On the other hand, they could have been introduced for religious purposes, as referred to above. The origin of the Balearic populations of the false smooth snake is likely Tunisia, while the viperine snake populations originated from Europe, either from the Iberian Peninsula or France (Pleguezuelos 2004; Guicking et al. 2008; Silva-Rocha et al. 2015). The impacts of the false smooth snake extends beyond the native herpetofauna (i.e. Lilford's wall lizard), as they are also able to predate birds and mammals, which can cause a substantial disturbance in these insular ecological communities.

5.2.2.4 Recent Introductions (19th Century to Nowadays)

Over the past two centuries, a total of ten species were introduced in the Balearic Islands, as a consequence of increasing tourism and trade in this region (Fig. 5.2): one toad (the common midwife toad, *Alytes obstetricans*); three chelonians (the painted turtle *Chrysemys picta*, the Mediterranean turtle *Mauremys leprosa* and the pond slider *Trachemys scripta*); four lizards (the common chameleon *Chamaleo chameleon*, the occelated lizard *Timon lepidus*, the Ibiza wall lizard *Podarcis pityusensis* and the Algerian Psammodromus *Psammodromus algirus*); and three snakes (the horseshoe whip snake *Hemorrhois hippocrepis*, the Montpellier snake *Malpolon monspessulanus* and the ladder snake, the latter on islands other than Menorca where it had already been introduced).

The common midwife toad was found in Menorca in 2007, and its introduction is associated with the trade in exotic live plants for ornamental purposes (Carrera and Pons 2010); however, it has not been confirmed later than 2007. The geographical origin is unknown.

The chelonians have been introduced mostly due to the pet trade. It is important to notice that the pond slider is an invasive turtle species native to the eastern USA and adjacent areas of Mexico and introduced worldwide, which can impact on native ecosystems by predation and pathogen transmission. The common snapping turtle can also impact on local aquatic fauna, such as birds and amphibians. For the rest of the chelonians, the impacts are not known.

As to the lizards, an introduction due to the pet trade is assumed for the common chameleon, whereas for the ocellated lizard either pet trade or passive introductions through olive trees (Rivera et al. 2011) are equally possible. The origin of the former is not known, while the latter is suggested to come from southeastern Spain, based on genetic and phenotypic data (Mateo et al. 2011; Silva-Rocha 2012).

Three large snake species were introduced during the last decade: the horseshoe whip snake and the Montpellier snake during 2003 in Ibiza (the last not seen since 2010) and Mallorca; the ladder snake during 2003 in Ibiza, 2004 in Mallorca, and 2006 in Formentera (Álvarez et al. 2010; Mateo et al. 2011). In all cases, the introduction pathway is attributed to the nursery trade, through live plants for ornamental purposes (Kraus 2009; Álvarez et al. 2010).

Individuals from all the three species were found primarily in trunks of olive trees in the nursery centres of Capdepera (Mallorca) and Sant Llorenç de Balàfia (Ibiza). The origin of the first two species is thought to be the southern Iberian Peninsula. The origin of the ladder snakes is uncertain but its alien status in the Balearics is beyond doubt (Carretero and Silva-Rocha 2015). Similarly to the horseshoe whip snake and the Montpellier snake, it can be found near olive trees translocated by the importation industry (Álvarez et al. 2010). As reported by the same authors, at least one company from Spain is involved in the olive trees trade, while no importations from France and Portugal (countries where the species also ranges) are known.

The olive trade business has increased through the years in the Balearic Islands, as a consequence of a trend in garden decorations. Reptiles use the olives as a refuge and there is evidence of several species living together in old trees (Rivera et al. 2011; Graziani et al. 2006; pers. obs. of the authors), which increases the probability of introductions of multiple species in many sites. Thus, the olive trade represents an important pathway for the introduction of reptiles throughout this region, and therefore must be considered when devising prevention and conservation measures.

5.2.2.5 The Future

Ecological niche models calculated with scenarios of climate change (i.e. extreme temperature/humidity and moderate temperature/humidity), forecast an increased suitability in most of the island territory for the alien snakes (with the exception of the false smooth snake) (Silva-Rocha et al. 2015). Indeed, recent studies suggested that climate change is already increasing the activity period and benefiting the survival and reproduction of Montpellier snake and horseshoe whip snake in the Iberian Peninsula (Moreno-Rueda and Pleguezuelos 2009; Zamora-Camacho et al. 2010). Therefore, the population size and spread of some of these Mediterranean snake species is expected to increase, with an associated increase of their impact on native biota.

Unfortunately, a projection in the future was not performed for other introduced species due to lack of records. Nevertheless, in those species coming from warm regions with heterogeneous habitats, it may be expected they will also benefit from climate change.

5.3 Italian Wall Lizard: 'Let It Be' Does not Work

The Italian wall lizard *P. sicula* represents a case where nothing was done to prevent the expansion of an introduced species (Silva-Rocha et al. 2014), which leads to its wide dispersion across islands. Analysing what was (not) done with this species in other areas, allows us to forecast the trends of this introduced species in the Balearics. In addition, the analysis of what occurs on the Balearics allows us to check those trends and to understand them in an island environment.

The species is native to the Italian Peninsula and Sicily and has been introduced in several places, including islands and coastal areas of the Eastern Adriatic, Iberian Peninsula, Turkey, North Africa and the United States. This species often inhabits human modified areas and uses ornamental plants as refuges, being very prone to accidental transportation by man. This is likely the main pathway for its expansion.

Several ecological and behaviour characteristics make the Italian wall lizard a concerning invader, able to adapt easily to a new environment and to displace native lizard species. Behavioural interference was reported with native lizards such as the Dalmatian wall lizard *Podarcis melisellensis* which has gone extinct in some small islets of the Adriatic Sea after the introduction of the Italian wall lizard by competitive exclusion, namely of basking sites (Nevo et al. 1972). Hybridization between the Italian wall lizard and other *Podarcis* species has been also reported (the Tyrrhenian wall lizard *P. tiliguerta*, the Aeollian wall lizard *P. raffonei* and the Sicilian wall lizard *P. wagleriana*; (Capula 1993, 2002; Capula et al. 2002) and may be particularly harmful for native *Podarcis* populations in small islands. In California, the Italian wall lizard *Italian wall lizard* shows a diet which overlaps with native lizards (the Western fence lizard *Sceloporus occidentalis* and Southern alligator lizard *Elgaria miulticarinata*). It may also have an impact on native lizards due to predation (Kirschbaum and Pauly 2016) and competition (e.g. in Kansas with the great plains skink *Eumeces obsoletus*, Oliverio et al. 2001). Impacts on the invertebrate community are unknown, but likely.

In Menorca, the Italian wall lizard has been present at least since the Middle Ages (Alcover et al. 1981), and nowadays is all over the island. This case exemplifies the kind of population dynamics of this species following its introduction in absence of measures to prevent its spread. A species with rapid adaptation/acclimation, like the Italian wall lizards, can easily expand all over an island. The same probably happened earlier in Sardinia, where the species is now only absent at the highest altitudes.

The extinction of Lilford's wall lizard in Menorca was probably not due to this species but to the earlier introduction of alien predators (Mayol 1985; Pérez-Mellado 1998). However, a possible arrival of the Italian wall lizard to the islets surrounding the main islands represents a high risk to the survival of microinsular populations of Lilfordi's wall lizard, as the replacement of native populations following the arrival of the Italian wall lizard have already been documented in the case of the Dalmatian wall lizard in Adriatic islets (Nevo et al. 1972). The Italian Wall lizard has already reached Ses Mones, one islet off-Menorca where Lilfordi's wall lizard is still present (Speybroeck et al. 2010; van den Berg and Zawadzki 2010).

Thus, preventive measures are a priority over other actions to avoid translocations of the Italian wall lizard from Menorca to surrounding islets, where endemic Lilfordi's wall lizard is present. This could be implemented by inspections of cargo and boats, and a campaign of public awareness for both islanders and tourists.

5.4 Ibiza and Formentera: When Social Perception Helps Conservation

The Pityusic islands, Ibiza and Formentera, remained less affected by introductions until the beginning of the twenty-first century. Because of this, the recent invasion process still can be seen in progress. Therefore, these two islands offer the opportunity to study the first stages of the invasion process as well as the effectiveness of conservation measures adopted in an appropriate time frame, i.e. soon after the introduction, with the involvement of local people.

At some point in the Pleistocene, the fauna of the Pityusic Islands was affected by a crucial and determining circumstance within the Balearic Archipelago: a massive extinction happened (Bailon et al. 2010), with no correspondence on the rest of the Mediterranean Islands (Alcover and McMinn 1993). There is only evidence of two terrestrial survivors, lizards and snails, which used to live in rock fissures. This big extinction might have been caused by a catastrophic event, such as a volcanic process—for instance, the Columbretes Archipelago, 100 km to the northwest of Ibiza had volcanic activity until 300,000 years ago. Later, during Pleistocene glaciations, as a consequence of sea level regression Ibiza and Formentera formed a single large island of more than 700 km^2, the biggest island in the Mediterranean without terrestrial mammals. During that period, paleontological records show that the number of bird species inhabiting these two islands was rather high, since they are capable of overseas colonization and they had little competition for resources (i.e. food) and supposedly little predation pressure. Additionally, fossil raptor pellets show a large number of lizards, as well as fish (Alcover and McMinn 1993).

5.4.1 Human and Reptile Invasions

When humans arrived for the first time in the Pityusic Islands, around the end of the third millennium BCE, their dietary options would have been similar to those first human settlers found in the Polynesian islands; essentially terrestrial and sea birds, fishes, and sea mollusks. Lizards and terrestrial snails were likely too small to constitute a food resource. Hence, the existing fauna provided poor resources for sustaining a human population (Alcover and McMinn 1993).

Initially, humans brought only the Moorish Gecko (Rato et al. 2010; Pinya and Carretero 2011), the Mediterranean house gecko (Rato et al. 2010; Pinya and Carretero 2011) and the spur-thighed tortoise (Mateo et al. 2011) to the Pityusic islands. Remarkably no other reptiles, particularly no snakes, were introduced in the islands in that period (Pinya and Carretero 2011; Mateo 2015). The Phoenician newcomers ruled the entire island, placing it under the protection of the Canaanite god Bes (Mateo and Ayllón 2012). He was represented with a snake on one hand and a knife on the other, since he protected the family and the home from any evil, especially venomous snakes (Guirand 1960; Fig. 5.3). Consequently, Ibiza became the Bes' Island, its name probably coming from there (Ebusus; Mateo 2015). Almost all the coins minted in Ibiza during this Punic period showed the image of the snake-killer god (Fernández 1975; Fig. 5.3). There is a similar case: according to the tradition of the 4th century (CE), the absence of snakes in Ireland—an animal associated to the devil by Christianity—is attributed to the protection of Saint Patrick.

This aversion towards snakes and their absence on the island was adopted as an identity symbol by the Ibizan inhabitants. In contrast, on those Mediterranean locations where snakes were common and therefore considered as beneficial or neutral, their peoples worshiped gods related to snakes (e.g. Aesculapius, Astarté, Isis, Mitra; Fernández 1975; Velázquez Brieva 2007). Transport of snakes among those places was something usual and a high number of acclimatization and some naturalizations (i.e. species were able to reproduce) took place, some of them lasting until our days in most of the large and medium sized Mediterranean islands (Mateo et al. 2011).

In the 2nd century BCE, when Carthage was defeated, the Ibizan population surrendered to the Romans. They were able to keep the Canaanite dialect Punic, and the worship of the god Bes. Later, in the first century CE, when Phoenicians and Romans still coexisted unmixed in Ibiza, two Latin authors wrote about the island and the mysterious lack of snakes. The geographer Pomponius Mela, in his work *De Chorographia* (Mela, around 43 D.A.), stated:

Fig. 5.3 Coins and Bas-relief with god Bes holding the snake and the knife. Clapboard from the Ptolemaic necropolis of Saqqara (3rd century BCE). *Source* Allard Pierson Museum, Amsterdam

> (…) (Ebusus) lacks harmful or wild animals, to the point that it does not breed them nor tolerate those brought there. In front of it there is the Colubraria, that comes to my mind because, being very abundant in many malefic genus of snakes, it is completely uninhabitable; however, if someone enters a place previously surrounded by Ebusitan soil, it becomes a pleasant place without danger, because those same snakes that otherwise attack all they find so often, they flee away frightened by the appearance of the dust.

Thirty years later, Pliny the Elder, naturalist and historian, probably copying the previous author, included a similar reference in his work *Naturalis Historia* (Plinius the Elder, 77):

The soil of Ebusus banishes snakes, that from Colubraria begets them and it is very harmful for everyone, unless one brings with himself Ebusitan soil; …

Both Latin authors assigned a magical character to the unusual absence of ophidians, as the Pityusic Islands were the largest Mediterranean Islands without snakes. By saying this, they were indirectly suggesting the existence of Ibizan soil trade to the city of Rome, as an element with occulted properties (Salazar de Mendonza 1770).

If we compare the number of acclimated species in Ibiza and Formentera before 1975 with other Mediterranean Islands, such as Mallorca or Menorca (Mateo et al.

2011), the Pityusic Islands have suffered much less historical introductions than the rest. It was only at the beginning of the 21st century that three snake species were introduced in Ibiza and Formentera. The change in agricultural practices occurred during this period may have indirectly prepared the ground for such introductions. After Spain became a member of the European Union, in 1986, the more competitive market forced Spanish farmers to transform their traditional agriculture into a mechanized one. Hence, between 1996 and 2005, more than 900,000 olive trees were ripped out ending up as firewood or used for gardening (Fortuny Santos 2002) in order to gain more agricultural fields. The massive trade of these olive trees between the south of the Iberian Peninsula and the Pityusic Islands provoked the first introduction of snakes in these islands.

The Montpellier snake was introduced to Ibiza, but it has not been sighted since 2010, and we therefore presume it did not establish and disappeared from the island.

The Ladder snake has a low capture rate in Ibiza, but is the most abundant snake in Formentera, having invaded around 350 ha of the island by 2016 (4.2% of the territory; *unpub*. data of the Balearic Government).

The Horseshoe whip snake was introduced to Ibiza and to Formentera, but seems to have disappeared from the latter, given that not a single specimen was captured during 2016. It is the most widespread in Ibiza, increasing the occupancy area quickly −148 km^2 occupied by the species by 2015 (27% of the island area).

Even though not all the traits of the natural history of the last two introduced snakes have been studied, preliminary analysis and observations indicate that both have successfully naturalized.

5.4.2 Impacts of Snake Introductions on Biodiversity

Snakes are efficient predators, and commonly absent or poorly represented in island native fauna. Therefore, their introduction on islands often dramatically impacts on the native fauna (Rodda et al. 1996). The only terrestrial vertebrate endemic to the Pityusic Islands is seriously endangered by these alien snakes.

Information on prey type and size consumed by alien predators is a key to our understanding of the success of invasive species (Herrel et al. 2008), and helps in evaluating the threat to the native organisms (Salo et al. 2007). The source populations of both the horseshoe whip snake and the ladder snake are well studied, and we compared body size, diet and reproduction between source and invasive populations.

The horseshoe whip snake in Ibiza has shifted its diet towards lizards, with the native Ibiza wall lizard, representing 55.4% of the observed prey (Hinckley et al. 2017), whilst in the diet of horseshoe whip snake in the south of the Iberian Peninsula (the source area of introduced populations) lizards represent only 24.2% of prey items (Pleguezuelos and Moreno 1990). Moreover, the high body condition (mass related to length) and the larger body size of individuals found in Ibiza offers compelling proof of the good ecological conditions experienced by the horseshoe whip snake on this island. Remarkably, the record for the maximum body length and weight for the species in the Iberian-Balearic region (1830 mm and 1440 g) was found in Ibiza, surpassing those previously described by 105% and 213%, respectively (Hinckley et al. 2017). This evidence suggests that this species grows longer and more robust in Ibiza than in its continental range (see Table 1 in Gil and Pleguezuelos 2001). This shows a rapid functional response (likely phenotypic plasticity) of this snake's size and shape to the new biotic and abiotic situation on the island.

A similar dietary shift to the one observed in the horseshoe whip snake in Ibiza is probably occurring with the ladder snake in Formentera. Continental populations of this latter species show an endotherm-based diet (i.e. small mammals and birds) with a negligible percentage of reptiles (Pleguezuelos et al. 2007). In contrast, the preliminary study of the diet in Formentera specimens shows that more than half of their prey is constituted by the endemic Ibiza wall lizard (Samuel Pinya, pers. com.).

The secondary prey type of these ladder snakes in frequency, and primary in biomass, are micromammals, which are aliens in Ibiza, abundant, and of no conservation concern. However, these alien prey of early arrival to the island provide food resources for later aliens like the horseshoe whip snake, in a process of invasional meltdown (Simberloff and Von Holle 1999). This situation will probably have negative repercussions on the Ibiza wall lizard by a hyperpredation process (Bull and Courchamp 2009; Hinckley et al. 2017).

Snakes may also be influencing the diet of other insular, native predators, with shared prey, such as the Barn owl (*Tyto alba*). Reproduction may be changing also to be more frequent (Shine 2003), with larger clutch size (Seigel and Ford 1987), larger hatchlings (Shine 1981) or earlier maturing individuals (Parker and Plummer 1987).

Populations of Ibiza wall lizard from islets surrounding Ibiza and Formentera are also potentially menaced by the arrival of snakes. A total of 39 islets hold 23 endemic subspecies (Salvador 2015; but see Rodríguez et al. 2013). Regardless their taxonomic status, most of these microinsular populations represent unique adaptations resulting from local ecological conditions and isolation, with very small sizes and undergoing strong demographic fluctuations. The arrival of snakes in these islets may produce a catastrophic and irrecoverable event for lizard populations as they would be the only available prey. On the other hand, the probability of such arrivals are not so unlikely as these islets are very close to the main islands' coast (1.17 km on average); six snakes have been observed swimming in the sea, and a snake skin was already found in one islet (unpub. data of the authors).

Besides Ibiza wall lizard, which is listed as Near Threatened (NT) (IUCN categories and criteria applied to regional scale of the Balearic Islands; Viada et al. 2006), there are 57 native birds that nest on the Pityusic islands whose adults or pulls are within the prey size range of these snakes. Among them, there are five species listed as Vulnerable (the common quail *Coturnix coturnix*, the little ringed plover *Charadrius dubius*, the Kentish plover *C. alexandrinus*, the European turtle dove *Streptopelia turtur* and the Woodchat shrike *Lanius senator*), two as

Endangered (the Cory's shearwater *Calonectris diomedea* and the barn owl *Tyto alba*), one as Critically Endangered (the Balearic shearwater *Puffinus mauritanicus*), and six as Near Threatened. Two breeding birds are Balearic endemics: the Balearic Shearwater, that nests in surrounding islets of Ibiza and in the main island of Formentera, and the Balearic Warbler (*Sylvia balearica*), occurring in both islands.

5.4.3 Impacts of Snake Invasions on Humans

Native species of Ibiza have a great significance not only from a biological point of view, but also for the inhabitants of this island. The endemic Ibiza Wall Lizard is considered a symbol of the Pityusic Islands (Dappen et al. 2013). Ibizan and Formenteran people are proud of their lizards and their images are present everywhere: on clothes, jewelry, lizard-shaped stickers on the cars, in decorative elements such as lamps, wall figures, mirrors, etc. Magazines and pamphlets frequently exhibit the lizard, and several companies use it in their logos. It is used as a tourist attraction too, and any tourist information about the island will have the symbol on it (Fig. 5.4a and b).

What does this symbol mean? Why is it so easy to relate Ibiza and Formentera with it, instead of any other animal or plant? To answer these questions, we have to remember that the first humans that arrived to the Pityusic Islands found only lizards within the community of ground dwelling vertebrates of these islands (Bover et al. 2008). The sole terrestrial vertebrate on such area was this attractive and harmless reptile. It is the only vertebrate exclusive to Ibiza and Formentera. Different civilizations introduced other vertebrates like genets (*Genetta genetta*)

Fig. 5.4 Different examples of the presence of Ibiza wall lizard, *Podarcis pityusensis,* in the everyday cultural life of Ibiza and Formentera. Photos by E. Montes

or hedgehogs (*Erinaceus europaeus*). In a way, the lizard symbolizes the naiveté and the purity of the original Ibiza and Formentera, as well as the harmless and innocuous fauna to humans that every visitor would find there. It is the best advertising anyone can make for an idyllic place like the Pityusic Islands. As a consequence, the invasive snakes are destroying the safety sense that secularly characterized Ibiza and Formentera, islands with no dangerous species until now. In fact, rural hotels are concerned and claim that the snakes are jeopardizing their business, as they have clients that come to Ibiza precisely because no dangerous animals can be found there.

Pityusic society is also having a very strong response to the presence of snakes. They are not used to snakes so their observation causes strong social alarm. Every spring and autumn, with the increasing activity of snakes, the island government receives hundreds of calls from frightened people that have seen a snake in their properties or just want to warn the authorities and give information, eager to collaborate in solving the problem. Rural inhabitants from the high-density snake zones tell us that they do not see lizards anymore, with a mix of sadness and anger. And maybe that is the main reason why they are so eager to help; the majority of these neighbors volunteer to take care of snake-traps (see below) in order to help control the invasion. The embrace of the endemic lizards as a symbol by the locals may be the key to its conservation, and the control of snakes (Bowen-Jones and Entwistle 2002).

5.4.4 Science and Management: An Inevitable Cross-Road

Eleven years after the first report of snake introduction, during 2014 and 2015, the Ibiza Island Council (island government) carried out a pilot project to control snake populations under the scientific advice and participation of the Spanish Herpetological Society (AHE). This first approach gave useful information about distribution, density, and the methods that best worked to eradicate the snakes. The main goals of this project consisted of promoting public awareness (Boudjelas 2009) and testing methods to capture snakes. Pamphlets in three different languages were distributed among the community; informative meetings were held for neighbors, as well as formative sessions for authority agents who had to deal with emergency calls related to snakes. A unified protocol was agreed between all the authority agents.

Among the capture methods tested in 2014 (plywood cover boards, PVC double funnel traps, and box-traps—baited and unbaited), lab mice baited box-traps gave the best results. Therefore, in the second year of the project, the Ibiza Island Council arranged the manufacturing of wooden box-traps, according to their guidance, with the Arts School (Secondary Level) of Ibiza. A total of 121 snakes were captured in 2015 by 200 box traps (Table 5.1, Fig. 5.5). Trained dogs were also used and proved quite effective in detecting snakes, but not very practical in the study area,

Fig. 5.5 Wooden box trap for capturing snakes on Ibiza Island. Note the access hatch on the top, a funnel in the lateral, and the small cage for restraining the lab mouse within the snake trap. Photo by E. Ayllón

Table 5.1 Individuals of the Horseshoe Whip Snake, *Hemorrhois hippocrepis*, and the Ladder Snake, *Rhinechis scalaris*, captured in Ibiza Island during the period 2011–2016, and invaded area by the Horseshoe whip snake according to years (Minimum Convex Polygon method, from the data in Fig. 5.6)

Year	Individuals		Area (km^2)
	Horseshoe whip snake	Ladder snake	Horseshoe whip snake
2011	12	7	63.2
2012	15	5	63.7
2013	38	10	109.4
2014	95	8	96.4
2015	302	10	149.3
2016	317	38	142.8
Total	779	78	

which is covered by hundreds of kilometers of stone fences where the snakes were difficult to catch (Table 5.1).

With the information gathered from the different trapping methods, we mapped the area covered by snakes each year, to evaluate the progression of the invasion.

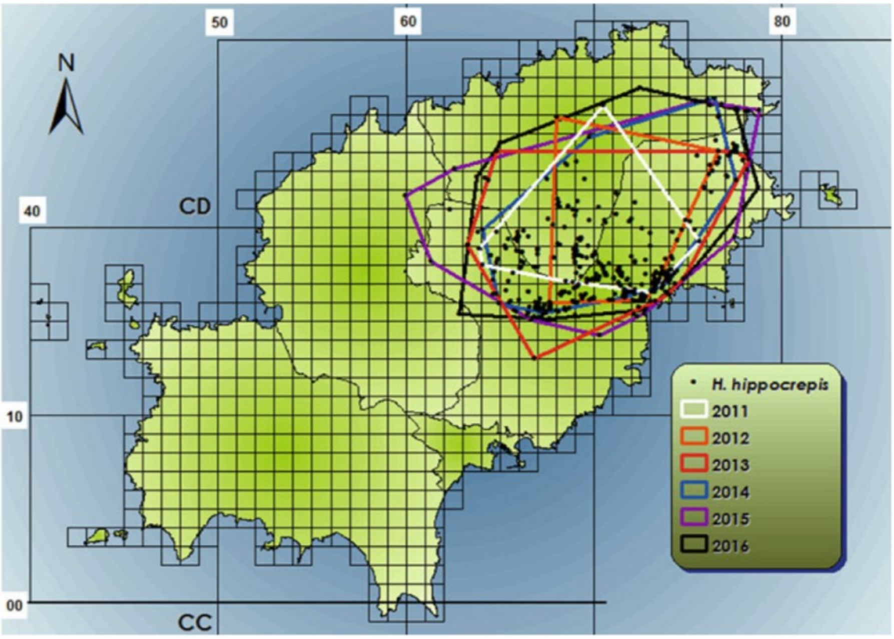

Fig. 5.6 Range of the invasive Horseshoe Whip Snake, *Hemorrhois hippocrepis*, in Ibiza Island in the period 2011–2016 (Minimum Convex Polygon method). Yearly sample size and area in Table 5.1. Figure prepared by Pedro Luis Hernandez -Sastre

As observed (Table 5.1, Fig. 5.6), the invasive population covers the northeastern sector of the island of Ibiza and the area increased in 2015, but stabilized after the intense trapping campaign of 2015–2016. These results have to be taken with caution, given that records increased inter-annually not only with the growth of the snake population within the island, but with the awareness of people and the stronger and more effective efforts to capture them (Table 5.1).

Fortunately, it seems the invasive snakes still show a contagious distribution pattern nearby the nurseries that acted as the introduction way, which is typical of the first stage of biological invasions (Williamson 1996). The apparent fast expansion observed is expected if we take into account that two of the main abiotic factors explaining the range of the reptiles, the mean annual temperature and average yearly rainfall of Ibiza, perfectly fit within the range of mean annual temperature and rainfall in their source range (Feriche 2015; Silva-Rocha et al. 2015). It is evident that the island is ideal for the spatial and demographic expansion of the species, and climate conditions will become even more favorable if predictions for climate change in this century are confirmed.

During 2015 we frequently observed scales and feces in empty traps, meaning that some snakes were able to escape. In 2016, when the Balearic Government took the control of the project, the traps were upgraded eliminating the funnels and installing just a hole of approximately 3 cm with a tilting door, only opening towards the inside of the box. This resulted in a very high increased rate of captures (2.2 captures/day/100 traps in 2015 vs. 10.5 captures/day/100 traps in 2016). The maximum result found elsewhere in trapping invasive snakes is 2.13 (Rodda et al. 1999).

Regarding the collaboration with the local community, which has given the most important contribution to the total snake captures, 400 new traps were made in 2016 by the Ibiza Island Council and two town councils (Santa Eulària des Riu, and Sant Joan de Labritja) and were sold for a subsidized price to any citizen who was willing to take care of them, after filling out and signing a commitment. This measure comes from the people themselves, since there have been repeated requests by the community for this type of action. It has been extended and more traps are being ordered, given that the demand is not falling.

These actions were not free of conflict, though: due to the lack of staff, collaborators have to sacrifice the snakes without professional guidance. This situation leads to two complex matters; animal cruelty and government responsibility regarding eradication of invasive species. Moreover, following the current procedure, researchers do not have the control on the distribution and sampling effort of traps. Common people do not know the techniques to manipulate snakes nor the regulation about what they can do or what they are not allowed to do with them. Putting such a responsibility on people's hands is risky, as they can spread the snakes by accident. Notwithstanding these potential problems, we encourage involving citizenship in invasive animal eradication programs (Boudjelas 2009; Gallo and Waitt 2011). Public participation in invasive alien species management is important, from ethical, legal, and practical standpoints (Boudjelas 2009).

From now on, the project should grow not only in staff but also in trap numbers and spread, as the priority should be avoiding the expansion of the snakes throughout the territory of the Pityusic islands. That can be done by placing traps along the edge of the currently invaded zone, before the snakes can invade further and affect populations of the endemic Ibiza Wall Lizard in snake-free zones (Grice 2009; Melero et al. 2010). The current ground perimeter of the invaded area is approximately 36 km (Fig. 5.6). Estimating one trap every 25–30 m (Rodda et al. 1999), we will require around 1400 traps to be placed around the perimeter of the invaded area just to control the expansion, plus 200–400 more to capture and reduce the population in the high-density zone of the core areas (close to the olive tree nurseries). The effectiveness of traps increases in combination with drift fences that intercept and guide snakes towards the traps (Fitzgerald 2012). However, that procedure represents a time and economic expense even greater than the cost of the traps; that is why the abundant rock walls on the island are being used as drift fences.

The study of the natural history of invasive snakes ought to be included in the project, since it may help in understanding the biological processes that make them successful and, therefore, in fighting them more accurately (Sakai et al. 2001; Stohlgren and Jarnevich 2009). This is a typical case of island invasion: a snake-free island, poorly populated in non-flying vertebrate fauna, where invasive snakes thrive. Numerous animals have been already studied after their inclusion as vouchers in scientific collections (Hinckley et al. 2017).

5.5 Conclusion

The Balearic Islands represent another striking example of the negative effect of human-mediated species introductions on native biota as well as on local people. Here, we presented two case studies which reflect two different attitudes regarding biological invasions. First, the case of the Italian wall lizard which represents the outcomes of a negligent attitude and taught us that if we ignore the problem, it will not solve itself but will simply get worse. In this particular case, a potentially invasive species was not ever considered to be dangerous in the Balearics. As a result, it spread throughout the islands where it was introduced, threatening the native biota, namely the endemic lizards which local people care about. The second case study reflects an active attitude which resulted in a strong involvement and a close collaboration with governments and general public to face the spread of invasive species, especially of introduced snakes. A project was created to understand how the invasion is progressing and how to deal with it.

Preliminary results on snakes' density control are encouraging, indicating the effectiveness of this collaboration, but we are only at the beginning of a long-term action which also includes preventing new introductions and monitoring the status of native species populations.

While capture campaigns may allow controlling the population size and spread of introduced snakes, a major priority for the conservation of native biota is to prevent new species from arriving on the island (Wittenberg and Cock 2001). The importation of big and old trees with cozy holes which can serve as shelters for alien species need to be limited, at least during critical periods (hibernation and egg-laying period, Shine et al. 1997). That limitation would leave a safe frame of two and a half months during spring time (April–June). Moreover, it is recommended that trees entering the Pityusic Islands within those periods are kept in quarantine at the entry point (any of the two Ibiza harbors); there are some who claim to have seen a snake falling from a moving trailer full of olive trees in spring. One-month quarantine in a walled enclosure (a minimum of 1.5 m height) with a half a dozen baited box-traps, should be enough to draw every hidden species in the cargo. The benefits from selling big olive trees are so high that the economic repercussions of such measures would be easily supported by the sellers, if a regulation obliged them (McNeely 2001).

Social collaboration, turning an eradication program into a publicly accepted project, has been shown to be vital for the project. It is strongly recommended to keep that work-line involving the public through a studied strategy that allows, on one hand, that Ibizan people feel they are working for their own island and symbol, contributing with their participation to achieve the maximum number of captures throughout the island. On the other hand, means the collaborators become a useful tool to technically improve the project, facilitating the collection of data in a programmed and organized way.

After all, the main concern of this invasion is, without any doubt, the same for everybody: the serious threat to the endemic fauna. Therefore, monitoring endemic populations is also crucial to determine whether and to what extent snake predation on lizards results on demographic impacts on lizard populations.

In conclusion, Balearic Islands exemplify an archipelago where aliens conquered the main islands and that has implications not only for biodiversity but also for the communities present. The future will determine if alien species will continue to conquer, or if the joint effort of science, policy and social participation will mitigate this invasion.

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Annex V. ARTICLE IN *QUERCUS* JOURNAL

Conflicto entre culebras y lagartijas en las islas Pitiusas

La biodiversidad de Ibiza, en grave peligro por las serpientes invasoras

por Elba Montes

Las lagartijas que habitan en Ibiza y Formentera son formas exclusivas de sus islas e islotes, mientras que todas las culebras de las Baleares han sido introducidas por el hombre en tiempos históricos. Un largo conflicto entre depredadores alóctonos y presas autóctonas que, pese a las medidas adoptadas, aún está lejos de resolverse.

Ibiza y Formentera, esos dos pequeños paraísos de nuestro mar Mediterráneo, parece que nada tengan que envidiar a cualquier isla de la Polinesia. Sus playas de mar turquesa y sus bosques sencillos –éstos de pino y sabina–, suave orografía y casas tradicionales, convierten a las llamadas islas Pitiusas en territorios con elementos similares a los de esas islas remotas del Pacífico. Sorprendentemente, esta similitud se extiende más allá de su apariencia: resulta que, al estudiar su registro fósil, encontramos una peculiar historia geológica.

Como el resto de las islas mediterráneas, hacia finales del Mioceno estuvieron conectadas a las actuales tierras continentales, con el consiguiente tráfico de animales entre ambos territorios, hasta que el estrecho de Gibraltar volvió a abrirse definitivamente, hace 5’3 millones de años, inundando la cuenca mediterránea y creando las islas que ahora conocemos. Sin embargo, en algún momento del Pleistoceno, época que comenzó hace 2’5 millones de años, desaparecieron de manera repentina los mamíferos y demás vertebrados terrestres no voladores que habitaban Ibiza y Formentera, así como varios invertebrados. El origen de esta abrupta ruptura faunística, que tan sólo ocurrió en estas dos islas mediterráneas, se relaciona con alguna clase de evento catastrófico, quizá de tipo volcánico. Los únicos supervivientes terrestres fueron los animales que habitaban en las fisuras de las rocas y les sirvieron de refugio: las lagartijas (*Podarcis pityusensis*), llamadas localmente *sargantanas*, y algunos caracoles. No era esperable la llegada de ningún otro vertebrado, pero aun así ocurrió. Hace un millón de años arribó, probablemente sobre una balsa de restos vegetales, una víbora enana a la isla de Ibiza (1).

Tres polizones

Cuando aparecieron los primeros humanos en las Pitiusas hace unos 4.000 años, en la Edad del Bronce, encontraron una versión mediterránea de las islas polinésicas en cuanto a fauna se refiere: muchas aves, pero ningún mamífero o vertebrado no volador, a excepción de las lagartijas y las pequeñas víboras. Fueron ellos los que empezaron a introducir animales, principalmente como fuente de alimento en unas islas con pocos recursos, pero también de forma accidental (como las salamanquesas o los erizos), o bien para controlar otros animales molestos. Uno de aquellos animales introducidos, el lirón careto (*Eliomys quercinus*), fue el que probablemente terminó con las víboras en muy poco tiempo.

Curiosamente, y al contrario que la mayoría de sus islas vecinas, las Pitiusas se conservaron libres de serpientes introducidas quizá debido a un antiguo culto fenicio, el del dios Bes, protector de la casa y la familia contra las serpientes venenosas. El cual, por cierto, dio nombre a la isla de Ibiza. Este culto fue perpetuado por las civilizaciones posteriores y, ya en el siglo I de nuestra era, Pomponio Mela y Plinio el Viejo dejaron constancia escrita de la singularidad de Ibiza, atribuyendo a su mágica tierra la capacidad de repeler a las serpientes venenosas (2).

Corría ya el año 2003 y en los campos y bosques de las Pitiusas nunca se había visto una serpiente. El poder de Bes, según los místicos y las palabras de Plinio el Viejo, seguía vigente. Pero las islas empezaron a ceder ante el tigre de la globalización. Los payeses vendieron sus casas a extranjeros adinerados, que convirtieron los antiguos cultivos en ostentosos jardines y los modestos chiringuitos en lujosos *beach clubs*. En aquellos momentos, dos factores confluyeron con consecuencias nefastas: por un lado, debido a la mecanización de la agricultura en España a raíz de su entrada en la Unión Europea, entre 1996 y 2005 se arrancaron más de 900.000 olivos para leña o jardinería. Mientras que, por otro lado, a nuestros pequeños paraísos pitiusos llegaba la moda del jardín mediterráneo, que incluye árboles centenarios con oquedades que precisan poco o ningún riego, como muy bien son los olivos. Las plataformas cargadas de olivos empezaron a ser habituales en los ferris que llegaban de la Península y, silenciosamente, tres polizones inadvertidos aterrizaron en la tierra mágica de Ibiza, anulando el supuesto poder antiofídico de su tierra: la culebra de herradura (*Hemorrhois hippocrepis*), la culebra de escalera (*Zamenis scalaris*) y la culebra bastarda (*Malpolon monspessulanus*). Esta última dejó de observarse en 2010, mientras que la culebra de escalera ha mantenido una población pequeña pero estable en Ibiza y ha proliferado en Formentera. En cuanto a la culebra de herradura, está mostrando todo su potencial invasor a los residentes en Ibiza (2).

Tesoros isleños

Algunos animales de aquel edén que encontraron los primeros pobladores humanos de Ibiza merecen una atención especial. La lagartija superviviente constituye una especie endémica de las islas, lo cual quiere decir que es propia y única de las Pitiusas. Pero esto no es todo: en muchos de los islotes que rodean las dos islas principales encontramos subespecies (o poblaciones con características únicas) que son a su vez endémicas de cada uno de ellos. Es decir, que cada islote guarda un tesoro que no existe en ningún otro lugar del mundo. Por otro lado, encontramos en esos mismos islotes, así como en algunos acantilados de Formentera, un ave muy especial, la pardela balear (*Puffinus mauretanicus*), también endémica, aunque esta vez del conjunto de las Islas Baleares. Dicha pardela tiene la particularidad de ser una de las aves más amenazadas de Europa y actualmente se considera en peligro crítico de extinción. Por último, existe otro endemismo balear, la curruca balear (*Sylvia baleárica*), un paseriforme propio del archipiélago. Las islas son territorios singulares y con un alto valor ecológico, pues su biodiversidad ha evolucionado de manera diferenciada y única. Eso las hace precisamente más vulnerables, ya que sus organismos no están preparados para competir o defenderse de invasores recién llegados, que no existían previamente o quedaron muy atrás en su memoria genética.

Por este motivo, las invasiones biológicas de las islas merecen una mayor atención que en los continentes. Pero en las Pitiusas no fue así hasta el año 2014. En ese momento, el Consell Insular de Ibiza emprendió un proyecto piloto para el control de los ofidios en ambas islas, trabajo que ejecuta actualmente el Gobierno de las Islas Baleares. Es una tarea ardua, porque difícilmente tiene un final, pero muy necesaria para mantener a raya las poblaciones de culebras. De hecho, está obteniendo magníficos resultados en ambas islas, especialmente en Formentera, ya que allí encontramos una población de culebra de escalera arrinconada contra un acantilado, bastante delimitada en el espacio (Cuadro).

Lagartija de las Pitiusas (*Podarcis pityusensis*) localizada en Formentera, en la península de La Mola (foto: Baravi Thaman).

En 2017 se publicó un estudio sobre la culebra de herradura que destacaba cómo habían cambiado sus hábitos alimenticios en Ibiza: las lagartijas representan el 56% de su dieta, mientras que en la población fuente ese porcentaje no supera el 24% (3). Por otro lado, los trabajos de trampeo en Formentera y la posterior necropsia demuestran que la culebra de escalera, que en la península es un depredador casi exclusivo de animales endotermos (de "sangre caliente"), en la isla devora lagartijas. De regreso a Ibiza y sus culebras de herradura, allí alcanzan récords para la especie en cuanto a tamaño, peso y porcentaje de grasa, lo que da una idea de lo bien alimentadas que deben estar y de los pocos enemigos naturales que tienen en la isla. Todo esto confirma la grave amenaza que suponen las culebras para nuestro único vertebrado terrestre no volador. Si acaban con las *sargantanas*, extremo que empieza a parecer posible, ¿cuál sería su siguiente presa fácil? Recordemos que tanto la pardela balear como la curruca balear están a su alcance.

Algunos de los islotes que rodean la isla de Ibiza, pertenecientes a la Reserva Natural de Es Vedrà, Es Vedranell y los Islotes de Poniente (foto: Elba Montes).

Grandes olivos en un vivero de Ibiza procedentes de la Península, uno de los medios que utilizan las culebras para llegar hasta las islas (foto: Baravi Thaman).

Cap de la Mola, en la isla de Formentera, zona donde han quedado arrinconadas las serpientes introducidas en esta isla (foto: Elba Montes).

¿Cómo evitar la entrada y expansión de las culebras?

Veinte años después de los primeros avistamientos de culebras, hoy contamos con campañas anuales de control que han dado muy buenos resultados. De hecho, las trampas han

Culebras acorraladas en Formentera

En Formentera aún hay lugar para la esperanza. La palabra "erradicación" está casi prohibida entre la gente que trabaja con especies invasoras, pues es realmente difícil conseguir eliminar hasta el último individuo de una población. Pero, en Formentera, la culebra de escalera se encuentra arrinconada en la península de La Mola y las capturas han empezado a decaer, si bien es cierto que la especie aún se está dispersando ligeramente. ¿Podríamos encontrarnos frente a la primera isla en la que se erradica un ofidio invasor? Si fuera así, el experimento serviría para poner de manifiesto que el éxito de las campañas radica en la contundencia y perseverancia, en lo rápido que se actúe, en la cantidad de trampas por kilómetro cuadrado… Es decir, en la calidad del proyecto.

La autora junto a una trampa utilizada para capturar ofidios en Ibiza, en este caso con dos ejemplares de culebra de herradura (foto: Federico Rey).

Culebra de herradura, un ejemplar de gran tamaño, atropellada en los alrededores de la localidad ibicenca de Jesús (foto: Elba Montes).

demostrado ser muy eficientes y son lo más parecido a un depredador que existe para ellas en Ibiza. Pero la mesa cojea. Por un lado, el grifo de los olivos sigue abierto. Podrían aplicarse medidas sencillas para reducir drásticamente la entrada de culebras, como restringir la llegada de olivos a los meses de primavera: se tratarían de evitar los meses de invierno, cuando las serpientes hibernan en los huecos de los troncos, y también los de verano, pues podrían esconder puestas de sus huevos.

Es muy improbable que una culebra activa, en plena época de búsqueda de pareja y alimento, con buena temperatura ambiental, se mantenga dentro de un árbol que es arrancado y transportado durante cientos de kilómetros. Si a esta medida se añade, en el puerto de destino, un periodo de cuarentena de unas pocas semanas en un recinto sembrado de trampas, entonces se minimiza el riesgo de introducción de ofidios (¡y de otros animales invasores!) de manera muy eficaz. También sería interesante sembrar con trampas los alrededores de cada vivero para controlar los posibles traslados dentro de las propias islas, así como los alrededores de cada nuevo foco o avistamiento fuera de los núcleos principales. Pero si no se toman medidas para controlar la entrada, seguir trampeando es como pretender vaciar el mar con un cubo de playa.

Al pie del muro de piedra seca, muda de culebra de herradura encontrada en Ibiza (foto: Elba Montes).

En Ibiza se han dedicado muchos esfuerzos a trampear centenares de culebras en las zonas donde alcanzan sus mayores densidades, pero no han contribuido a contener la población de aquellos primeros núcleos que surgieron al norte y al este de la isla. Tampoco se ha evitado que, desde allí, la plaga se extendiera al resto del territorio. Ibiza tiene una extensión de 572 kilómetros cuadrados y está dividida por la carretera que va desde la capital hasta San Antonio. Esa carretera separa precisamente la zona más afectada de la que hasta ahora no había albergado poblaciones consolidadas, aunque sí se producen avistamientos puntuales que habría que controlar. Viene a ser una barrera artificial de la que podría sacarse muchísimo provecho si se colocaran trampas en toda su longitud, al menos para preservar la zona suroeste.

Culebra de herradura nadando en aguas de la Cala de Sant Vicent, en la isla de Ibiza (foto: Daniel Ferrer).

No hay tiempo que perder

Habría que establecer zonas prioritarias, de acuerdo con su valor ecológico, como el Parque Natural de Ses Salines o los islotes que albergan poblaciones singulares y vulnerables de lagartijas. Tales espacios deberían ocupar los primeros lugares en la lista de entornos que precisan protección inmediata ante la presencia de serpientes en Ibiza. Una vez alcanzado este objetivo, podrían aplicarse medidas contra las culebras en el resto de la isla. Desgraciadamente, da la sensación de que los acontecimientos que ponen en peligro a las *sargantanas* aumentan de forma exponencial, como apremiándonos a actuar antes de que sea demasiado tarde. Se han registrado numerosos avistamientos de culebras de herradura en el aeropuerto de Ibiza, contiguo al Parque Natural, e incluso una culebra de escalera hallada dentro de este mismo espacio protegido.

Culebra de collar sacrificada en Roca Llisa (Ibiza) en junio de 2018 (foto: cortesía de Pepe Fernández).

A todo lo anterior habría que sumar los 15 avistamientos de culebras de herradura nadando en el mar en los alrededores de Ibiza, a una distancia media de 200 metros de la costa, además de las dos mudas encontradas en el islote de S'Espartar. A título de ejemplo, una de esas culebras descubiertas cuando nadaban en el mar se encontraba a 110 metros de la costa de Es Figueral y a 20 metros del islote de S'Ora, donde se localiza la subespecie *Podarcis pityusensis hortae*. O, mejor dicho, donde se localizaba, pues sólo unos meses después pude constatar que esa población ya no existía.

Por si todo esto fuera poco, en junio de 2018 un ciudadano capturó y sacrificó una culebra de collar mediterránea (*Natrix astreptophora*) en la urbanización de Roca Llisa, al sur del municipio de Santa Eulària des Riu. Por las fotos, podría tratarse de una culebra de collar europea (*Natrix helvetica*), pero, en cualquier caso, sería una nueva especie de ofidio a añadir a la lista de las Pitiusas. Este hallazgo nos golpea duramente en la cara y nos recuerda el constante peligro biológico que supone la llegada de cualquier especie.

Para terminar, es inevitable hacerse las siguientes preguntas. ¿No hay ya suficientes alarmas ya encendidas? ¿No es evidente que, si no se toman medidas contundentes, estamos permitiendo que nuestra biodiversidad viva bajo amenaza? Y, en definitiva, ¿qué más tiene que ocurrir para que nos apuremos a proteger nuestro paraíso insular?

Elba Montes durante su estancia doctoral en la isla de Guam, con una serpiente arbórea café (*Boiga irregularis*) en las manos (foto: Mary Joy Viernes).

Autora

Elba M. Montes Vadillo es licenciada en Ciencias Ambientales por la Universidad de Valencia. Tras varios voluntariados en Parques Nacionales, empezó a trabajar en el Consell Insular d'Eivissa como técnica superior de Medio Ambiente, donde lideró el proyecto piloto de control de ofidios en Ibiza. En el marco de sus estudios doctorales sobre la invasión de la culebra de herradura en Ibiza, viajó a la isla de Guam (Pacífico) para familiarizarse con la gestión de las serpientes invasoras. Actualmente participa en un proyecto de investigación financiado por National Geographic para estudiar los cambios en el comportamiento de las lagartijas ibicencas causados por la invasión de serpientes.

Agradecimientos

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Annex VI. DOCTORAL STAY Report-Summary on Guam, Saipan and Tinian (USGS and USDA)

INFORMATION ABOUT THE PhD STUDENT

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INFORMATION ABOUT THE STAY

Reception Center: United States Geological Survey (USGS)

Project: USGS Brown Tree Snake Project (Guam)

Length and dates: 1 month, from 5th January through 4th February 2017

Responsible Investigators: Dr. Robert N. Reed and Dr. Aaron Collins

JUSTIFICATION, ACTIVITIES AND RESULTS OF THE STAY

Reason for choosing this destination: In the years following the World War II, the brown tree-snake (BTS) (*Boiga irregularis*) was introduced by accident to the island of Guam. This snake was brought by cargo in ships coming from other south Pacific islands and due to the absence of natural predators the population grew fast and exhausted the native vertebrates within three decades (many of them were endemic). Since the 90's, the United States Government began applying control campaigns that have allowed the development and improvement of trapping and detection of these animals along the years.

Since my Doctorate goal is focused on a snake invasion on the island of Ibiza (which has a similar area to Guam, about 550 sq km), the justification of carrying out this stay was based on the opportunity that it meant to me: I learned from the most relevant case regarding a snakes invasion on an island environment, being a worldwide reference to this type of invasions.

Activities during the stay: I joined 4 different teams during the stay:

- USGS BTS team (in Guam): formed by 6 to 8 biologists and the manager biologist (Dr. Aaron Collins), they carry out different scientific research supported by the USGS and different Universities. This research aims to acquire knowledge about the BTS invasion in order to apply it to fight against the snake.

Their offices and laboratory are located at the Guam National Wildlife Refuge: they use this building as an operational base for their work. There are some offices, a laboratory, a workshop where they can build traps and nest-boxes, several storage spaces, a room where the mice are bred and a space for preparing the mouse food, a room for the sacrifice and measurement of the BTS, and a big cage where they keep two big BTS for environmental education. They also use three outdoors enclosures for experiments: a small concrete enclosure of about 20 m^2, used for trap studies and snake resistant bird nest-boxes; a large concrete enclosure, used for reproduction experiments, of about 900 m^2; and a double barrier enclosure, at the Air Force Base, named Closed Population (CP), of 5 Ha. The latter has 14 transects, and virtually all the snakes inside it are marked (there are 110 with microchips and they can't go outside nor outsiders can go in). This was the enclosure where all the experiments in which I participated took place.

Within this enclosure, they must follow a protocol for humane handling of the animals. This means that even when the bait has enough food for one week, the traps are checked every day to avoid the snakes being more than 24 hours without water. They don't work to control the snakes' population; therefore, they don't usually remove them or kill them. When they do, they use a humane method which consists of firmly holding the neck of the snake against a board and smashing the head with determination with a heavy hammer, twice if necessary, and then cutting the head off the body.

- USDA-APHIS-WS (in Guam): the US Department of Agriculture's Animal and Plant Health Inspection Service, Wildlife Services has been responsible for the control of BTS. Its goal is to control number of BTS at ports of exit to prevent its spread to other islands, as well as trying to keep the snakes power station equipment and transmission lines, in order to minimize interactions with humans and power outages.

In their office at Barrigada, Guam, they have the different prototypes of traps and doors that they tried and developed until they have found the most effective door design. They use the cylindrical traps that provide the best results, they utilize a similar system as USGS team, for food and water for the mice (a wax block with rodent chow and a potato instead of water). They are not subject to the humane protocol, and capture large numbers of snakes, so the traps are checked once a week and the method of euthanasia is freezing.

- University of Georgia (in Guam): this research team studies the effects of the dead BTS bodies on the soil organisms. This extra input is important since the BTS does not have natural predators, and great numbers of dead bodies are likely to fall from the trees (where the BTS lives) and become a new input to the living organisms on the soil.

- University of Iowa's EBL group (in Saipan Island): the Ecology of Bird Loss research group is studying the cascading effects of bird extinction on Guam, by comparing some variables to other islands (like Saipan) without snakes and with birds. The effects they were studying during my stay were those caused by the loss of seed dispersal, as well as the diversity of plants in the native forest.

- DLNR-DFW (in Saipan and Tinian islands): the Department of Lands and Natural Resources' Division of Fish and Wildlife is in charge of the interdiction measures to avoid the entrance of BTS to the rest of the Marianas receiving cargo from Guam.

1. Research activities that I accomplished in Guam

- Fish fertilizer experiment (USGS BTS Team): the goal was to try different substances in order to determine if any of them could be used to attract and lead snakes into a trap. The experiment begins at the sunset; three of the transects are sprayed with the fish fertilizer and then all of the transects are checked looking for snakes, to see if they find more snakes in the sprayed ones. So far, the results were inconclusive. They finished this 5-year experiment during my first week on Guam. I participated during 2 nights.

- The new project was one of three simultaneous projects (USGS BTS): pre NWFN TOXDROP population census (they will begin deploying acetaminophen laced mice on April 1st) with visual and trap surveys to ensure they get as close to the total population of CP as possible. This is how they can try to determine how many snakes are dying as they try to eradicate the population. The second project is TRAP ENHANCE: they try different prototypes of traps to see if they are better than the standard modified minnow trap that has been used for the last 20 years. The third project is TRAPCHAR HEIGHT where they set the standard modified minnow traps at three different heights; 0.5-0.6 m, 0.8 m (standard height for trapping) and 1.8 m from bottom of trap to ground. They want to see if they can increase captures of smaller sized snakes, as observations during night surveys found they tend to make contact with lower traps. I helped in making some of the traps during one day, also in setting the traps the morning it had to be done, and in checking the traps during 7 work days.

- Night search at the swiftlet caves (USGS BTS): there are three caves were populations of Mariana swiftlet (*Aerodramus bartschi*) live. They were highly threatened by the BTS and the USDA-APHIS-WS placed traps close to their colonies. This action, together with the night-searches that the USGS BTS team has been carrying on, is helping the population of swiftlets to recover. The experiment consists of two persons staying for 30 minutes inside the cave, each one in one part of the cave, with night-vision binoculars, searching for BTS. After that time, they shift positions and repeat the search. These birds nest on the ceiling of the caves and are so vulnerable that they cannot be disturbed by light or noise. I visited the caves one night and helped with the search.

- Effects of dead BTS on the ground life activity (University of Georgia): the experiment consisted on placing video cameras in front of mesh boxes with different dead animals inside. The aim is to compare the effects of different dead animals, including dead BTS (given the high numbers of BTS that may die and fall on the ground), on ground life activity. They put them in a mesh box to avoid that monitor lizards can eat them. I participated and helped during one day.

- Nest-boxes for the Mariana starlings and the extinct kingfisher (USGS BTS): the Mariana starling (*Aplonis opaca*) populations in Guam suffered an important decrease due to predation pressure by the BTS, but they did not go extinct. This experiment tries different designs of nest-boxes and baffles to stop the snakes from getting to them. The person in charge checks the nest-boxes periodically in order to assess the success of each different design. They are placed in high positions in poles or palm trees, therefore they check the boxes with a camera system using a long stick. The fact that the starlings use cavities for nesting makes this experiment possible, and it also gives hope in trying a similar experiment for the extinct in the wild Guam kingfisher (*Todiramphus cinnamominus*), that counts with only a few specimens kept in captivity. This would allow reintroducing and increasing the population of both species. I visited and helped checking the nest-boxes during one day.

2. Control activities on Guam

- Snake trapping (USDA-APHIS-WS): they use cylindrical traps baited with mice placed in strategic spots (military lands, power stations and transmission lines, ports, airport, and industrial areas where containers with cargo are sealed). They also place small PVC tubes baited with a dead neonate mouse with acetaminophen (80 mm) in it. The snakes eat the mouse and die due to the high toxicity that this medicine causes to snakes. A total of 3,755 traps that result in

12,000 captures every year are placed on Guam. Approximately 70 employees carry out this work. I helped trap checking during 5 workdays.

Standard cylindrical traps used for capturing BTS

Compartment for the mouse, with food and potato

- Night search (USDA-APHIS-WS): this work takes place on Naval Base Guam, Andersen Air Force Base, Won Pat International, and the Commercial Port of Guam. The search is carried on from a vehicle with one or two spotlights along the perimeter fence, to supress the BTS population around these ports of exit. I participated during 2 night-searches.

- Trained dog inspections (USDA-APHIS-WS): the team of trained dogs is responsible for checking all cargo that leaves Guam to any other island and to the U.S. mainland. This includes all military cargo, aerial cargo, sea cargo and household goods moving from Guam to high risk areas. The goal is to inspect a 100% of the cargo that goes outside the island. The dogs are trained with live BTS that the workers hide in the inspections to test the dog teams periodically. The dog needs to feel rewarded often to keep the teams proficient at finding BTS in cargo. They are very careful in order to avoid that the dogs associate other smells with the treat (such as the human that hides the snake, or the box where the snake is kept). I was able to attend three dog inspections.

3. Research activities on Saipan

- Seedling experiment (EBL group): some of the native plant species need to be dispersed away from parent plants in order to have a better chance of survival. The EBL group was carrying out an experiment in which groups of 5 seedlings of different species were planted in different marked spots within the forest, some of them near adult specimens of the same species and some of them far away from adults of the same species, in order to better understand density or distance depending mortality in maintaining diversity and species abundance. During the days I helped we did work with the Guamia (*Guamia mariannae*), an endemic tree to the Mariana Islands and Guam. The seedlings were measured and watered with the same exact amount of water, and then watered during two consecutive days. There are different factors that kill seeds/seedlings when they are not dispersed away from the parent tree, a common one observed in other systems being fungus. Therefore, dispersal can be really important to the success of forests structure/diversity/abundance. This project is looking more specifically in the Mariana Islands and looking at specific species to see how distance dependence plays a role in each species survival (if it does). This could just show one more way in which the loss of birds on Guam has larger trophic level effects. I helped carrying on this experiment during 3 days.

4. Control activities on Saipan and Tinian

- Trained dog inspections (DLNR-DFW): the DLNR-DFW BTS team is in charge of controlling all cargo coming from Guam to Saipan and Tinian. This includes flight and sea cargo. They have an office next to Saipan airport and another one next to Tinian port, where they keep the dogs. When a plane with cargo comes to Saipan, there is a conveyor belt from the plane to a container, and the team trainer-dog is on top of it. The dog smells every box and package. From time to time, a different person places a mesh box with a snake in it, hidden inside different packages every time. It is the same procedure they use on Guam. I attended two dog inspections.

- Port BTS Barrier (DLNR-DFW): there is a square concrete barrier at the port of both islands, about 1.5m tall and 800 sq m (28 m each side). The upper part of the fence bends towards the interior of the enclosure, so that snakes wouldn't be able of escaping. The metallic door has the same shape. When cargo from Guam arrives, the containers are left inside for about a week and traps are placed inside the perimeter. The barrier in Saipan was destroyed by a typhoon and they are about to rebuild it. I visited the fence at Saipan and Tinian.

Port fence at Tinian

Conclusions and results: The experience has been enriching and positive. It gave me an idea of the possible outcome in Ibiza if the necessary work is not done: a population of 2,000,000 BTS is estimated for Guam, the eradication is virtually impossible, and the USDA-APHIS-WS is focused on controlling and preventing the associated problems they cause (power outages and human health and safety). Meanwhile, most of the bird species are extinct on the island and as a result, big-sized insects and spiders are literally everywhere; also the native forest faces serious trouble surviving because of the lack of seed dispersal and the invasion of foreign plant species, such as vines.

It also gave a useful view of how intense control measures need to be in order to be effective taking into account the area of the island, and the importance of stopping the snakes from going to other islands. The same type of fence could definitely be used in the port of Ibiza to control the entrance of snakes. The potato is an excellent idea to avoid carrying water, and the wax blocks are also something practical and useful.

I gained practical experience in handling snakes, manufacturing and fixing traps, placing traps on the field, spotting snakes in the wild, and in general, I collaborated in all the activities named in this report.

Regarding the research work that is being carried on, it reveals how basic it is to acquire knowledge about an invasive species that, until the moment it arrived to the island, nothing was known about how it would behave in that new environment. Cascading effects can be prevented if they are investigated on time. Research gives also the answer to what methods work best to fight the invasive snakes.

Responsible USGS-BTS: ResponsibleUSDA-APHIS-WS: Responsible DLNR-DFW:

Dr. Robert N. Reed Jeffrey Flores Kevin Donmoyer

Dr. Juan Manuel Pleguezuelos Gómez, Dra. Mónica Feriche Fernández-Castanys and Dra. Pilar Navarro Gómez as advisor, co-advisor and tutor of the student, state their conformity with this summary-report:

Signed: Signed: Signed:

Date: 16 March 2017

The student: Elba M. Montes Vadillo

Signed:

Annex VII. DIVULGATION ACTIVITY

During my PhD years, I realized that the invasive snakes became not only a biodiversity issue, but also a social problem that deserved special attention. Thus, it was necessary to spread reliable information and to raise awareness about how much needed it is to involve everyone in it. I gave the best of me in every talk and every interview.

Talks:

- Schools on Ibiza:
  - CEIP S'Olivera (2016 and 2018).

Talk to 1st Primary class in CEIP S'Olivera, March 2016. Photo: Xesús Ballesteros

- <u>High schools</u> on Ibiza:
    - Colegio Nuestra Señora de la Consolación (2018)
    - IES Sant Agustí des Vedrà (2019)

Talk to 1st Baccalaureate class in IES Sant Agustí des Vedrà, 2019. Photo: Marisol Torres

- <u>University</u> (Balearic Islands):
    - Universitat Oberta de Majors (Universitat de les Illes Balears – UIB, March 2021).
- Several talks taken place on Formentera and Ibiza, organized by the Regional Governments (Govern de les Illes Balears and Consell Insular d'Eivissa) addressed to general public from both islands (from 2015 to 2019).
- <u>Scientific Conferences</u>:
    - Island Biology Conference (Azores Islands, 2016 and La Réunion, 2019)
    - Congreso Luso-Español de Herpetología (Lleida, 2016 and Salamanca, 2018)
    - Island Invasives Conference (Scotland, 2017).

Talk in the Island Invasives Conference, in Dundee (Scotland), July 2017. Photo: M.Á. Miranda

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Annex VIII. JOURNALS

Complete reference and authors' affiliation for each article/chapter:

Chapter 1:

Hinckley, A., Montes, E., Ayllón, E. and Pleguezuelos, J.M., 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*.** *European Journal of Wildlife Research*, *63*(1), pp.1-8. https://doi.org/10.1007/s10344-016-1068-z.

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Chapter 2:

Montes, E., Kraus, F., Chergui, B. and Pleguezuelos, J.M., 2021. **Collapse of the endemic lizard *Podarcis pityusensis* on the island of Ibiza mediated

by an invasive snake. *Current Zoology.* zoab022, https://doi.org/10.1093/cz/zoab022.

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Chapter 3:

Montes, E., Feriche, M., Ruiz-Sueiro, L., Alaminos, E. and Pleguezuelos, J.M., 2020. **Reproduction ecology of the recently invasive snake *Hemorrhois hippocrepis* on the island of Ibiza**. *Current Zoology*, *66*(4), pp.363-371. https://doi.org/10.1093/cz/zoz059.

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Chapter 4:

Montes, E., Feriche, M., Alaminos, E. and Pleguezuelos, J.M., 2020. **The Horseshoe whip snake (*Hemorrhois hippocrepis*) on Ibiza: predator release in an invasive population**. *Amphibia-Reptilia*, *42*(2), pp.1-6. https://doi.org/10.1163/15685381-bja10039.

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Chapter 5:

Montes, E., Feriche, M., Pleguezuelos, J.M., Alaminos, E. and Navarro, P. **Parasites and enemy release: the case of the invasive snake *Hemorrhois hippocrepis* on the island of Ibiza**. *Herpetological Conservation & Biology*, in review.

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Chapter 6:

Montes E, Kraus F, Pleguezuelos JM. **Rapid endangerment of the lizard *Podarcis pityusensis* by an invasive snake demands immediate conservation response**. *Amphibian & Reptile Conservation*, in review.

Elba Montes[1]*, Juan M. Pleguezuelos[2], Fred Kraus[3]

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Annex I:

Montes, E., Gallo-Barneto, R. and Cabrera-Pérez, M.A., in press. **Presence of the horseshoe whip snake (*Hemorrhois hippocrepis*) on Gran Canaria, Spain**. *Boletín de la Asociación Herpetológica Española.*

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Annex II:

Montes, E., Ruiz, M., in press. ***Natrix astreptophora* and *Anguis fragilis* on the island of Ibiza**. *Boletín de la Asociación Herpetológica Española*.

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