

La ecología de los reptiles en un parque natural antropizado: factores que afectan a su distribución, gestión y conservación



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Tesis presentada por Robby Marcel Drechsler para optar al grado de Doctor en
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A handwritten signature in blue ink, consisting of stylized initials 'RD' followed by a diagonal stroke.

Firmado: Robby Marcel Drechsler

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Firmado: Juan Salvador Monrós González

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Resumen

El desarrollo de la actividad humana ha llevado a una pérdida importante de la biodiversidad a nivel global. Muchos ecosistemas son alterados a distintos niveles, entrando en un desequilibrio que en algunas ocasiones lleva a un colapso prácticamente total. Además, el bienestar de la población humana está muchas veces ligado al buen funcionamiento de los ecosistemas. Por ello, la sociedad es cada vez más consciente de la importancia de la conservación de los ecosistemas y de reducir su impacto ambiental. Una de las zonas que ha pasado por todas estas etapas es la Albufera de Valencia. Después de un uso tradicional durante siglos, el desarrollo industrial a principios del siglo XX ha llevado al colapso ecológico de la zona. Ante tal situación y la evidencia de sus efectos sobre la población, despertó un gran interés por la conservación y posterior restauración de la zona, realizándose toda una serie de actuaciones para cumplir con este fin.

Sin embargo, el esfuerzo de seguimiento y conservación de la fauna no se distribuye de forma uniforme a todos los grupos, sino que se centra en las especies más “atractivas” o de interés comercial, como son las aves o los peces. Uno de los grupos que pasó desapercibido de forma prácticamente total es el de los reptiles. La información que se tiene sobre este grupo es muy escasa y, generalmente, anticuada. No obstante, los reptiles, dada su estrecha relación con el medio ambiente y su importante papel ecológico en los ecosistemas, son excelentes bioindicadores de la calidad ambiental e incluso útiles para evaluar el efecto que tienen las medidas de conservación tomadas. Por lo tanto, es esencial promover el interés de la sociedad, las instituciones y la comunidad científica por los reptiles de la zona. El objetivo de esta tesis es actualizar la información sobre distintos aspectos ecológicos de las especies y aportar una base sobre la cual en un futuro se puedan desarrollar distintos trabajos enfocados a la conservación o el estudio de los reptiles presentes en el Parque Natural de la Albufera de Valencia.

Para cumplir este objetivo se ha realizado un seguimiento intensivo de la población de reptiles en distintos puntos del parque que consistió básicamente en la realización de censos y la toma de medidas biométricas. Los resultados obtenidos muestran que uno de los principales problemas a los que se enfrentan las poblaciones de reptiles en la zona es el grado de aislamiento. Existen diversas zonas donde se concentra una diversidad importante de reptiles, sin embargo están muy aisladas. Aumentando la conectividad entre estos puntos calientes se podría potenciar su capacidad conservadora de forma drástica.

También se han encontrado indicios de que la concentración de un gran número de individuos en áreas reducidas puede conllevar un alto grado de competencia tanto inter- como intraespecífica, que, a su vez, puede alterar otros aspectos de la ecología de las especies. Así, el seguimiento de las poblaciones de lagartijas mostró que se pueden asociar alteraciones de la dinámica poblacional (avance de la época reproductora, crecimiento acelerado, aumento de la proporción de machos) y de la ecología trófica con un alto nivel de competencia. También se ha aportado información de la ecología básica de algunas especies y se ha descrito por primera vez de forma detallada el

crecimiento de la lagartija colirroja, al igual que la dieta de las distintas especies de lagartijas.

En el caso de la zona húmeda, el seguimiento de las poblaciones de la culebra viperina ha podido evidenciar un efecto negativo de la actividad humana sobre sus poblaciones, siendo estas menos diversas y menos complejas en zonas con una alta presión antrópica. Para las especies de culebras acuáticas, las reservas biológicas (Tancat de la Pipa, Tancat de Milia y Tancat de Illa) son importantes zonas de refugio. Una posible forma de mejorar la conservación de estas especies es la creación de una red interconectada de reservas alrededor del perímetro de la laguna central.

Finalmente también se evaluaron los proyectos de conservación de galápagos y de la tortuga mediterránea que se están llevando a cabo en la zona mediante el análisis de sus movimientos, del uso de hábitat y del tamaño de su dominio vital. En ambos casos los resultados muestran que los proyectos son un éxito y, además, aportan información útil para mejorar la planificación de futuros proyectos similares.

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El marco ecológico

La actividad humana está alterando el medio ambiente a nivel global (Jordan et al., 1990), afectando básicamente a todos los ecosistemas y, en la mayoría de los casos, con efectos negativos (Hooper et al., 2005). Estas perturbaciones llevan a importantes desequilibrios en los ecosistemas y uno de los problemas más graves es la pérdida de biodiversidad (Naeem et al., 1994). Existen numerosos trabajos en los que se demuestra que existe una relación íntima entre la biodiversidad y el nivel de estabilidad de los ecosistemas (por ejemplo, Johnson et al., 1996; Hooper et al., 2005; Mazur, 2013). Además, en muchos casos el bienestar humano también depende del buen estado de los ecosistemas, por ejemplo, por la aparición de plagas o el desarrollo de enfermedades en ambientes alterados (Pongsiri et al 2009; Pecl et al., 2017).

Sin embargo, estas alteraciones no son puntuales y sus consecuencias son muy complejas (Sinclair & Bryom, 2006). Las perturbaciones de los ecosistemas se dan a diferentes niveles: desde la modificación del paisaje y la destrucción y fragmentación de hábitats, por ejemplo por la construcción de una infraestructura de carreteras (Tellería et al., 2011), hasta la alteración de las redes tróficas y el flujo de materia y energía en el ecosistema, por ejemplo, por la introducción de especies exóticas invasoras (Chapin et al., 1996). Por lo tanto, realizar proyectos de conservación en estos ambientes alterados es un trabajo igualmente complicado y costoso. Para que estos proyectos sean exitosos se deben tener en cuenta diferentes aspectos ecológicos. En el caso de la conservación animal, algunos de los aspectos más importantes a tener en cuenta son:

- La diversidad y la distribución de las especies (por ejemplo, Chapin et al., 1996). Cada especie realiza una función en el ecosistema, ayudando a mantener el equilibrio del mismo, pero a su vez requiere de determinadas condiciones para poder desarrollarse. Asimismo, dependen del contacto con otras poblaciones para permitir el flujo génico y evitar la acumulación de mutaciones desfavorables (Madsen et al., 1996).
- La dinámica poblacional de las especies (por ejemplo, Salvidio & Delaunoy, 2003). Se debe tener en cuenta todo el ciclo vital, si presentan momentos de letargia, cuándo es el periodo reproductivo, cuánto tiempo tardan en llegar a la madurez sexual, etc. Para que una especie pueda desarrollarse de forma correcta su dinámica poblacional debe funcionar correctamente y, en muchos casos, la alteración de alguno de los aspectos de la dinámica poblacional puede llevar a su desaparición.

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- Las relaciones tróficas (por ejemplo, Pace et al., 1999). Las especies en un ecosistema no actúan de forma independiente, están conectadas entre sí. La conexión más directa quizás sea la trófica, la relación depredador-presa es esencial a la hora de determinar el flujo de energía y materia en la red ecológica. Existen ejemplos en los que las alteraciones de una especie se han transmitido por la red trófica al resto del sistema, lo que se llama “cascadas tróficas” (Pace et al., 1999).

Aunque se trate de un trabajo largo, complicado y costoso, la protección y conservación de la biodiversidad es un reto esencial, ya que la extinción de una especie es un proceso irreversible.

El Parque Natural de la Albufera de Valencia

El Parque Natural de la Albufera de Valencia se sitúa unos 10 km al sur de la ciudad de Valencia en la costa este de España. Con una extensión de aproximadamente 21.000 hectáreas representa uno de los humedales más importantes de la península ibérica. Su utilización por el hombre se remonta hasta la prehistoria, aunque parece ser que no es hasta la llegada de los romanos cuando comienzan a consolidarse los primeros asentamientos importantes (Ferrando & Jambrino, 2014). Hasta la Edad Media el principal uso que tenía la Albufera era pesquero y salero, sin embargo, a partir del siglo XIII se empieza a implementar un complejo sistema de riego y el uso agrícola va ganando más y más importancia.

Ante la modificación del uso para la producción agraria y su creciente demanda y explotación del agua como recurso de riego, rápidamente surgió la necesidad de poder controlar las afluencias hídricas de la zona para poder regular los niveles de agua. Esto supuso un cambio radical en la naturaleza de los ecosistemas del humedal. La flora, la fauna e, incluso, la actividad cultural debieron adaptarse a estas nuevas condiciones (Sanchís Ibor, 2001). Este nuevo uso agrícola y el pesquero se mantuvo prácticamente sin cambios hasta mediados del siglo XX. El importante desarrollo industrial durante esta época, el vertido de aguas residuales urbanas e industriales y la proliferación urbanística de la costa, al igual que la mecanización de la agricultura y el uso masivo de productos químicos hicieron que entre los años 60 y 70 del siglo XX, la Albufera entrase en una crisis ecológica por la masiva eutrofización y reducción de la calidad acuática y ambiental (Soria, 2006; Ferrando & Jambrino, 2014).

Para frenar este deterioro y recuperar su valor original, la Albufera fue declarada como Parque Natural en 1986 por su alto valor ambiental, cultural y paisajístico (Generalitat Valenciana, 1990). Además, en 1989, fue incluida en la lista de Humedales Internacionales (según la Convención de Ramsar) y, en la Red Natura 2000 (según la Directiva Europea de Hábitats y Aves). A partir de este momento empieza a crecer el interés por conservar los paisajes y los ecosistemas de la zona. Uno de los primeros eventos a destacar es la restauración del cordón dunar en el límite Este del Parque. En los años 60, se arrasó prácticamente la totalidad del cordón dunar iniciando la construcción de un paseo marítimo de considerables dimensiones, así como una infraestructura de carreteras y edificios con el objetivo de fomentar el turismo de sol y playa (Olmos et al., 2014). En 1982, en respuesta a una importante

presión ciudadana ante tal alteración del paisaje se aprobó el Plan Especial de Protección del Monte de la Devesa de El Saler, con el objetivo de recuperar y conservar el ambiente natural de la zona. El éxito del proyecto fue excepcional y uno de los hitos más importantes en conservación de la zona. Varias décadas después y a día de hoy, el cordón dunar ha recuperado no sólo su aspecto, sino también su función ecológica, albergando una importante y peculiar diversidad de flora y fauna. Esta zona incluso ha servido para el desarrollo de diversos proyectos de conservación de fauna, como la reintroducción de la tortuga mediterránea o el seguimiento de la población de erizos.

Otro evento a destacar es la creación, entre 2006 y 2011, de áreas de reserva para fomentar la conservación biológica y la mejora de la calidad del agua. En concreto se crearon tres reservas: el Tancat de la Pipa, el Tancat de Milia y el Tancat de Illa; antiguos campos de arroz transformados en humedales artificiales que han recuperado hábitats palustres y su biodiversidad asociada, restaurando en pequeños espacios el estado natural de la albufera. Estas áreas protegidas han servido de base para la realización de numerosos estudios científicos relacionados con la conservación ambiental (por ejemplo Martín et al., 2013; Rodrigo et al., 2013). También el uso público y la educación ambiental juegan un papel importante en el uso que se les da a estas reservas, realizándose visitas de escuelas locales y cursos y voluntariados ambientales de todo tipo.

La fauna reptiliana

Según el Banco de datos de Biodiversidad de la Comunidad Valenciana (libremente accesible en <http://www.bdb.gva.es/es/inicio>), en los límites del Parque Natural de la Albufera de Valencia se han descrito estas 17 especies de reptiles autóctonas (dejando de lado las especies marinas):

- | | | |
|-------------------------------------|------------------------------------|---------------------------|
| - <i>Acanthodactylus erythrurus</i> | - <i>Mauremys leprosa</i> | - <i>Testudo hermanni</i> |
| - <i>Chalcides bedriagai</i> | - <i>Natrix maura</i> | - <i>Timon lepidus</i> |
| - <i>Coronella girondica</i> | - <i>Natrix astreptophora</i> | - <i>Zamenis scalaris</i> |
| - <i>Emys orbicularis</i> | - <i>Podarcis hispanica</i> | |
| - <i>Hemorrhois hippocrepis</i> | - <i>Psammodromus algirus</i> | |
| - <i>Hemidactylus turcicus</i> | - <i>Psammodromus edwardsianus</i> | |
| - <i>Malpolon monspessulanus</i> | - <i>Tarentola mauritanica</i> | |

Considerando que en la península ibérica hay unas 54 especies de reptiles autóctonas, dentro de los límites del Parque Natural se acoge aproximadamente el 30% de la biodiversidad reptiliana ibérica. Aunque la diversidad de reptiles es excepcionalmente alta, el interés por este grupo es mínimo, por lo que muchas de estas citas son anticuadas y el conocimiento general sobre el estado de las poblaciones de reptiles en el parque es muy exiguo. De hecho, apenas se realizaron estudios ecológicos sobre los reptiles en la zona. Existe algún trabajo antiguo relacionado con la ecología parasitaria de reptiles (por ejemplo Roca & Lluch, 1986) y algún trabajo anecdótico relacionado con características comportamentales de lagartijas (Guillén-Salazar et al., 2007). Algo más de interés

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han despertado las tortugas, en especial los galápagos, cuyas poblaciones se ven gravemente afectadas por la introducción de la tortuga de Florida (*Trachemys scripta elegans*) (por ejemplo, Sancho & Lacomba, 1999; Andueza & Alcayde, 2004). En la implementación y el seguimiento de estos proyectos, las reservas biológicas mencionadas anteriormente han jugado un papel fundamental (Fernández et al., 2013). También la tortuga mediterránea (*Testudo hermanni hermanni*) ha sido objeto de un proyecto de conservación. Viendo que únicamente presentaba poblaciones naturales en Cataluña y Baleares (Soler-Massana, 1995; Llorente et al., 2002), y teniendo datos arqueológicos de su presencia en el pasado en la cuenca Valenciana (Bailón, 2001; Pérez & Serra, 2009), en 2011 se inició un proyecto de reintroducción en la Devesa de El Saler, en el cordón dunar restaurado anteriormente.

Las amenazas

Cada vez es más evidente que las poblaciones de reptiles en general presentan problemas de conservación, incluso se habla de un declive general de reptiles, similar al que ocurre en anfibios (Gibbons et al., 2000). Las amenazas que afectan a los reptiles son diversas, entre ellas:

- Destrucción y fragmentación de los hábitats.
- Deterioro de la calidad ambiental (acumulación de contaminantes, eutrofización de las aguas...).
- Disminución en la abundancia de presas.
- Incremento en la abundancia de depredadores naturales.
- Expansión de las infraestructuras viarias y aumento de la intensidad del tráfico, que conlleva un incremento en la mortalidad por atropello.
- La mala fama de estas especies en la población general, sobre todo de los ofidios, conlleva un desinterés general por el estado de sus poblaciones e incluso una persecución activa.

Todas estas amenazas tienen un punto en común: la actividad humana. Viendo la historia y la situación actual de la zona de estudio, el alto (y cada vez más intenso) grado de antropización supone un peligro considerable para el bienestar de esta excepcional diversidad de especies reptilianas. Más aún, considerando los resultados obtenidos en estudios realizados en zonas muy similares, como es el Delta del Ebro. En esta zona, Santos & Llorente (2009) detectaron un declive de aproximadamente un 50%, en algunos casos, incluso 100% de la población de *N. maura* en tan solo 13 años y atribuyen este efecto a las amenazas relacionadas con la presencia humana (la industrialización, la modernización de las técnicas de plantación y siega del arroz, el uso masivo de fertilizantes, etc.). También la introducción de especies exóticas supone una presión ecológica adicional y no solamente en el caso de las tortugas, comentado anteriormente, también otras especies sufren estos efectos negativos. Por ejemplo, se ha descrito que la introducción de peces exóticos con espinas dorsales duras implica una mortalidad adicional en serpientes piscívoras, ya que al ingerir sus presas, las espinas penetran la pared corporal (Alarcos et al., 2009; Pérez-Bote & Roso, 2009).

Objetivos

Ante esta situación preocupante y la falta total de información sobre el estado de las poblaciones en el Parque Natural de la Albufera de Valencia, se propuso la realización de esta tesis doctoral cuyo objetivo principal fue actualizar y ampliar el conocimiento sobre el estado de las poblaciones de reptiles en la zona mediante el estudio de la distribución y abundancia de sus poblaciones. También se pretendió estudiar qué factores, tanto naturales como antropogénicos, afectan a las especies de estudio y, en base a los resultados obtenidos, proponer posibles medidas de gestión y conservación de estas especies de reptiles. En concreto, los objetivos específicos fueron:

1. Estudiar la distribución de todos los reptiles en el Parque Natural de la Albufera de Valencia y los factores que puedan afectar a la misma. Este objetivo también incluye la verificación de la presencia de las especies citadas en el parque y detectar especies exóticas, al igual que identificar las zonas más favorables y desfavorables para cada una de ellas (Capítulo I).
2. Conocer con más detalle la ecología y el estado de las poblaciones de lacértidos. Esto incluye el estudio de los factores que influyen en su abundancia y dinámica poblacional, al igual que el estudio del estado corporal de los animales y factores relacionados (como la dieta) (Capítulos II, III y IV).
3. Analizar el estado de las poblaciones de culebras de agua (*Natrix* sp.) y conocer más acerca del efecto que tiene la actividad humana sobre el mismo, mediante el estudio de su condición corporal en diferentes ambientes (más y menos antropizados) (Capítulo V).
4. Evaluar el éxito del reforzamiento poblacional realizado para el galápago europeo (*Emys orbicularis*) (Capítulo VI) y de la reintroducción de la tortuga mediterránea (*Testudo hermanni hermanni*) en la Devesa de El Saler (Capítulo VII), mediante el estudio de sus movimientos y su selección de hábitat .

Estructura de la tesis

Esta tesis se presenta como compendio de publicaciones donde cada capítulo corresponde a un artículo científico. Los artículos originales de los Capítulos III, VI y VII ya fueron aceptados y publicados por revistas científicas (la referencia concreta se encuentra en la página titular del capítulo correspondiente). Los artículos de los otros capítulos se encuentran en proceso de revisión por diferentes revistas científicas, por lo que se les asigna el estado “En revisión”. De todas formas, los resultados de todos los capítulos se discuten conjuntamente en un apartado especial al final de la tesis, seguido de una recopilación de las principales conclusiones de la tesis. Los capítulos no se presentan por orden cronológico, si no que se ordenan en base a las temáticas que trata cada uno de ellos:

Capítulo I Drechsler, R.M. & Monrós, J.S. Using an habitability index to build a predictive distribution model of reptiles at a local scale. *Animal Biodiversity and Conservation* (En revisión).

Capítulo II Drechsler, R.M. & Monrós, J.S. Can interspecific competition alter population dynamics? A possible

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case of three lizard species in a coastal area in Eastern Spain. *Herpetological Conservation and Biology* (En revisión).

Capítulo III Drechsler, R.M. & Monrós, J.S. (2018). Body growth and its implications in population dynamics of *Acanthodactylus erythrurus* (Schinz, 1834) in the Eastern Iberian peninsula. *Amphibia-Reptilia*, 1(aop): 1-8.

Capítulo IV Drechsler, R.M. & Monrós, J.S. Diet composition and trophic ecology of three sympatric insectivorous lizard species in a highly anthropized area in the eastern Iberian peninsula. *Basic and Applied Herpetology* (En revisión).

Capítulo V Drechsler, R.M., Vera, P., Martínez, D.C. & Monrós, J.S. The effect of biological microreserves in a highly anthropized environment on the biology of *Natrix maura* (Linnaeus, 1758). *Amphibian and Reptile Conservation* (En revisión).

Capítulo VI Drechsler, R.M., Fernández, L.M., Lassalle, M. & Monrós, J.S. (2018). Movement Patterns and Home Range Sizes of Translocated European Pond Turtles (*Emys orbicularis*, Linnaeus, 1758) in Eastern Spain. *Herpetological Conservation and Biology*, 13: 1-9.

Capítulo VII Drechsler, R.M., Vilalta, M. & Monrós, J.S. (2016). Analysis of movement patterns and macrohabitat use in Hermann's tortoises (*Testudo hermanni hermanni*, Gmelin 1789) reintroduced in a coastal area dominated by pinewood in eastern Spain. *Amphibia-Reptilia*, 37: 359-371.

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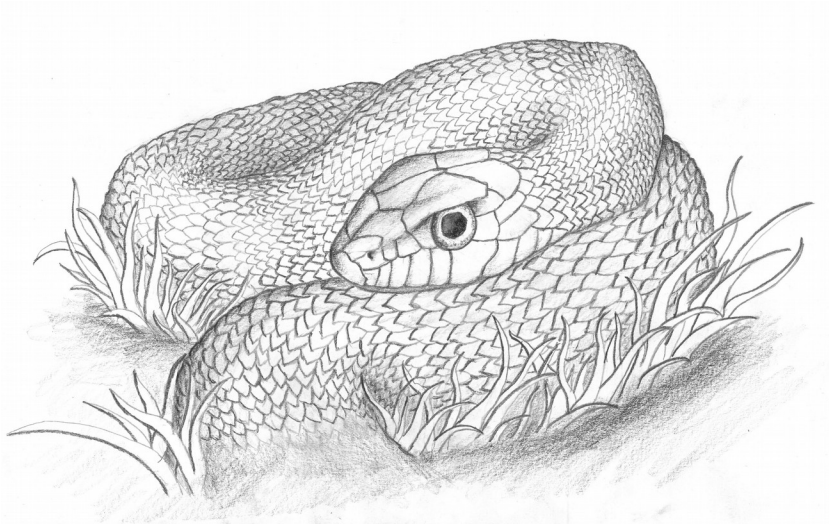
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Capítulo I

Using an habitability index to build a predictive distribution model of reptiles at a local scale.

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Animal Biodiversity and Conservation (En revisión)

Using an habitability index to build a predictive distribution model of reptiles at a local scale.

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Abstract

Models able to reliably predict the distribution of a species at a small scale are valuable tools in conservation biology as they can help to focus and direct conservation efforts, improving the success rates of such projects. As the capacity of a species to colonize a certain habitat depends on several factors, a model based on the habitat availability and quality is a good predictor for determining if a species is present or absent in an area. We constructed a model to predict the distribution of reptiles in the Albufera de Valencia Natural Park (Eastern Spain) evaluating the habitability of each habitat type in the area for each species and considering their availability in 1 km² squares. We tested our results drawing a Receiver Operating Characteristic curve (ROC) and calculating the Area Under the Curve (AUC). Our model showed high verisimilitude values for lacertid species (AUC above 0.9), moderate values for snakes (AUC ~ 0.6) and nearly random values for geckos (AUC ~ 0.5). We also carried out a diversity study of nine different points in the area. Our results indicate that the most important area for reptiles in the Natural Park is a NE line of dunes and Aleppo pine forest. However, this area is very isolated and we suggest to take measures to facilitate the contact to other populations, especially in the case of lacertids.

Keywords: *Conservation, Distribution, Habitability, Management, Modeling, Reptiles.*

Introduction

From the perspective of biodiversity conservation, knowing in detail the distribution of each species is essential (e.g. Guisan et al., 2013). However, surveying the entire area of distribution at a small scale is almost impossible. Thus, in the context of global threats like climate change the regional scale has gained more and more importance. Those large-scale distribution models often lack a sufficient fine resolution to be used as tools for species management and conservation at a local scale (Barbosa et al., 2010). In the last years, the advance in computational technologies has eased the access to large data bases and citations and it allowed to develop methodologies to predictively model species distributions at different scales (Rodríguez et al., 2007). Although it

is evident that such models have to be critically evaluated and applied with caution, they result to be a valuable tool when directing conservation measures (Loiselle et al., 2003).

The capacity of a species to be able to use or colonize a certain habitat type depends on many factors. These factors can be intrinsic to the species, like the conditions necessary for egg development (Löwenborg et al., 2010), the type of food they consume (Díaz & Carrascal, 1991) or the thermal biology (Monasterio et al., 2009). But they can also be extrinsic, i.e. imposed by the environment, like predator density (Whitaker, 1973), refuge availability (Monasterio et al., 2009), the degree of anthropic alteration (Mangianotti et al., 2013), etc.

The Albufera de Valencia Natural Park, located at the East of the Iberian peninsula, is an area of special interest. Given its extension, its history and actual land uses, it offers a wide spectrum of habitats with very different characteristics (Soria, 2006). However, the tracking of vertebrates was mostly centered on groups like birds or fish (e.g. Jambrino & Fernández-Anero, 1997; Soria, 2006). In the case of reptiles, the information is antiquated and poor. Only some punctual studies were carried out in the area focusing on reptiles (Roca & Lluch, 1986; Guillén-Salazar et al., 2007; Drechsler et al., 2016; Drechsler et al., 2018; Drechsler & Monrós, 2018). In fact, it is unknown where some of the cited species are located or even if they are still present in the area. In this context, having a tool which allows to identify the most favorable areas for each species is of great importance when proposing and planning management, tracking or conservation projects for these species.

The main objective of this work is to model the distribution of reptiles within the limits of the Albufera de Valencia Natural Park using a habitability index for each species based on the habitat types. We pretend to identify the most and least favorable areas for the reptilian fauna, with the aim of localizing and managing those areas in order to improve the general management and conservation of reptiles in the Natural Park. In addition, we pretend to study the diversity of reptiles at the different sampling points.

Material and methods

Study area

Our study area is the Albufera de Valencia Natural Park, located about 10 km South of Valencia city (39° 21' 18.7" N 0° 21' 38.4" W). It is one of the most important wetlands of the Iberian peninsula (RAMSAR area since 1990 and part of the Natura 2000 network) with an area of approximately 21000 ha. About 3000 ha correspond to the central lake, the remaining 18000 ha are mainly rice crops. The water input of this area has several origins: Júcar river, rain water from surface runoff from highly urbanized watersheds, subterranean aquifers, urban or industrial effluents (refined waste waters) and watering returns from the agriculture in the area. It is a highly anthropized area focused on the agricultural and fishing use. In the East, touching the Mediterranean sea, there is a line of dunes with approximately 1 km width with dunes of different degree of maturity.

Habitat characterization and Habitability index

To model the distribution of the different species we distinguished 16 habitat types in the area:

- Train rails, with a stony substrate and rail traffic.
- Roads, with an asphalted substrate and abundant high velocity traffic.
- Pathways, not asphalted, with a stony substrate, lower traffic level than roads and with lower velocity.
- Canals, constructed for the water distribution, constantly flooded, with flowing water and a dense vegetation at the shores formed by Common Reed (*Phragmites australis*) and Southern Cattail (*Typha domingensis*).
- Urban areas, human settlements, areas with a high human presence.
- Abandoned areas, areas without a certain use, abandoned crops, ruins, large road borders.
- Marsh vegetation, relatively large masses of dense vegetation formed mainly by Common Reed (*Phragmites australis*) and Southern Cattail (*Typha domingensis*), generally flooded, at least temporally.
- *Mallaes*, depressions in the dune line, temporally flooded, with a vegetation formed by rushes (*Juncus* sp.) and plants adapted to high salinity levels, like *Salicornia* sp.
- Forest, fixed dunes, with a dense arboreal vegetation mainly formed by Aleppo pine (*Pinus halepensis*) and a dense undergrowth with species like *Smilax aspera*, *Asparragus officinalis*, *Chamaerops humilis* or *Pistacia lentiscus*.
- Dunes, an area of mobile dunes with a variable degree of maturity and a vegetation formed by several herbaceous and bush species, generally less than 1 m tall, like *Ammophila arenaria*, *Helichrysum stoechas*, *Euphorbia paralias*, *Medicago marina* or *Rhamnus alaternus*.
- Beach, directly touching the Mediterranean sea, nearly free of vegetation and an important human presence, especially during the summer months.
- Golf tracks, very open areas constructed on the dune line.
- Biological reserves (*tancats*), there are three within the limits of the Natural Park: Tancat de la Pipa, Tancat de Milia and Tancat de Illa. All three areas are old rice fields, transformed into artificial wetlands with the objective to improve water quality and also biodiversity conservation and environmental education.
- Rice fields, crops dedicated to the cultivation of Bomba rice (*Oryza sativa*). They remain dry from February to May.
- Crops, areas dedicated to the cultivation of different plant species of commercial interest (tomatoes, oranges, etc.). In contrast to rice fields, these are never flooded.
- Water, large bodies of open water, relatively static and free of marsh vegetation. This habitat is mainly formed by the central lagoon.

In order to evaluate how habitable each habitat type is we rated 22 parameters (11 positive and 11 negative) for each habitat type and each species (Table 1). The chosen parameters had to fulfill the following conditions: 1) be relatively easy to evaluate; 2) be applicable to all species and all habitats; 3) have an effect on basic aspects of the biology of every species (feeding, reproduction, mortality, natality, migration, etc.). We assigned a value to each of

the parameters between 0 and 3 for each species and habitat, depending on the expectable effect on the habitability (0 = negligible, 1 = low, 2 = moderate and 3 = high). We obtained the habitability of each habitat type for each species adding up the values for the positive parameters and subtracting the values for the negative parameters. To minimize the level of arbitrariness and to evaluate the aspects in the most objective way possible we tried to support the election of the parameters and each value assignment with bibliography (Table 1). For example, we considered the feeding of adults and juveniles separately because in most species an ontogenetic shift of the trophic niche was described.

Once we obtained the habitability values of each habitat type for each species, using the QGIS v2.18 (2018) software, we drew a layer of 1x1 km squares over the area of the Natural Park. For each of these squares we calculated the proportion of cover of each habitat type. Then, we calculated the mean habitability of the square for a certain species adding up the products of the habitability value of each habitat type and the respective cover proportion.

Test of verisimilitude of the model

To test the results of the model we used independent citation data obtained from the Biodiversity Database of the Valencian Community (freely accessible at <http://www.bdb.gva.es/es/inicio>), roadkill data ceded by the Ministry of Agriculture, Environment, Climate Change and Rural Development of the Regional Government of Valencia and data obtained during samplings carried out by the main author between 2015 and 2018. With these data we drew the Receiver Operating Characteristic curve (ROC), following Newbold et al. (2010), which measure the proportion of correct hits of the model considering a species present at different habitability thresholds. The Area Under the Curve (AUC) indicated the adjustment of the model to the data, being a value of 1 a perfect adjustment and a value of 0.5 pure randomness.

Study of the diversity of the reptile community

We used the above cited samplings to confirm the presence of cited species and to study the general diversity of the reptilian population of the Albufera de Valencia Natural Park. The samplings were carried out between 2015 and 2018 and consisted in randomly walking nine different sites (Fig. 1), annotating and identifying the species of each seen individual. The censuses began about two to three hours after sunrise and had a duration between 1.5 and two hours. Once we obtained these data, we calculated the species richness (S), the Shannon diversity index (H') (Shannon & Weaver, 1949) and the equitativity (J) (Pielou, 1966), applying the following formulas, where p_i are the proportions of individuals of each species respect the total:

$$H' = - \sum_{i=1}^S p_i * \ln p_i \qquad J = \frac{H}{\ln S}$$

Results

During the samplings we could not verify the actual presence of in the past very rarely cited species like *Hemorrohis hipocrepris*, *Coronella gironica* or *Timon lepidus*, thus, we did not include them in this work. The detected species can be found in Table 2.

Table 1: List of considered aspects for the habitability evaluation.

Considered aspects	References
Positive	
A Food availability for adults	Valverde (1967), Santos et al. (2000), Santos et al. (2006), unpubl. data
B Food availability for juveniles	
C Refuge availability for hibernation	Seva (1982), Santos & Llorente (2001a), Salvador (2016), Pleguezuelos (2017a, b)
D Meeting probability between males and females (density of individuals)	Santos & Llorente (2001b)
E Suitability for egg laying	
F Suitability for egg development	Blázquez & Villafuerte (1990), Iraeta et al. (2007), Santos et al. (2008), Salvador (2016)
G Refuge availability to avoid predators	Blázquez (1995), Monrós (1997), Santos et al. (2008), Salvador (2015), Belliure (2015)
H Can it be used as ecological corridor? (Does it facilitate migration and dispersion?)	Pernetta et al. (2011), Dick & Mebert (2017)
I Substrate suitability for the species	Belliure (2015), Santos (2015), Salvador (2015, 2016), Pleguezuelos (2017a, b), Pleguezuelos (2018)
J Does it allow thermoregulation? (sunny and shady patches)	Belliure (2015), Santos (2015), Salvador (2015, 2016), Pleguezuelos (2017a, b), Pleguezuelos (2018)
K Degree of biodiversity protection	Unpubl. data
Negative	
L Predation risk for adults	
M Predation risk for juveniles	Galán (2013), Belliure (2015), Pleguezuelos (2017)
N Degree of human disturbance	Belliure (2015), Santos (2015), Salvador (2015, 2016), Pleguezuelos (2017a, b), Pleguezuelos (2018)
O Risk of road mortality	Belliure (2015), Santos (2015), Salvador (2015, 2016), Pleguezuelos (2017a, b), Pleguezuelos (2018)
P Risk of mortality by human activities (large individuals)	
Q Risk of mortality by human activities (small individuals)	Galán (2005), Santos (2015), Pleguezuelos (2017)
R Does it induce habitat fragmentation?	Telleria et al. (2011)
S Does it hinder migration or dispersion? (obstacles like walls, etc.)	Dick & Mebert (2017), Leon et al. (2015) Pernetta et al. (2011)
T Proportion of the year with adverse conditions for the species	Santos & Llorente (2001a)
U Risk of infections or illness contagion, expectable density of parasites	Santos (2015)
V Risk of intoxication (degree of chemical pollution)	Santos et al. (1999)

The values we assigned to evaluate the habitability are summarized in APPENDIX I. As some results for the habitability were practically identical between some species, we considered them together. Thus, *M. monspessulanus* and *Z. scalaris* form a group; the lizards *A. erythrurus*. *P. algirus* and *P. edwardsianus* form another, and, finally, the geckos *T. mauritanica* and *H. turcicus* another.

Table 2: Detected species during the samplings between 2015 and 2018

Sample point	AR	LR	Palmar	MS	SC	Pipa	Milia	Illa	Dunes
Sampled hours	84	72	38	12	14	95	82	62	268
<i>Malpolon monspessulanus</i>	X	X	X			X	X	X	X
<i>Zamenis scalaris</i>							X		X
<i>Natrix maura</i>	X	X	X	X	X	X	X	X	
<i>Natrix astreptophora</i>	X	X	X			X	X	X	
<i>Tarentola mauritanica</i>	X	X	X	X	X	X	X	X	X
<i>Hemidactylus turcicus</i>	X								
<i>Acanthodactylus erythrurus</i>									X
<i>Psammodromus algirus</i>									X
<i>Psammodromus edwardsianus</i>									X
<i>Chalcides bedriagai</i>									X

The habitability results show that for most species the NE area of the Natural Park is especially important (Figure 2). This area corresponds to a line of dunes and Aleppo pine forest. Especially for lizards and *C. bedriagai* it results to be the only area with good conditions, although there is also an area at the South with more or less favorable conditions and where we would expect these species to be present. In the case of snakes, they seem to be more generalists, finding habitable areas throughout the entire surface of the Natural Park.

However, the preferences of the different species can also be observed. While the two *Natrix* species prefer more humid areas, especially the surroundings of the central lagoon, *M. monspessulanus* and *Z. scalaris*, although they can also be found in rice field areas, they prefer the NE forest area. The geckos, in contrast, are mainly found associated to human settlements, although they are also present in forest areas.

The verisimilitude tests of the model gave very good results for the lizards (AUC = 0.98) and *C. bedriagai* (AUC = 0.96); moderately good results for snakes (AUC = 0.60 for *M. monspessulanus* and *Z. scalaris*; AUC = 0.66 for *N. maura* and AUC = 0.62 for *N. astreptophora*) and results close to random for geckos (AUC = 0.55) (Figure 2).

The diversity and equitativity indexes for the nine sampled points (Table 3) show that the areas with higher reptile species diversity are the NE area of dunes and forest and the northern areas, close to the central lagoon (Pipa and LR). Instead, the area with the lowest diversity is characterized by a high human presence (AR).



Figure 1: Localizations of the different sampling points

Table 3: Values of species richness, equitativity and diversity of reptiles for each sampling point.

Sample point	Sampled hours	Species richness	Equitativity (J)	Shannon (H')
AR	84	5	0.35	0.82
LR	72	4	0.64	1.28
Dunes	268	6	0.66	1.71
Illa	62	4	0.45	0.90
Milia	82	6	0.38	0.99
MS	12	2	1.00	1.00
Palmar	38	4	0.52	1.05
Pipa	95	4	0.63	1.26
SC	14	2	0.80	0.80

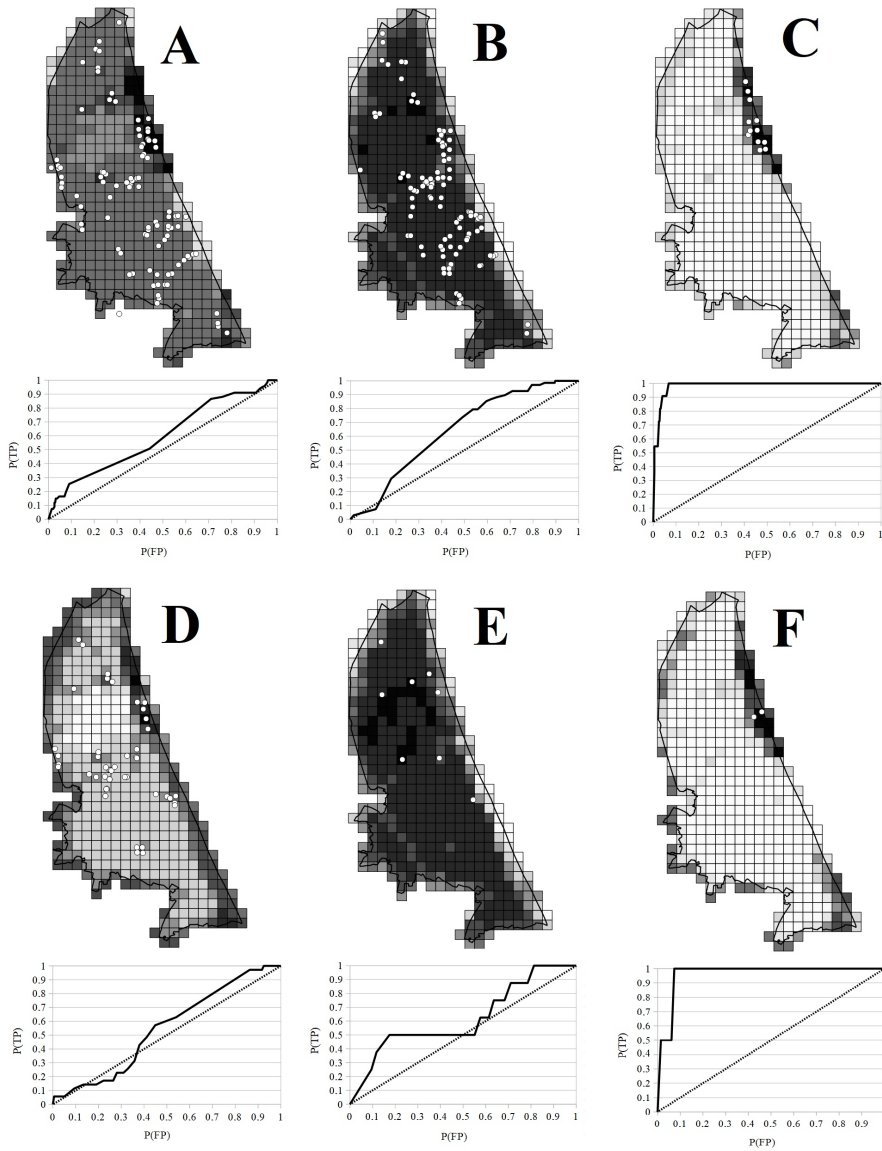


Figure 2: Results of the mean habitability for each 1x1 km square for the different species or groups: *M. monspessulanus* + *Z. scalaris* (A); *N. maura* (B); Lizards (C); Geckos (D); *N. astreptophora* (E) and *C. bedriagai* (F); darker colors indicating higher habitability. In addition, we represent on each map the citations for each species or group (white points) and the resulting ROC curve after the evaluation of each distribution model

Discussion

Although in the past there were made predictive models for species distributions based on present habitat types (e.g. Cowley et al., 2000; Guisan & Hofer, 2003), the way we evaluate habitat habitability for the different species and the scale we apply such a model are novel. The greatest problem with this type of models is the degree of arbitrariness of the researcher (Ray & Burgman 2006). In our case we minimized this effect by two ways: 1) making a relatively rough evaluation (with only four categories) of the effect of the different aspects on a certain species; and 2) consulting in each case studies and bibliographic references which could give us hints and facilitate our decision. For example we took into account that in Galan & Fernández-Arias (1993) the authors state that *N. astreptophora* prefers to lay eggs in mounds of plant matter in decomposition and we evaluated in each habitat type how abundant we expect to be such microhabitats when rating if a certain habitat is suitable for egg laying for this species.

The verisimilitude of our results can also be observed in the values of the adjustment tests, especially for lizards and *C. bedriagai*. Although in the case of snakes the values seem poorly significant (AUC a bit over 0.6), we have to take into account that the data we used to evaluate the model are totally sporadic (road kills and citations from amateurs) and they, by far, do not cover all squares of the study area. But still the model gives positive results for all groups, excepting geckos. Given the different ecological characteristics of the different species, not all models are adequate to predict the distribution of all species (McPherson & Jetz, 2007).

The problem with geckos can be broken down in two: 1) they present very small home ranges, with barely some m² (Salvador, 2016); and 2) they are capable of using vertical environments. These two characteristics allow them to colonize small structures embedded in an on the first look unfavorable environment (like motor shacks in the rice fields, small walls, ruins, etc.). In this case, the scale of our model is not fine enough to be able to reliably predict the presence or absence of these species. In addition, we have to consider that between the two species forming the group (*T. mauritanica* and *H. turcicus*) an important degree of interspecific competition was described (Lisičić et al., 2012). This competition is generally biased in favor of *T. mauritanica*, given its higher sturdiness, larger body size of adults and higher aggression (Lisičić et al., 2012). In fact, *H. turcicus* results to be very rare in the Albufera de Valencia Natural Park, only being detected in two areas (cited in MS and captured in AR). Hence, this competition with *T. mauritanica* seems to considerably reduce its distribution.

The results of the distribution model and also the diversity results indicate that the most interesting and important area for reptiles in the Albufera de Valencia Natural Park is the NE coastal line with dunes and forest. This area is almost the only habitable area for the lizard species and *C. bedriagai* (Fitze, 2012; Belliure, 2015; Pollo, 2015; Salvador, 2015). It is also a preferable area for *M. monspessulanus* and *Z. scalaris*. Among the most decisive factors are the high prey availability and a reduced mortality risk related to predation or human presence. In the case of *Z. scalaris* it is expectable that this preference is even more important (Pleguezuelos, 2017b). The citations

of this species were located mostly in or relatively close to the forest habitat. However, we also saw several individuals in Milia, maybe using the marsh vegetation on the perimeter of the central lagoon as an ecological corridor.

One of the biggest problems of the dune area is its isolated character. The present species, especially lacertids, have no possibility to contact other near populations. This high degree of isolation and the concentration of a high number of individuals in a relatively small area can lead to an additional reproductive cost and a reduction in adaptability of these populations (Díaz et al., 2005). In addition to lead to a genetic deterioration by endogamy (Madsen et al., 1996). However, specific studies are needed to confirm that.

Another important problem is the CV-500 road, a very transited road which “cuts” the dune area from the rest of the Natural Park. In fact, a high number of fauna road kills were registered on this road, not only reptiles, because of the lack of wildlife passages. This type of roads has already been described as important physical barriers which limit the species distribution, especially those with reduced dispersion capacities (Tellería et al., 2011). We suggest the construction of wildlife passages which facilitate the crossing of the road and the implementation of ecological corridors in order to improve the dispersion of individuals and the contact with other populations.

In the case of water snakes (*Natrix* sp.), rice fields seem to be suitable habitats for these species. However, it is more and more evident that the intensification of the agriculture, the massive use of chemical products and the use of larger machinery threatens these populations (Santos & Llorente, 2009; unpubl. data). In this context, in the case of the Albuera de Valencia, the conservation of the perimeter of the central lagoon is especially important. Likewise, it is important to foment the creation of protected areas like Pipa, Milia or Illa, as we could detect a positive effect of such areas on snake populations (unpubl. data).

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APPENDIX I: Evaluations of the habitability of each habitat type for each species

		Species: <i>Malpolon monspessulanus</i> + <i>Zamenis scalaris</i>																
Habitat type	Rails	Roads	Pathways	Canals	Urb.	Beach	Mallae	Forest	Golf	Dunes	Marsh veg.	Reserves	Abandoned	Crops	Water	Rice		
Habitability	-13	-19	-9	11	-15	-11	23	30	-8	28	21	21	19	5	-1	3		
A(+)	0	0	1	3	2	0	3	3	1	3	3	3	2	3	0	3		
B(+)	0	0	0	3	1	0	3	3	1	3	3	3	2	3	0	3		
C(+)	0	0	0	2	1	0	1	3	0	3	3	3	3	2	0	1		
D(+)	0	0	1	3	0	0	3	3	1	3	3	3	3	2	0	2		
E(+)	0	0	0	3	1	0	2	3	0	3	2	3	3	2	0	1		
F(+)	0	0	0	3	1	0	2	3	2	3	3	3	3	3	0	2		
G(+)	0	0	0	3	2	0	3	3	0	3	3	3	3	2	3	1		
H(+)	0	0	1	1	0	1	3	3	0	3	3	0	2	0	3	3		
I(+)	3	0	3	3	1	3	3	3	3	3	3	3	3	3	3	3		
J(+)	0	0	1	3	3	0	3	3	1	3	3	3	3	3	0	1		
K(+)	0	0	0	0	0	0	1	2	0	2	0	3	0	0	0	0		
L(-)	3	1	3	3	1	3	2	0	3	1	3	3	1	1	2	3		
M(-)	3	0	3	3	3	3	1	2	3	1	2	3	2	3	3	1		
N(-)	3	3	2	1	3	2	0	0	3	1	0	0	2	2	0	2		
O(-)	1	3	2	0	3	0	0	0	1	0	0	1	0	1	0	0		
P(-)	1	1	1	2	3	2	1	0	3	1	0	1	0	3	1	3		
Q(-)	0	0	1	1	3	2	0	0	3	0	0	0	0	2	0	1		
R(-)	1	3	0	0	2	0	0	0	0	0	0	0	0	1	0	0		
S(-)	1	3	0	0	3	0	0	0	1	0	0	0	1	2	0	0		
T(-)	3	3	3	0	3	3	0	0	0	0	0	0	0	0	0	2		
U(-)	0	0	0	3	1	0	0	0	0	0	2	1	2	0	2	2		
V(-)	0	2	1	3	2	0	0	0	0	0	1	0	0	3	2	3		

Species: *Natrix maura*

Habitat type	Rails	Roads	Pathways	Canals	Urb.	Beach	Maltales	Forest	Golf	Dunes	Marsh veg.	Reserves	Abandoned	Crops	Water	Rice
Habitability	-14	-19	-10	16	-23	-16	15	15	-15	-1	21	20	18	-3	14	12
A(+)	0	0	0	3	0	0	2	0	0	0	3	3	1	0	3	3
B(+)	0	0	0	3	0	0	2	1	0	0	3	3	2	1	3	3
C(+)	0	0	0	3	1	0	1	3	0	0	3	3	3	2	0	1
D(+)	0	0	1	3	0	0	3	0	0	0	3	3	3	0	3	3
E(+)	0	0	0	3	0	0	1	3	0	0	3	3	3	2	0	2
F(+)	0	0	0	3	0	0	2	1	0	0	3	3	3	1	0	3
G(+)	0	0	0	3	2	0	3	3	0	1	3	3	3	2	2	2
H(+)	0	0	1	3	0	0	1	2	0	0	3	0	1	2	3	3
I(+)	2	0	3	3	1	1	3	2	1	2	3	3	2	2	3	3
J(+)	0	0	1	3	3	0	3	3	1	1	3	3	3	2	3	3
K(+)	0	0	0	0	0	0	1	2	0	2	0	3	0	0	0	0
L(-)	3	1	3	3	3	3	2	2	3	1	3	3	1	1	1	2
M(-)	3	0	3	3	3	3	1	3	3	1	2	3	2	3	1	1
N(-)	3	3	2	1	3	2	0	0	3	1	0	0	2	2	0	2
O(-)	1	3	2	0	3	0	0	0	1	0	0	1	0	1	0	0
P(-)	1	1	1	1	3	3	1	0	3	1	0	1	0	3	0	2
Q(-)	0	0	1	0	3	3	0	0	3	0	0	0	0	2	0	1
R(-)	1	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0
S(-)	1	3	0	0	3	0	0	0	1	0	0	0	1	2	0	0
T(-)	3	3	3	0	3	3	2	0	0	3	0	0	0	0	0	2
U(-)	0	0	0	3	1	0	1	0	0	0	3	2	0	0	2	1
V(-)	0	2	1	3	2	0	0	0	0	0	1	0	0	3	2	3

Species: Natrix asreptophora

Habitat type	Rails	Roads	Pathways	Canals	Urb.	Beach	Millales	Forest	Golf	Dunes	Marsh veg.	Reserves	Abandoned	Crops	Water	Rice
Habitability	-15	-19	-10	17	-23	-17	10	8	-15	-2	21	20	14	-3	15	13
A(+)	0	0	0	3	0	0	2	0	0	0	3	3	1	0	3	3
B(+)	0	0	0	3	0	0	2	0	0	0	3	3	2	0	3	3
C(+)	0	0	0	3	1	0	1	3	0	0	3	3	3	2	0	1
D(+)	0	0	1	3	0	0	3	0	0	0	3	3	3	0	3	3
E(+)	0	0	0	3	0	0	0	0	0	0	3	3	2	2	0	3
F(+)	0	0	0	3	0	0	0	0	0	0	3	3	2	2	0	3
G(+)	0	0	0	3	1	0	3	3	0	1	3	3	3	2	3	2
H(+)	0	0	1	3	0	0	1	1	0	0	3	0	0	1	3	3
I(+)	1	0	3	3	1	0	1	1	1	1	3	3	2	2	3	3
J(+)	0	0	1	3	3	0	3	3	0	1	3	3	3	3	3	3
K(+)	0	0	0	0	0	0	1	2	0	2	0	3	0	0	0	0
L(-)	3	1	3	3	2	3	2	2	3	1	3	3	1	1	1	2
M(-)	3	0	3	3	3	3	1	3	3	1	2	3	2	3	1	1
N(-)	3	3	2	1	3	2	0	0	3	1	0	0	2	2	0	2
O(-)	1	3	2	0	3	0	0	0	1	0	0	1	0	1	0	0
P(-)	1	1	1	0	3	3	1	0	3	1	0	1	1	3	0	2
Q(-)	0	0	1	0	3	3	0	0	3	0	0	0	1	2	0	1
R(-)	1	3	0	0	3	0	0	0	0	0	0	0	0	0	0	0
S(-)	1	3	0	0	3	0	0	0	0	0	0	0	0	2	0	0
T(-)	3	3	3	0	3	3	2	0	0	3	0	0	0	0	0	2
U(-)	0	0	0	3	1	0	1	0	0	0	3	2	0	0	2	1
V(-)	0	2	1	3	2	0	0	0	0	0	1	0	0	3	2	3

Species: Lizards (*Acanthodactylus erythrinus* + *Psammotromus algrinus* + *Psammotromus edwardsianus*)

Habitat type	Rails	Roads	Pathways	Canals	Urb.	Beach	<i>Mallaea</i>	Forest	Golf	Dunes	Marsh veg.	Reserves	Abandoned	Crops	Water	Rice
Habitability	-4	-23	-3	-13	-22	-4	22	23	-8	24	3	2	13	-5	-17	-19
A(+)	1	0	3	0	1	1	3	3	1	3	3	3	3	3	0	3
B(+)	1	0	3	0	1	1	3	3	1	3	3	3	3	3	0	3
C(+)	1	0	0	0	2	0	3	3	0	3	0	0	3	0	0	0
D(+)	0	0	3	0	0	1	3	3	0	3	0	0	3	0	0	0
E(+)	0	0	0	0	0	1	3	3	0	3	0	0	2	0	0	0
F(+)	0	0	0	0	0	1	3	3	3	3	0	0	2	0	0	0
G(+)	1	0	0	3	2	0	3	3	0	3	3	3	3	2	0	1
H(+)	1	0	1	0	0	2	0	3	0	3	0	0	0	0	0	0
I(+)	2	0	2	0	0	3	3	3	2	3	1	0	1	1	0	0
J(+)	0	0	1	3	1	0	3	3	1	3	3	3	3	3	0	0
K(+)	0	0	0	0	0	0	1	2	0	2	0	3	0	0	0	0
L(-)	3	3	3	3	3	3	1	3	3	2	3	3	3	3	3	3
M(-)	3	3	3	3	3	3	1	3	3	2	3	3	3	3	3	3
N(-)	3	3	2	1	3	2	0	0	3	1	0	0	2	2	0	2
O(-)	1	3	3	0	3	0	0	0	2	0	0	1	0	1	0	0
P(-)	0	0	0	0	3	2	0	0	2	0	0	0	0	1	0	3
Q(-)	0	0	0	0	3	2	0	0	2	0	0	0	0	1	0	3
R(-)	1	3	1	3	3	0	0	0	1	0	1	0	0	0	3	3
S(-)	0	3	0	3	3	0	0	0	0	0	0	3	1	2	3	3
T(-)	0	3	3	3	3	1	1	0	0	0	2	3	0	1	3	3
U(-)	0	0	0	0	0	1	3	3	0	3	0	0	1	0	0	0
V(-)	0	2	1	3	2	0	0	0	0	0	1	0	0	3	2	3

Species: *Geckonids (Tarentola mauritanica + Hemidactylus erythrurus)*

Habitat type	Rails	Roads	Pathways	Canals	Urb.	Beach	Mallaeas	Forest	Golf	Dunes	Marsh	veg.	Reserves	Abandoned	Crops	Water	Rice
Habitability	-1	-25	-2	-13	11	-13	13	23	-8	7	10	10	20	17	10	-17	-6
A(+)	1	0	1	0	3	0	3	3	1	3	3	3	3	3	3	0	2
B(+)	1	0	1	0	3	0	3	3	1	3	3	3	3	3	3	0	2
C(+)	1	0	1	0	3	0	2	3	0	1	1	3	3	3	2	0	2
D(+)	1	0	1	0	3	0	2	3	0	1	1	2	3	3	2	0	1
E(+)	1	0	1	0	3	0	2	3	0	0	1	3	3	3	2	0	1
F(+)	3	0	3	0	3	0	2	3	0	1	2	3	3	3	3	0	1
G(+)	1	0	1	3	3	0	2	3	0	1	3	3	3	3	2	0	2
H(+)	1	0	2	0	3	0	0	3	0	1	2	0	0	0	3	0	1
I(+)	3	0	3	0	3	0	3	3	3	1	2	3	3	3	3	0	1
J(+)	0	0	1	3	3	0	3	3	0	3	3	3	3	3	3	0	3
K(+)	0	0	0	0	0	0	1	2	0	2	0	3	0	0	0	0	0
L(+)	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3	3	3
M(+)	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3	3	3
N(+)	3	3	2	1	3	2	0	0	3	1	0	0	0	2	2	0	2
O(+)	2	3	3	0	3	0	0	0	1	0	0	1	0	0	1	0	0
P(+)	1	1	1	0	3	1	0	0	1	0	0	0	0	0	1	0	2
Q(+)	1	1	1	0	3	1	0	0	1	0	0	0	0	0	1	0	2
R(+)	1	3	2	3	0	0	0	0	1	0	0	0	0	0	0	3	2
S(+)	0	3	1	3	0	0	0	0	0	0	0	0	0	0	0	3	2
T(+)	0	3	0	3	0	3	1	0	0	0	1	0	0	0	0	3	2
U(+)	0	0	0	0	1	0	3	3	0	3	3	2	2	2	2	0	1
V(+)	0	2	1	3	2	0	0	0	0	0	1	0	0	0	3	2	3

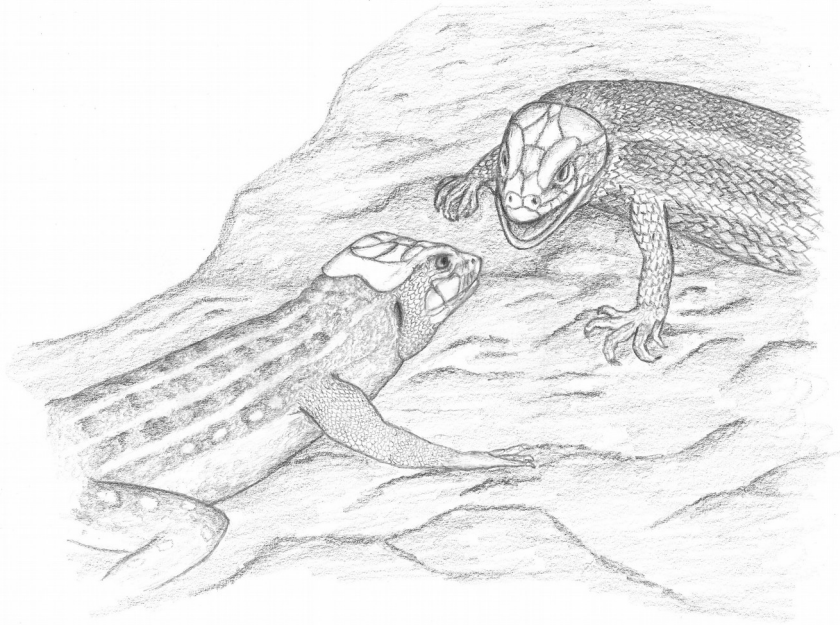
Species: *Chalcidius bedriagai*

Habitat type	Rails	Roads	Pathways	Canals	Urb.	Beach	Millruas	Forest	Golf	Dunes	Marsh	veg.	Reserves	Abandoned	Crops	Water	Rice
Habitability	-6	-23	-18	-16	-22	-9	20	27	-7	24	3	3	2	13	4	-17	-19
A(+)	1	0	1	0	1	0	3	3	1	3	3	3	3	3	3	0	3
B(+)	1	0	1	0	1	0	3	3	1	3	3	3	3	3	3	0	3
C(+)	0	0	0	0	2	0	3	3	0	3	0	0	0	3	2	0	0
D(+)	0	0	0	0	0	0	2	3	0	3	0	0	0	3	2	0	0
E(+)	0	0	0	0	0	0	2	3	1	3	0	0	0	2	1	0	0
F(+)	0	0	0	0	0	0	2	3	1	3	0	0	0	2	1	0	0
G(+)	1	0	0	3	2	3	3	3	1	3	3	3	3	3	2	0	1
H(+)	0	0	0	0	0	0	0	3	0	3	0	0	0	0	2	0	0
I(+)	2	0	1	0	0	3	2	3	1	3	1	0	0	1	2	0	0
J(+)	0	0	0	0	1	0	3	3	1	3	3	3	3	3	3	0	0
K(+)	0	0	0	0	0	0	1	2	0	2	0	0	3	0	0	0	0
L(-)	3	3	3	3	3	3	1	1	2	2	3	3	3	3	3	3	3
M(-)	3	3	3	3	3	3	1	1	2	2	3	3	3	3	3	3	3
N(-)	3	3	2	1	3	2	0	0	3	1	0	0	0	2	2	0	2
O(-)	1	3	3	0	3	0	0	0	2	0	0	0	1	0	1	0	0
P(-)	0	0	1	0	3	2	0	0	2	0	0	0	0	0	1	0	3
Q(-)	0	0	1	0	3	2	0	0	2	0	0	0	0	0	1	0	3
R(-)	1	3	3	3	3	0	0	0	1	0	1	0	0	0	0	3	3
S(-)	0	3	1	3	3	0	0	0	0	0	0	0	3	1	2	3	3
T(-)	0	3	3	3	3	3	1	0	0	0	2	3	3	0	1	3	3
U(-)	0	0	0	0	0	0	1	3	0	3	0	0	0	1	0	0	0
V(-)	0	2	1	3	2	0	0	0	0	0	1	0	0	0	3	2	3

Capítulo II

Can interspecific competition alter population dynamics? A possible case of three lizard species in a coastal area in Eastern Spain

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Can interspecific competition alter population dynamics? A possible case of three lizard species in a coastal area in Eastern Spain

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Abstract

There are many factors affecting population dynamics, both abiotic and biotic. One of the most important biotic factors affecting different ecological aspects of a species is competition. But there is relatively little research focussing on the effect of competition on population dynamics. Thus, we studied population dynamics of three insectivorous lizard species (*Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus edwardsianus*) which cohabit in our study area. We carried out periodic censuses and samplings during 2015 and 2017. Our results seem to confirm that a high level of competition can alter some aspects of population dynamics. Also body size seems to play a role, as most adjustments we detected were related to small size classes and the most affected species was *P. edwardsianus*. Some possible responses to competition we detected were an advance of the reproduction period, increased growth rates and biasing the sex ratio notably towards males (as higher testosterone levels lead to more aggression and this improves success rates in interspecific encounters). However, our study area is highly anthropized and further research is needed to discern if these adjustments are really exclusively related to competition or if human disturbance also plays a role.

Keywords *Acanthodactylus erythrurus*, Competition, Ecology, Population dynamics, *Psammodromus algirus*, *Psammodromus edwardsianus*, Spain.

Introduction

The species in the Mediterranean region adapted their life cycles to the peculiarities of the Mediterranean climate, leading to very characteristic phenologies (Crucitti, 2012). This has also an effect on population dynamics, observing different reproductive strategies to grant the survival of the populations. Some species present annual cycles, so that nearly the entire population is renewed every year (Carretero & Llorente, 1991), others opt for a longer generation time, so that individuals reproduce various times during their life (Galán, 1999; Carretero, 2006).

However, in addition to climatic conditions and other abiotic factors, there are also biotic factors that can influence population dynamics. One of the most important is competition (Werner & Gilliam, 1984). For example, it has been described that a high level of (intraspecific) competition is one of the most important forces behind gigantism in isolated systems (e.g. Pafilis et al., 2009). Competition can also be responsible for changes in reproductive and phenotypic traits of a species (Svensson, & Sinervo, 2000; Du, 2006; Calsbeek & Cox, 2010). In interspecific relations, usually the larger species has higher competitive capacity (Werner & Gilliam, 1984). However, the recruitment of new individuals occurs through small size classes, so that the maximum level of competition can be expected in juveniles (Werner & Gilliam, 1984). One way to avoid this competition is using the plasticity of population dynamics, inherent to every species (Ford & Seigel, 1989; Carretero, 2006). This plasticity allows for example to advance or delay the hatching period or to enhance fertility in comparison to other populations, less exposed to the competitive pressure.

In our study area cohabit three lizard species *Acanthodactylus erythrurus* (Schinz, 1834), *Psammodromus algirus* (Linnaeus, 1758) and *Psammodromus edwardsianus* (Dugès, 1829). All three species share the same microhabitats and feed on the same prey (insects). Thus, we expect a high competitive pressure between them, maybe leading to alterations of their “normal” population dynamics. There were carried out some studies in the past regarding population dynamics and demography of the species, as show the information compilations from Belliure (2015) for *A. erythrurus*; Salvador (2011) for *P. algirus* and Fitze (2012) for *P. edwardsianus*. Especially for *P. algirus* and *P. edwardsianus* there is a good amount of information, however, the studies are basically descriptive and focussed on each species independently. In the case of *A. erythrurus* interactions with other species are completely unknown (Belliure, 2015). There are no studies which focus on the three species at once and the effect this coexistence could have on their population dynamics. Additionally, the studies show a great geographic variability of different aspects of population dynamics. For example, the body size at which *P. algirus* reaches sexual maturity varies from 55 to 67 mm snout-vent length (Busack et al., 2006 and Salvador & Veiga, 2001, respectively) and the mean number of eggs found per female varies from 4.5 (Carretero & Llorente, 1997) to 6 (Pollo & Pérez-Mellado, 1990). Another interesting case is *P. edwardsianus*, where important interannual fluctuations of population densities were described, passing from values of 60 individuals per hour to 2 individuals per hour between 2006 and 2010 (Fitze, 2012). This is associated to the fact that *P. edwardsianus* seems to be an opportunistic species, very abundant in highly altered areas and less abundant as habitat maturity increases (Fitze, 2012).

The hypothesis we want to test is, given the expected high competitive pressure and the high degree of variability of different aspects of population dynamics, we expect alterations of some of these aspects, with the objective to minimize the negative effects of such interactions, especially at the forest habitat where we expect the maximum values of lizard densities. Therefore, our main objective is to record these alterations and provide the first data regarding annual demographic variations of three sympatric lizard species in our study area.

Material and methods

The study area is located about 10 km South of Valencia city and is part of the Albufera de Valencia Natural Park (39°20'32"N 0°18'36"W). It represents a coastal line about 10 km long (N-S) and about 1 km wide (E-W).

The study area presents typical Mediterranean vegetation, with two distinct macrohabitat types. A “Dune” habitat with an area of mobile dunes with different degree of maturity and a vegetation formed by diverse herbaceous and shrub species, generally less than 1 m tall, like *Ammophila arenaria*, *Helichrysum stoechas*, *Euphorbia paralias*, *Medicago marina* or *Rhamnus alaternus*, among others; and a “Forest” habitat, an area of fixed dunes with an arboreal vegetation mainly formed by Aleppo pine (*Pinus halepensis*) and a dense undergrowth with species like *Smilax aspera*, *Asparagus officinalis*, *Chamaerops humilis* or *Pistacia lentiscus*.

The samplings were carried out between April and October (both included) of 2015 and 2017. In 2015 we carried out one sampling in each habitat every two weeks, and in 2017 we intensified the sampling effort to 2 times per week in each habitat. We only sampled on days with favourable weather conditions, starting approximately three hours after sunrise. We also measured the temperature with sunlight and with shade before and after each sampling.

Each sampling consisted in a census randomly walking the area for two hours, recording all detected individuals, annotating species, age class and sex every time possible. We also captured all possible individuals by hand or looping, putting all captures in individual cloth bags. After the census, we processed all captured individuals, measuring basic biometry (total length, SVL, weight) and counted abdominal eggs in females performing a gentle massage. We marked each individual with a code of amputated phalanges in order to control recaptures (Drechsler & Monrós, 2018). After the measuring, each individual was released near the capture point.

In the case of *A. erythrurus* we considered an individual as adult if its Snout-Vent Length (SVL) was over 60 mm (males) (Seva, 1982) or 55 mm (females) (minimum size we observed a gravid female); in the case of *P. algirus* we considered adults from SVL > 52 mm (males) or SVL > 53 mm (females); and in the case of *P. edwardsianus* we considered adults from SVL > 34 mm. These criteria were considered following results in previous studies in similar areas as our study area (Salvador, 2011; Fitze 2012; Belliure, 2015, Drechsler & Monrós, 2018). We considered an individual as hatchling if its body size was close to those described for newly hatched individuals for each species.

For the abundance estimation we standardized the counts by the duration of each census in hours, obtaining abundance values in individuals per hour. Then, we grouped the data by months and habitats, calculating the mean and standard error. We evidenced the statistical significance of the observed differences performing Kruskal-Wallis tests, given that the distribution of our data was not normal (Shapiro-Wilks Test, $W = 0.979$, $p = 0,039$ for *A.*

erythrurus; $W = 0.854$, $p < 0.001$ for *P. algirus* and $W = 0.930$, $p < 0.001$ for *P. edwardsianus*). Afterwards, we calculated the proportions of the different age classes for each month, each species and each habitat; and the sex ratio in each case. In the case of females, we also evaluated if there are differences in the amount of eggs produced per female between habitats, also performing Kruskal-Wallis test as these data did not have a normal distribution either (Shapiro-Wilks Test, $W = 0.849$, $p < 0.001$ for *A. erythrurus*; $W = 0.922$, $p = 0.141$ for *P. algirus* and $W = 0.827$, $p = 0.019$ for *P. edwardsianus*).

Results

The analysis of the abundance phenology of the three species showed significant differences between them (Kruskal-Wallis Test, $X^2 = 110.16$, $df = 2$, $p < 0.001$). While *A. erythrurus* presents two abundance peaks (one in May and one in September), the abundance of *P. edwardsianus* tends to increase throughout the year and *P. algirus* maintains similar (but relatively low) levels throughout the year (Fig. 1).

The comparison between the two habitat types also showed significant differences for all three species (Kruskal-Wallis Test, $X^2 = 6.607$, $df = 1$, $p = 0.010$ for *A. erythrurus*; $X^2 = 6.374$, $df = 1$, $p = 0.012$ for *P. algirus*; and $X^2 = 69.174$, $df = 1$, $p < 0.001$ for *P. edwardsianus*). In the case of *A. erythrurus* we observed a clear dominance in both habitats which was especially important in the “Dune” habitat. We recorded in all three species a preference for the “Forest” habitat, but especially for the two *Psammodromus* species, with higher abundance values in relation to the “Dune” habitat during the entire year. Although, in the case of *P. algirus* we observed a decrease in abundance in the “Forest” habitat going from values of about 4 ind./h in spring to 1 ind./h in autumn (Fig. 1).

Comparing the data from 2015 and 2017, we detected a very subtle increase of abundance in 2017 for all three species, but in neither case it was statistically significant. Considering the global data (without distinguishing between both habitat types or seasons), *A. erythrurus* went from a mean value of 6.2 ind./h to 6.4 ind./h (Kruskal-Wallis Test, $X^2 = 0.444$, $df = 1$, $p = 0.505$); *P. algirus* went from 1.6 ind./h to 1.9 ind./h (Kruskal-Wallis Test, $X^2 = 1.018$, $df = 1$, $p = 0.313$) and *P. edwardsianus* went from 3 ind./h to 3.9 ind./h (Kruskal-Wallis Test, $X^2 = 2.886$, $df = 1$, $p = 0.089$).

The demographic analysis of *A. erythrurus* showed that at the beginning of the year, slightly over the half of the population is composed by immature individuals (Fig. 2). This proportion is reduced to <10% at the beginning of the hatching period in July. In the “Dunes” habitat, we observed the first gravid female on the 4th of May and the last on the 8th of July; while in the “Forest” habitat, the first gravid female appeared on the 12th of May and the last was observed on the 6th of August. The mean number of palpated eggs per female was 3.25 ± 0.62 ($n = 12$) in the “Forest” habitat and 3.33 ± 0.84 ($n = 18$) in the “Dunes” habitat (Kruskal-Wallis Test, $X^2 = 0.104$, $df = 1$, $p = 0.748$). The first hatchling of *A. erythrurus* appeared on the 13th of July in the “Dunes” habitat and on the 14th of July in the “Forest” habitat, being the maximum of hatchlings in August. This maximum was especially important

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in the “Forest” habitat. At the end of the year, the proportion of immature individuals in the population was >90% (Fig. 2). The sex ratio was practically identical between both habitat types, with 64.7%/35.3% (M/F) in the “Forest” habitat and 65.6%/34.4% (M/F) in the “Dunes” habitat.

The demographic analysis of *P. algirus* showed a high proportion of adults in the population during the first half of the year, which is reduced at the beginning of the hatching period in July (Fig. 3). The first gravid female appeared in the “Forest” habitat on the 22nd of April and the last on the 23rd of July; while in the “Dunes” habitat we observed the first one on the 2nd of May and the last one on the 10th of July. The mean number of palpated eggs per female in the “Forest” habitat was 3.73 ± 1.68 ($n = 11$) and in the “Dunes” habitat 3.86 ± 0.69 ($n = 7$) (Kruskal-Wallis Test, $X^2 = 0.020$, $df = 1$, $p = 0.886$). We observed the first hatchling of *P. algirus* on the 14th of July in the “Forest” habitat and on the 12th of August in the “Dunes” habitat. Regarding the phenology of the appearance of hatchlings, we observed a difference between both habitat types, as in the “Dunes” habitat hatching seems to occur later (August) than in the “Forest” habitat (July). In both cases the proportion of immature individuals increased to the end of the year to values >80% (even 100% in the “Dunes” habitat) (Fig. 3). The sex ratio is very similar between both habitat types, with 54.5%/45.5% (M/F) in the “Forest” habitat and 57.1%/42.9% (M/F) in the “Dunes” habitat.

Finally, the demographic analysis of *P. edwardsianus* showed that in both habitats at the beginning of the year the entire population is adult (Fig. 4). In the “Forest” habitat, the first gravid female appeared on the 7th of April and the last on the 17th of July; while in the “Dunes” habitat, we observed the first one on the 5th of April and the last one on the 9th of June. The mean number of palpated eggs per female was 2.25 ± 0.89 ($n = 8$) in the “Forest” habitat and 2.75 ± 1.50 ($n = 4$) in the “Dunes” habitat (Kruskal-Wallis Test, $X^2 = 0.302$, $df = 1$, $p = 0.583$). The first hatchling of *P. edwardsianus* appeared on the 22nd of June in the “Dunes” habitat and on the 13th of August in the “Forest” habitat. Although, due to the very low detectability of *P. edwardsianus* hatchlings we only observed these two individuals the entire sampling period, so that we can not infer on the hatching phenology of this species. The posterior increase of immature individuals in the population reaches maximum values in August with about 80%. Until the end of the year, the proportion of adult individuals increases to 50% in the “Forest” habitat and even 70% in the “Dunes” habitat (Fig. 4). The sex ratio showed differences between both habitat types, being in the “Forest” habitat 67.4%/32.6% (M/F) and in the “Dunes” habitat 80.3%/19.7% (M/F).

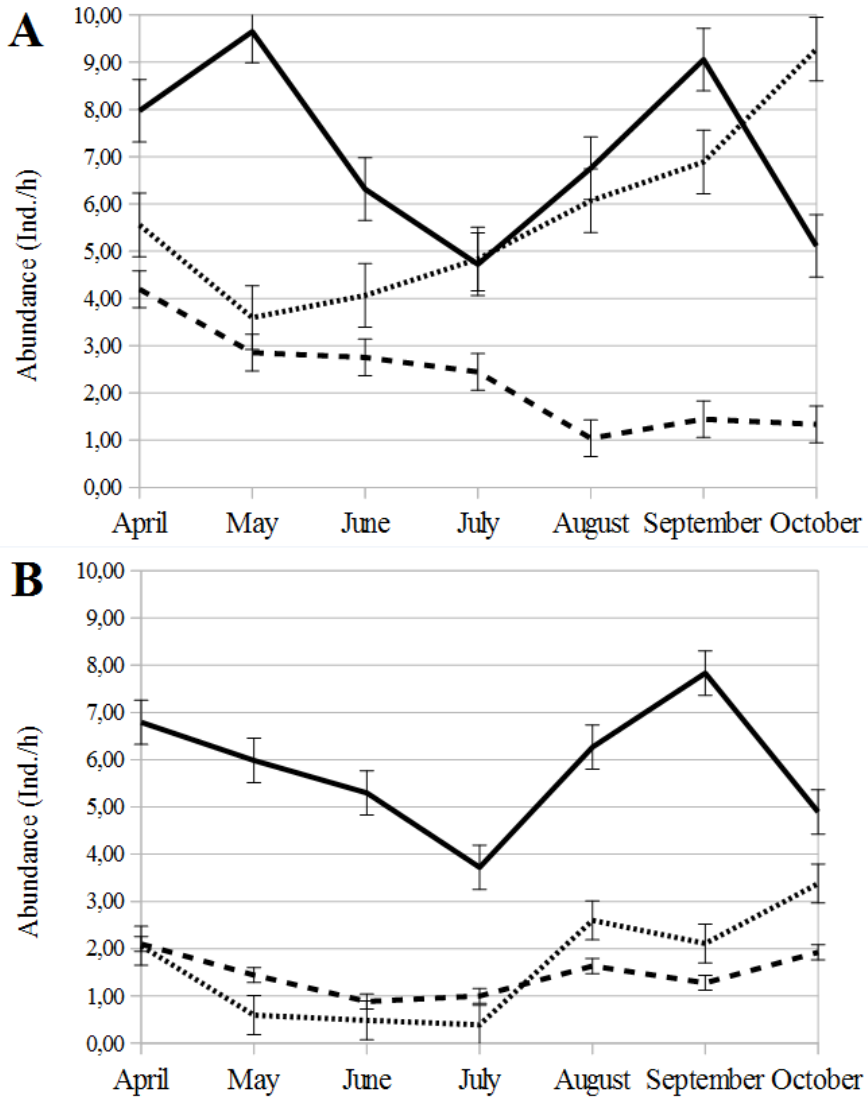


Figure 1: Representation of the abundance variation of *A. erythrurus* (continuous line), *P. algirus* (large dashed line) and *P. edwardsianus* (small dashed line) in the “Forest” habitat (A) and the “Dunes” habitat (B) during the sampling period. We represent the mean value and the standard error in each case.

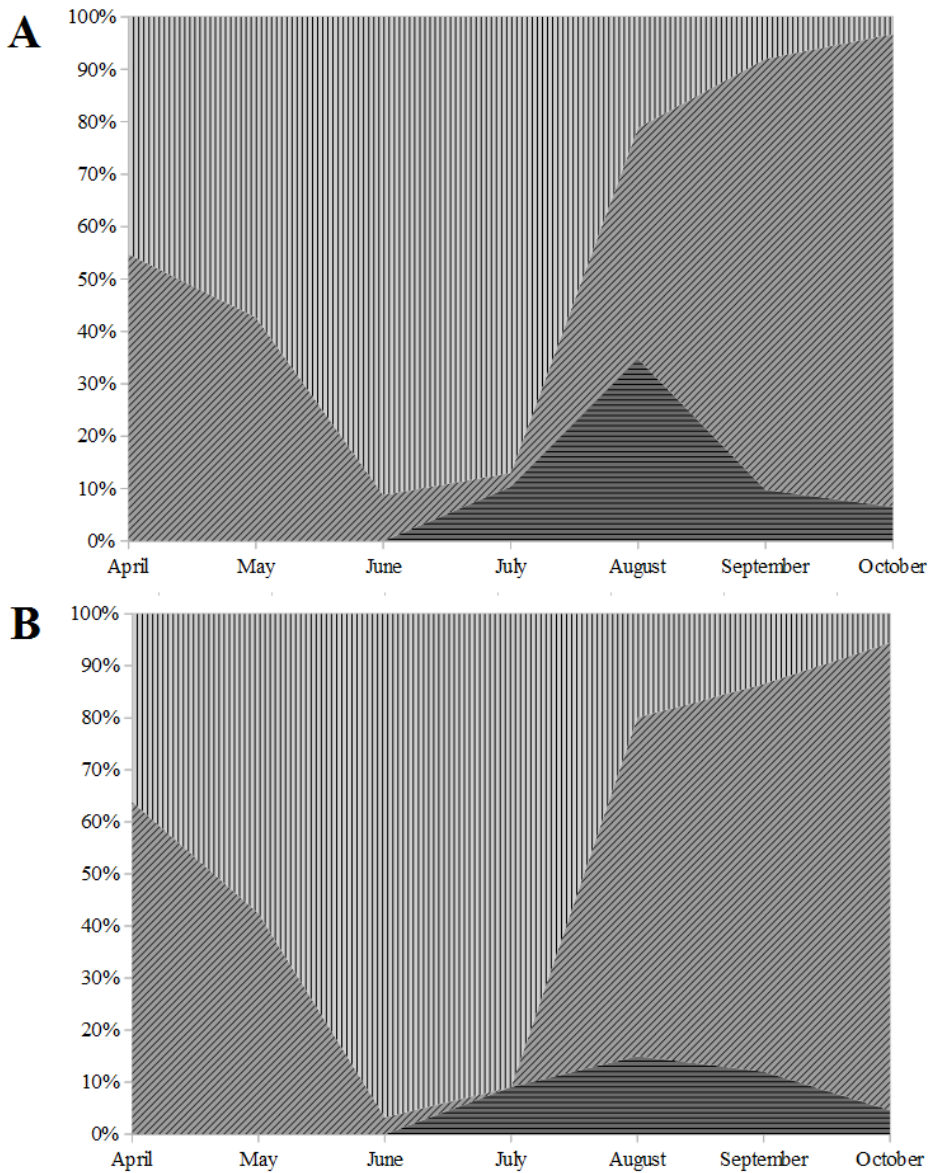


Figure 2: Representation of the variation of the proportions of adults (■), juveniles (▨) and hatchlings (■) of *A. erythrus* during the sampling period in the "Forest" habitat (A) and the "Dunes" habitat (B).

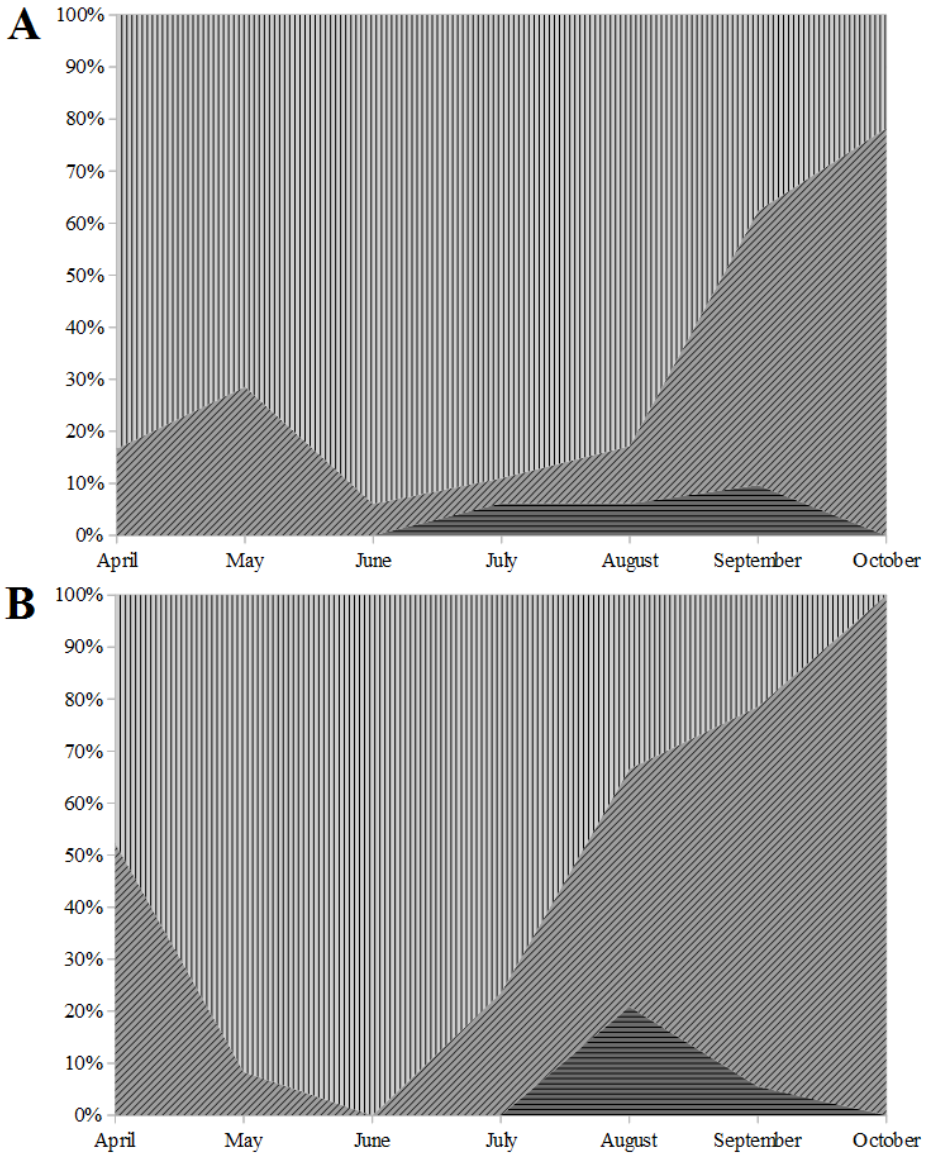


Figure 3: Representation of the variation of the proportions of adults (□), juveniles (▨) and hatchlings (▩) of *P. algirus* during the sampling period in the “Forest” habitat (A) and the “Dunes” habitat (B).

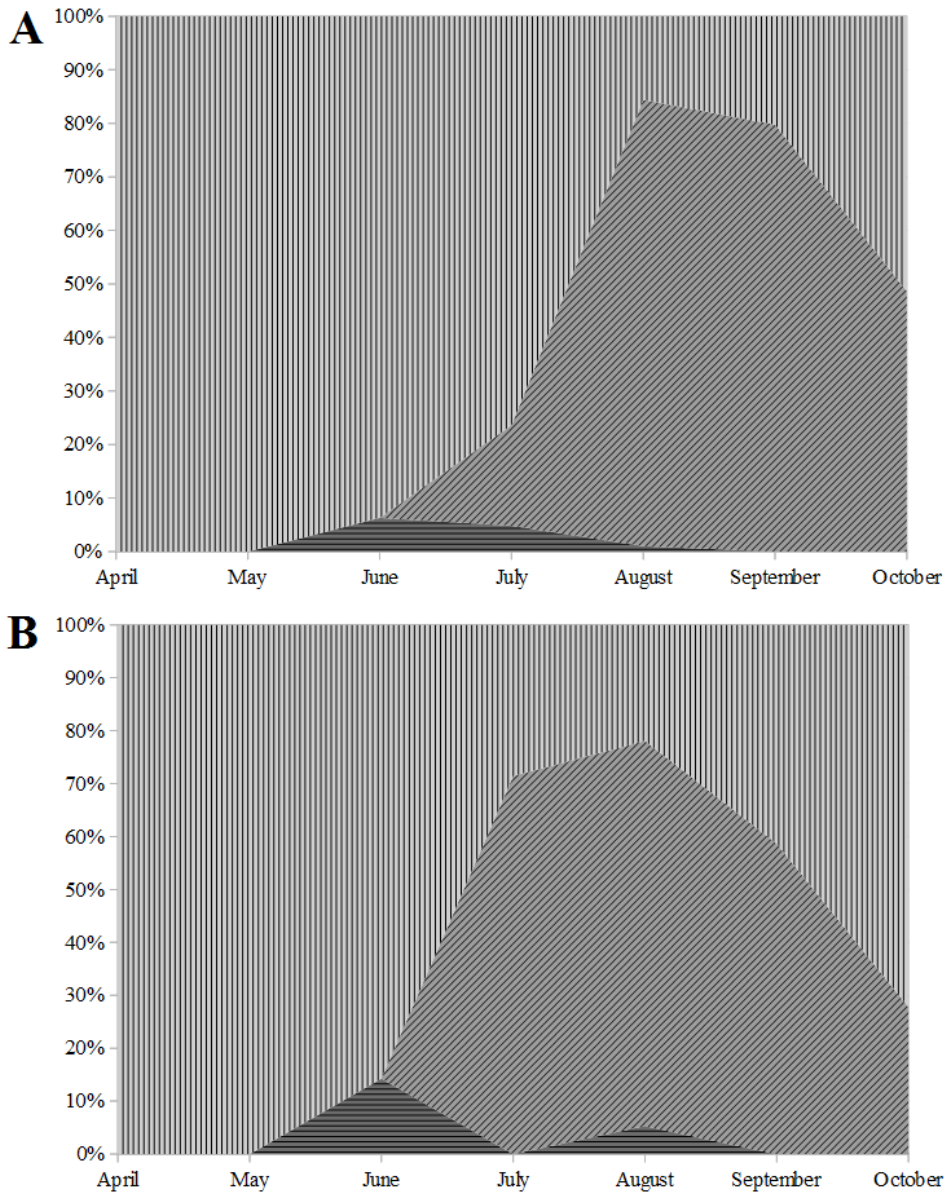


Figure 4: Representation of the variation of the proportions of adults (▨), juveniles (▧) and hatchlings (▩) of *P. edwardsianus* during the sampling period in the "Forest" habitat (A) and the "Dunes" habitat (B).

Discussion

Our results show several independent hints favouring our hypothesis. In the “Forest” habitat, where we expected a higher competitive pressure due to maximum abundance values, each species showed a different phenologic pattern. We found that *A. erythrurus* presented two abundance peeks, the first one can be explained by an increased activity during mating season (Busack & Klosterman, 1987), and the second one by the appearance of hatchlings (Pérez-Quintero, 1996). In the case of *P. edwardsianus*, we observed a clear tendency to increase abundance throughout the year. To explain this fact we have to take into account that the life cycle of this species is annual (Carretero & Llorente, 1991). This annuality also leads to high interannual fluctuations of the abundance of this species (Fitze, 2012), as the effect of environmental conditions on the population levels is much more direct than in other species. The fluctuations in abundance of *P. edwardsianus* were also associated to the ecological succession, as this species tends to occupy preferably the initial states (Fitze, 2012). Thus, reduced densities in mature environments could be, at least partly, related to interspecific competition. As new species colonize the habitat, *P. edwardsianus* keeps “loosing terrain”, being less competitive, maybe because of their small body size, especially juveniles. The unique reproduction of most individuals also implies a higher susceptibility to adverse periods and even spontaneous local extinctions (e.g. Jonsson & Ebenman, 2001; Jeppsson & Forslund, 2012). In the case of *P. algirus*, in neither of the two habitats we detected an abundance peek related to hatchling appearance. This could also be interpreted as a response to high competition levels between individuals of small body sizes, given the massive input of juveniles in summer, especially from *A. erythrurus*.

Another detail supporting the theory of competition between small size classes is that in the case of *P. edwardsianus*, the proportion of adults increases at the end of the year, indicating that some individuals reach sexual maturity the same year they hatched. If this is confirmed, it would be very interesting, as previous studies indicate that individuals reach sexual maturity in spring (Carretero & Llorente, 1991). An increased growth rate could be associated with competitive pressure. Moreover, the relatively small body size of *P. edwardsianus* also implies that adult individuals compete with juveniles of the other two species. In these conditions, an accelerated growth rate could be a great advantage. In addition, our results show that *P. edwardsianus* has an advanced phenology in comparison to the other two species. Juveniles hatch between one to two months earlier and also the appearance of gravid females indicates that the reproduction of this species is previous to the other species. In fact, in our case the hatching period is even earlier than the periods described for other *P. edwardsianus* populations, beginning in June (Fitze, 2012). This could be an important advantage for *P. edwardsianus* hatchlings regarding resource use, microhabitat occupation and territory knowledge.

Also in the case of *A. erythrurus* we evidenced a considerably higher growth rate than in previously described populations (Drechsler & Monrós, 2018). In our case, the variations of age class proportions indicates a mainly annual cycle of the population, very different results from previous studies, where the authors stated that individuals reach sexual maturity at 1.5 years of age (Busack & Jaksic, 1982; Belliure, 2015). Additionally, we

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detected an extreme peak of hatchlings in August in the “Forest” habitat. We could exclude that it is an artefact related to the representation of proportions (that in reality it is a low proportion of another age class), given that the mean values of abundance for the other age classes are practically identical in both habitats. Considering our hypothesis, this massive input of juveniles to the population can be advantageous for *A. erythrurus*.

The sex ratio also hints in favour to our hypothesis, as in all three species it is biased towards males. Higher levels of testosterone in males lead to higher aggression and, thus, a higher probability of success in interspecific encounters. Following our hypothesis, the smallest species (*P. edwardsianus*) would be the most affected, and that is exactly what we observed, although a higher proportion of males had been described previously in other populations, it did not reach such extreme values (Carretero, 1992). In the case of *A. erythrurus*, the sex ratio seems to be 2:1 biased towards males, which is also a higher proportion of males than previously described for this species (Busack & Jaksic, 1982). However, the sex ratio of *P. algirus* is very similar to those described in other populations (Salvador & Veiga, 2001).

We could not detect an possible effect of competition on the other aspects of population dynamics. In the case of *A. erythrurus*, hatching occurs between July and October, a period traditionally described for this species (Pérez-Quintero, 1996). The period we observed gravid females indicates that egg laying takes place from mid May to mid August, which also accords to previous results (Castilla et al., 1992, Carretero & Llorente et al., 1995). The fact that we only observed one hatchling peak indicates that in our population the majority of females only lays eggs once per year, although in other populations the capacity of various clutches per year was described (Castilla et al., 1992). The mean number of eggs per female (3.25 ± 0.62 for “Forest” and 3.33 ± 0.84 for “Dunes”) is a bit lower than in other populations (Belluire, 2015).

In the case of *P. algirus*, the variation of age class proportions showed differences between habitats. In the “Forest” habitat the obtained pattern seems to be similar to other populations, with a high proportion of adults until August, which is then reduced due to the input of juveniles to values of about 25% at the end of the year. In fact, this is exactly the percentage a previous study described for individuals surviving from spring to autumn (Civantos & Forsman, 2000). The period we observed gravid females is the same as described in other populations (Salvador & Veiga, 2001). However, the values of eggs per female (3.73 ± 1.68 for “Forest” and 3.86 ± 0.69 for “Dunes”) are among the lowest registered for this species, but very similar those described in the Ebro Delta, a habitat very similar to our study area (Salvador, 2011). Finally, in the case of *P. edwardsianus*, the variation of age class proportions throughout the year clearly reflects the annual character of this species, and the mean number of eggs per female (2.25 ± 0.89 for “Forest” and 2.75 ± 1.50 for “Dunes”) is similar to values described in other populations (Fitze, 2012).

Regarding the variation of abundance, the analysis showed differences between species and between habitats. In the “Dunes” habitat, *A. erythrurus* is clearly the dominant species, with values that generally triplicate the values

of the other two species. This is expectable, as previous studies described that *A. erythrurus* prefers more open areas and that it is more thermophile than the other two species (Belliure et al., 1996). These, in contrast, prefer denser habitats (Camacho, 1980; Bons, 1989; Martín & López, 2002). However it is curious that *A. erythrurus* also dominates in the “Forest” habitat, even with higher abundance values than in “Dunes”. This in some way contradicts the previously described preference. Although the comparison of our abundance results with other studies is difficult as they are usually expressed in individuals per hectare, and not individuals per hour. In addition, they refer to other habitat types, different from our study area. In fact, in the case of *P. algirus* we did not find any values for coastal or dune habitats, only for oak forests (Salvador, 2011). But given the high heterogeneity on a small scale in our study area, the estimation of abundance in relation to time is more reliable than in relation to surface, and this method is also more suitable for long term monitoring.

In conclusion, the detailed analysis of population dynamics of the three lizard species in the study area showed several hints favouring our hypothesis. However, there could also be other factors we did not consider playing a role. We have to take into account that the study area presents a high anthropic pressure, especially the “Forest” habitat, being a very frequented area by bicycles, cars and even buses, which imply an additional mortality. Although comparing 2015 and 2017 there was a subtle increase in abundance of all species, in neither case it was significant. Previous studies also showed that human alteration of a dune habitat can affect each lizard species differently (e.g. Vega et al., 2000). Thus we suggest to carry out similar studies in other areas where the three lizard species cohabit in order to discern if the described effects are really caused by competition or if they are more a local effect related to human activity.

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Capítulo III

Body growth and its implications in population dynamics of *Acanthodactylus erythrurus* (Schinz, 1834) in the Eastern Iberian peninsula

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Amphibia-Reptilia (2018), aop: 1-8.

Body growth and its implications in population dynamics of *Acanthodactylus erythrurus* (Schinz, 1834) in the Eastern Iberian peninsula

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Abstract

We calculated growth rate for the spiny-footed lizard (*Acanthodactylus erythrurus*) inhabiting coastal eastern Spain from long-term mark-recapture data. Growth curves differ between sexes, with males growing faster than females and achieving larger size maximums. In this population each sex reaches maturity at about 300 days of age, approximately 34% faster than males, and 28% faster than females studied in a population further south and west in Iberia. Our logarithmic growth model has an accuracy of 96.8% and high statistical significance ($r = 0.96$ for males and $r = 0.97$ for females). Although both the exponential curve of “best fit” for growth estimated for males ($r = 0.81$), and the linear curve of “best fit” estimated for females ($r = 0.77$) in a population from Cádiz (Busack & Jaksic, 1982) are also significant. The overlap between growth curves and the general data cloud of the population showed that at the end of the year the proportion of individuals younger than one year was 80% and the proportion of individuals older than one year was 20%. Our data, in agreement with calculated maximum life spans for males (1.9 years) and females (2.1 years) in Cádiz, suggest a life span of approximately two years for both sexes. Females seem to reproduce only in a unique season in their lives, at this locality, as in Cádiz (Busack & Klosterman, 1987) they likely lay only one clutch, whereas females in Morocco (Bons, 1962) may produce two.

Keywords: *Acanthodactylus erythrurus*, growth rates, population dynamics, Spain

Introduction

A species' growth pattern is closely related to its life history (Case, 1978) and influences both functional age of reproductive maturity and species longevity (Tinkle, 1969). Because of this it is an important factor to be considered in ecology and population dynamics.

Body size and age in reptiles are positively correlated (Halliday & Verrel, 1986) and there is still important

information lacking regard to growth patterns and lifespan, age of sexual maturity, differing growth models or variability within different populations of the same species. There are only two reliable methods for estimating age of an individual available today: skeletochronology and mark-recapture (Halliday & Verrel, 1986), but with the advance of molecular techniques, age may eventually be estimated accurately by studying telomeres (Hatase et al., 2008). Skeletochronology is effective for long-lived species (e.g. turtles; Avens & Snover, 2013), but is error prone for species with short life cycles (e.g. Eden et al., 2007). The mark-recapture method is most reliable for these species (e.g. Znari & Brown, 1999), but to use it reliably, long-term population monitoring is required.

The dominant species in the study area is the spiny-footed lizard *Acanthodactylus erythurus* (Schinz, 1834), a relatively large, insectivorous species with Mediterranean distribution. It has a remarkable preference for open and arid habitats, what makes that in the Iberian peninsula it is especially abundant in coastal dune environments (Pérez-Mellado, 1982). *A. erythurus* is one of the cases where there are still unknowns regarding the relation between growth and population dynamics, what can also be perceived in the information compilation of the species done by Belliure (2015).

Therefore, we proposed this study with the objective of describing in detail the growth pattern of *A. erythurus* from a coastal population in the East of the Iberian peninsula. Moreover, assessing the implications it has on ecological parameters like population dynamics. All in the context of improving the knowledge regarding these characteristics in order to favour future conservation plans for this species.

Materials and methods

Study area

The study area is situated in the East of the Iberian peninsula, at about 10 km south Valencia city and it is part of the Albufera de Valencia Natural Park (39°20'29"N 0°18'43"W). It is formed by a coastal line of about 10 km length (N-S) and 1 km wide (E-W).

The sampling site presents a typical Mediterranean vegetation. Adjacent to the shore, mobile dunes with a variable degree of maturity and a vegetation formed mainly by different grass and bush species (generally less than 1 m tall) like *Ammophila arenaria*, *Helichrysum stoechas*, *Euphorbia paralias*, *Medicago marina* or *Rhamnus alaternus*, among others. Then, further away from the coast line, also an area of fixed dunes with a forest vegetation mainly formed by Aleppo pine (*Pinus halepensis*) and a dense undergrowth of species like *Smilax aspera*, *Asparagus officinalis*, *Chamaerops humilis* or *Pistacia lentiscus*.

Methods

Samplings were carried out between April and October (both included) of 2015 and 2017. In the first year we did two samplings every two weeks, while in 2017 we intensified the sampling effort to four times a week. That means a total of 131 sampling days.

Each sampling consisted in a random track census with two hours of duration, where we recorded all seen individuals of *A. erythrurus*, distinguishing age class and sex, when possible. We began sampling two to three hours after sunrise. In parallel to the countings, we captured every individual possible by hand or looping (Fitzgerald, 2012), stopping the census timer during the duration of each capture try.

We put all captured individuals in individualized cloth bags for the posterior measurement. Once we finished the sampling we processed the captured individuals, recording sex, age class and other observations. Then we measured the basic biometry (snout-vent length [SVL], total length [TL] and weight) (similar to other studies like Sacchi et al., 2007). Finally, we marked each individual with an unique code of amputated phalanges, a method commonly used for marking lizards (e.g. Perry et al., 2011). Once finished the measuring we released each individual near the point of capture.

Data analysis

For the abundance estimation we standardized the countings by the duration time of each census, obtaining abundance values in individuals/hour. Then, we grouped the data by months, calculating the mean and standard error in each case.

For the growth curve estimation we used biometric data of recaptures (45 individuals with 116 datasets). We calculated the growth rate for each recapture by dividing the increment in SVL by the number of elapsed days (eg. Haenel & John-Alder, 2002). Then, we grouped the obtained values by intervals of 10 mm SVL (of the individual), calculating the mean value of growth rate for each interval. Afterwards, we drew a tendency line, which equation allowed us to assign a growth rate value (in mm/day) to every value of SVL. The inverse value of the growth rate (in days/mm) allowed us to estimate the theoretical time an individual needs to grow from 30 mm SVL to 31 mm, from 31 mm to 32 mm and so on. The representation of this increment in size in relation to time is the growth curve. We applied this procedure separately for each sex. In order to evaluate the precision of our model we carried out an intensive sampling in April 2018, obtaining a total of 20 recaptures of different sizes and sexes.

For the study of age composition of the population in a certain moment of the year, we estimated the highest value of SVL individuals hatched in summer are able to reach (according to our model). In order to obtain this value, we

drew the growth curve on the largest individual of each sex at the end of October that according to our model hatched in the previous summer. We set the initial point of the growth curves on the first day we observed hatchlings in the field (13th of July). According to this model, individuals situated over the maximum line in spring and summer of the following year are too big to have hatched the previous year and, thus, can be considered second year individuals.

Results

The analysis of the censuses showed that juveniles of *A. erythrurus* hatch from July to October. The maximum in hatchings occurs in August (Fig. 1). The calculation of the growth rate shows that the relation between the size of an individual (*SVL*, in mm) and its theoretical growth rate (*GR*, in mm/day) is expressed by the following formula for each sex:

Males ($R^2 = 0.995$):

$$GR = 5.28 \cdot 10^{-5} \cdot SVL^2 - 0.01 \cdot SVL + 0.46$$

Females ($R^2 = 0.998$):

$$GR = 4.86 \cdot 10^{-5} \cdot SVL^2 - 0.01 \cdot SVL + 0.48$$

The application of these formula for each value of *SVL* in intervals of 1 mm allowed the estimation of the number of days an individual needs to reach a certain size (Table 1). The representation of these values allowed us to draw the growth curves, which adjust to the following logarithmic formula, where *SVL* is the size of an individual (in mm) and *t* is time (in days):

Males ($R^2 = 0.923$):

$$SVL = 9.65 \cdot \ln(t) + 3.34$$

Females ($R^2 = 0.937$):

$$SVL = 7.50 \cdot \ln(t) + 10.61$$

The testing of the model showed a precision of 93.9% comparing the predicted and the real, observed, values. Nevertheless, it also showed quite high error values (~16%) in individuals which passed the hibernation during the initial phase of their growth, that means individuals which hatched late (from the middle of September) the previous year. Supposing that the growth during hibernation is null or negligible, we subtracted effective growth days in each of these individuals until the error of the model respect the real value was minimal. This showed a mean duration of the hibernation of 117 ± 23 days. Considering this and correcting the effective days of growth in the mentioned individuals, the error of the prediction went down to 3.2% in these cases and the precision of the general model went up to 96.8%.

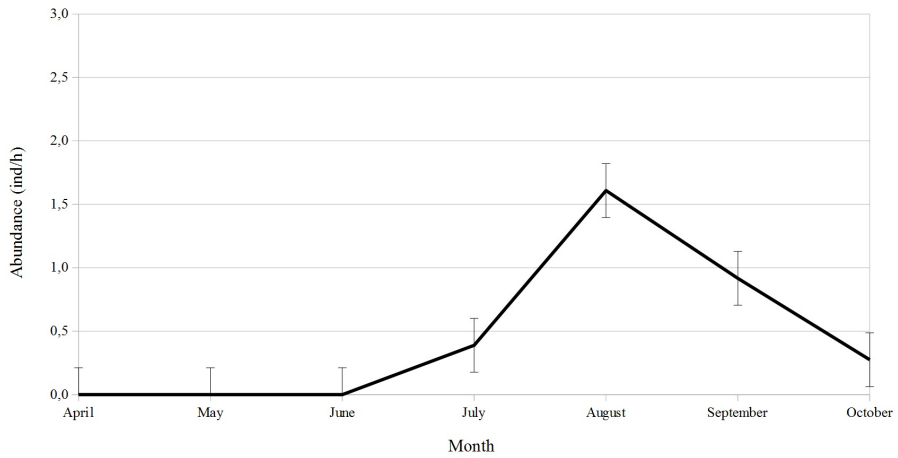


Figure 1: Representation of the mean and standard error of the variation in hatchling abundance (in individuals/hour) during the year.

Table 1: Estimated age in days according to our growth model in intervals of 1 mm SVL, considering an initial SVL of 30 mm.

SVL (mm)	Estimated age (days)		SVL (mm)	Estimated age (days)	
	Males	Females		Males	Females
31	5	5	54	188	240
32	10	10	55	201	264
33	15	16	56	215	292
34	20	21	57	230	324
35	26	27	58	246	363
36	32	33	59	263	412
37	38	40	60	281	476
38	44	47	61	300	571
39	50	54	62	321	742
40	57	61	63	344	1639
41	64	69	64	368	-
42	71	77	65	395	-
43	78	86	66	423	-
44	86	95	67	455	-
45	94	105	68	490	-
46	103	116	69	528	-
47	112	127	70	572	-
48	121	139	71	620	-
49	131	153	72	676	-
50	141	167	73	740	-
51	152	183	74	815	-
52	163	200	75	905	-
53	175	219	76	1015	-

The overlap of the growth curves with the data cloud of all captures (Fig. 2) allowed us to estimate the age class composition of the population during the year (Fig. 3). We can remark from this representation the disappearance of second year individuals in September, what can be a hint to the lifespan. Moreover, the proportion of individuals younger than one year at the end of the activity period is over 80%. Therefore, the proportion of second year individuals at the beginning of the year is about 20%.

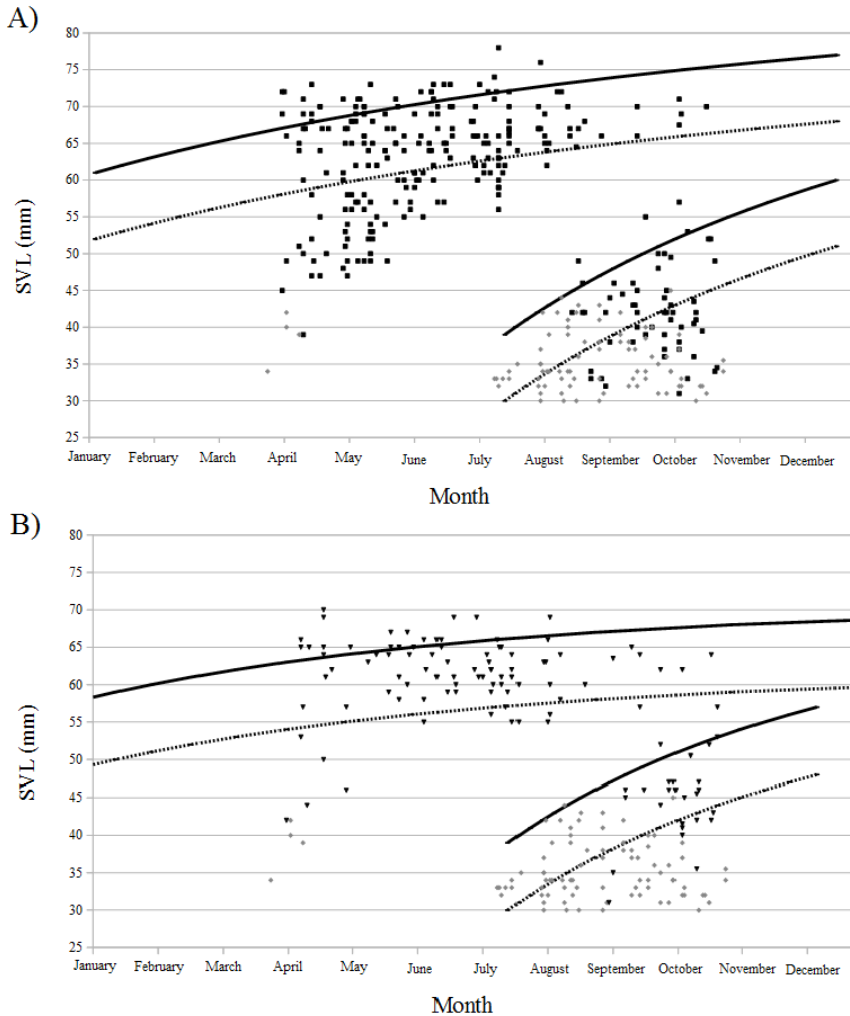


Figure 2: Overlap between the growth curves and the general data cloud obtained during the samplings. We represent the mean curve (dotted line) and the maximum curve (continuous line) for each sex: males (A) and females (B). In the data cloud we distinguish males (black squares), females (black triangles) and individuals with unknown sex (grey diamonds).

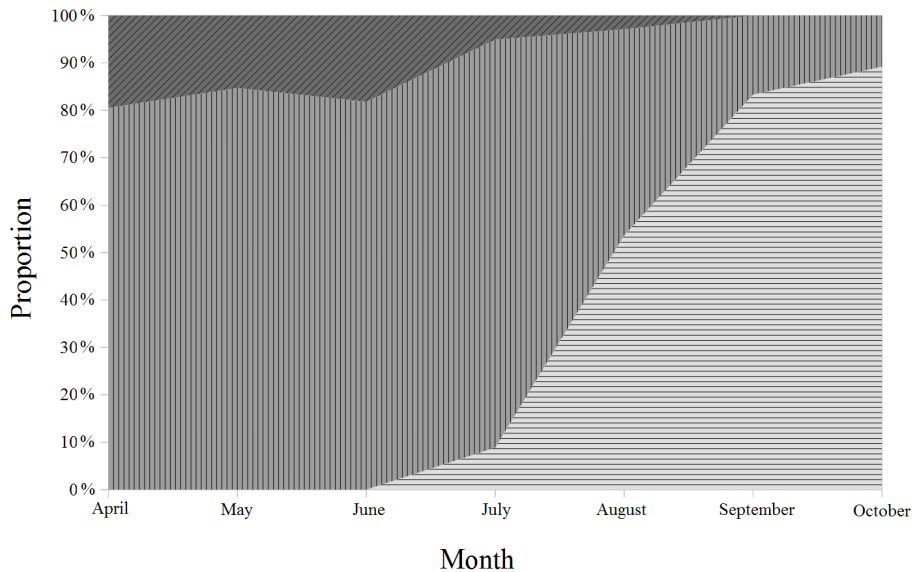


Figure 3: Representation of the variation of age class proportions in the population during the year, according to our growth model. We distinguish the proportion of present year individuals (clear area with horizontal lines); first year individuals (intermediate dark area with vertical lines) and second year individuals (dark area with diagonal lines).

Discussion

The beginning (13th of July) and maximum (August) of the appearance of hatchlings coincide with the observed in other populations (Pollo & Pérez-Mellado, 1990). Therefore, the temporal calibration of our growth curve model is valid and applicable or comparable to other populations. In previous studies it was described that juveniles hatch with a size between 28 and 31 mm (Pérez-Quintero, 1996; Belliure, 2015). Thus, also the consideration to use the minimum observed SVL in the field (30 mm) as the initial point of the model is valid.

There is only one previous study where growth rates of *A. erythrurus* were estimated (Busack & Jaksic, 1982). This study was carried out in a region in South Spain, about 273km South and 534km West of our study site. Climate data from both sites are quite similar, ours being a bit drier, hence we do not expect great differences in the general performance of the species. Our recorded growth rates are considerably higher than the ones described in Busack & Jaksic (1982). The authors estimated growth rates of 0.06 mm/day for males and 0.05 mm/day for females. However, this calculation has a high error margin as they calculated the growth rate for a large size interval (from hatching to sexual maturity) using preserved individuals. Our study allows a much finer evaluation

of growth. In addition, in the cited study the authors hypothesize an exponential growth curve for males and a lineal one for females. Although both curves were significant ($r = 0.81$ for males and $r = 0.77$ for females) (Busack & Jaksic, 1982), our results show that the growth rate varies while the individual is growing. Smaller individuals have considerably higher growth rates (around 0.2 mm/day) than larger ones. This results in a logarithmic type of growth curve, with a high slope at the beginning, which gets flatter as time passes. This is also reflected by the higher statistical significance of our model ($r = 0.96$ for males and $r = 0.97$ for females).

This type of growth curve is very common. Back in 1938 the so called Bertalanfy Equation was described (Von Bertalanfy, 1938), or its more generalized version from Richards (1959), and it has already been applied to reptiles (Shine & Charnov, 1992). However, as Busack & Jaksic (1982), we found a sexual dimorphism, presenting males higher growth rates than females. This is also consistent with the fact that adult males tend to be larger than females (Castilla, Barbadillo & Bauwens, 1992; Barbadillo & Bauwens, 1997).

Previously it was described that *A. erythrurus* reaches sexual maturity at an age of about 1.5 years (Busack & Jaksic, 1982; Seva, 1982). Considering that males reach sexual maturity at 60 mm SVL (Seva, 1982), and females at 55 mm SVL (minimum size we observed a gravid female), according to our model, in our population both sexes reach sexual maturity after about 300 days. That means a considerably shorter time than previously described, approximately 34% faster than males, and 28% faster than females studied in Cádiz (Busack & Jaksic, 1982). In fact, the very first hatchlings could be able to reproduce the following year. Nevertheless, endocrinological studies of the population should be carried out in order to evaluate the exact moment when each sex reaches sexual maturity, moreover considering the quite large variability in sizes of reproductive maturity described in different populations of this species (Belluire, 2015).

The results we recorded regarding population dynamics are very interesting. The maximum value that according to our model an individual hatched in summer is able to reach at the end of the year suggests that more than 80% of the population is renewed every year. That means only 20% of the individuals reach the second winter. This, in combination with the described in the previous paragraph, could mean that there is an important selective pressure on the moment of hatching. In Busack & Jaksic (1982), although the authors estimated higher annual survival rates (around 55%), the estimated lifespan is approximately two years. Our model is coherent with this, given that second year individuals disappear exactly two years after the maximum of hatchings in the present year. Although, we have to remark that from that point the growth rate is so low that our model is not able to distinguish one year individuals and older.

This has also repercussions on the reproductive strategy *A. erythrurus* follows. The almost entire annual renovation of the population indicates that this species follows a strategy based on a single reproduction. That means, the majority of females only reproduces in a unique season in their lives, being able to lay up to two clutches. Although the number of clutches is variable between different populations (Bons, 1962; Busack &

Klosterman, 1987; Castilla, Barbadillo & Bauwens, 1992; Carretero & Llorente, 1995). Some females reach the second year. These females would act as a “reproductive reserve” if one year results to be very unfavourable. If this theory shows to be correct, it would mean that *A. erythrurus* is a much more fragile species than previously thought, as a single reproduction leads to a higher susceptibility to unfavourable conditions and, in consequence, increases the risk of extinction (e.g. Jonsson & Ebenman, 2001; Jeppson & Forslund, 2012). In fact, we found one case of a female which in 2017 was gravid and in 2018 was recaptured with the typical red coloured tail indicating heat, evidencing that she participates in a second reproductive event. This hypothesis is coherent with the recorded data, as the proportion of females in second year individuals (58%) is considerably higher than the general mean adult sex ratio of the population (35%) (unpublished data). This may also indicate that lifespan for females is longer than for males.

In conclusion, this is the first work which describes in detail the growth of *A. erythrurus* and, in addition, analyses the repercussion it has on population dynamics and reproductive ecology of the species. In fact, we obtained interesting results, which show that some data previously described should be revised or profiled. Our results and analyses will be of great importance when elaborating future managing and conservation protocols for this species.

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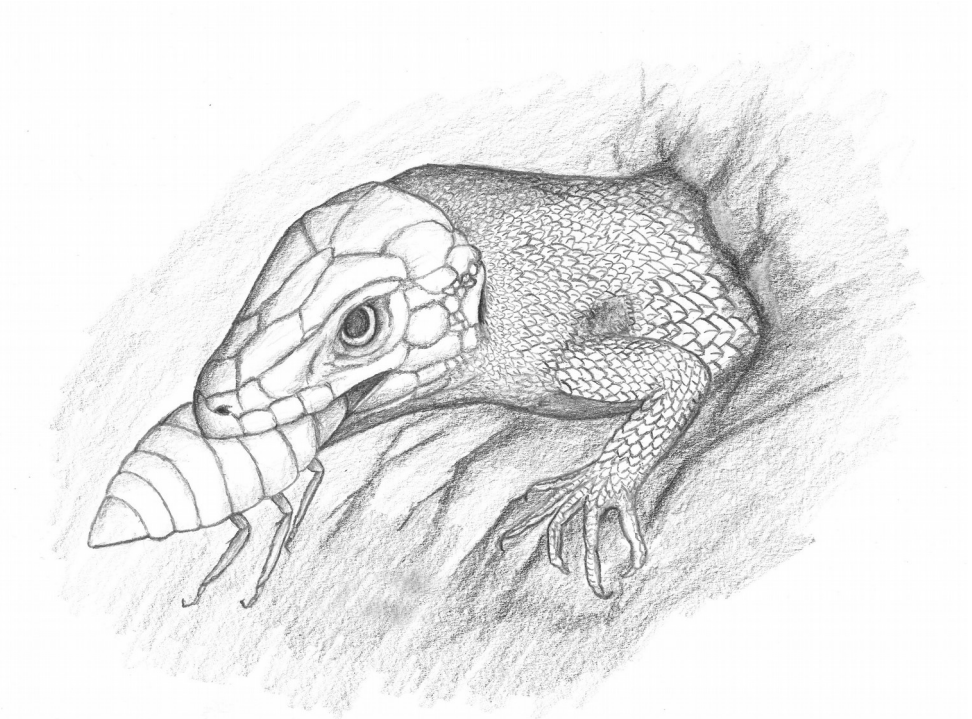
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Capítulo IV

Diet composition and trophic ecology of three sympatric insectivorous lizard species in a highly anthropized area in the eastern Iberian peninsula

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Basic and Applied Herpetology (En revisión).

Diet composition and trophic ecology of three sympatric insectivorous lizard species in a highly anthropized area in the eastern Iberian peninsula

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Abstract

Trophic ecology is one of the most important aspects of a species' ecology and it is crucial when trying to assess how different species interact in an ecosystem. Showing how the diet intraspecifically changes in different body sizes, sexes or habitats and how trophic resources are shared interspecifically allows to understand how the ecosystem functions. With this objective, we studied the diet and trophic ecology of *Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus edwardsianus*, which are in syntropy in the Albufera de Valencia Natural Park. We collected a total of 485 faecal samples and could identify 18 different prey groups. The main prey groups in *A. erythrurus* were Hymenoptera, Coleoptera and Hemiptera; in *P. algirus*, Lepidoptera, Arachnida, Coleoptera, Diptera, Hemiptera and Orthoptera; and in *P. edwardsianus*, Coleoptera, Hemiptera and Arachnida. Our results show that *A. erythrurus* seems to be the most specialized species, having the lowest values of trophic niche amplitude and the lowest intraspecific diet variation. Although this species is known to feed mainly on ants, our results indicate that mirmecophagy seems to be especially important in juveniles. Indeed we observed in all three species a niche separation between small and big individuals, indicating that diet changes with age. We could also evidence a resource partitioning between *A. erythrurus* and *P. algirus*, presenting a niche overlap of only 51.6%. In conclusion, there are various factors playing together shaping the diet of a species in a certain environment: behavioural, ecological, environmental and physiological factors.

Keywords: Coastal habitat, Diet, Lizard, Trophic ecology, Spain.

Introduction

The Mediterranean region of the Iberian peninsula presents a typical climate, characterized by a noticeable seasonality, with hot and dry summers, cold winters and humid springs and autumns with softer temperatures, and

an important interannual variability (e.g. Lionello et al., 2006). These peculiar environmental conditions allowed the formation of a relatively rich and singular biodiversity which deserves to be conserved. Although the conservation of biodiversity is being a more and more complicated task. Human activity lead to the extinction of many species in the past decades and its effects can be noticed in nearly every ecosystem on the planet (Jordan et al., 1990). One of the most interesting aspects to consider in this context of biodiversity loss is the study of trophic webs in communities and the function each species has in them. The alteration of a single species' function can be transmitted to the rest of the ecosystem by the trophic web, which is known as trophic cascades (Pace et al., 1999). These negative effects of species loss by trophic cascades could be evidenced for example in tropical ecosystems, where the disappearance of insectivorous lizards lead to an uncontrolled increase in the density of herbivorous arthropods and, in consequence, to a higher leaf damage of the plants they consumed (Spiller & Schoener, 1994; Dial & Roughgarden, 1995). On the other side, there are also cases where the feeding of a species plays a major role in its conservation. In reptiles, we can cite the case of different elapid species in Australia, where the type of foraging is correlated with its vulnerability to extinction (Reed & Shine, 2002).

However, trophic ecology is not limited to only describing the diet of a species, it is much more complex. For example, there could be variations in the diet from one population to another of the same species (Vitt et al., 1997); or even within the same population, given that sex, different size ranges or the phenology could lead to diet variations (Best & Pfaffenberger, 1987; Perry, 1996; Verwajen et al., 2002). Thus, we have to contemplate trophic ecology studies of species from different perspectives. Also, the presence of other species with a similar trophic niche can result in a resource partitioning and a specialization in one particular food type or even a total change in diet. It has been proved that there is an inverse relation between resource partitioning, or the separation of trophic niches, and trophic competition between species (Pacala & Roughgarden, 1982).

In the study area cohabit three species of lizards: *Acanthodactylus erythrurus* (Schinz, 1834), *Psammodromus algirus* (Linnaeus, 1758) and *Psammodromus edwardsianus* (Dugès, 1829). These species share the same microhabitats as the same trophic resource. Thus, we would expect, if the resources are limited, a high level of competition between the species. In fact, there are studies that describe a higher specific aggression between species in syntropy (Ortiz & Jenssen, 1982). This competition, which clearly would reduce the fitness of involved species, could be avoided reducing the trophic niche amplitude (specialization) and the degree of niche overlap (Pacala & Roughgarden, 1982). There are previous works on the diet of the three study species (for example Busack & Jaksic, 1982, for *A. erythrurus*; Pérez-Mellado, 1982, for *P. algirus*; or Carretero-Llorente, 1991, for *P. edwardsianus*). In some cases the authors even considered the ecological interaction between *A. erythrurus* and *P. algirus* (Seva, 1984; Rouag et al., 2007). But these studies never considered *P. edwardsianus* and, in addition, were carried out in areas with low anthropic pressure.

The objective of this study is the description of the trophic ecology of three sympatric insectivorous lizard species (*Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus edwardsianus*). Thus, on one hand, we

will describe in detail the diet of each species and we will evaluate if there are interspecific differences. On the other hand, in each species we will study if there are intraspecific differences related to sex, size, gravidity, used macrohabitat type and month. Finally, we will analyse trophic niche amplitude and overlap.

Material and Methods

Study area

The study area is situated about 10km South from Valencia city and is part of the Albufera de Valencia Natural Park (39°20'20"N 0°18'43"W). It represents a coastal line about 10km long (N-S) and 1km wide (E-W). It is a very human-frequented area, in summer there is much activity related to touristic use of the beach, but it is also an area with a great interest in the ecotouristic and cycling sectors because of its distinct and naturalized landscapes.

The area presents a typical Mediterranean vegetation. It is a dune habitat with an area of mobile dunes with a variable degree of maturation and a vegetation formed mainly by herbaceous and bush species, generally less than 1m tall, like *Ammophila arenaria*, *Helichrysum stoechas*, *Euphorbia paralias*, *Medicago marina* or *Rhamnus alaternus*, among others (this is what we call "Dune" habitat). Behind this habitat there is an area of fixed dunes with an arboreal vegetation formed mainly by Aleppo pine (*Pinus halepensis*) and a dense undergrowth with species like *Smilax aspera*, *Asparagus officinalis*, *Chamaerops humilis* or *Pistacia lentiscus* (this is what we call "Forest" habitat).

Fieldwork

Field samplings were carried out between April and October (both included) of 2015 and 2017. In 2015 we did one sampling every two weeks in each habitat type, while in 2017 we intensified the sampling effort to four times a week (two in each habitat type).

In every sampling we captured lizards by hand or looping (e.g. Guillén-Salazar et al., 2007). We put the captured individuals in individual cloth bags until the later processing. At the end of the sampling, we measured basic biometric data (snout-vent length or SVL and weight), we identified the species, age class, sex (in females we annotated if they were gravid or not) every time possible. We obtained faecal samples deposited in the cloth bags or by performing a gentle abdominal massage on each individual. We kept the faecal samples friezed at -20°C until their processing in the laboratory.

Faecal sample processing and data analysis

All obtained samples were analysed in the laboratory. We put every sample on a petri dish with some drops of

water and carefully separated with tweezers the different items. Then, using a binocular magnifier and with the help of an arthropod identification guide (Melic, 2005), we tried to identify every item found in every sample, at least to the order level. Finally, we conserved every sample in an eppendorf with 70% ethanol.

We could distinguish a total of 18 groups (prey groups), which in general correspond to arthropod orders, except some lower levels, considered separately because of their peculiar characteristics. Thus, we considered the family Formicidae a part from the rest of Hymenoptera given their small size, very high abundance in the environment and the absence of wings; and scorpions from the rest of Arachnida given their harder exoskeleton, and generally bigger body size. With the obtained data we built a presence/absence matrix of each prey group in each sample, assigning 1 to presence and 0 to absence. Afterwards, we grouped the data by species, sex, size, habitat, gravidity and month. In the case of the size, we grouped the data by intervals of SVL (of 10mm for *A. erythrurus* and *P. algirus*, and 5mm for *P. edwardsianus*). In order to simplify the graphic representation of the proportions of the different prey groups in the detailed diet analysis for each species we unified all minor prey groups (with less than 5% presence in all species) in a single group called “Others”.

For the study of diet composition, in each comparison we calculated the proportion of presence of each prey group, respect the total of samples. In order to evidence statistical significance of the observed differences, we performed a non parametric Kruskal-Wallis (1952) test for each prey group in each comparison.

For the study of the trophic ecology we used the same method as in Sasa & Monrós (2000). We calculated niche amplitude in each case as the Levins (1968) niche amplitude index, using the following formula:

$$L = \frac{1}{n \sum_{i=1}^n p_i^2}$$

Where p_i are the proportions of presence of each prey group respect the total.

Once we obtained the values of trophic niche amplitude, we proceeded to calculate the degree of niche overlap for each comparison, using the Pianka (1973) index, applying the following formula:

$$O = \frac{\sum p_1 * p_2}{\sqrt{\sum p_1^2 * \sum p_2^2}}$$

Where p_1 and p_2 are the proportion of a certain prey group in the grouping 1 and 2, respectively. For the percentages of niche overlap we followed Krebs (1989), applying the following formula:

$$\% \text{ Overlap} = 100 * \sum \text{minimum of } p_1, p_2$$

All statistical analysis were carried out using R (2016) v3.2.3.

Results

Comparison of the diet between species

During the samplings we obtained a total of 485 samples: 246 from *A. erythrurus*, 101 from *P. algirus* and 138 from *P. edwardsianus*. The analysis of diet composition of the three species showed significant differences in the consumption of the different prey groups (Table 1). In the case of *A. erythrurus* we can remark the proportions of Hymenoptera, ants, Coleoptera and Hemiptera, being the major groups present (Fig. 1). In the case of *P. algirus*, we observed maximum values in Lepidoptera and non-scorpion Arachnida, followed by a relatively equivalent composition of Coleoptera, Diptera, Hemiptera and Orthoptera. We can also remark that this species consumes the highest proportion of scorpions from the three studied lizards, finding remains in approximately 15% of the samples (Fig. 1). Finally, in the case of *P. edwardsianus*, the most consumed prey groups were Coleoptera, Hemiptera and non-scorpion Arachnida. This species was also the only one consuming cockroach oothecae (Fig. 1).

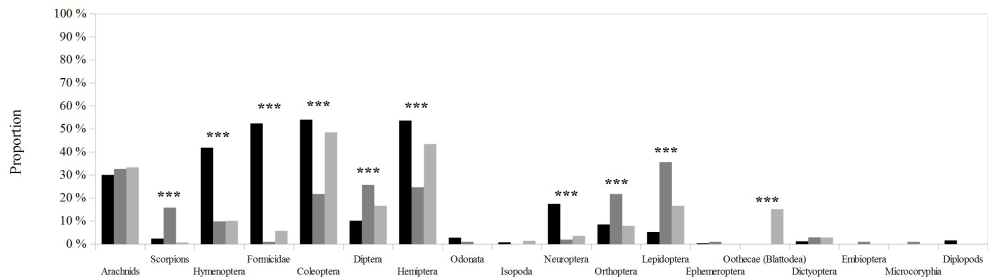


Figure 1: Representation of presence proportions in samples of the different prey groups, comparing the three lizard species (■ *A. erythrurus*; ■ *P. algirus*; ■ *P. edwardsianus*). We show significant results of the Krushkal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**) and $p < 0.001$ (***).

Diet analysis by species

The detailed diet composition analysis of *A. erythrurus* did not show significant differences in diet between sexes nor gravid and not gravid females (Table 1, Fig. 2). Although, we did find significant differences between the different SVL ranges in Hymenoptera, ants, Coleoptera and Odonata (Table 1). The most remarkable fact in this case is that there seems to be an increment in Hymenoptera consumption as the individuals grow, going from values of about 25% in small individuals to values of about 60% in big individuals. The opposite occurs in ants, where the proportions in small individuals lie by about 60%, while in big individuals it is reduced to 30%. In the case of Coleoptera we can remark the relatively low proportion in very small individuals (Fig. 2).

When comparing the diet of *A. erythrurus* in the two different habitat types, we found significant differences in the proportions of ants, Coleoptera and Diplopoda (Table 1), being ants more abundant in the Dune habitat and Coleoptera more abundant in the Forest habitat. Diplopoda was only found in the Forest habitat. Finally, the phenological analysis of diet composition showed significant differences in the consumption of scorpions, Hymenoptera, ants, Coleoptera and Hemiptera (Table 1). In this case, scorpions present maximum values in April; Hymenoptera are more consumed in spring and the beginning of summer; Coleoptera had also maximum values in spring (reaching values up to 90% in April) and Hemiptera, in contrast, are more consumed in summer (with values up to 80% in July). We did also detect individual cases of ingestion of vegetal items (small sticks, flowers, seeds), which were not included in the analysis as we think they were accidental ingestions while hunting prey sitting on the vegetation.

The detailed diet composition analysis of *P. algirus* did not show differences between sexes or by gravidity either (Table 1, Fig. 3). When comparing diet composition in the different SVL ranges we did observe some interesting differences, although most of them were not statistically significant (Table 1). The statistically significant differences correspond to the consumption of scorpions, being more consumed by large individuals, and Diptera, being more consumed by small individuals (Table 1, Fig. 3). In the comparison of diet composition between habitats we found significant differences in the consumption of Diptera, presenting higher values (about 35%) in the Dune habitat, and Hemiptera, presenting higher values in the Forest habitat (about 40%) (Table 1). Finally, the phenological analysis showed significant differences in Arachnida (being especially abundant in April, with about 65%), scorpions (being quite abundant in June, with more than 50%) and Coleoptera (being less abundant in June, August and October) (Table 1, Fig. 3). We also recorded individual ingestions of plant matter and some snail shells, what we interpret as accidental ingestions, and thus did not include it in the analysis. In addition, we recorded one case of interspecific predation: an adult male of *P. algirus* consumed a juvenile of *A. erythrurus*.

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Table 1: Kruskal-Wallis test results of the comparisons of the proportions between the different groupings. Values with a significance $p < 0.05$ are highlighted in bold.

		Arachnids	Scorpions	Hymenoptera	Formicidae	Coleoptera	Diptera	Hemiptera	Odonata	Isopoda
Between species		0.762	< 0.001	< 0.001	< 0.001	< 0.001	0.001	< 0.001	0.094	0.476
<i>A. erythrurus</i>	Sex	0.432	0.595	0.163	0.073	0.969	0.772	0.201	0.963	0.325
	Gravidity	0.519	0.130	0.118	0.114	0.678	0.724	0.733	0.542	NA
	Habitat	0.841	0.200	0.245	< 0.001	0.045	0.128	0.469	0.114	0.098
	Size	0.944	0.560	0.044	0.007	0.027	0.419	0.918	0.042	0.377
	Phenology	0.278	0.020	0.006	0.001	0.015	0.393	0.044	0.596	0.483
<i>P. algirus</i>	Sex	0.649	0.629	0.418	NA	0.930	0.418	0.420	0.306	NA
	Gravidity	0.512	0.218	0.522	NA	0.892	0.121	0.221	0.178	NA
	Habitat	0.800	0.074	0.201	0.493	0.041	0.002	0.014	0.493	NA
	Size	0.064	0.014	0.670	0.530	0.154	0.016	0.400	0.406	NA
	Phenology	0.021	< 0.001	0.340	0.602	0.007	0.070	0.892	0.462	NA
<i>P. edwardsianus</i>	Sex	0.389	NA	0.668	0.827	0.734	0.516	0.780	NA	0.665
	Gravidity	0.335	NA	0.645	0.346	0.204	0.685	0.398	NA	0.588
	Habitat	0.903	0.409	0.058	0.042	< 0.001	0.009	0.413	NA	0.785
	Size	0.995	0.670	0.329	0.222	0.049	0.732	0.283	NA	0.819
	Phenology	0.964	0.959	0.724	0.195	0.508	0.867	0.694	NA	0.375
		Neuroptera	Orthoptera	Lepidoptera	Ephemeroptera	Oothecae (Blattodea)	Dictyoptera	Embiopoda	Microcoryphia	Diplopoda
Between species		< 0.001	0.001	< 0.001	0.499	< 0.001	0.417	0.149	0.149	0.142
<i>A. erythrurus</i>	Sex	0.929	0.381	0.398	0.149	NA	0.325	NA	NA	0.226
	Gravidity	0.436	0.811	0.346	0.509	NA	NA	NA	NA	NA
	Habitat	0.952	0.387	0.387	0.243	NA	0.753	NA	NA	0.019
	Size	0.372	0.565	0.988	0.305	NA	0.620	NA	NA	0.024
	Phenology	0.460	0.497	0.821	0.254	NA	0.813	NA	NA	0.782
<i>P. algirus</i>	Sex	NA	0.234	0.563	0.340	NA	0.946	0.294	NA	NA
	Gravidity	NA	0.437	0.181	NA	NA	0.286	0.458	NA	NA
	Habitat	0.583	0.592	0.831	0.496	NA	0.951	0.496	0.496	NA
	Size	0.171	0.077	0.422	0.330	NA	0.149	0.432	0.524	NA
	Phenology	0.496	0.233	0.357	0.454	NA	0.655	0.116	0.595	NA
<i>P. edwardsianus</i>	Sex	0.251	0.534	0.101	NA	0.510	0.192	NA	NA	NA
	Gravidity	0.346	0.346	0.065	NA	0.432	NA	NA	NA	NA
	Habitat	0.979	0.106	0.217	NA	0.225	0.698	NA	NA	NA
	Size	0.264	0.132	0.504	NA	0.983	0.287	NA	NA	NA
	Phenology	0.091	0.555	0.237	NA	0.136	0.914	NA	NA	NA

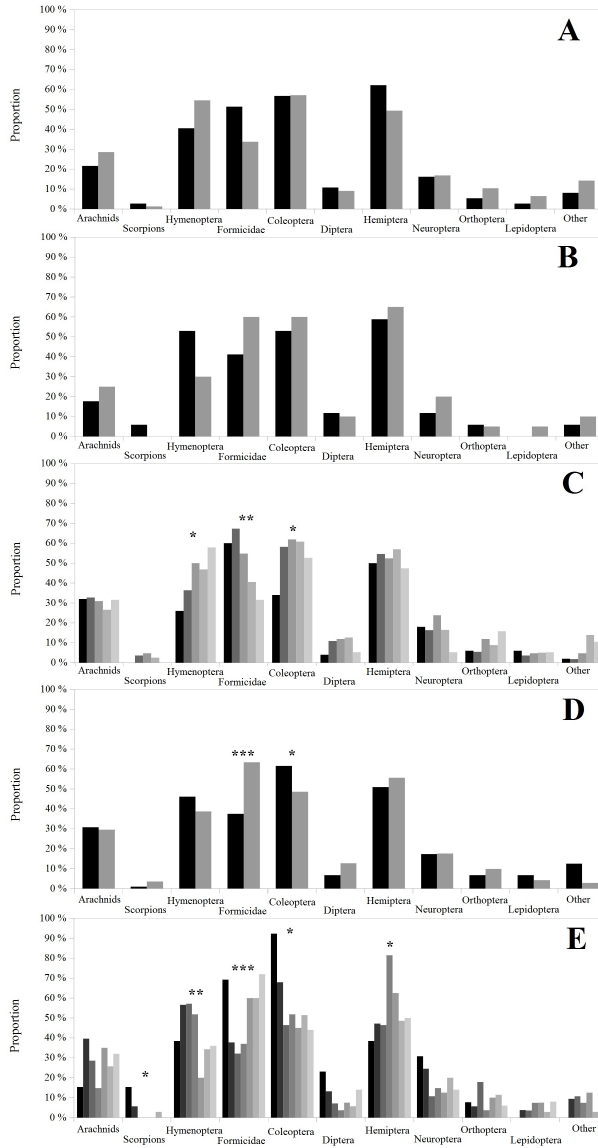


Figure 2: Representation of presence proportions in samples of the different prey groups in *A. erythrurus*. We show the comparison between sexes (A, ■ females; ■ males), by gravidity in females (B, ■ gravid; ■ not gravid), SVL ranges in mm (C, ■ 30-39; ■ 40-49; ■ 50-59; ■ 60-69; ■ 70-79), habitat types (D, ■ Forest; ■ Dunes) and months (E, ■ April; ■ May; ■ June; ■ July; ■ August; ■ September; ■ October). We show significant results of the Kruskal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**) and $p < 0.001$ (***).

Last but not least, in the detailed analysis of diet composition in *P. edwardsianus* as in the other two species we did not find significant differences between sexes nor by gravidity (Table 1, Fig 4). Considering body size ranges, we did only find significant differences in the consumption of Coleoptera, being more consumed by large individuals (Table 1, Fig. 4). The comparison of diet composition in the different habitat types showed significant differences in the consumption of ants, Coleoptera and Diptera (Table 1). While Coleoptera are especially abundant in the Forest habitat (about 65%), ants and Diptera are more abundant in the diet of individuals in the Dune habitat. The phenological analysis did not show any significant differences in any prey group (Table 1, Fig. 4).

Niche amplitude and overlap

Our values regarding niche amplitude show that *A. erythrurus* is the species with the smallest trophic niche and *P. algirus* is the one with the biggest niche (Table 2). At the intraspecific level we can remark that, in the case of *P. algirus*, females tend to have considerably greater trophic niche than males. This is not the case in the other two species (Table 2). In all three species, gravid females seemed to have slightly greater trophic niche amplitudes than non gravid females (Table 2). Regarding body size ranges, in general smaller (younger) individuals in all three species seem to present wider trophic niches than older individuals (Table 2). Considering the habitat types, we found that both *Psammodromus* species had wider trophic niches in the Dune habitat than in the Forest habitat (Table 2). Finally, regarding the variations of the values during the year, we could not detect a clear pattern, but there is a light trend to increase trophic niche amplitude during hotter months (especially in both *Psammodromus* species) (Table 2).

Considering the values of trophic niche overlap, we found that the diets of *A. erythrurus* and *P. algirus* are the most different, with an overlap of only 51.6%. The other comparisons lay by about 67% (Table 3). At the intraspecific level, we observed results according to the described above (Table 3). In neither species we observed differences between sexes, with overlaps of more than 80% (Table 3). The analysis considering gravidity did not show great differences in *A. erythrurus*, but in *P. algirus* and *P. edwardsianus*, with overlaps of 68.3% and 71.0%, respectively (Table 3). Regarding body size ranges, we could see in all three species the same pattern: a trophic niche separation as individuals grow, that means the values of niche overlap are lower comparing small and big individuals (Table 3). Comparing both habitat types, we observed that trophic niche overlap values are relatively high for both *Psammoromus* species (about 70%), but are especially high for *A. erythrurus* (86.3%). Finally, considering the phenological analysis, in the case of *A. erythrurus* we observed relatively high values (>70%) in all comparisons. In the case of *P. algirus*, values were between 50% and 70%, and the lowest values in general correspond to summer months. In the case of *P. edwardsianus* all values were located above 75%, with the exception of May (Table 3).

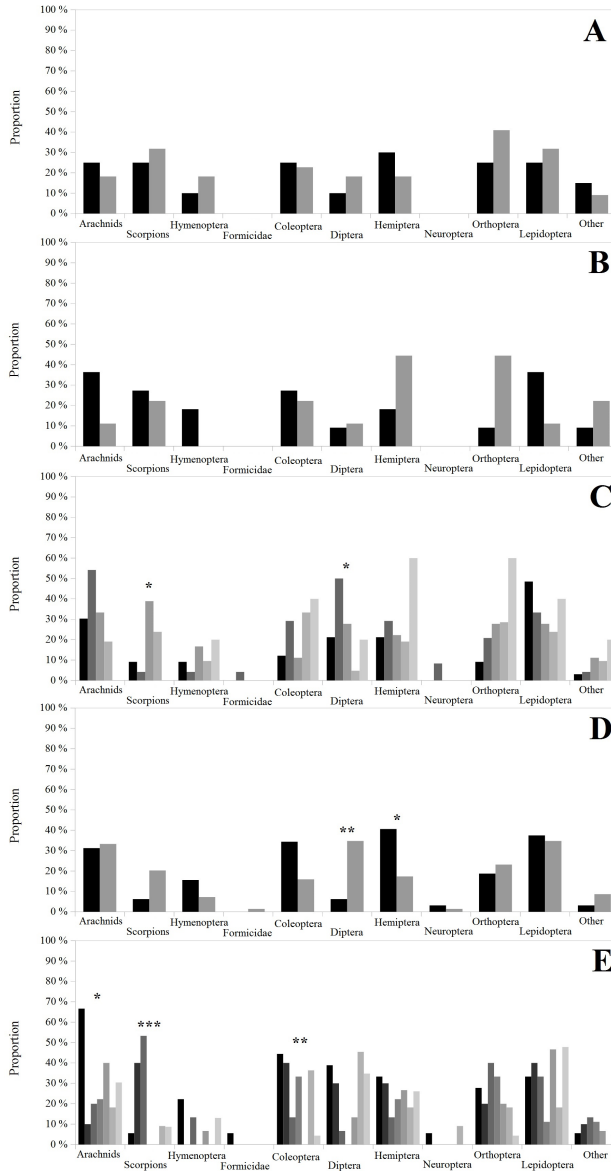


Figure 3: Representation of presence proportions in samples of the different prey groups in *P. algirus*. We show the comparison between sexes (A, ■ females; ■ males), by gravidity in females (B, ■ gravid; ■ not gravid), SVL ranges in mm (C, ■ 30-39; ■ 40-49; ■ 50-59; ■ 60-69; ■ 70-79), habitat types (D, ■ Forest; ■ Dunes) and months (E, ■ April; ■ May; ■ June; ■ July; ■ August; ■ September; ■ October). We show significant results of the Kruskal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**) and $p < 0.001$ (***)

Discussion

The global diet analysis accords to data obtained in previous studies in the case of *A. erythrurus* (Belliure, 2015). The major prey groups in this species were Hymenoptera, ants, Coleoptera and Hemiptera, the same as in a similar study carried out in Alicante (Seva, 1984), although our results show a higher diversity of minor prey groups. In the case of *P. algirus*, we observed some discrepancies with results obtained in previous works. The most remarkable is the relatively high proportion of Lepidoptera, a group which has not been described as such important in the diet of this species yet, in fact in the majority of studies it is not even mentioned (Salvador, 2011; Mamou et al., 2016). In addition, we found other minor prey groups which were not described previously in the diet of *P. algirus*, as scorpions and Neuroptera. Finally, in the case of *P. edwardsianus*, our results in general adjust to the ones obtained in previous studies, although we can remark some differences. On the one hand, Hymenoptera had been described as a very abundant prey group in this species (Fitze, 2012), but in our case it is more a minor prey group. On the other hand, in none of the previous studies the consumption of cockroach oothecae by *P. edwardsianus* was described, while in our case they appeared in about 15% of the samples.

The diet analysis at the intraspecific level did not show significant differences between sexes in any species. This is not surprising, as this was already described in previous studies (Busack & Jaksic, 1982; Pollo & Pérez-Mellado, 1991; Fitze, 2012). Although we observed considerably higher values in niche amplitude for females than for males in the case of *P. algirus*. We found no significant differences between gravid and non gravid adult females in neither species. This seems to contradict the results of niche amplitude, but the lack of significance can also be due to a too low sample size. Moreover, the differences in niche amplitude are relatively subtle. Also the values of niche overlap in this case are low. Although it is not significant, there seems to be a very subtle trend of gravid *P. algirus* females to consume more soft preys (Lepidoptera, Arachnida, Hymenoptera) and less hard preys (Hemiptera, Orthoptera). We could not find any references regarding this issue, but it could be explained by a better digestion or an easier hunting of these types of prey, what would give a more positive energetic balance, important, as egg production and incubation is a very energetically demanding task. Another explanation could be that the eggs in the abdomen occupy much volume, leading to a more difficult digestion of very hard or very big preys (Weiss, 2001). The effect of gravidity on diet composition is a topic that should be more studied in the future, also in other reptile species.

The phenologic analysis of diet composition showed a nearly absent variation in diversity in the case of *A. erythrurus*, with trophic niche overlaps above 70% in nearly all cases. A similar result as in a previous study (Seva, 1984). Although we recorded variations in the proportions of the different prey groups. Coleoptera seem to be ingested more in spring, ants are consumed less during the dry period, opposed to Hemiptera. These variations could be the result of variations in abundance of the different prey groups in relation to changes in the physical conditions of the environment. Especially the preference for mirmecophagy in this species leads in this direction.

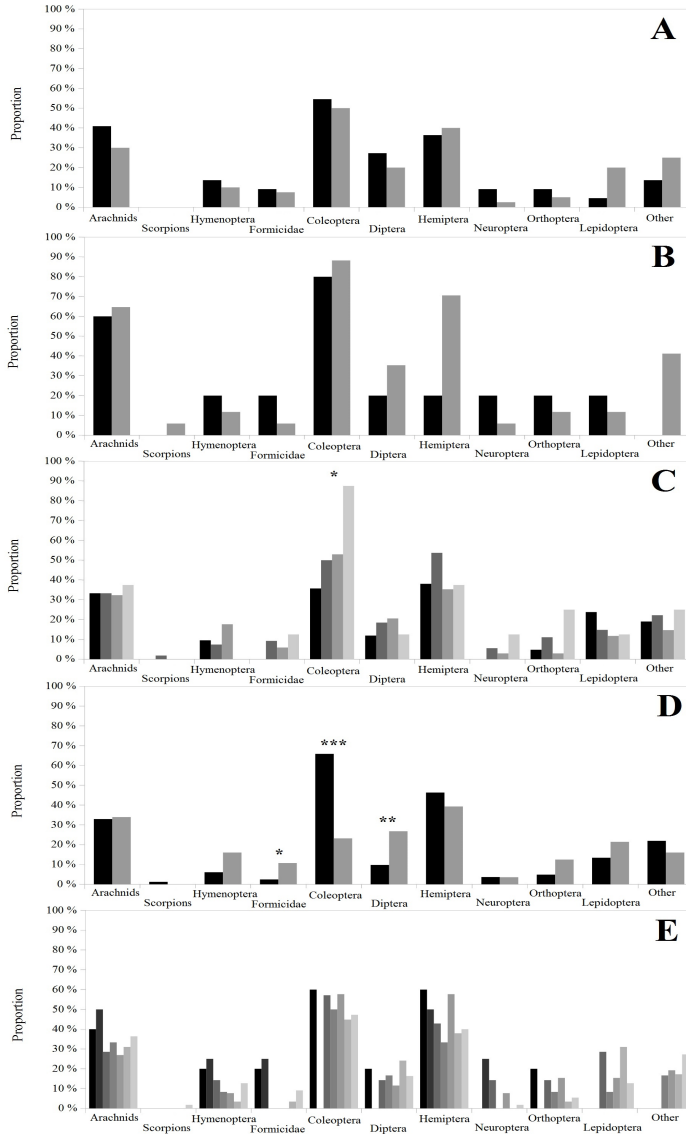


Figure 4: Representation of presence proportions in samples of the different prey groups in *P. edwardsianus*. We show the comparisons between sexes (A, ■ females; ■ males), by gravidity in females (B, ■ gravid; ■ not gravid), SVL ranges in mm (C, ■ <35; ■ 35-39; ■ 40-44; ■ >44), habitat types (D, ■ Forest; ■ Dunes) and months (E, ■ April; ■ May; ■ June; ■ July; ■ August; ■ September; ■ October). We show significant results of the Kruskal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**); $p < 0.001$ (***)

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In the case of *P. algirus*, we could record a higher variation in diet diversity, with some values below 60% of trophic niche overlap. This is coherent with the higher values in niche amplitude during summer months. Thus, it seems that *P. algirus* in fact presents a higher diet diversity in summer, resulting from a reduction in prey selectivity during less favourable periods.

Finally, in the case of *P. edwardsianus*, we did not detect differences except for May, but this month is only represented by 4 samples, what let us doubt on its representativeness. However, that we did not detect great variations in diet composition is an interesting result, given that this species was previously described as euriphage and opportunistic (Carretero & Llorente, 1991). In this case, seasonal variations in prey group abundance should be reflected in the diet of this species. This indicates that *P. edwardsianus* seems to be more selective as previously thought, given that it is hard to imagine that arthropod abundance and composition does not change during the year.

The values of trophic niche amplitude seem to indicate that *A. erythrurus* is the species with the most specialized diet. On the one hand, it presents the lowest values of niche amplitude of all three species. But it also has the lowest intraspecific variability in all comparisons. This is coherent with previous studies (Seva, 1984). That in all three species we recorded that gravid females have wider trophic niches also leads to the conclusion that gravidity has indeed an effect on the females' diet (Van Leeuwen et al., 2011). Another interesting result regarding niche amplitude is that in all three species the smallest (youngest) individuals have the largest trophic niches. This can basically be explained in two ways: 1) a higher diversity of small preys which for adult individuals result to be not profitable to hunt; or 2) neophilia, a young individual instinctively tends to try a greater diversity of preys and with time it specialises on certain types of prey. Considering our results for trophic niche overlap, indicating a separation of niches between small and large individuals, the first explanation seems to be the most correct. In the second case an individual would still be preying on (a reduced part of) the same pool of prey, thus we would expect higher niche overlap values. In fact, a shift in diet related to age had been observed in various lizards and it is mostly related to changes in energy requirements of the individual (e.g. Ballinger et al., 1977; Troyer, 1984; Mautz & Nagy, 1987).

Regarding the comparison between both habitat types, our results show that *A. erythrurus* presents very similar values in both habitats and in the other two species the most diverse diet is found in the Dune habitat. This is curious, as this habitat presents extremer environmental characteristics, with less vegetation and a high degree of insulation what leads to higher temperatures, especially in summer. It is known that abundance and diversity of arthropods tends to increase in dune systems with the increasing complexity of the vegetation (McLachlan, 1991). Our data, in contrast, show the complete opposite. As *A. erythrurus* is a more thermophile species (Carretero & Llorente, 1995; Belliure et al., 1996), a dune environment is an optimal environment for this species. But, the other two species are less thermophile and this type of habitat presents suboptimal conditions (Patterson & Davies, 1984). Thus, our conclusion is that an extremer environment induces a lower selectivity in the diet of these

Table 2: Trophic niche amplitudes, calculated as the niche amplitude index from Levins (L), with the sample size in each case (n). In the case of size ranges, the values in brackets refer to *P. edwardsianus*.

Species	n	L				
<i>A. erythrurus</i>	246	0.85				
<i>P. algirus</i>	101	2.03				
<i>P. edwardsianus</i>	138	1.57				
			<i>A. erythrurus</i>	<i>P. algirus</i>	<i>P. edwardsianus</i>	
Sex	n	L	n	L	n	L
F	37	0.81	20	2.33	22	1.38
M	77	0.89	22	1.79	40	1.59
Gravidity						
Gravid	17	0.87	11	1.98	5	0.78
Not gravid	20	0.74	9	1.80	17	0.50
Size (mm)						
30-39 (<35)	50	1.07	33	2.19	42	2.05
40-49 (35-39)	55	0.73	24	1.13	54	1.31
50-59 (40-44)	42	0.72	18	1.70	34	1.60
60-69 (>44)	79	0.83	21	2.53	8	0.83
70-79	19	0.93	5	0.86	-	-
Habitat						
Forest	104	0.88	32	1.69	82	1.21
Dunes	142	0.80	69	1.96	56	1.97
Phenology						
April	13	0.55	18	0.87	5	0.96
May	53	0.72	10	1.39	4	1.45
June	28	1.00	15	1.51	7	1.32
July	27	0.72	9	2.89	12	1.87
August	40	0.86	15	1.94	26	1.21
September	35	0.91	11	2.05	29	1.61
Octobre	50	0.80	23	1.85	55	1.53

species, favouring opportunism. This had been described in other organisms, like the snake *Natrix tessellata* (Weiperth et al., 2014), but we could not find any reference describing it in lizards. Although, it would also explain the tendency of the *Psammodomus* species to increase trophic niches during summer.

Our results regarding trophic niche overlap show that there is a resource partitioning between the species, at least between *A. erythrurus* and *P. algirus*. While the first tends to consume a greater proportion of hard preys like Coleoptera and Hemiptera, the second one, although it also consumes these prey groups, it tends to consume more soft preys like Lepidoptera, Arachnida or Diptera. These results are curious given that in another area where both species coexist a high degree of trophic niche overlap and diet similarity was described (Rouag et al., 2007). But in older studies (Pérez-Mellado, 1982; Seva, 1984) the authors found niche overlaps of 63% and 66%, respectively, more similar values to our case (51.6%), but still greater values. In Seva (1984) the author explains these

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differences in diet composition by differences in feeding strategies. *A. erythrurus* is more specialized (mirmecophagy) and *P. algirus* is more opportunistic. In addition to a behavioural factor, as *P. algirus* tends to climb through the vegetation, while *A. erythrurus* remains mostly on the ground.

Table 3: Trophic niche overlap, calculated as the Pianka index below the diagonal and as the percentage of overlap above the diagonal for all three species and intraspecific comparisons. In the case of size ranges, the values in brackets refer to *P. edwardsianus*.

Species	<i>A. erythrurus</i>	<i>P. algirus</i>	<i>P. edwardsianus</i>				
<i>A. erythrurus</i>	1	51.6	67.7				
<i>P. algirus</i>	0.61	1	67.8				
<i>P. edwardsianus</i>	0.82	0.81	1				
<i>A. erythrurus</i> <i>P. algirus</i> <i>P. edwardsianus</i>							
Sex	F	M					
F	1 1 1	86.4 80.4 83.6					
M	0.97 0.93 0.96	1 1 1					
Gravidity	G	NG					
G	1 1 1	86.1 68.3 71.0					
NG	0.96 0.63 0.88	1 1 1					
Habitat	Forest	Dunes					
Forest	1 1 1	86.3 71.9 72.8					
Dunes	0.96 0.82 0.84	1 1 1					
Size (mm)	30-39 (<35)	40-49 (35-39)	50-59 (40-44)	60-69 (>44)	70-79		
30-39 (<35)	1 1 1	88.8 73.8 85.2	82.8 74.9 82.3	80.3 63.0 67.2	75.4 56.4 -		
40-49 (35-39)	0.98 0.87 0.96	1 1 1	90.4 59.9 85.1	88.3 62.9 78.5	80.9 56.0 -		
50-59 (40-44)	0.95 0.83 0.95	0.98 0.82 0.96	1 1 1	91.1 74.4 75.7	84.7 59.0 -		
60-69 (>44)	0.93 0.75 0.86	0.96 0.73 0.91	0.99 0.85 0.92	1 1 1	84.3 65.4 -		
70-79	0.88 0.92 -	0.92 0.65 -	0.96 0.67 -	0.97 0.80 -	1 1 -		
Phenology	April	May	June	July	August	September	October
April	1 1 1	85.7 67.5 58.3	67.2 55.3 78.3	68.4 59.7 78.6	70.7 68.3 78.1	81.3 73.9 71.5	76.9 81.4 78.7
May	0.92 0.74 0.71	1 1 1	84.7 64.1 46.7	81.1 53.8 42.9	77.3 58.0 45.6	83.5 71.8 38.6	80.6 62.5 47.4
June	0.86 0.62 0.90	0.97 0.81 0.59	1 1 1	81.8 50.3 80.0	78.7 52.2 84.6	82.2 53.0 79.0	80.3 51.9 76.9
July	0.83 0.79 0.94	0.92 0.67 0.58	0.94 0.60 0.94	1 1 1	78.0 54.2 79.5	78.2 61.0 77.2	76.8 45.0 79.4
August	0.87 0.82 0.94	0.89 0.65 0.61	0.88 0.63 0.96	0.91 0.63 0.94	1 1 1	87.9 50.4 77.2	86.9 77.5 77.2
September	0.94 0.85 0.86	0.94 0.84 0.55	0.93 0.57 0.94	0.92 0.69 0.92	0.97 0.60 0.92	1 1 1	89.4 61.6 84.1
October	0.90 0.82 0.92	0.91 0.75 0.66	0.90 0.61 0.90	0.89 0.48 0.92	0.97 0.91 0.94	0.98 0.74 0.95	1 1 1

Although we would like to remark another (physiological) factor that affects diet composition: bite force. It is already known that *A. erythrurus* has generally a higher bite force than *P. algirus* (Verwajen & Van Damme, 2007) and this grants it better access to harder prey types. This factor also allows to explain some of the other tendencies we observed regarding diet shifts related to body size. In *P. algirus* the proportions of hard preys (Orthoptera, Hemiptera, Coleoptera) increase with body size, while soft preys (Diptera, Arachnida, Lepidoptera) decrease with body size. The same can be observed in *P. edwardsianus*, where the proportion of Coleoptera increases with body

size and the proportion of Lepidoptera decreases. In this context, we can also remark that, although it had been described that *A. erythrurus* has a marked tendency to mirmecophagy (Pérez-Mellado, 1982; Seva, 1984), the consumption of ants seems to be especially important for juvenile individuals, appearing in over 60% of the samples. In adult individuals (>60mm SVL) the proportion of ants in the diet decreases about 20-30%.

In conclusion, we can say that there are multiple factors (environmental, behavioural, physiological, competition...) that affect diet composition of a species. Some of these factors had not been considered yet when describing the diet of the object species (like bite force). This may open a path for future studies which consider all these factors together and evaluate the importance each factor has on shaping such an important part of the ecology of a species like the trophic niche.

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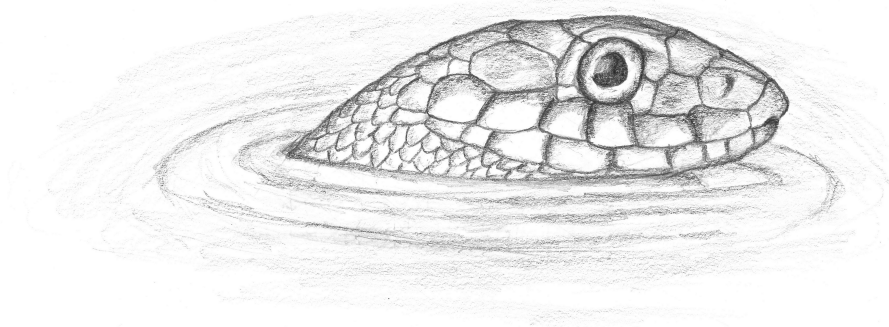
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Capítulo V

The effect of biological microreserves in a highly anthropized environment on the biology of *Natrix maura* (Linnaeus, 1758).

Robby M. Drechsler, Pablo Vera, Daniel C. Martínez & Juan S. Monrós



Amphibian and Reptile Conservation (En revisión).

The effect of biological microreserves in a highly anthropized environment on the biology of *Natrix maura* (Linnaeus, 1758).

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Abstract

Human disturbance in highly anthropized areas is known to have many negative effects on biodiversity. Reptiles, and snakes in particular, due to their close relation to the environment (e.g. thermoregulation) and their limited movement capacities, are excellent bioindicators of environmental quality. In addition they carry out essential ecological functions, acting as prey and predator at the same time. However, studies focusing on the effect taken conservation efforts have on their populations are scarce. Often such studies are focussed on so called “umbrella” species, like birds, as in theory they act as a representation of the general environmental quality. But the conservation of one group does not necessarily imply the conservation of the others. Hence, the aim of this study is to evaluate the effect of small protected areas on one of the most common snake species in the Iberian peninsula: *Natrix maura*. During 2015 and 2018 we carried out samplings in eight different points in the Albufera de Valencia Natural Park, three of them being biological reserves. Our results show that such protected areas have positive effects on the *N. maura* population on different levels. In protected areas, population structures are more complex, the body condition of large individuals is better and reproductive periods seem to have a larger magnitude and be longer than in not protected areas. We also studied predatory pressure, but did not find a significant correlation between the abundance of predatory birds (herons) and injured individuals. In conclusion, such areas can be essential for snakes to maintain their biological cycles and in some cases even to avoid their disappearance in highly anthropized environments and we strongly recommend the creation of more protected areas in order to promote the conservation of biodiversity in these areas.

Keywords: Conservation, Ecology, Snakes, Spain, Wetlands.

Introduction

In a more and more anthropized world, the conservation of biodiversity is becoming an increasingly important challenge. However, there is an imbalance on the partitioning of conservation efforts among different animal groups (Czech et al., 1998). Especially in the general society poorly accepted groups tend to be the ones receiving less attention when planning and carrying out conservation and management projects (Czech et al., 1998). One of the groups where this results to be most evident is snakes. Performing as predators and prey at the same time, snakes are of vital importance to the function of many ecosystems. Moreover, given their tight relationship with environmental conditions and their limited moving capacities they represent an ideal group for being used as bioindicators of environmental quality and to evaluate the success of already taken conservation measures (Pleguezuelos et al., 2002; Beaupre & Douglas, 2009).

Natrix maura is one of the most common snake species of the Iberian fauna and clearly the most abundant snake in water related habitats, being fresh water, brackish water or, in some cases even sea water (e.g. Cabot & Olea, 1978; Fuentes & Escoriza, 2015). This great ecological plasticity allowed this species also to persist in highly human disturbed areas, like agricultural areas (Santos, 2015). However, in many localities there is still a total lack of knowledge regarding their population status and the effect human disturbances have on it. This is concerning, as in areas where this had been studied a very negative effect of human activity on *N. maura* populations was detected (Miras et al., 2009; Santos & Llorente, 2009; Santos, 2015).

The threats *N. maura* populations are facing are divers. Even though there are natural factors affecting negatively *N. maura* populations, as the improvement of natural predator populations like herons (e.g. Garrido et al., 2012), the great majority of the threats are related to human activity. Road mortality is an important factor, especially in wetlands as roads usually go in parallel with canals or water channels (Llorente et al., 2005; Santos, 2015). Also the destruction, fragmentation and disturbance of its habitats are important threats (Santos et al., 2002). The massive use of plant protection products in agriculture and contaminants poured into rivers from urbanizations have reduced noticeably the water quality in the species' habitats. Given that prey items of *Natrix maura* are mainly found in the water, it was already evidenced that *N. maura* has a great capacity of bioaccumulation of contaminants (Santos et al., 1999). In addition, ecological alterations of the ecosystems by the introduction of exotic species also had direct or indirect negative effects on *N. maura* populations (e.g. Alarcos et al., 2009). Finally, the fear and bad image ophidians have in the general population leads to that encounters with humans usually end with the snakes' death, even being absolutely inoffensive (Hailey & Davies, 1987). The effects of all those factors were seen for example in the Ebro Delta, when Santos & Llorente (2009) detected a dramatic reduction in the abundance of *Natrix maura* in only 13 years.

As in the Ebro Delta, in the Albufera de Valencia Natural Park the major terrain use is the plantation of rice (Sánchez, 2008). This intensive agriculture has promoted the massive use of fertilizers, herbicides and pesticides,

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which in the past decades lead to a massive eutrophication and a drastic decrease in general water quality (e.g. Soria, 2006). Facing this problem, between 2006 and 2011 several natural reserves were created in order to foment biological conservation and the recovery of water quality. These reserves are the Tancat de la Pipa, the Tancat de Milia and the Tancat de Illa, old rice fields which were transformed in artificial wetlands, recovering marshy habitats and the associated biodiversity, restoring in small areas the natural state of the Albufera wetland.

The importance of such type of biological reserves was already evidenced for various groups of organisms, like birds (Sebastián-González et al., 2013; Rodrigo et al., 2018), amphibians (Reques, 2004) or turtles (Drechsler et al., 2018). Fauna conservation studies often are focused on “umbrella” or “indicator” species or zoological groups, as for example birds. Although, this implies a simplification of the ecological relationships and it was already criticized, as the conservation of one group not necessarily entails the conservation of the others (e.g. Figuerola & Green, 2003). In the case of reptiles (with the exception of turtles with conservation problems), there are barely any studies which evaluate the effect of conservation measures on their populations.

The aim of this study is to evaluate the effect of the existence of small biological reserves in highly anthropized environments on different aspects of the biology, especially population dynamics, of *Natrix maura*. Given that this species is the most common reptile in aquatic environments in the Iberian peninsula, our data will be of great use when comparing biological quality of different areas and to evaluate if conservation measures have to be taken, and at the same time evaluate the success of taken measures.

Material and Methods

Study area

The study area is the Albufera de Valencia Natural Park, located about 10 km south of Valencia city (39° 21' 18.7" N 0° 21' 38.4" W). It is one of the most important wetlands of the Iberian peninsula, with an area of about 21000 ha. Approximately 3000 ha correspond to the central lagoon, while the remaining 18000 ha mainly correspond to intensive rice crops (*Oryza sativa*). The water supply of this environment has different origins: Júcar river, rain water from highly urbanized watersheds, springs from subterranean aquifers, urban or industrial effluents (depurated wastewater) and irrigation returns from the agriculture in the area.

The study area is highly anthropized for the agricultural use, so that natural marsh vegetation is restricted to canals and the perimeter of the central lagoon, and is mainly formed by common reed (*Phragmites australis*) and southern cattail (*Thypha dominguensis*).

Embedded in this anthropized environment are the three studied biological reserves: Tancat de la Pipa, Tancat de Milia and Tancat de Illa. All three reserves are old rice fields, transformed in artificial wetlands in order to restore

water quality, foment the conservation of biodiversity and environmental education. The access to this areas is restricted to the fulfilment of these objectives. The Tancat de la Pipa (Pipa) is the largest reserve, with an area of about 40 ha, and in it different types of shallow marshy habitats are recreated, including canals with dense vegetation on the shores and permanent lagoons. The other two reserves are characterized by a more active management of water levels and vegetation. The Tancat de Milia (Milia) has an intermediate area of 33.4 ha and the Tancat de Illa (Illa) is the smallest with only 16 ha. In addition to the reserves, we sampled five more points: the Catarroja port and the surrounding rice fields (AR), an area far away from the central lagoon and high anthropic pressure due to the presence of bars, frequently used roads, fishing and boat traffic; rice fields near the Silla port (LR), an area close to the central lagoon and less anthropic pressure; the surroundings of El Palmar (Palmar), an area with a relatively high anthropic pressure, abundant vehicle traffic and fishing activity; Socarrada (SC), an area close to Illa and the Muntañeta dels Sants (MS), a small urbanized area embedded in the rice field environment (Fig. 1).

Fieldwork

Between March and November of 2015 and 2018 we carried out random searchings for *N. maura* with a duration between 1.5 and 2 hours at the 8 indicated sampling points. We initiated the censuses two to three hours after sunrise. We repeated the sampling at each point with a periodicity of once every two weeks in 2015 and once per week in 2018. In each sampling we annotated adverse weather conditions like clouds, wind or rain. We also recorded all seen individuals of *N. maura*, indicating if they were adults or juveniles every time possible. Individuals were considered adults from SVL > 250 mm (males) and SVL > 300 mm (females) (Santos, 2015). In parallel to the counts, we captured all possible individuals by hand and put them in individual cloth bags until the posterior measuring. Once finished the censuses we processed the captured individuals, measuring basic biometry (Snout-Vent Length or SVL, total length, weight), in addition, we recorded the presence of injuries or a broken tail, if the individual was in digestion and other observations. We marked each individual with a unique code of small notches at the ventral scales. After measuring, each individual was released at the capture point.

Data analysis

To study the abundance, we standardized the number of seen individuals with the duration of each census (in hours), obtaining the values in individuals/hour. We grouped the data by areas, years and seasons (being March, April and May “Spring”; June, July and August “Summer” and September, October and November “Autumn”). In order to evidence statistical significance of the observed differences we performed a multifactorial ANOVA, considering the three factors. In order to evaluate the degree of predatory pressure in each area we calculated the proportion of individuals with injuries or broken tails respect the total captured (Santos et al., 2011) comparing data from 2015 and 2018. In addition, in the case of the reserves, we compared these data with abundances of birds that are potential predators of *N. maura*, especially large herons (great egret *Egretta alba*, grey heron *Ardea*

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cinerea and purple heron *Ardea purpurea*). We obtained the number of birds carrying out weekly counts during the same period as the snake censuses. The bird counts were carried out with binoculars and telescopes, always during the first four hours after sunrise and avoiding adverse meteorological conditions like wind, rain or fog. In the cases of Pipa and Illa we went on foot, recording all seen individuals, while in the case of Milia, with less vegetation surrounding open water areas, we counted from inside a car.

For the construction of the population pyramids, we used the data from both years, without discriminating periods. For each area we grouped the captured individuals in intervals of 150 mm SVL and calculated the proportion of individuals corresponding to each interval respect the total of the area.

To study the hatching phenology, we considered individuals with SVL < 145 mm as hatchlings, following Duguay & Saint Girons (1966), and calculated the proportion of these respect the total captured each month, comparing protected (Pipa, Milia and Illa) with not protected areas (LR, AR, Palmar, MS and SC).

Finally, to study the body condition we represented the relation between weight (g) and size (SVL, en mm) of the individuals and drew the tendency line. We excluded individuals with a SVL above 600 mm as only in two areas (Pipa and Milia) appeared such individuals. The tendency line of the global data cloud served as reference function. Afterwards, we separated the data by areas and calculated the correlation coefficient (R) and determination coefficient (R^2) of the corresponding data cloud with the reference function. A low coefficient in an area indicates that the gain of weight of the individuals in this area does not follow the mean increase of the general population. In order to analyse more in detail the evolution of weight in the different areas, we calculated the mean value for different size intervals in each area and grouped the data by protected and not protected areas.

Results

We discarded an effect of the presence of clouds or other adverse meteorological conditions on the censuses comparing the days with such conditions with the days immediately before and after with favourable conditions (ANOVA, $F_{1,102} = 0.626$, $p = 0.431$).

The abundance analysis showed a significant reduction between 2015 and 2018 in Illa and almost significant in LR and Milia (Table 1, Fig. 2). This decrease is evident especially in adult individuals in LR and Milia and in adult and juvenile individuals in Illa (Fig. 2).

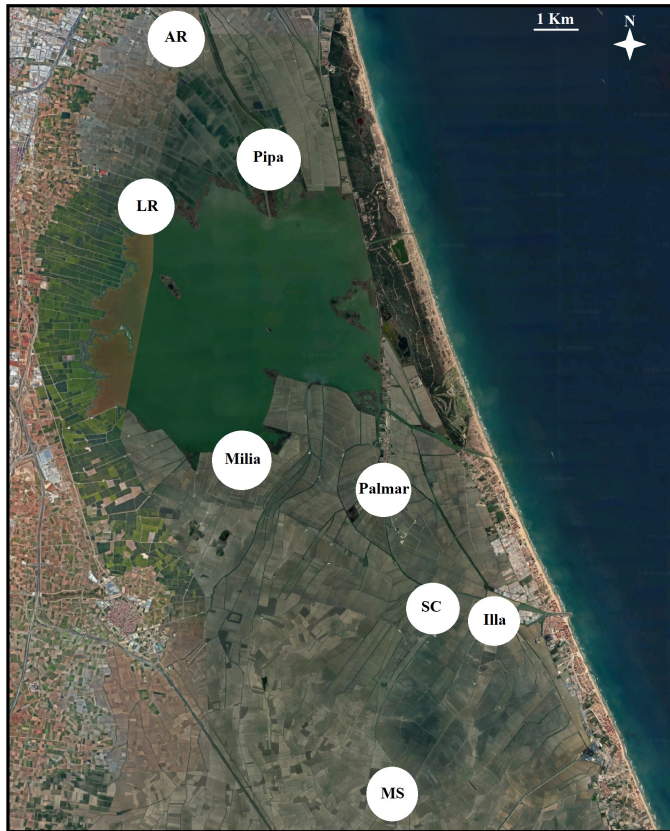


Figure 1: Satellite image of the study area, the Albufera de Valencia Natural Park, obtained via Google Maps (accessed on January 25th of 2019), indicating the location of the eight sampling points.

We found significant differences in the distribution of sizes between areas ($\chi^2 = 362.2$, $df = 7$ $p < 0.001$). The population pyramids (Fig. 3) show that the most mature populations, i.e. with the highest proportion of large individuals, correspond to Pipa and Milia, presenting approximately 10-15% of individuals above 600 mm SVL. In the other areas, the populations are mainly formed by immature individuals, specifically individuals between 150 and 299 mm SVL. The second most abundant group ranges from 300 to 449 mm SVL, and is formed by young adults. In these areas, very few individuals (~5%) reach a SVL above 450 mm.

Table 1: Results of the multifactorial ANOVA comparing the variation in abundance of *N. maura* throughout the year between 2015 and 2018 in each sampling point (MS, SC and Palmar were excluded due to lack of data).

	Year			Season			Year+Season		
	DF/n	F	p	DF/n	F	p	DF/n	F	p
AR	1 44	1.769	0.192	1 44	10.481	< 0.001	1 44	0.959	0.392
LR	1 36	1.703	0.202	1 36	16.759	< 0.001	1 36	3.198	0.055
Illa	1 39	4.023	0.053	1 39	4.589	0.017	1 39	7.170	0.003
Milia	1 42	0.218	0.643	1 42	7.466	0.002	1 42	2.862	0.070
Pipa	1 49	0.150	0.701	1 49	2.330	0.110	1 49	0.656	0.524

The analysis of the hatching phenology clearly shows two spikes, one more important in Spring and one less important in Autumn (Fig. 4). Also the comparison between protected and not protected areas showed significant differences ($\chi^2 = 29.08$, $df = 1$, $p < 0.001$). In not protected areas, hatching peaks seemed to delay one month and be of less magnitude, compared to protected areas.

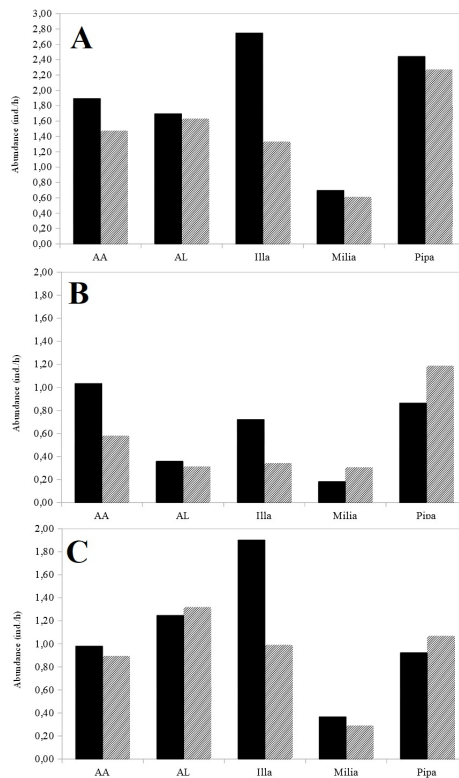


Figure 2: Representation of the abundances of *N. maura* in the different study areas in 2015 (filled bars) and 2018 (striped bars). We represent the total population (A), adults only (B) and juveniles only (C).

The results obtained regarding predatory pressure indicate that the proportion of individuals with injuries or broken tails is maximum in Milia, followed by Pipa (Fig. 5). Illa presents the smallest values among the reserves. The areas AR and LR present relatively high values, in comparison with the other not protected areas (Fig. 5). We also have to mention that, although there were no statistical significant differences in the general proportions of injured individuals between 2015 and 2018 (ANOVA, $F_{1,14} = 0.252$, $p = 0.624$), in some areas the differences were considerable. So, in AR the proportion of injured individuals went down from 24% to 14%, while in LR it increased from 5% to 20% (Fig. 5). In the protected areas (Pipa, Milia and Illa) the values remain similar between years, except for Illa where the values decrease from 20% to 5% (Fig. 5).

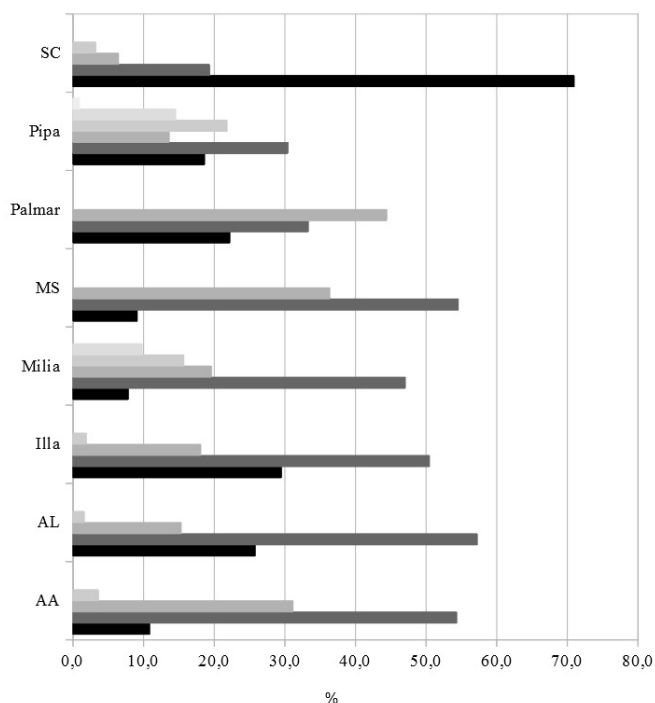


Figure 3: Population pyramids of each area representing the proportion of individuals of each SVL interval in the population: < 150 mm (■); 150-299 mm (■); 300-449 mm (■); 450-599 mm (■); 600-749 mm (■) y >750 mm (■).

We did not find a significant correlation between the abundance of potential predator birds (expressed as number of birds detected per census and ha of the reserve) and the proportion of injured individuals of *N. maura*, although the results were relatively close to significance (Lineal Regression Model, $F_{3,10} = 4.424$, $p = 0.126$, considering only the three mentioned large heron species; and Lineal Regression Model, $F_{3,10} = 2.757$, $p = 0.195$ for all heron species).

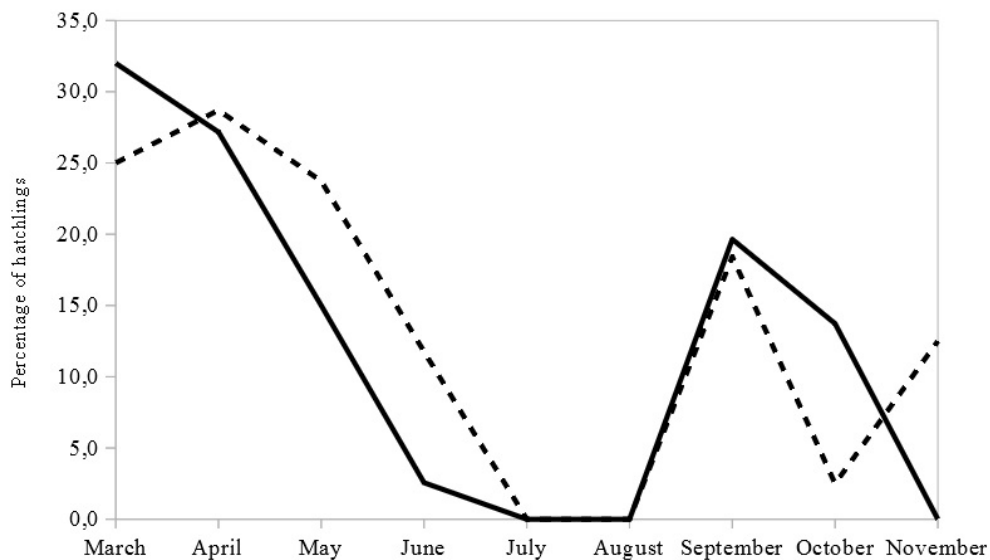


Figure 4: Representation of the variation of the proportion of hatchlings in the population throughout the sampling period. We compare the results from protected areas (continuous line) and not protected areas (dashed line).

The analysis of body condition showed that in the sampled population of *Natrix maura* in the Albufera de Valencia Natural Park, weight (W , in g) varies with body size (SVL, in mm) according to the following function:

$$W = 0.787328 e^{0.009809 SVL} \quad R^2 = 0.95$$

The comparison of the data clouds of each area with this reference function showed that MS and Illa were the less correlated areas, and SC and LR the most correlated areas (Table 2). Considering the biological reserves, Illa was the less correlated and Pipa the most correlated. Comparing protected areas with not protected areas, we detected a clear difference regarding the relation of weight and body size. Being the values identical for juveniles, large individuals (over 450 mm SVL) are significantly heavier in protected areas than in not protected areas (Table 2) (multifactorial ANOVA, $F_{3,649} = 35.851$, $p < 0.001$).

Discussion

Our results show that biological reserves are local areas of importance for the conservation of snakes in the Albufera de Valencia Natural Park. The population structure in protected areas is more complex, individuals reach larger body sizes and their body condition is better in comparison to not protected areas. In addition, reproductive periods are longer. The effect of such reserves as natural environments can reduce noticeably some threats and pressures on snakes like agricultural activities and human presence, which imply higher mortality (due to

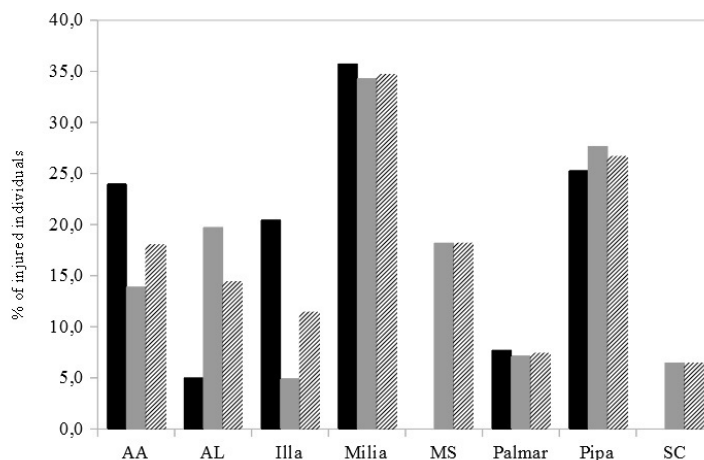


Figure 5: Representation of the proportion of injured individuals or with broken tail for each area in 2015 (black bars), 2018 (grey bars) and considering both years (striped bars).

Table 2: Values of the correlation and determination coefficients of the increase of weight with body size respect the reference function for each area and mean values of weight (in g) of the individuals in different ranges of body size for each area and comparing protected (Illa, Milia and Pipa) and not protected areas (AR, LR, MS, Palmar and SC).

	Correlation coefficient (<i>R</i>)		Determination coefficient (<i>R</i> ²)	
SC	0.982		0.965	
LR	0.953		0.908	
AR	0.950		0.903	
Pipa	0.942		0.888	
Palmar	0.939		0.881	
Milia	0.929		0.863	
Illa	0.888		0.789	
MS	0.886		0.785	
	SVL (mm)			
	< 150	150-299	300-449	450-599
SC	2.31	3.67	26.50	80.80
LR	2.74	6.68	31.51	91.92
AR	2.51	9.50	30.04	60.28
Pipa	2.53	6.45	34.06	131.70
Palmar	2.96	11.09	37.57	-
Milia	2.39	8.16	30.08	100.71
Illa	2.64	6.92	35.47	91.17
MS	2.30	15.39	30.64	-
Protected	2.57	6.91	33.97	127.14
Not protected	2.57	8.38	31.48	70.75

machinery, road overruns or aggression caused by the aversion snakes cause in many people) (e.g. Whitaker & Shine, 2000). Precisely, it is expectable that this mortality is accentuated in large individuals. Moreover, in not protected areas, the low environmental quality and human disturbance also negatively affects the availability of prey (fish and amphibians) (Lawler, 2001; Marco, 2002). The introduction of exotic species can also result in additional mortalities (Alarcos et al., 2009; Pérez-Bote & Roso, 2009). Finally, it was demonstrated that the bioaccumulation rate of toxics in *N. maura* is more important in large individuals than in small ones (Santos et al., 1999; Lemaire et al., 2018). All these factors could play a synergetic role and explain the results of this study.

Our results also show that the size and the management of protected areas play an important role in their ability to conserve *N. maura* populations. In the case of Illa, although it is a protected area, its reduced size and the fact that it is surrounded by a very transited road can prevent the development of a population as complex as the ones observed in Milia and Pipa. In addition, in this area we detected the most important decrease in *N. maura* abundance of all areas. In Milia, although the individuals reach large body sizes and the population seems to be stable, the density of individuals is minimal. The reasons behind this are not very clear yet and we require a longer term monitoring to be able to get possible explanations.

One possible explanation could be the presence of predators, especially birds like herons. These birds also use to concentrate in the reserves, using it for reproduction, feeding or as temporal roosts during migration (e.g. Gosálvez et al., 2012; Pérez-Granados et al., 2013). Many birds, especially herons, predate on *N. maura* (e.g. Amat & Herrera, 1977; González & González-Solís, 1990). In fact, the proportion of injured individuals of *N. maura* is higher in Pipa and Milia than in the other areas. Although, in this study we could not evidence a significant effect of bird density on the state of *N. maura* populations, in most cases the correlations were even negative. This can be explained by the denser vegetation in protected areas, offering to the snakes more refuges and possibilities to hide and escape from predators. We also have to take into account the effect of the “bias of the survivor”, as we only see and measure failed predation tries. A study more centred on the predator-prey relationship between birds and snakes may show that there is an important effect.

The abundance spikes of hatchlings seem to delay about one month in not protected areas and be of less magnitude. This plasticity in the temporal adjustment of reproduction was already observed in other areas (Santos & Llorente, 2001; Santos et al., 2005). In Santos et al. (2005), the authors associate this adjustment to prey availability, as females initiate reproduction once they reach a certain amount of fat reserves (Naulleau & Bonet, 1996; Bonet et al., 2002). Although we have to remark that the phenology of hatchlings in our case was very different to the observed in other populations, where the reproduction is once per year in Spring (even though some authors also saw matings in Autumn) and the hatchlings appear from August (Duguy & Saint Girons, 1966; Santos & Llorente, 2001; Santos et al., 2005; Santos, 2015). This could be a methodology error, related to the size we considered individuals as hatchlings, although our criterium (SVL < 145 mm) is according to hatchling sizes described in Duguy & Saint Girons (1966), and is even lower than the sizes described by other authors (Santos,

2015). We require a more detailed study of this issue to clarify our doubts.

Our results do not allow to infer the long term tendency of the populations in the studied areas or the general population of *N. maura* in the Albufera de Valencia Natural Park. However, the fact that in neither area we detected an increase in snake density and that in some areas the decrease was significant, can be interpreted as an indicator that the populations may be suffering a decline. In fact, it has been described that snake populations in general are declining considerably, indicating that in Europe the most probable causes are habitat deterioration, low prey availability and pollution (Reading et al., 2010). In the case of Iberian wetlands, industrialisation, the modernisation of sowing and harvesting techniques, the massive use of fertilizers, habitat loss and fragmentation, among other factors have already caused an important decrease in snake populations in the Ebro Delta, a very similar area to our study area (Santos & Llorente, 2009). Specifically, the authors detected a decline of about 50%, in some cases even 100%, of the *N. maura* population in only 13 years. However, the lack of data in the Albufera de Valencia Natural Park on the status of the *N. maura* population in the past does not allow to confirm that something similar is happening in this area.

In conclusion, we can state that the existence of biological reserves in a highly anthropized environment has a positive effect on *N. maura* populations on different levels. Considering that human disturbance and the effects of an intensive agriculture (landscape homogenization, loss of boundaries, temporality and used chemical products) are getting stronger and that a general decline of snake populations has already been described, we could even affirm that such protected areas are essential for snakes to maintain their biological cycles and, in extreme cases, even to avoid the disappearance of populations of species like *N. maura* in this type of environments. Taking all this into account, it is evident that the creation of more such protected areas is important and has to be promoted in highly anthropized areas, with the aim to conserve and protect snakes, a group of predators essential for the function of many ecosystems and on which it is increasingly necessary to pay attention.

Acknowledgements

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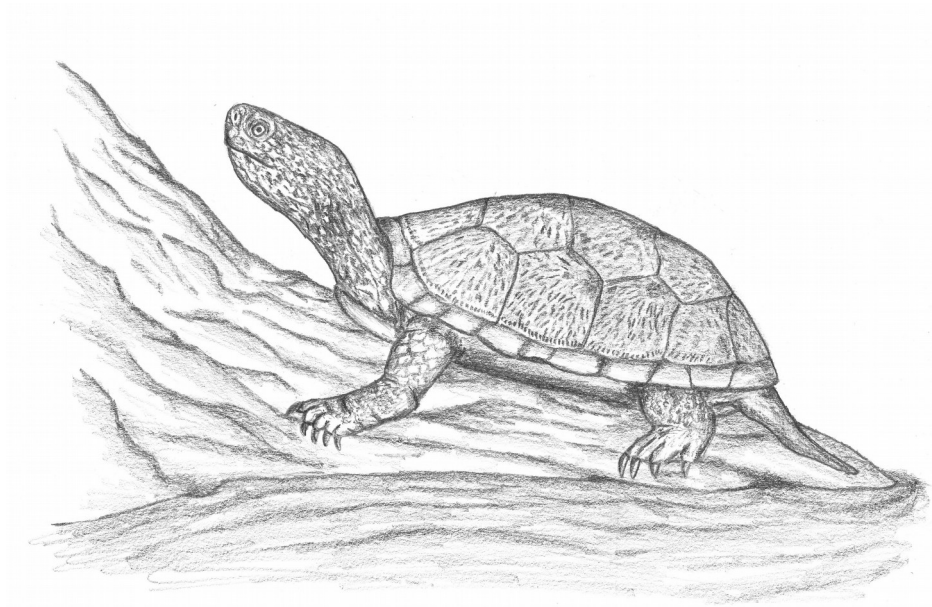
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Capítulo VI

Movement Patterns and Home Range Sizes of Translocated European Pond Turtles (*Emys orbicularis*, Linnaeus, 1758) in Eastern Spain

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Movement Patterns and Home Range Sizes of Translocated European Pond Turtles (*Emys orbicularis*, Linnaeus, 1758) in Eastern Spain

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Abstract

Populations of European Pond Turtles (*Emys orbicularis*) suffer from various threats, including habitat loss and fragmentation, and the introduction of invasive species. The aim of this study was an evaluation of the status and population viability of *E. orbicularis* in the Tancat de la Pipa Reserve, located in the Albufera de Valencia Natural Park (Spain). We analyzed activity and habitat use data from 14 introduced individuals. For this purpose, we radio tracked *E. orbicularis* between 2010 and 2015. Our results indicate movement similar to those documented in previous studies, with differences demonstrated between individuals released in different habitat types. We did not detect an effect of translocation on movement distances. We calculated home range areas using MCP and Kernel methods, noting differences according to release site habitat type. We did not detect differences between sexes nor a significant correlation between the extent of the home range and the size of an individual. Our data reveal a clear preference for dense vegetation of different plant species like paspalum grasses (*Paspalum* sp.), spiny rush (*Juncus acutus*), and sea club-rush (*Bolboschoenus maritimus*) in addition to reed (*Phragmites australis*) and cattail (*Typha domingensis*) and a water depth of about 15–20 cm. This information will be useful for designing future *E. orbicularis* conservation projects.

Keywords: biology; ecology; habitat use; in situ conservation; radio tracking; turtles

Resumen

Las poblaciones de galápago europeo (*Emys orbicularis*) se enfrentan a varias amenazas, entre las que se encuentran la pérdida y fragmentación de hábitats y la introducción de especies invasoras. El objetivo de este estudio fue la evaluación del estatus y la viabilidad poblacional de *E. orbicularis* en la reserva natural del Tancat de la Pipa, situada en el Parque Natural de la Albufera de Valencia (España). Para ello se analizaron datos de la

actividad y el uso de hábitat de individuos introducidos en el área de estudio, obtenidos mediante el radioseguimiento de 14 *E. orbicularis* entre 2010 y 2015. Los resultados indican un movimiento similar al descrito en estudios previos, con diferencias demostradas entre individuos liberados en diferentes tipos de hábitats. No se observó un efecto de la translocación de los individuos sobre las distancias recorridas. Se calcularon los tamaños de los dominios vitales usando los métodos MCP y Kernel, evidenciando diferencias en relación al tipo de hábitat en donde se soltaron. No se detectaron diferencias entre sexos ni una correlación significativa entre el tamaño del dominio vital y el del individuo. Los resultados muestran una clara preferencia por una vegetación densa de diferentes especies vegetales como hierbas del género *Paspallum*, junco espinoso (*Juncus acutus*) o castañuela (*Bolboschoenus maritimus*), también carrizo (*Phragmites australis*) y enea (*Typha domingensis*), además de una profundidad de agua de unos 15-20 cm. Esta información será útil a la hora de diseñar futuros proyectos de conservación de *E. orbicularis*.

Palabras clave: *biología; conservación in situ; ecología; radioseguimiento; tortugas; uso de hábitat*

Introduction

Biodiversity is a critical attribute of an ecosystem as it plays a fundamental role in maintaining or enhancing ecosystem function (Naeem et al., 1994). Higher biodiversity has been associated with higher stability and productivity of ecosystems (e.g., Johnson et al., 1996; Hooper et al., 2005; Mazur, 2013). Human activity has altered biodiversity of ecosystems in many ways, having an important and often negative effect (Hooper et al., 2005). Thus, conservation of biodiversity is essential to maintaining or increasing ecosystem function. Nevertheless, not all animal classes are treated the same way. Reptiles often suffer from reduced conservation efforts due to a bad image in society caused by a multitude of popular beliefs, most of which are false (e.g., Alves et al., 2012). However, turtles and tortoises are the most accepted reptiles in society and very often are held as pets, given that they are not perceived to be dangerous and are easy to handle in general. This acceptance by the general public leads to a greater conservation effort dedicated to turtles, accruing up to 75% of the financial investments dedicated to reptile conservation (Jiménez & Lacomba, 2002).

A high proportion of turtle species require conservation measures due to alteration and exploitation of their habitats. Turtles are a special case among vertebrates that colonize aquatic environments because their semi-aquatic behavior allows us to study and understand the close connection between terrestrial and aquatic environments (Bodie & Semlitsch, 2000). The conservation of turtles not only depends on the quality of the aquatic habitat but also on the quality of the terrestrial habitat surrounding it. This makes the conservation of turtles a complicated and expensive undertaking (Turtle Conservation Fund, 2002).

Rangewise the European Pond Turtle (*Emys orbicularis*; Fig. 1) is listed as Near Threatened (NT) in the International Union for the Conservation of Nature (IUCN) Red List (IUCN, 2017). In Spain, specifically, it is

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considered Vulnerable (VU) in the Red List of Endangered Species (Keller & Andreu, 2002). The same authors indicate that even this category is optimistic, considering the status of most *E. orbicularis* populations in Spain and that it should be elevated to Endangered (EN) (Keller & Andreu, 2002). Its populations are mainly threatened by habitat destruction and fragmentation due to an extensive and intensive agriculture, construction of infrastructure, and urbanization (Cordero & Ayres, 2004, Vicente Sancho, unpubl. report). The introduction of exotic species also represents a serious problem, especially Red-eared Sliders (*Trachemys scripta elegans*; Pérez-Santigosa et al., 2013). To a lesser extent, poaching for pet trade or consumption also affects Iberian populations negatively. Additionally, populations occupying temporal humid areas suffer from recent severe droughts, especially in areas with unsustainable water extraction for agriculture (Fahd et al., 2009). The Valencian region of Spain is known to be a relatively dry region, with regularly occurring droughts (Estrela et al., 2000; Vicente-Serrano et al., 2004), although dry periods are becoming more common. For example in 2013, the accumulated annual mean precipitation was only 50% of the average value (Agencia Estatal de Meteorología. 2017. Resúmenes Climatológicos. Available from http://www.aemet.es/en/serviciosclimaticos/vigilancia_clima/resumenes?w=0&datos=2 [Accessed 1 June 2017]).

Various international conservation projects have been carried out in Europe where, on a regional scale, numerous researchers are working on the conservation of the species and its habitats and the eradication of invasive species like *T. scripta elegans* (Ayres et al., 2013). *In situ* conservation activities, such as introduction or translocation of individuals can be a valuable tool for projects aimed at reversing negative impacts on wild populations (Griffith et al., 1989). In these cases, it is essential to evaluate the success of each project; however, this leads to high costs. The best way to evaluate success of translocation projects is long-term monitoring of the released individuals (Bertolero et al., 2007). A common method for monitoring and evaluating such projects is the attachment of radio transmitters to animals (e.g., Bremner-Harrison et al., 2004 in mammals; Sanz & Grajal, 1998 in birds; or Plummer & Mills, 2000 in reptiles). The aim of this study was to evaluate activity patterns and habitat use data of introduced *E. orbicularis*, information useful for designing future conservation projects for this species.

Materials and Methods

Study site.—The study area is located in the Tancat de la Pipa Reserve, an artificial wetland in the Albufera de Valencia Natural Park (coordinates 39.36374 -0.346283), Spain, which covers an area of about 40 ha. The vegetation is formed mainly by Common Reed (*Phragmites australis*) and Southern Cattail (*Thypha dominguensis*). The study site was surrounded by Bomba Rice (*Oryza sativa*) fields, except at the south, where it was close to the Albufera Lagoon (Fig. 1).

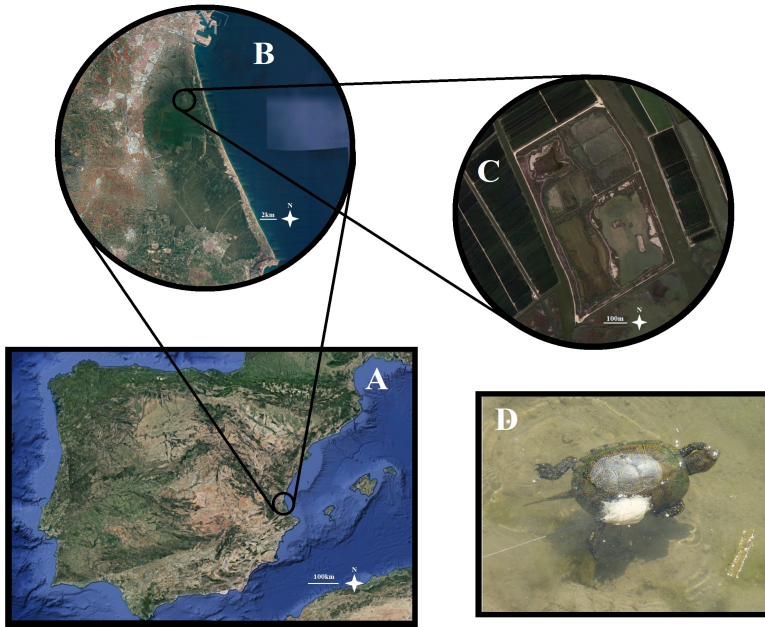


Figure 1: Location of the study area using satellite images obtained with Google Maps (on 30th of May 2017): Iberian Peninsula (A), Albufera de Valencia Natural Park (B) and Tancat de la Pipa reserve (C) and a photo of one individual of *E. orbicularis* used in this study (D) (Photographed by Lucía Moreno at the Tancat de la Pipa Reserve).

Between 2010 and 2015, we released 14 *E. orbicularis* (six in June 2010; two in July 2010; four in July 2011, and two in April 2015). Although the exact origin of these individuals was unknown, they did come from the region of the Albufera de Valencia Natural Park in Spain, including south of the Turia River. We housed all individuals at the El Saler Wildlife Center *La Granja*. Turtles we used in this study included wild individuals found by people and individuals held as pets. To identify the turtles, we marked each individual with a code of small notches on the marginals of the carapace (Cagle, 1939). We then attached 15 g radio-transmitters (Dexilon Automation, Valencia, Spain) to the carapace of each individual with epoxy resin. The transmitters emit 30 pulses per minute and we programmed them to work 12 h a day, with an estimated battery life time of about 24 months. We tracked individuals one or two times a week using an ICOM receiver (model IC-R20, Biotrack, Wareham, UK) and a directional Yagi antenna (Biotrack, Wareham, UK). We recorded the UTM coordinates each time we located a turtle, similar to other studies (Cadi et al., 2004; Meeske & Mühlenberg, 2004; Mignet et al., 2014).

We collected data from 11 females and three males, with a total of 365 locations (or tracking events). The weight of turtles at their release ranged from 220 to 492 g (two < 300 g; four 300–400 g; seven > 400 g; we did not record the weight of one individual). We analyzed GPS data using QGIS (2016) v2.12.3 software. This allowed us to obtain information about turtle activity patterns, size of home ranges, and habitat use. Due to defects in some transmitters, seven individuals produced fewer than 10 locations. We did not include these individuals in the estimation of home range size after observing a significant correlation between the number of locations and the size of the home range (Spearman Correlation Test, $\rho = 0.858$, $P < 0.001$). We did not find a significant correlation for turtles with > 10 locations (Spearman Correlation Test, $\rho = 0.627$, $P = 0.097$). We also excluded turtles with fewer than 10 locations from the analysis of habitat use. We made all statistical analysis using R (2016) v3.2.3.

To investigate turtle activity, we estimated mean distance traveled per day. We obtained this mean distance by standardizing the distance between two consecutive locations by the days elapsed between them. We grouped the data in periods of 15 d throughout the year, calculating the mean distance traveled in each period. The representation of these values allowed us to obtain the phenologic variation of the activity. Afterwards, we grouped the data in periods of 10 d elapsed after release, until day 370 (approximately one year). This allowed us to see how the activity of a turtle changed after being released. We performed a Shapiro-Wilk test in order to determine if the data are normally distributed and a Levene test for each variable in order to determine homogeneity of variances. The results of these tests showed that the data had no normal distribution ($W = 0.90934$, $P < 0.001$ for phenologic grouped data and $W = 0.74998$, $P < 0.001$ for post-release grouped data), but confirmed homoscedasticity in both cases ($F = 1.455$, $P = 0.240$ for “habitat”; $F = 0.960$, $P = 0.492$ for “month”, $F = 0.433$, $P = 0.651$ for “weight class” and $F = 0.588$, $P = 0.446$ for “sex”; for phenologic grouped data) and ($F = 1.431$, $P = 0.241$ for “habitat”; $F = 1.809$, $P = 0.167$ for “weight class” and $F = 2.336$, $P = 0.128$ for “sex”; for post-release grouped data). Then, we performed a Kruskal-Wallis test to evaluate differences in movement based on sex, weight classes at release (< 300 g, 300–400 g, > 400 g), and individuals released in different habitats. We distinguished five types of macrohabitats in the study area (Fig. 2): Canal were narrow areas where there was a constant water flow and a dense reed vegetation on the sides; Filter were areas characterized by a dense vegetation of different plant species like paspalum grass, Spiny Rush (*Juncus acutus*), and Sea Club-rush (*Scirpus maritimus*). These areas also had Common Reed and Southern Cattail on the shores and some areas inside this habitat and a water depth of about 15–20 cm; Subaquatic Fountain was a habitat that originated from a 250 m deep sounding and the vegetation is mainly formed by Southern Cattail; Marsh included two shallow lagoons that recreated the outline of the Albufera Lagoon at its healthy state, with areas of abundant subaquatic macrophytes and a high biodiversity; Swampy Areas where variations of the water level cause temporal inundation; and, Exterior for locations situated outside the limits of the reserve.

For the analysis of home ranges, we calculated the size of the home range of each individual by the Minimum Convex Polygon (MCP) (Mohr, 1947) method, using 100% of the locations, and by the Kernel method (at 90% for

the representative area and at 50% for the core area) (Worton, 1989). We performed linear regression to determine if there was a relationship between the size of an individual (weight at time of release) and home range size. We also analyzed if there were significant differences in home range size between sexes or individuals released in different habitats. We then associated each location with the type of habitat and calculated the percentage of locations each individual turtle had in each habitat type. We performed an ANOVA to test for differences in macrohabitat use. In addition, we performed a *post hoc* Tukey test to elucidate proportional habitat use. Because percentages do not have a normal distribution, we transformed percentages using the Arcsine Transformation (Zar, 1999), applying the following formula, p' being the transformed value and p the original value (expressed as proportion from 0 to 1)

$$p' = \frac{\arcsin(\sqrt{p}) * 180}{\pi}$$



Figure 2: Photos of the different habitat types considered in this study: Canal (A) (photographed by Matthieu Lassale), Filter (B) (Photographed by Lucía Moreno), Subaquatic fountain (C) (Photographed by Lucía Moreno), Marsh (D) (Photographed by Lucía Moreno), Swampy Areas (E) (Photographed by Lucía Moreno) and Exterior (F) (Photographed by Matthieu Lassale).

Results

Analysis of movements

In winter (December to the end of February), movement of turtles was relatively low, between 0 and 10 m/d, corresponding with their period of torpor. Movement peaked in spring with turtles moving 31.8 ± 34.0 [0.0-132.6] m/d between March and April. During the first month of summer (June), movement decreased to values of 14.56 ± 19.29 [0.0-83.9] m/d, until a second peak spikes in July, then movement progressively decreased in fall until hibernation (Fig. 2A). We did not observe differences in movement between sexes ($\chi^2 = 0.789$, $P = 0.374$) nor between weight classes ($\chi^2 = 0.480$, $P = 0.787$) but between individuals released in different habitats ($\chi^2 = 7.353$, $P = 0.025$). The analysis of the movement among individuals released in different habitats showed that the peak of movement of three individuals released in Filter habitat in March, while in summer they were quite inactive, with a small peak in August (Fig. 2B). The four individuals we released in Subaquatic Fountain moved less than in other habitats, but they were active longer, from March to October, with greatest distances moved at the end of spring and the beginning of summer (Fig. 2B).

Considering days elapsed after release, we observed a clear decrease in movement distances at the first 150 d, with values of about 300 m/d dropping to values approximating 5 m/d. Activity maintains this level until day 250 and then returns to the initial values. If we draw a tendency line for the first year after release, it has a slope near to 0 (Fig. 4). If we consider that the majority of individuals were released in summer, the variations in activity adjust very well to known movement patterns for the species. We did not observe differences in movements post-release based on sex ($\chi^2 = 3.693$, $P = 0.055$), weight classes ($\chi^2 = 0.776$, $P = 0.679$), but for individuals released in different habitat types ($\chi^2 = 12.242$, $P = 0.002$).

Home ranges and habitat use

Home ranges were quite variable. We observed significant differences in the extension of the core areas (Kernel 50) between individuals released in different habitats, with the turtles released in Filter habitat having the smallest values and the ones released in Swampy Areas exhibiting the highest values (Table 1). This pattern was also observed considering the representative area of the home range (Kernel 90) and the home range obtained by the MCP method, although in these cases the differences were not significant (Table 1).

We did not detect differences between sexes in either case (Table 2), nor a significant correlation between the extension of the home range and the size of an individual, considering its weight at release ($F_{4,8} = 0.175$, $P = 0.908$). Considering the percentages of locations in each habitat type ($7.7 \pm 11.9\%$ for “Canal”; $54.0 \pm 36.2\%$ for “Filter”; $16.3 \pm 24.6\%$ for “Marsh”; $13.7 \pm 26.8\%$ for “Subaquatic fountain”; $7.4 \pm 9.7\%$ for “Swampy areas” and $0.9 \pm 2.6\%$ for “Exterior”), we found significant differences in habitat use with Filter the most used and Exterior

used the least ($F_{5,72} = 8.821, P < 0.001$). The only habitat with significant differences was Filter ($P < 0.001$ for Filter – Canal, Filter – Exterior, Filter – Subaquatic fountain, Filter – Marsh and Filter – Swampy areas).

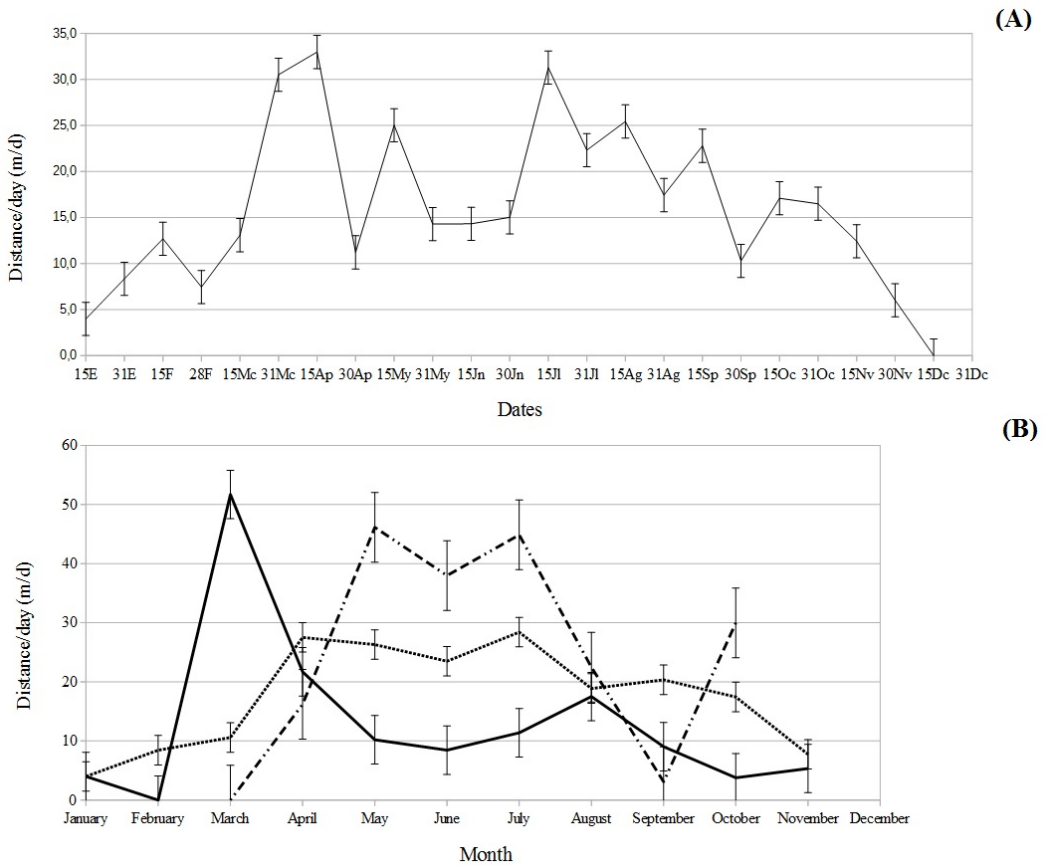


Figure 3: (A) Representation of the mean and standard error of the movements per day every 15 d. (B) Representation of the mean and standard error of the movements per day every month, separating the individuals by the habitat they were released in: Filter (continuous line), Subaquatic Fountain (regularly dashed line) and Swampy Areas (irregularly dashed line).

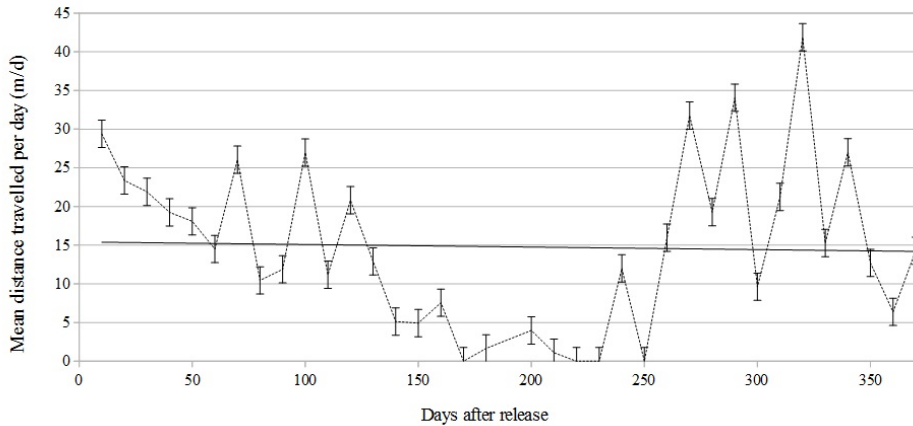


Figure 4. Representation of the mean and standard error of the movements per day every 10 days after release.

Table 1: Means and standard deviations of home range size in hectares, calculated using the MCP method and the kernel method (at 90% and 50%), for individuals grouped by the habitat they were released in. The results from the ANOVAs: degrees of freedom and sample sizes (df/n), F statistics and significance levels (P).

	Filter	Subaquatic	Swampy	df/n	F	P
		Fountain	Areas			
MCP 100	5.80 ± 5.07	13.36 ± 8.10	24.95 ± 0.00	2 8	2.927	0.144
Kernel 90	6.12 ± 5.05	24.15 ± 15.50	50.12 ± 0.00	2 8	5.021	0.064
Kernel 50	1.53 ± 1.17	6.61 ± 4.26	15.21 ± 0.00	2 8	6.369	< 0.05

Table 2: Means and standard deviations of home range size in hectares, calculated using the MCP method and the kernel method (at 90% and 50%), for individuals grouped by sex. The results from the ANOVAs: degrees of freedom and sample sizes (df/n), F statistics and significance levels (P).

	Males	Females	df/n	F	P
MCP 100	10.46 ± 1.56	12.48 ± 10.30	1 8	0.068	0.802
Kernel 90	15.52 ± 5.07	22.33 ± 21.11	1 8	0.185	0.682
Kernel 50	3.48 ± 0.91	6.55 ± 6.13	1 8	0.450	0.527

Discussion

Movements of turtles in our study were similar to those obtained in previous reintroduction studies (Cadi et al., 2004; Mignet et al., 2014). In a study in France (Cadi & Miquet, 2004), peak of turtle movement began in May, two months later than at our site. This may be due to the difference in latitude, given that in lower latitudes favorable temperatures for the initiation of activity are reached earlier. We observed decreased activity in June, despite that fact that most of the individuals in our study were females. Typical movement patterns in *E. orbicularis* are that males travel large distances from April to May to search for females for mating and females move the most from May to June for egg laying (Duguy & Baron, 1998; Schneeweiss et al., 1998; Cadi & Miquet, 2004; Cadi et al., 2004; Mignet et al., 2014). The difference we saw might be because our study area is surrounded by rice fields and the lagoon (at the south), and that these exterior environments are not favorable for egg laying, so females are forced to lay eggs inside the study area. This is supported by the presence of juveniles in the study area after the hatching period (pers. obs.), given that juveniles do not tend to make large movements.

It is also interesting that we found differences in movements among individuals released in different habitat types, although interpretation of this is difficult because the individuals were changing habitats while moving around the study area. However, individuals released in Filter generally presented lower activity levels compared to individuals released in the other habitat types. In addition, the data regarding the habitat use indicate a clear preference for Filter. This may suggest that this type of habitat is the most favorable. We also have to consider that the majority of individuals were released in June and July, where the differences between movement phenologies were most significant. This could indicate that the type of habitat a turtle is released in affects the initial movement pattern, and we indeed detected differences in movement distances post-release among individuals released in different habitat types.

Our post-release activity matches phenology previously described for reintroduced individuals of the species (Mignet et al., 2014). We did not observe a decrease in movement after a year, contrary to what Mignet et al. (2014) observed with their study population. Their individuals also had smaller home ranges than newly released turtles. This reduction in activity could be the conclusion of an initial phase of exploration just after the release and with the establishment of a new territory near the releasing site. We did not detect such a decrease, which could be interpreted as our study area offered a selection of habitats that were adequate so that the individuals rapidly settled down near the release site.

Home range sizes between sexes did not show significant differences. Neither Cadi et al. (2004) and Mignet et al. (2014) observed significant differences between sexes. Values of home range sizes obtained for each sex (10.46 ha for males and 7.30 ha for females using MCP 100%) were similar to the values obtained in other studies (7.74 ± 3.63 ha for males and 12.51 ± 8.38 ha for females, using MCP 95% in Cadi et al. 2004).

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We did not detect a correlation between the size of an individual and the size of its home range, although this correlation has been found in another study of turtles in Spain (Pérez-Santigosa et al., 2013). Correlations of animal size and home range size have also been found in other ectothermic organisms: lizards (Perry & Garland, 2002) and tortoises (Drechsler et al., 2016). Our small sample size may have contributed to the lack of correlation, but also a recent study (Slavenko et al., 2016) concluded that in turtles, energy requirements are not a reliable predictor for home range size and that there must be other, much more reliable factors such as the cost of locomotion in each habitat to be considered.

Regarding habitat use, we recorded that Filter was the most used habitat, probably indicating that this type of habitat is the most favorable. This agrees with the comparisons of home range sizes between individuals released in different habitats: individuals released in Filter also had smaller home ranges, meaning that they remained near the release site. In previous studies, habitats similar to this have been described as appropriate for the winter torpor of *E. orbicularis* (Segurado & Araújo, 2004; Thienpont et al., 2004).

In conclusion we think that the Tancat de la Pipa Reserve is a favorable area for releasing individuals of *E. orbicularis*. It also represents an important wildlife refuge given the exploitation of the Albufera area for rice cultivation and fishing. We also have to remark that until now, we have not found any *Trachemys scripta elegans* or other invasive turtles, increasing the population stability. We have also found successful reproduction by *E. orbicularis* inside the study area. The isolated nature of the site means that it would be difficult for invasive species to find, but it also means that immigration by native turtles will be difficult. We suggest creating ecological corridors to enhance the dispersion of turtles, combined with intensive monitoring in such corridors to avoid an influx of invasive species. A more economical approach may be to establish a stable native population inside the reserve, which can be used as a source of individuals for introduction or population reinforcement projects.

Acknowledgments

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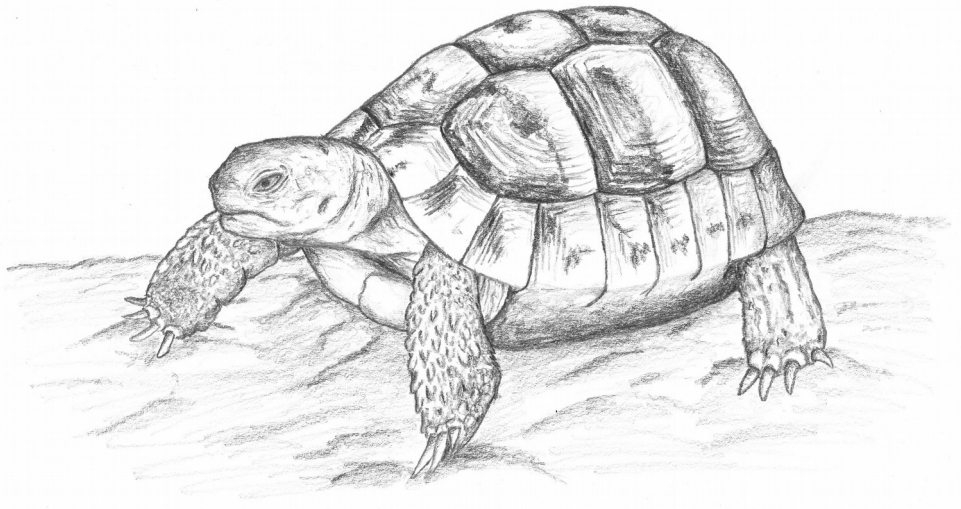
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Capítulo VII

**Analysis of movement patterns and macrohabitat use
in Hermann's tortoises (*Testudo hermanni hermanni*,
Gmelin 1789) reintroduced in a coastal area
dominated by pinewood in eastern Spain.**

Robby Drechsler, Mercè Vilalta & Juan S. Monrós.



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Analysis of movement patterns and macrohabitat use in Hermann's tortoises (*Testudo hermanni hermanni*, Gmelin 1789) reintroduced in a coastal area dominated by pinewood in eastern Spain.

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Abstract

The Hermann's tortoise is a strictly European species found mostly in areas with Mediterranean and sub-Mediterranean climates and, especially the subspecies *T. hermanni hermanni*, has to deal with various threats which reduced its geographic distribution to only a few isolated populations. Thus, with the objective of recovering natural populations of the species, numerous reintroduction projects are being carried out throughout its historical and prehistorical geographic distribution. The aim of our study is to evaluate the success of the *T. hermanni* reintroduction project carried out in the Albufera de Valencia Natural Park since 2011, through the analysis of movements, home range sizes and habitat use in a new environment. The recorded activity pattern presents two peaks, one in spring and another in August, and the hibernation period (from December to February) is the same as observed in other populations. We did not find significant differences in home range sizes between sexes, but a tight relation between home range sizes and body sizes with larger individuals having larger home ranges. This relation was not observed for core areas (Kernel at 50%). Considering the habitat use, we did not find differences between the groups of individuals we defined, but different types of habitats were used differently. “Scrub” was the most frequented (~50%), followed by “dunes” (~20%), “mallaes” (~20%) and “forest” (<20%). Our results can be used to improve the success of future reintroduction projects by directing ideal habitat, timing and carapace size of released Hermann's tortoises.

Keywords: ecology, habitat use, home range, in situ conservation, radiotracking, reintroduction.

Introduction

Biodiversity is one of the most important attributes of an ecosystem, because it has a tight relation to maintaining or enhancing ecosystem function (Naeem et al., 1994). In the past it has been shown that higher biodiversity can

be associated with higher stability and productivity of ecosystems (e.g., Johnson et al., 1996; Hooper et al., 2005; Mazur, 2013). Human activity has altered biodiversity of many ecosystems in many different ways, having an important and often negative effect on them (Hooper et al., 2005). Thus, the conservation of biodiversity is essential to maintaining or increasing ecosystem function. Nevertheless, various animal classes are not treated the same way, and certain inequalities exist within them. For example, in López & Barberá (2011) it is said that "... environmental impact assessments of infrastructures do not use to value the effect on groups of small vertebrates and invertebrates, centering all corrective measures to minimize the effects on the most emblematic fauna, like birds or large mammals". One group suffering such an inequality is the reptile group, due to a bad image caused by a multitude of popular beliefs, most of them being absolutely untrue. However, within the group of reptiles, turtles and tortoises have a relatively high acceptance in society, which leads to a higher conservation effort, gathering up to a 75% of financial investments dedicated to the conservation of reptiles (Jiménez & Lacomba, 2002).

The distribution of tortoises is mainly determined by the climate (Anadón et al., 2006a). The Hermann's tortoise is a species found in regions with Mediterranean and sub-Mediterranean climates of Europe (Celse et al., 2014). It is known that the Hermann's tortoise *Testudo hermanni* has serious conservation problems (Pleguezuelos, Márquez & Lizana, 2002; Celse et al., 2014). Especially the subspecies *T. hermanni hermanni* is in decline due to various threats as habitat loss, forest fires or poaching for pet trade. These threats took the species to the limit of extinction in most parts of its geographic distribution (Pleguezuelos, Márquez & Lizana, 2002). In Spain, the Hermann's tortoise has natural populations remaining only in Catalonia and the Balearic Islands (Soler-Massana, 1995; Llorente et al., 2002). If we except island populations because of being the result of multiple historical introductions, there is only one natural population remaining in the northern peninsula (Albera population), which in 1986 was affected by a fire. The density of tortoises before the fire was estimated at 10.95 individuals/ha (Félix et al., 1989). Twenty years later, at the same area, the density was estimated again and was found to be 0.3 individuals/ha (Bertolero, Oro & Besnard, 2007). This density is considered to be extremely low and, therefore, the situation of the species is at high risk, with an unpredictable future (Bertolero, 2010).

Due to this critical situation of the species, numerous reintroduction projects are being carried out throughout its historic and prehistoric geographic distribution with the objective of recovering natural populations (Soler et al., 2002; Bertolero, Oro & Besnard, 2007; Mateo, 2011). In the Valencian Community one of these projects is being carried out since 2005 at the Sierra de Irta Natural Parc, trying to establish a viable population (Vilalta, 2010). As the individuals adapted well to the environment and even reproduced, this project was extended in 2011 to the Albufera de Valencia Natural Parc. In this area, no natural population is known historically but there are several archeological hints that the pre-historical distribution of this and closely related species was much wider than today and that the species was present in the Valencian Community (Bailón, 2001; Pérez & Serra, 2009), so it was considered to be extinct from the local fauna (Jiménez & Lacomba, 2002).

Reintroduction of individuals is a valuable tool within the *in situ* conservation, used in animal conservation programs in order to reverse negative trends in natural populations (Griffith et al., 1989) or, as in our case, to recover an extinct population (e.g., Hereida, 1992). In these cases it is essential to evaluate the success of each project that is carried out. However, this is a very expensive task because the best way of success evaluation is a long-term monitoring of the released individuals (Bertolero, Oro & Besnard, 2007).

We also have to remark that some aspects of the phenological variability or plasticity of wild *T. hermanni* populations are still unknown. Nevertheless, it is essential to know those aspects for determining activity ranges, habitat preferences or reproduction patterns, because a better understanding of the biological and ecological aspects of tortoise populations will be fundamental for the development of more effective management and protection plans (Corti & Zuffi, 2003). In order to best understand future reintroductions and habitat usage of *T. hermanni*, we should fully understand key moments of movement for releasing the individuals. With successful monitoring of habitat usage and movement of reintroduced *T. hermanni*, we expect to assist the further viability of *T. hermanni* populations.

Among the most often used monitoring methods for evaluation of conservation projects is the attachment of radio transmitters to animals (e.g. Sanz & Grajal, 1998, with birds; Plummer & Mills, 2000, with reptiles; Bremner-Harrison, Prodohl & Elwood, 2004, with mammals). In some cases the attachment of the transmitters to the animals' body can be a complex task. For example, in snakes it is necessary to implant the transmitter into the animal's body (Monrós, 1997). In the case of terrestrial tortoises, the attachment of the transmitter to the tortoise's shell is much easier. In addition, this method allows easy relocation of individuals in the field during their life span and, thus, understanding their total home range and movement patterns throughout various habitats. For those reasons, radio tracking is a highly appreciated and widely used method in terrestrial tortoises (Calzolari & Chelazzi, 1991; Casamitjana, Loaliza & Frigola, 2013; Vilardell-Bartino et al., 2015).

The aim of our study is to assess the success of the *T. hermanni* reintroduction project carried out in the Albufera de Valencia Natural Park since 2011, analyzing the movements, home range sizes and habitat use after the translocation to the new environment. The evaluation of the data will be useful in future planning of similar projects when choosing ideal habitat, timing and carapace size of released Hermann's tortoises, enhancing their survival and, in conclusion, the success of the project.

Materials and methods

The study was carried out in a coastal area dominated by pinewood in the Albufera de Valencia Natural Park (39°20'20"N 0°18'43"W), located about 10 km south of the Valencia city. Our study site is situated between a brackish lagoon and the sea, being about 10 km long and 1 km wide and having an area of about 850 ha (Fig. 1).

The study area has a variety of habitats, mainly mobile dunes, fixed dunes and the “mallaes”, with typical Mediterranean vegetation. The mobile dunes are colonized by herbaceous vegetation, including different species of grasses and creepers, whilst the fixed dunes have a dense vegetation and pinewood, mainly formed by aleppo pine. Last but not least, the “mallaes” are environments where the drainage of rain water and the proximity of the water table causes temporal inundation, leading to a vegetation mainly formed by reeds and succulents adapted to different levels of salinity and inundation.

To investigate the macrohabitat use of the different individuals, we distinguished four types of macrohabitats within the study area: “forest”, characterized by a relatively dense tree cover of aleppo pine; “scrub”, with a bush cover of different plant species exceeding in general one meter in height; “dunes”, characterized by a less dense bush vegetation of different species usually less than one meter high; and, finally, the “mallaes” with temporal inundation, and a vegetation mainly formed by reeds and succulents.

Between the years 2011 and 2015, 215 individuals of *T. hermanni* were released at the study site (118 males and 97 females). The animals came from wildlife centers from Menorca, but detailed information about their origin is not available (wild animals which may have suffered an accident, some may have been kept as pets). They did not come from breeding facilities, but were held in captivity until release.

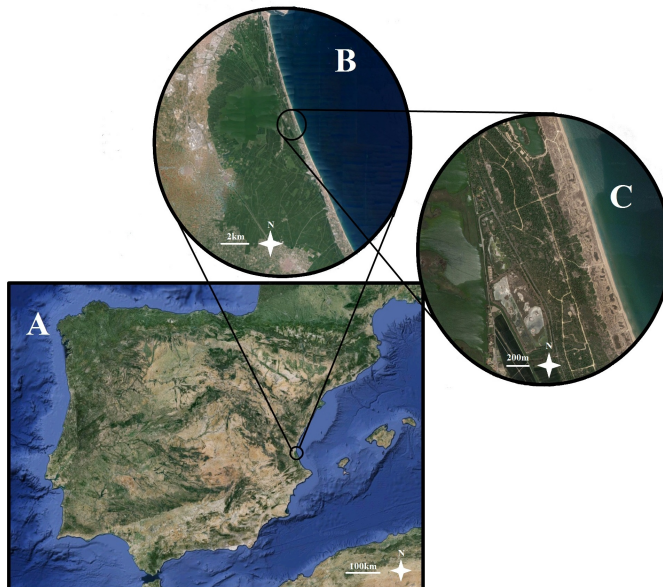


Figure 1: Location of the study area using satellite images obtained with Google Maps (on 28th of June 2016): Iberian Peninsula (A), Albufera de Valencia Natural Park (B) and study area (C).

All individuals were marked permanently with unique codes of small incisions at the border of their shell (Cagle, 1939). To 29 individuals we also attached transmitters to be able to track them at any time in the field (Calzolari & Chelazzi, 1991; Casamitjana, Loaiza & Frigola, 2013; Vilardell-Bartino et al., 2015). We recorded a mean of 63 locations (events of tracking) per animal. The individuals were penned for three months in the study area before being released (soft-release, e.g. Tuberville et al., 2005). We released the tracked individuals in different moments of consecutive years: 20 in October 2011, 2 in July 2012 and 7 were released in April 2013. For radio tracking we used TW-3 radio transmitters from Biotrack (which emit 20ms pulses, 40 pulses/minute, and have an expected battery life of 18 months). We attached the transmitters to the tortoises' shell using Demotec resin, between the second and third costal plate in females, and in the center of the shell in males, so they do not interfere with activity of the animals (reproduction, feeding, hibernation...). We tracked the individuals once a week (once every 15 days in winter) using an ICOM receptor model IC-R20 and a directional Yagi antenna with about 800g, both from Biotrack. We recorded the UTM coordinates and the weight of each individual every time we located them.

We analyzed the UTM coordinates with QGIS v2.10.1 (2015) software. For the analysis of movements, first, we grouped the data by date and calculated the mean value of the distance travelled per day every 15 days of the year. Then, we grouped the data by days elapsed after the release of each individual, calculating the mean value of the distance travelled per day every 10 days until the day 200 after release. Because the number of days that elapsed between the locations was variable (we tracked the individuals once a week, not exactly every 7 days), we standardized the distances for the days passed between the locations, obtaining the mean distance moved per day as an indicator for the activity of each individual. As there were several cases of long-distance movements, to avoid statistical aberrations, for statistical analysis we did not consider values over 100m/d.

We also calculated the individual home range size using the Minimum Convex Polygon method (MCP) with 100% of the locations, and using the kernel method (at 90% for the representative area and at 50% for the core area). As the tortoises were introduced into a new unfamiliar environment, and to minimize serial correlation of the data, for home range size estimation we did not consider the locations of the first month after release. Finally, we did a Spearman correlation test for each individual with the number of locations and the obtained home range size.

As we were working with relocated individuals, and for most of them we have data of several years, we estimated the home range size in the period of maximum activity (spring) and evaluated if there are differences between consecutive years after release, performing an ANOVA for repeated measures.

For the analysis of macrohabitat use, we created a layer in QGIS which represents different types of macrohabitats at the study site (forest, dunes, scrub and "mallaes") and associated to each location the habitat type the animal was found in. The locations that could not be put in one of the described macrohabitats were grouped as "others" (for example individuals found at the beach). As not all individuals had the same amount of locations, to be able to compare them we calculated the percentage of locations found in each type of macrohabitat relative to the total for

each individual, considering a certain period of time (e.g. hibernation, the entire activity period, mating period, etc.). Given that percentages do not have a normal distribution, for statistical analysis they were transformed using the arcsine transformation (Zar,1999), applying the following formula, p' being the transformed value and p the original value (expressed as proportion from 0 to 1).

$$p' = \frac{\arcsin(\sqrt{p}) * 180}{\pi}$$

We analyzed if there were statistically significant differences between the sexes, individual body sizes and moments of release performing ANOVAs. As we did not have measures of the carapace size, we used the weight at the moment of release. For the statistical analysis we separated the sample in two groups (<700g and >700g, a value close to the mean, having n = 14 and n = 15, respectively). For the analysis of habitat use, the differences between the different types of habitat within a group (sexes, body sizes and moments of release) were tested with a *post hoc* Tukey test, so we could know which habitats are used significantly differently. All statistical analysis were performed using R v3.2.3 (2015).

Results

Movements

Grouping the distances travelled per day by date, we could see clearly that the hibernation period starts in December and lasts until February. Then, there was a period of maximum activity in spring and a second one at the end of summer. Finally, there was a progressive decrease in activity in autumn until hibernation (Fig. 2). We did not find differences in phenology between individuals with different body sizes (multifactorial ANOVA, $F_{23,1775} = 0.984$, $p = 0.484$), but there were statistically significant differences between the sexes (multifactorial ANOVA, $F_{23,1775} = 1.609$, $p < 0.05$). Thus, we analyzed which periods of 15 days showed a significant difference in average distance travelled per day performing an ANOVA for each period, observing significant differences on 15 January (ANOVA, $F_{1,51} = 6.412$, $p < 0.05$), 31 May (ANOVA, $F_{1,86} = 5.898$, $p < 0.05$) and 31 October (ANOVA, $F_{1,157} = 12.85$, $p < 0.001$) (Fig. 2).

Grouping the distances travelled per day by days elapsed after release, we could see clear and significant differences between periods of 10 days (multifactorial ANOVA, $F_{13,1778} = 5.407$, $p < 0.001$), so that the activity was decreasing during the first 50 days post-release, and, then, increasing to initial values at about day 90. We have to keep in mind that, although there were individuals released in April or July, the majority was released in October (20 of 29 individuals), before hibernation.

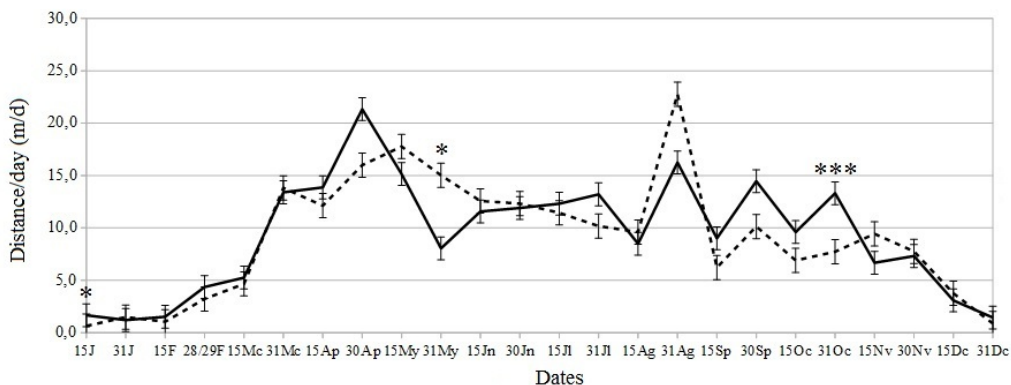


Figure 2: Representation of the mean and standard error of the movements per day every 15 days in males (continuous line) and females (dashed line). We represented the statistical significance (ANOVA) of the differences with asterisks: $p < 0.05$ (*), $p < 0.001$ (***).

Home range

The home range sizes recorded by the MCP method did not show significant differences between sexes nor between individuals released in April and October (Table 1). The same was with the home range sizes recorded by the kernel method, both for the kernel 90 and for the kernel 50 (Table 1). But, we observed a tight relation between the body size of an individual, considering its weight at release, and the size of its home range. Indeed, we could see significant correlations in home range size recorded by the MCP method (linear regression test, $F_{21,29} = 10.22$, $p < 0.01$) and by the kernel method in the case of the kernel 90 (linear regression test, $F_{21,29} = 5.926$, $p < 0.05$), with larger individuals having larger home ranges (Fig. 3). In the case of the kernel 50, which corresponds to the core area of the home range, we did not observe this correlation (linear regression test, $F_{21,29} = 3.358$, $p = 0.081$). The Spearman correlation test did not show a correlation between the number of locations and the size of the home range in any case: MCP ($\rho = 0.190$, $p = 0.384$), kernel 90 ($\rho = -0.201$, $p = 0.359$) and kernel 50 ($\rho = -0.182$, $p = 0.406$). The analysis of home range sizes during spring in consecutive years after release did not show significant differences between years (ANOVA for repeated measures, $F_{3,37} = 2.471$, $p = 0.117$).

Habitat use

The analysis of the percentage of locations in each type of habitat, considering the whole activity period [March – November] did not show differences in habitat use between different groups of individuals (sexes, weight classes and releasing cohorts) (Table 2). But, we observed differences in use of various types of habitats. The *post hoc* Tukey analysis showed that the habitat “scrub” had the most significant differences, being the most used (Table 3).

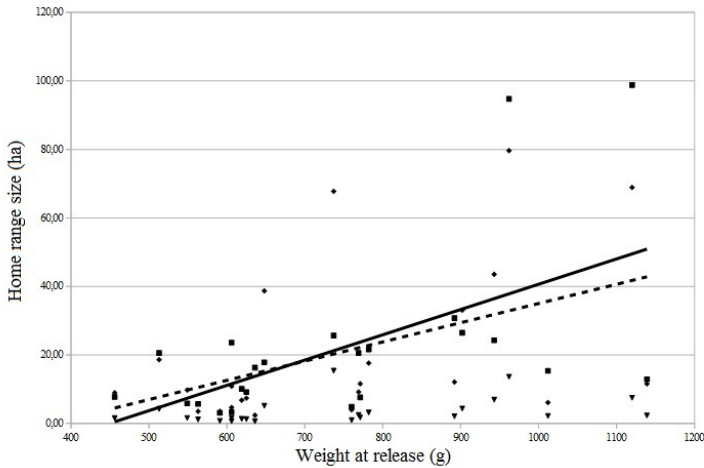


Figure 3: Representation of the correlation between the home range size and the body size of an individual, calculated by the MCP method (square points) and by the kernel method (rhomboids for kernel 90 and triangles for kernel 50) The continuous line represents the regression for MCP ($R^2 = 0.327$) and the dashed line represents the regression for kernel 90 ($R^2 = 0.220$).

Table 1: Means and standard deviations of home range size in hectares, calculated using the MCP method and the kernel method (at 90% and 50%), for the different groups of individuals. The results from the ANOVAs: degrees of freedom and sample sizes (DF/n), F statistics and significance levels (p).

	Males	Females	DF/n	F	p
MCP (100%) (ha)	12.5 ± 9.0	32.5 ± 32.5	1 23	4.226	0.052
Kernel 90 (ha)	16.2 ± 20.1	26.0 ± 26.1	1 23	1.017	0.325
Kernel 50 (ha)	2.9 ± 4.2	4.3 ± 3.7	1 23	0.717	0.407
	April	October	DF/n	F	p
MCP (100%) (ha)	35.0 ± 33.7	19.3 ± 23.1	1 21	1.436	0.246
Kernel 90 (ha)	35.2 ± 27.9	18.3 ± 21.7	1 21	2.039	0.170
Kernel 50 (ha)	5.9 ± 4.5	3.2 ± 3.8	1 21	1.791	0.197

During hibernation [December – February], we also did not observe significant differences between groups of individuals (Table 2) and the *post hoc* Tukey test showed again the habitat “scrub” had the most significant differences, being the most used (Table 3). For the mating period [March – May and August – September] and the nesting period [May – June], the results were very similar to those obtained for the whole activity period, without differences between groups of individuals and with similar results for the *post hoc* Tukey test.

Discussion

Movements

The activity period of the Hermann's tortoise is quite variable through its distribution range. In the Ebro delta, for example, the annual activity pattern for the whole population presents one peak during spring (Bertolero, 2002). The activity pattern we recorded presents two peaks, one in spring and another in August. Nevertheless, the hibernation period (from December to February) was the same as obtained in other populations (Bertolero, 2002).

Two peaks in activity pattern were also observed in Italy (Rugiero & Luiselli, 2006) and in the Ebro delta population (Bertolero, 2002). In the latter case, the two peaks correspond to differences between the sexes at the moment of maximal activity, the first peak corresponding to females and the second peak to males. Seasonal differences in travelled distances between sexes were also described in other tortoise species, for example *T. kleinmanni* (Geffen & Mendelssohn, 1988). But, in our study, we did not detect such a difference, although, there were some differences between the sexes. The only significant difference detected with biological sense is the observed at 31 May, because the major activity of females at this point can be associated with nesting. Hailey (1989), although with another subspecies (*T. hermanni boettgeri*), also found that the general movement patterns were similar between sexes, so the need of males to search for receptive females does not seem to have an effect on the activity level of males and vice versa.

Another possible explanation is that both peaks can be related to the mating behavior in general. Although detection of successful mating in the wild is quite rare, we can count mating attempts, which are observed more frequently. The mating begins just after the hibernation and lasts throughout the activity period (Bertolero, 2010). But the frequency of observed mating attempts is not homogeneous throughout the year, detecting two peaks which present variations between different populations (Bertolero, 2010; Celse et al., 2014). These peaks of mating attempts can be associated with an increased activity (i.e. movements). The two peaks do not necessarily have the same intensity. While it has been described in Corsica that the peak in spring is the most important (Nougarède, 1998), in Mauritius, the Peloponnese and the Ebro delta, the most important peak is in summer (Stubbs & Swingland, 1985; Willemsen, 1991; Bertolero, 2002). In our study, both movement peaks seem to have the same magnitude, although the spring peak lasts longer.

We suppose that released animals are initially highly active due to their need to explore the new environment and that the activity level decreases after a certain period (e.g. Muñoz & Thorbjarnarson, 2000, in crocodiles). Considering all monitored tortoises, we indeed, observed this trend. An unpublished study with the population in the Sierra de Irta Natural Park also provided a similar result, recording that the individuals' activity decreased after 90 days. But, in our case, performing the analysis taking into account the moment when each individual was released, we observed clear differences between the individuals released in October and the ones released in April

Table 2: Means and standard deviations of percentages of locations in each type of habitat for the different groups of individuals, considering the whole activity period [March – November] and the hibernation period [December – February]. The results from the ANOVAs: degrees of freedom and sample sizes (*DF*/*n*), *F* statistics and significance levels (*p*).

	March – November					December – February				
	Males	Females	<i>DF</i> / <i>n</i>	<i>F</i>	<i>p</i>	Males	Females	<i>DF</i> / <i>n</i>	<i>F</i>	<i>p</i>
<i>Mallaes</i>	13.1 ± 10.7	17.6 ± 16.4	1 29	0.243	0.626	5.2 ± 9.0	17.9 ± 36.9	1 29	1.308	0.263
<i>Scrub</i>	51.8 ± 22.6	49.6 ± 28.7	1 29	0.032	0.860	52.4 ± 41.5	51.6 ± 41.0	1 29	0.001	0.982
<i>Dunes</i>	19.9 ± 20.1	18.7 ± 25.8	1 29	0.001	0.977	14.7 ± 32.6	7.3 ± 18.7	1 29	0.444	0.511
<i>Forest</i>	12.6 ± 13.4	11.5 ± 20.7	1 29	0.663	0.423	15.1 ± 31.4	13.8 ± 25.2	1 29	0.007	0.934
<i>Other</i>	2.6 ± 4.1	2.5 ± 4.8	1 29	0.000	0.995	0.0 ± 0.0	1.7 ± 6.2	1 29	1.241	0.275
	<700g	>700g	<i>DF</i> / <i>n</i>	<i>F</i>	<i>p</i>	<700g	>700g	<i>DF</i> / <i>n</i>	<i>F</i>	<i>p</i>
<i>Mallaes</i>	14.7 ± 11.6	15.6 ± 15.4	1 29	0.028	0.869	5.9 ± 9.4	15.5 ± 34.8	1 29	0.574	0.455
<i>Scrub</i>	54.6 ± 24.5	47.3 ± 25.9	1 29	0.551	0.465	55.2 ± 37.5	49.2 ± 44.3	1 29	0.142	0.709
<i>Dunes</i>	21.3 ± 29.0	17.6 ± 14.7	1 29	0.002	0.961	12.1 ± 25.5	10.8 ± 29.3	1 29	0.142	0.908
<i>Forest</i>	7.7 ± 8.9	16.3 ± 21.1	1 29	1.289	0.266	12.6 ± 23.8	16.4 ± 32.7	1 29	0.093	0.762
<i>Other</i>	1.8 ± 3.6	3.3 ± 4.9	1 29	1.153	0.292	0.0 ± 0.0	1.5 ± 5.7	1 29	0.931	0.343
	April	October	<i>DF</i> / <i>n</i>	<i>F</i>	<i>p</i>	April	October	<i>DF</i> / <i>n</i>	<i>F</i>	<i>p</i>
<i>Mallaes</i>	11.7 ± 13.6	16.4 ± 14.1	1 27	1.049	0.316	0.0 ± 0.0	14.6 ± 30.2	1 27	2.233	0.148
<i>Scrub</i>	40.5 ± 33.3	52.5 ± 21.6	1 27	1.608	0.216	26.5 ± 36.5	57.5 ± 39.8	1 27	4.155	0.052
<i>Dunes</i>	31.3 ± 34.8	15.8 ± 16.8	1 27	1.956	0.174	4.8 ± 12.6	14.9 ± 31.4	1 27	0.504	0.484
<i>Forest</i>	16.1 ± 18.3	11.8 ± 16.9	1 27	0.228	0.637	22.7 ± 36.1	13.1 ± 26.8	1 27	1.076	0.310
<i>Other</i>	0.5 ± 1.2	3.4 ± 4.9	1 27	3.677	0.067	3.2 ± 8.4	0.0 ± 0.0	1 27	3.086	0.091

and July. At least in our study, this observed “releasing effect” can be considered as an artifact attributable to the normal phenology of the tortoises, because the individuals released in October (20 of 29 individuals) hibernate shortly after release. This result can be useful when planning future conservation projects since the moment of release could have an effect on the success of the project. In this case, we think it is more favorable to release the individuals in spring or early summer so they can investigate the new environment adequately and prepare themselves correctly for hibernation. But more investigation is needed to assess the effect on parameters like survival or body condition.

Home range

We did not find significant differences in home range size between sexes, agreeing with results obtained in other studies (Rozyłowicz & Popescu, 2013, in *T. hermanni boettgeri*; Vilardell-Bartino et al., 2015, in *T. hermanni hermanni*). Nevertheless, there are also studies which describe sexual differences in home range size (using the MCP method), for example, in an oak forest in north Italy where the females' home range (7.4 ha) was almost twice the size of the males' (4.6 ha; Mazzotti, Pisapia & Fasola, 2002).

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Table 3: Results of the *post hoc* Tukey test, showing the significance (p) of the differences in percentages of locations between different types of habitat in each group of individuals (only significant values $p < 0.05$), considering the whole activity period [March – November] and the hibernation period [December – February].

Group	Habitat type	March –	December –
		November	February
		p	p
Males	Scrub – Forest	<0.001	<0.01
	Scrub – Dunes	<0.001	<0.01
	Scrub – “Mallaes”	<0.001	<0.001
	Scrub – Other	<0.001	<0.001
	Dunes – Other	<0.05	
Females	Scrub – Forest	<0.001	<0.05
	Scrub – Dunes	<0.01	
	Scrub – “Mallaes”	<0.01	<0.05
	Scrub – Other	<0.001	<0.001
<700g	Scrub – Forest	<0.001	<0.001
	Scrub – Dunes	<0.001	<0.001
	Scrub – “Mallaes”	<0.001	<0.001
	Scrub – Other	<0.001	<0.001
	Dunes – Other	<0.05	
>700g	Scrub – Forest	<0.001	
	Scrub – Dunes	<0.01	<0.05
	Scrub – “Mallaes”	<0.001	
	Scrub – Other	<0.001	<0.01
April	Scrub – Other	<0.01	
October	Scrub – Forest	<0.001	<0.001
	Scrub – Dunes	<0.001	<0.001
	Scrub – “Mallaes”	<0.001	<0.001
	Scrub – Other	<0.001	<0.001
	“Mallaes” – Other	<0.05	

We have to remark that our values (12.5 ± 9.0 ha for males and 32.5 ± 32.5 ha for females) are considerably higher than the cited. In Mazzotti, Pisapia & Fasola (2002), where the values were also higher than other recorded home range sizes for *T. hermanni hermanni*, the authors associate this fact with a poor habitat. In our case this large home ranges could mean that the study area is not able to support a high number of individuals, and thus is not a favorable habitat for release. But, the areas in question differ strongly: the study area in Mazzotti, Pisapia & Fasola, (2002) is a coastal oak forest of about 1000 ha, characterized by warm and humid summers and cold and dry winters. Instead, our study area is characterized by warm and dry summers and cold and humid winters and the predominant vegetation is an aleppo pine forest. On the other hand, Longpierre, Hailey & Grenot (2001) indicated that a large home range size can also be associated with a more complex habitat. Given the multitude of different

environments in our study area, this could be a valid explanation. In a recent study (Slavenko et al., 2016) the authors analyzed different predictors of home range size in different species of tortoises and concluded that large home range sizes could also be explained by a low energy cost of locomotion. But we also have to take into account that our individuals were relocated, and thus could behave differently than the native ones. Rittenhouse et al. (2007), although with a different species (*Terrapene carolina triunguis*), found that relocated individuals had an increased activity, longer moving distances and larger home range sizes compared to native turtles. Our results could also be explained in this manner, but we did not detect a difference in home range size during spring in consecutive years (up to 4) after release, which would be expected as the individuals settle down.

An interesting result we obtained is that, independently of the method used for calculating the home range size, we observed clear differences according to the size of the tortoise. Indeed, we detected a significant relation between the size of a tortoise (considering its weight at release) and the size of its home range. This relation was not detected for core areas. Larger tortoises seem to have larger home ranges than smaller ones but with similar core areas. A possible explanation to this could be that the size of the home range is directly related to energetic requirements of the individual, as it was described before (e.g. Perry & Garland (2002) in lizards). As it has been described in other studies (Bertolero, 2002), the major part of the time the individuals are not active, remaining in the core areas, hiding under the vegetation, leaving their refuges only to satisfy their needs. Thus, larger tortoises have larger energy requirements and, in consequence, larger home ranges, with similar core areas. Although, a recent study (Slavenko et al 2016) showed that energy requirement in the case of ectotherm animals, specifically tortoises, is not a good predictor for home range size. Instead, other factors like the cost of locomotion act as major factors for predicting home range size. In our case, this would mean that the cost of locomotion in larger tortoises is less than the cost of locomotion in smaller tortoises in relation to their energy input. Further research is needed to clarify that.

In the context of the reintroduction project carried out, all this is interesting because for the establishment of a resident and self-sustaining population it is favorable that the released individuals have lower requirements and smaller home ranges. A similar statement is made by Attum et al. (2011) regarding the translocation of individuals of *T. graeca*. In this study, the authors released the individuals just before aestivation “forcing” them to spend time in the area. Also in Tuberville et al. (2005) the authors penned individuals of the gopher tortoise leading to a significantly increased site fidelity and smaller activity areas. There is no territoriality described in *T. hermanni*, their spreading throughout the area will be mainly determined by the availability of resources. Thus, in a first step, smaller individuals should be released, because they would, supposedly, move less. On one hand, this makes their tracking easier and more individuals can be released, but more important is that they will not spread widely to other habitats unless the habitat chosen for release is unfavorable. Once the tracking of these individuals shows that the habitat is favorable, larger individuals can be released to enhance their spreading throughout the area and expand the limits of the population so that all available resources in the area are used.

Our study did not include hatchlings, because all individuals were translocated, but personal observations indicate that the introduced individuals are reproducing in the study area. This is a good opportunity to describe movement patterns of hatchlings of a translocated population and record information about important aspects like the dispersal and behavior of those individuals. This has been done in other species, with very interesting results (see e.g. Pike, 2006, about gopher tortoise hatchlings). We suggest doing a similar study for *T. hermanni*.

Habitat use

The analysis of percentages of locations in each type of habitat, considering the whole activity period [March – November] did not show significant differences in habitat use between the groups of individuals we defined, but, we found that different types of habitats were used differently. “Scrub” was the most frequented by all groups (~50%), followed by “dunes” (~20%), “mallaes” (~20%) and “forest” (<20%). The “other” types of habitats were the least frequented (<10%), maybe because they are quite rare in the study area or because they are adverse habitats. Our results are similar to those recorded in other studies (Rugiero and Luiselli, 2006; Rozyłowicz & Popescu, 2013; Vilardell-Bartino et al., 2015). Del Vecchio et al. (2011) indicate that Hermann's tortoises look for small patches of desirable habitat, using the most part of the habitat only for locomotion. These patches are defined by the presence of five plant species (*Arbutus unedo*, *Arenaria serpyllifolia*, *Andryala integrifolia*, *Asparagus acutifolius* and *Smilax aspera*). The presence or absence of these or some other specific plant species in our defined macrohabitats could explain their different use, but more research is needed in our study site to confirm that.

Anadón et al. (2006b) indicate that ecological requirements such as food resources, places for egg laying or thermoregulation may not be important when trying to explain habitat use considering the entire annual cycle, but could be significant for particular periods. Thus, we applied the same procedure to different periods within the activity period (mating [March – May and August – September] and nesting [May – June]), but we did not find significant differences between the groups of individuals we defined. This is curious, because in other studies it has been described for example that females move from forest areas to more open areas to lay eggs (Stubbs & Swingland, 1985). But the cited study was carried out in higher latitudes. This could imply different behaviors due to colder temperatures, because the tortoises require more open areas with more insolation for nesting. Moreover, as said before, in our case and in general, the tortoises prefer more open areas during the whole activity period, so the females will also nest there (supported by personal observations of females nesting in this areas).

During hibernation [December – February] “scrub” was also the most preferred habitat (~50%), and, in general, there are no significant differences in the use of different habitat types compared to the activity period. In other studies it has been described that the tortoises tend to hibernate in more densely vegetated areas, given the major protection from predators and meteorological events (Stubbs & Swingland, 1985; Vilardell-Bartino et al., 2015). The fact that in our case we did not observe this behavior could indicate that the selective pressure induced by

predators like foxes or dogs is not very high and the meteorological conditions are mild enough to allow the hibernation in more open areas.

In conclusion, in future reintroduction projects the success of the project can drastically be increased choosing the correct habitat for the release, especially in areas with patches of clearly different habitats. Also temporal requirements have to be considered and the best moment for release has to be chosen (e.g. preactivation release). Finally, the animals that will be released, especially at the beginning of the reintroduction, have to be well selected and their body condition should be monitored in order to evaluate the success of the reintroduction. The correct combination of habitat, timing and condition [\pm (age, size, weight...)] of released individuals could significantly increase the success of the project overall.

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Discusión general y perspectivas

Los reptiles realizan funciones importantes en los ecosistemas, ayudando a mantener el equilibrio, principalmente a nivel trófico, promoviendo el flujo energético (actuando como presas y depredadores a la vez) o, en el caso de especies semiacuáticas, mejorando la interconexión entre el medio terrestre y el acuático (por ejemplo, Cortés-Gomez et al., 2015). La presencia humana ha alterado prácticamente todos los ecosistemas del planeta, induciendo un desequilibrio que en algunos casos está llevando a resultados catastróficos (por ejemplo, MacDougall et al., 2013). Además, en muchos casos, el bienestar de la población humana también está condicionado por el buen estado y funcionamiento de los ecosistemas (Ostfield & Hold, 2004; Pongsiri et al., 2009; Pecl et al., 2017). Un ejemplo es la Albufera de Valencia, donde la actividad humana ha provocado hace unas décadas una crisis ecológica importante (Soria, 2006), que también está repercutiendo en la población humana (Ferrando & Jambino, 2014). Probablemente esta fue la llama que encendió el interés de la sociedad de la zona para proteger, conservar y restaurar todos estos ambientes. Aunque el esfuerzo realizado desde entonces hasta ahora es importante, las medidas de conservación y seguimiento de fauna se han centrado sobre todo en aves (por ejemplo, Prosper & Hafner, 1996; Rodrigo et al., 2018) y, en menor medida, en otros grupos como peces (Blanco & Romo, 2006). El grupo de los reptiles pasó casi totalmente desapercibido y, de hecho, hasta la actualidad es desconocido cuáles son las especies realmente presentes y el estado de sus poblaciones o cómo afectan las medidas de conservación a este grupo de animales, porque la información que se tiene es escasa y bastante anticuada. Únicamente el subgrupo de las quelonios ha recibido atención en los últimos años, realizándose diversos proyectos de conservación, tanto de las tortugas acuáticas (Andueza & Alcayde, 2004; Campos-Such, 2016), como de la tortuga mediterránea (Vilalta, 2010).

Esta tesis aporta información básica sobre el estado de los reptiles en el Parque Natural de la Albufera de Valencia. En el Capítulo I se evidencia que algunas de las especies citadas en el parque, bien nunca estuvieron presentes (citas erróneas), bien ocupan áreas periféricas no muestreadas o bien ya se extinguieron de la fauna local. Los resultados también muestran que la diversidad de la fauna reptiliana se ve afectada por el grado de actividad humana, siendo las zonas menos antropizadas las más diversas. Esto está en consonancia con los resultados del Capítulo V, que muestra que la presencia humana también tiene un efecto negativo sobre el estado de las poblaciones y la condición corporal de los individuos de la culebra viperina (*Natrix maura*), lo cual es congruente con estudios similares realizados, por ejemplo, en el Delta del Ebro (Santos & Llorente, 2009). Las principales causas de este efecto negativo son aparentemente la mecanización de la agricultura, el aumento del tráfico de vehículos y el uso masivo de productos químicos, entre otras. En ambos capítulos también se evidencia la importancia que tienen las reservas biológicas. Estas reservas permiten a la fauna local refugiarse de la intensa actividad humana, de forma que incluso podrían ser un elemento clave a la hora de evitar la desaparición total de algunas especies. Sin embargo, actualmente actúan de forma aislada. Su potencial conservador se podría incrementar considerablemente creando una red de reservas interconectadas en el perímetro de la laguna central, el

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cual, con la vegetación palustre, también es la zona más favorable para los reptiles acuáticos, como se muestra en el Capítulo I.

Respecto las especies terrestres, en el Capítulo I se muestra que la zona más favorable para ellas es la Devesa de El Saler. Para los lacértidos representa prácticamente la única zona en la que hay condiciones para desarrollarse. Es un área que en el pasado estuvo muy alterada y donde, más recientemente, se hizo un gran esfuerzo para restaurar el aspecto natural y su funcionalidad ecológica (Olmos et al., 2014). Sin embargo, también esta zona padece de un importante grado de aislamiento. Aunque las especies de culebras puedan moverse por las áreas húmedas, lo que facilita la dispersión y la conectividad con otras poblaciones, los lacértidos no tienen esta posibilidad. La zona está rodeada de un ambiente prácticamente inhabitable para estas especies, lo que evita su dispersión e imposibilita el contacto con otras poblaciones. Esto a medio o largo plazo puede llevar a problemas de conservación graves (Madsen et al. 1996; Findlay & Bourdages, 2000; Díaz et al. 2005), relacionados principalmente con el deterioro genético, aunque se requieren estudios de esta índole para confirmarlo. Pero, además, la concentración de un alto número de individuos de especies ecológicamente muy similares, puede conllevar un alto grado de competencia tanto inter- como intraespecífica (Pafilis et al., 2009).

Efectivamente, los resultados de los Capítulos II y IV parecen soportar esta afirmación. En el Capítulo II se han encontrado diversos indicios de que la competencia ecológica puede alterar algunos aspectos de la dinámica poblacional de las especies de lagartijas. Las posibles alteraciones que se pudieron detectar son un avance de la época reproductora, un crecimiento más acelerado y un desequilibrio de la relación de sexos en favor de los machos. Dejando de lado el incremento en la proporción de machos, cuyos niveles de testosterona conllevan una mayor agresividad, las otras dos respuestas indican que el factor tamaño también juega un papel. La relación entre competencia y tamaño ya se ha descrito en el caso del gigantismo insular (Pafilis et al., 2009). De hecho, los resultados del Capítulo II parecen indicar que la competencia es especialmente alta en rangos de tamaños pequeños, lo cual es lógico ya que son los rangos en los que hay más individuos. Esto también es soportado por los resultados del Capítulo IV, en el cual se describe que existe un cambio ontogénico de la dieta en las tres especies y que los individuos pequeños son los que presentan una amplitud de nicho trófico mayor. La imagen general de los resultados del Capítulo IV parece mostrar que uno de los factores de mayor impacto a la hora de determinar la dieta de un individuo es la fuerza de mordedura. La combinación de los resultados de ambos capítulos parece apuntar a que la competencia ecológica a la que se ven sometidos los individuos se da principalmente a nivel trófico y que una manera de aliviar esta presión competitiva es aumentar lo más rápido posible la fuerza de mordedura para tener acceso a presas más duras y permitir un manejo general de las presas más eficiente (Verwajen et al., 2002). De forma que la fuerza de mordedura parece ser el elemento clave a la hora de determinar la competencia inter- e intraespecífica, teniendo repercusiones incluso a nivel de dinámica poblacional. Trabajos anteriores ya plantearon que la fuerza de mordedura tiene repercusiones sobre el nivel de competencia (Herrel et al., 1996). Con lo cual, sería un punto de inicio muy interesante para un estudio en el que se mida directamente la fuerza de mordedura y se relacione con otros aspectos de la ecología de las especies de la zona de estudio.

Esta tesis, además, ha aportado información básica sobre aspectos de la ecología de diferentes especies, en especial la lagartija colirroja (*Acanthodactylus erythrurus*) de la que en el Capítulo III se ha descrito de forma detallada el crecimiento y se ha estudiado qué repercusiones tiene sobre su dinámica poblacional. Los resultados de este estudio son muy interesantes ya que hacen ver la necesidad de reevaluar la información que se tenía hasta el momento sobre estos aspectos ecológicos de la especie. El crecimiento resulta ser bastante más acelerado de lo que se pensaba anteriormente (Busack & Jaksic, 1982), incluso dándole a la especie un carácter casi anual, lo que aumenta considerablemente su riesgo de sufrir extinciones locales por eventos estocásticos desfavorables (Jonsson & Ebenman, 2001; Jeppson & Forslund, 2012). Considerando los resultados de los Capítulos II y IV este crecimiento tan acelerado podría estar relacionado con el alto grado de competencia, por eso es necesario que se realicen más estudios en diferentes poblaciones a lo largo de la distribución geográfica de la especie, al igual que aplicar la misma metodología a otras especies.

En general, los Capítulos I a V hacen ver que la falta de información básica acerca de las poblaciones de reptiles presentes en el Parque Natural es un problema importante. Considerando que ya se ha realizado un gran esfuerzo para la conservación de la biodiversidad, cabría enfatizar la atención a este grupo de animales. De hecho, los reptiles, dada su estrecha relación con el medio ambiente (por ejemplo debido a su ectotermia) y sus limitadas capacidades de desplazamiento, son excelentes bioindicadores de la calidad ambiental, especialmente de las zonas húmedas al conectar el ambiente acuático y el terrestre, y también útiles para evaluar el éxito de las medidas de conservación tomadas (Lambert, 1997; Pleguezuelos et al., 2002; White & Burgin, 2004; Beaupre & Douglas, 2009).

Un buen ejemplo a seguir es el esfuerzo que se está realizando para la conservación de las tortugas. En los Capítulos VI y VII se evaluaron los dos proyectos de conservación que actualmente se están realizando en la zona de estudio. Los datos de radioseguimiento que se han obtenido de las tortugas no solamente han permitido afirmar que los trabajos están siendo exitosos, sino que también aportan información útil a la hora de gestionar estos proyectos, con el objetivo de maximizar el éxito. Al igual que en los Capítulos I y V, en el Capítulo VI se evidencia la importancia que tienen las reservas biológicas, en este caso prácticamente esenciales para poder controlar y monitorear las poblaciones de galápagos. Otro aspecto importante es que acercan estos proyectos a la sociedad general e incluso permiten que ayude activamente en el manejo de los mismos mediante voluntariados, seminarios, etc. El Capítulo VII, además, vuelve a mostrar la importancia de la Devesa de El Saler como punto caliente en la diversidad de reptiles de la zona. El hecho que incluso se haya podido detectar la reproducción de la tortuga mediterránea introducida en el área, muestra que el proyecto está siendo un éxito. Los datos de radioseguimiento obtenidos desde 2011, además son útiles a la hora de plantear y gestionar proyectos similares en otras zonas, ajustando el momento y la zona de suelta y el tamaño de los individuos que se liberan.

En conclusión, la tesis ha mostrado que el esfuerzo que se ha realizado para la conservación de la biodiversidad en el Parque Natural de la Albufera de Valencia es importante. Sin embargo, los reptiles pasaron desapercibidos

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demasiado tiempo, por lo que el principal problema que presenta este grupo de animales es la falta de información básica. Dado el papel de estos vertebrados en mantener el equilibrio de los ecosistemas y de su capacidad de servir como buenos bioindicadores, sobre todo de las zonas húmedas, es esencial que se realice un seguimiento de este grupo, aunque sea a nivel básico. Estos datos también son de interés científico, permitiendo mejorar las actuaciones de conservación y atrayendo la atención de científicos nacionales e internacionales. De forma que esta zona podría convertirse en una joya a nivel científico y un ejemplo a seguir en la conservación de la biodiversidad y los reptiles que forman parte de ella.

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Resumen ampliado

En las últimas décadas la actividad humana ha dejado huella en prácticamente todos los ecosistemas del planeta. El resultado de esta alteración es una importante pérdida de diversidad biológica (Hooper et al., 2005). Incluso se afirma que en la actualidad se está dando la sexta gran extinción (Barnosky et al., 2011). Esta pérdida de diversidad implica una alteración del funcionamiento de muchos ecosistemas e incluso un desequilibrio de los mismos (Hooper et al., 2005). En muchos casos esto también conlleva repercusiones negativas para el hombre (Pongsiri et al 2009; Pecl et al., 2017). Por ello la conservación de la biodiversidad es de suma importancia ya que la extinción de una especie es un proceso irreversible.

Llevar a cabo proyectos de conservación generalmente resulta ser un trabajo largo, complicado y costoso. Con lo cual, para su financiación muchas veces se requieren fondos públicos (Mansourian & Dudley, 2008), cuya inversión debe estar soportada por toda la población. El problema reside en que no todos los grupos animales presentan la misma imagen en la población en general (Czech et al., 1998; López & Barberá, 2011). En algunos casos la existencia de mitos urbanos y leyendas distorsionan la imagen de estos grupos y llevan a una aversión de la población frente ellos, independientemente de su importancia ecológica o incluso sus efectos positivos para el hombre. Uno de estos grupos es el de los reptiles, especialmente las serpientes. Aunque muchas especies de reptiles tengan efectos positivos para el hombre, como son las salamandras como insecticida natural o diversas especies de serpientes como control de plagas de roedores, su imagen es tan negativa que lleva a una persecución activa de estos animales y a un desinterés general por el estado de sus poblaciones. Esta falta de apoyo público también repercute en el interés de la comunidad científica (Czech et al., 1998), habiendo menos especialistas trabajando en este campo por la dificultad de financiación. Esto hace que, a día de hoy, todavía existan grandes incógnitas sobre aspectos básicos de muchas especies y que el estado de muchas poblaciones sea completamente desconocido.

En la zona de estudio, el Parque Natural de la Albufera de Valencia, el esfuerzo realizado para la conservación biológica en las últimas décadas es admirable: en 1982, la aprobación del Plan Especial de Protección del Monte de la Dehesa de El Saler, con el objetivo de recuperar y conservar el paisaje natural de la zona después de haber sido arrasada por el auge turístico; la declaración como Parque Natural en 1986; la inclusión en la lista de humedales RAMSAR en 1989 y en la Red Natura 2000; la creación, entre 2006 y 2011, de áreas de reserva para fomentar la conservación biológica y la mejora de la calidad del agua (Tancat de la Pipa, Tancat de Milia y Tancat de Illa), etc. Sin embargo, aún estando localizado apenas a 10 km de un centro urbano importante y albergando una diversidad extraordinaria de reptiles, se desconoce prácticamente cualquier aspecto de sus poblaciones. La información que se tiene en relación a los reptiles se limita básicamente a listas antiguas de especies presentes y algún trabajo científico suelto (Roca & Lluch, 1986; Guillén-Salazar et al., 2007). Esto es alarmante, ya que la

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antropización cada vez más intensa de los humedales (construcción de infraestructuras, desarrollo urbano, mecanización de la agricultura, uso masivo de productos químicos, introducción de especies exóticas, etc.) ha llevado a una importante alteración de estos ecosistemas (Soria, 2006; Ferrando & Jambrino, 2014). Los efectos negativos de estas alteraciones sobre los reptiles se pueden apreciar por ejemplo en el trabajo de Santos & Llorente (2009), donde se detectó una importante reducción en la abundancia de *Natrix maura*, uno de los reptiles más comunes de la fauna ibérica, en tan solo 13 años. Por ello se ha propuesto la realización de esta tesis, con el objetivo de evaluar el estado de los reptiles presentes en el Parque Natural y aportar una base para elaborar futuros proyectos de investigación y conservación de estas especies.

El primer objetivo que nos planteamos fue determinar qué especies realmente están presentes en la zona y cuál es su distribución, dado que desde el punto de vista de la conservación, conocer la distribución de las especies es esencial (Guisan et al., 2013). Por lo tanto, en el Capítulo I se evalúa cuáles son las especies presentes en el Parque Natural (considerando a parte las tortugas) y qué áreas son las más favorables y desfavorables para cada una de las especies. Para ello se construyó un modelo predictivo de distribución basado en los tipos de hábitats presentes en el área y la habitabilidad de cada uno de ellos para cada especie. Además, se realizaron censos periódicos en nueve puntos diferentes entre 2015 y 2018. Se pudo verificar la presencia de 10 de las 14 especies reptilianas citadas en el parque (obviando las tortugas). Como uno de los principales problemas de modelos de este estilo es el grado de arbitrariedad (Ray & Burgman, 2006), se intentó minimizar este efecto realizando una evaluación relativamente grosera (de tan solo cuatro categorías) del efecto sobre la habitabilidad y consultando en cada caso referencias bibliográficas para justificar la decisión tomada. Además, para dar un mayor peso al modelo y evaluar la verosimilitud de los resultados, se utilizaron datos de citas, de atropellos y de los muestreos para dibujar curvas de Característica Operativa del Receptor (ROC) (Newbold et al., 2010). Se calculó el área bajo la curva (AUC) para valorar el ajuste del modelo a la realidad. Aunque los datos utilizados para estas pruebas fueron totalmente esporádicos y no cubrían todas las cuadrículas, en todos los grupos salieron resultados positivos, a excepción de los geckónidos, cuyas características ecológicas hacen que el modelo no sea adecuado para predecir de forma fiable su distribución (McPherson & Jetz, 2007; Salvador, 2016).

El modelo de distribución mostró que la zona de más interés para los reptiles es la Devesa de El Saler, una franja de dunas móviles y dunas fijas con una vegetación arbórea de pino carrasco (*Pinus halepensis*) situada al noreste. Resulta ser el hábitat más adecuado para las culebras no acuáticas (*Malpolon monspessulanus* y *Zamenis scalaris*), aunque también se puedan encontrar en la zona de arrozales. Pero es especialmente importante para las especies de lacértidos, siendo prácticamente la única zona habitable para ellos. El mayor problema de esta área es su carácter aislado. Las poblaciones presentes no tienen posibilidad de entrar en contacto con otras poblaciones y esto podría llevar a medio o largo plazo a importantes problemas de conservación (Madsen et al., 1996; Díaz et al., 2005). Otra área de gran importancia, sobre todo de cara a las especies acuáticas, es el perímetro de la laguna central, el cual puede ser utilizado como corredor ecológico por algunas especies. Lo que remarca la importancia de fomentar la creación de áreas de reserva adicionales, en el mejor de los casos interconectadas entre ellas.

Viendo la situación de los lacértidos en la Devesa, en el Capítulo II se intenta evaluar el estado de sus poblaciones y si esta convivencia en un espacio tan reducido conlleva una competencia interespecífica, la cual podría llevar a alteraciones en determinados aspectos de la dinámica poblacional de estas especies (Werner & Gilliam, 1984). Para ello se realizaron muestreos periódicos en 2015 y 2017 en los que se anotaron todos los individuos vistos durante los censos de recorrido aleatorio de dos horas de duración. Además, se capturaron todos los individuos posibles para tomar medidas biométricas básicas. Los resultados obtenidos apuntan a que la competencia interespecífica es un factor que puede alterar la dinámica poblacional de las especies. Posibles respuestas que se detectaron incluyen un crecimiento más acelerado, un avance de la época reproductora y un decantamiento de la relación de sexos hacia los machos. Lo que se observa en estas respuestas es que el tamaño corporal parece jugar un papel importante, por lo que la competencia sería especialmente alta entre las clases de tamaño pequeñas. En el caso de la relación de sexos, la mayor agresividad de los machos aumenta la probabilidad de victoria en enfrentamientos interespecíficos. Sin embargo, también cabe tener en cuenta que la zona de estudio es un área con una alta presencia humana, especialmente el hábitat bosque es una zona muy transitada por bicicletas, coches e incluso buses, que conllevan una mortalidad por atropello adicional a la natural. Aunque los resultados comparando los años 2015 y 2017 muestran un ligero incremento en la abundancia de las tres especies, este no resulta ser significativo. En el pasado ya se ha descrito que la alteración humana de un hábitat dunar puede afectar de forma diferente a las distintas especies de lagartijas que habitan la zona (por ejemplo, Vega et al., 2000). Con lo cual habría que realizar estudios similares en otras zonas donde convivan las tres especies para poder discernir si los efectos descritos realmente son causados por la competencia, si son más bien un efecto local asociado a la actividad humana o si son producidos por otros factores ecológicos.

La especie de lagartija más abundante y claramente dominante del área es la lagartija colirroja (*Acanthodactylus erythrurus*). Por lo que se aprovechó la oportunidad de estudiar más específicamente la dinámica poblacional de esta especie. En el Capítulo III se describe por primera vez de forma detallada la curva de crecimiento de esta especie. Aunque en el pasado hubo un trabajo en el que ya se han descrito curvas de crecimiento de la especie (Busack & Jaksic, 1982), estas curvas se calcularon con datos de individuos preservados y no con datos de individuos vivos de la población. En nuestro caso, para obtener las curvas de crecimiento se utilizaron datos de recapturas de todo el rango de tamaños de la población. Con las variaciones de tamaño y el tiempo transcurrido entre cada captura se pudieron derivar tasas de crecimiento medio para los diferentes rangos de tamaños y dibujar así una curva de crecimiento. Los resultados muestran que el crecimiento resulta ser bastante diferente de lo que se había hipotetizado anteriormente, siendo considerablemente más acelerado de lo pensado (Busack & Jaksic, 1982). Este crecimiento tan rápido conlleva repercusiones importantes en la dinámica poblacional de la especie, otorgándole un carácter casi anual. Solapando las curvas de crecimiento con la nube de puntos de la población total se ha podido observar que más del 80% de la población se renueva cada año y que solamente una pequeña parte llega hasta la segunda primavera. Con lo cual, la mayoría de hembras se reproduce tan solo una única vez en su vida. Esto hace que la población sea bastante más susceptible a eventos catastróficos, y, en consecuencia, aumenta el riesgo de extinción local (Jonsson & Ebenman, 2001; Jeppson & Forslund, 2012). Además, indica que

existe una importante presión selectiva sobre el momento de eclosión.

Dado que uno de los factores más decisivos a la hora de determinar el grado de competencia que hay entre diferentes especies es el factor trófico, sobre todo entre especies que se alimentan del mismo grupo de presas (por ejemplo, Pacala & Roughgarden, 1982), otra característica ecológica de la población de lagartijas que se estudió fue su ecología trófica. En el Capítulo IV se describe y estudia detalladamente la dieta y aspectos de la ecología trófica, como la amplitud y el solapamiento de los nichos tróficos de cada una de las especies de lagartijas. Aunque existen trabajos en los que ya se estudia la dieta y la ecología trófica de las especies (Busack & Jaksic, 1982; Pérez-Mellado, 1982; Seva, 1984; Carretero & Llorente, 1991; Rouag et al., 2007) en ninguno de ellos se consideraron las tres especies en conjunto y las áreas de estudio fueron en la mayoría de los casos muy diferentes a la Devesa de El Saler. Con lo cual, para realizar el estudio se utilizaron muestras fecales tomadas durante los muestreos descritos en los capítulos II y III. Estas muestras fecales fueron estudiadas individualmente en el laboratorio con ayuda de una lupa binocular, identificando los grupos presa presentes en cada una de ellas. Los resultados mostraron, aún siendo las tres especies insectívoras, un cierto grado de reparto del recurso, tanto intercomo intraespecíficamente. Entre las tres especies destacó sobre todo el bajo solapamiento que hubo entre la lagartija colirroja y la colilarga (51.6%). *A. erythurus*, mostró, en general, ser la especie con la dieta más especializada de las tres, presentando una amplitud de nicho menor y una variabilidad intraespecífica muy reducida. Esto es coherente con trabajos anteriores (Seva, 1984). Su dieta se basa principalmente en Himenópteros, Coleópteros y Hemípteros. Sin embargo, aunque la notable tendencia a la mirmecofagia de esta especie ya fue descrita anteriormente (Pérez-Mellado, 1982; Seva, 1984), el consumo de hormigas parece ser especialmente importante en juveniles y menos en adultos. En general, en todas las especies se pudo evidenciar un cambio ontogénico en la dieta, habiendo un nivel de solapamiento de nichos tróficos mínimo entre los rangos de tamaño más grandes y más pequeños de cada especie. Una de las conclusiones más interesantes que se pudieron sacar de los resultados es que muchas de las tendencias y diferencias en la dieta observadas se pueden relacionar con la fuerza de mordedura, ya que una mordedura más fuerte permite el acceso a presas más duras y justamente este es el grupo que aumenta en la dieta de individuos más grandes. De forma que la fuerza de mordedura podría ser un factor clave a la hora de determinar el grado de competencia trófica entre las especies, lo cual sería coherente con los resultados mostrados en el Capítulo II.

Después del estudio detallado de la ecología de las lagartijas en los capítulos anteriores el foco de estudio pasó a centrarse en el ambiente acuático. La especie predominante, con diferencia, en este ambiente es la culebra viperina (*Natrix maura*). Siendo la especie reptiliana más representativa del área y considerando los resultados preocupantes en el Delta del Ebro mencionados anteriormente, se decidió evaluar el estado ecológico de esta especie en diferentes puntos del Parque Natural. La existencia de una serie de reservas biológicas en las que ya se están llevando a cabo proyectos de conservación, manejo y seguimiento de la fauna resultó ser un punto de partida muy interesante. Los efectos positivos de este tipo de reservas ya se habían descrito para varias especies animales (Reques, 2004; Sebastián-González et al., 2013; Rodrigo et al., 2018), sin embargo, en ningún momento se

tuvieron en cuenta las poblaciones de culebras. Por lo tanto, en el Capítulo V se estudia si estas reservas biológicas, en concreto los humedales artificiales Tancat de la Pipa, Tancat de Milia y Tancat de Illa, tienen también un efecto positivo sobre las poblaciones de *N. maura* y si este efecto positivo puede verse alterado por algunas características de estas reservas. Para ello, en 2015 y 2018 se realizaron muestreos periódicos en un total de 8 puntos diferentes (dentro y fuera de las reservas) realizando tanto censos de los individuos como tomando medidas biométricas básicas. Los resultados mostraron que reservas biológicas en un ambiente tan antropizado como es la Albufera de Valencia tienen un efecto muy positivo sobre las poblaciones de *N. maura*. Se pudo evidenciar que las poblaciones en el interior de las reservas son considerablemente más complejas, es decir, más individuos alcanzan tamaños mayores, que fuera de las mismas y que, además, los individuos presentan una mejor condición corporal. Especialmente los adultos fueron bastante más pesados en el interior de las reservas que fuera de ellas, considerando un mismo intervalo de tamaños. Esto puede estar relacionado con la disponibilidad de presas, la cual se espera que sea mayor dentro que fuera de las reservas. Pero también la actividad humana, el tráfico de vehículos, la siembra y siega mecánica del arroz, el uso de productos químicos, etc., podrían jugar un papel, evitando que los individuos alcancen tamaños grandes y ofreciendo una calidad ambiental general bastante baja en las zonas fuera de las reservas biológicas. Por otro lado, el tipo de reserva y su localización influyen en su capacidad conservadora de las culebras. Así, en el Tancat de Illa apenas se pudo detectar un efecto positivo, de hecho, la abundancia de culebras bajó significativamente entre 2015 y 2018. Algunos factores que pueden jugar un papel en este caso es que se trata de una reserva muy pequeña, de tan solo 16 ha, y que, además, se encuentra rodeada por una carretera muy transitada. También cabe decir que en ningún punto se pudo detectar un incremento significativo de la abundancia de culebras. Por lo tanto, se sugiere realizar un seguimiento anual o, al menos, plurianual de sus poblaciones para poder detectar a tiempo un declive y poder reaccionar debidamente.

Otro resultado interesante que se obtuvo en este estudio, es que no se pudo evidenciar una relación entre la abundancia de aves depredadoras y la proporción de individuos heridos de culebras. Como se ha mencionado anteriormente, los humedales artificiales tienen un efecto muy positivo sobre las poblaciones de aves, como garzas, cuyo número ha ido aumentando considerablemente en los últimos años (Garrido et al., 2012). Sin embargo, como estas aves depredan sobre culebras (Amat & Herrera, 1977; González & González-Solís, 1990) y se concentran en los humedales artificiales, estas zonas podrían tener un efecto incluso negativo sobre las poblaciones de culebras. Una posible explicación de no encontrar una relación entre estos dos hechos, podría ser debido a que la vegetación densa de las reservas aporta a las culebras suficientes refugios y posibilidades de huida ante sus depredadores. Aunque también cabe tener en cuenta que se midió la presión depredadora sobre las culebras como la proporción de individuos con colas rotas (intentos de captura fallidos), pero no se tienen datos sobre el número de intentos exitosos y un estudio que se centre en medir este número podría dar resultados bastante diferentes.

Finalmente, en los capítulos anteriores no se consideraron las tortugas dado que ya existen proyectos de conservación que se centran de forma específica en este grupo y uno de los objetivos de la presente tesis fue

evaluar el éxito de estos proyectos estudiando el patrón de desplazamientos, el dominio vital de los individuos y el uso de hábitat. El primer proyecto se presenta en el Capítulo VI, centrado en el galápagos europeo *Emys orbicularis*. En la península ibérica, la situación del galápagos europeo es muy alarmante. Las principales amenazas para sus poblaciones son la destrucción y fragmentación de su hábitat debido a una agricultura extensiva e intensiva, la construcción de infraestructuras y la urbanización (Cordero & Ayres, 2004). Además, la introducción de especies exóticas también representa un grave problema, sobre todo en el caso de la tortuga de Florida (*Trachemys scripta*) (por ejemplo, Pérez-Santigosa et al., 2013). En menor medida también es un problema la captura, bien para el consumo, bien para el mantenimiento como mascota, que afecta negativamente a las poblaciones ibéricas. Finalmente, las poblaciones que ocupan zonas húmedas temporales han sufrido el efecto de importantes sequías en los últimos años, sobre todo en aquellas zonas en las que se extrae agua para el uso agrícola de forma no sostenible (por ejemplo Fahd et al., 2009). Ante esta situación tan preocupante se han desarrollado varios proyectos LIFE a nivel europeo en los que, a nivel regional, se ha trabajado en la conservación de esta especie y su hábitat, y la erradicación de las especies invasoras, en especial el galápagos de Florida (Ayres et al., 2013).

Como parte de uno de estos proyectos, en el Tancat de la Pipa entre 2010 y 2015 se soltaron 14 individuos de galápagos europeo. Aunque el origen exacto de los individuos es desconocido, son individuos procedentes de la región, incluyendo también la zona sur del río Turia. Todos los individuos fueron entregados al centro de recuperación de la fauna de El Saler. Para poder hacer el seguimiento se les adhirieron emisores de radiofrecuencia y se localizaron periódicamente mediante antenas direccionales. Para el estudio de la actividad, se tomó la distancia media recorrida por día como un marcador de la misma; para el estudio del dominio vital, se calculó la extensión del dominio vital por el método Minimum Convex Polygon (MCP), con el 100% de los puntos y por el método Kernel, el área representativa al 90% y el área núcleo al 50%; y, finalmente, para el estudio del uso del hábitat se diferenciaron 6 tipos de hábitat y se asoció a cada localización el hábitat en el que se encontró. Los resultados mostraron que el Tancat de la Pipa es un lugar apropiado para la suelta de individuos de galápagos europeo y que un hábitat del tipo “filtro verde” parece ser el más óptimo para esta especie. Este hábitat se caracteriza por una vegetación densa formada por diferentes especies vegetales como *Paspallum* sp., *Juncus acutus* y *Scirpus maritimus*, además de carrizo y enea en las orillas y alguna zona puntual dentro de los filtros, y una profundidad del agua de unos 15-20 cm. En trabajos anteriores, hábitats de este tipo ya se han descrito como apropiados para la hibernación del galápagos europeo (Segurado & Araújo, 2004; Thienpont et al., 2004).

El segundo proyecto de conservación de tortugas realizado en el parque se presenta en el Capítulo VII y se centra en la tortuga mediterránea *Testudo hermanni hermanni*. Este proyecto se inició, junto con otros en diversos puntos de su distribución histórica y prehistórica (Soler et al., 2002; Bertolero et al., 2007; Mateo, 2011), en 2005 en la Sierra de Irtza en respuesta a que la tortuga mediterránea, y especialmente la subespecie *T. hermanni hermanni*, presentaba poblaciones naturales únicamente en Baleares y Cataluña (Soler-Massana, 1995; Llorente et al., 2002) y que se enfrentaba a toda una serie de amenazas, como pérdida y fragmentación de hábitats, incendios forestales,

caza furtiva para la comercialización, etc. (Pleguezuelos et al., 2002; Celse et al., 2014). Tras ver que el proyecto dio resultados muy positivos en esta área (Vilalta, 2010), se extendió a la Albufera de Valencia en 2011. El proyecto en sí consistió en la relocalización de individuos provenientes de centros de vida silvestre de Baleares. La introducción de individuos es una herramienta muy buena en la conservación de las especies y ya fue utilizada en el pasado en proyectos de conservación para revertir tendencias negativas en poblaciones naturales (Griffith et al., 1989) o, como en este caso, recuperar una población extinta (Heredia, 1992). Cada uno de estos individuos se marcó y se mantuvo en cautividad durante tres meses en la zona de suelta, que se corresponde con el cordón dunar de la Devesa de El Saler (suelta suave, Tuberville et al., 2005). Una vez transcurrido este tiempo los individuos se liberaron. A algunos de ellos se les adhirió un emisor de radiofrecuencia y se monitorearon periódicamente sus desplazamientos. En total se siguieron 29 ejemplares, cuyos datos fueron utilizados para realizar el estudio. Igual que en el Capítulo VI, se estudió el patrón de desplazamientos, el dominio vital y el uso de los diferentes tipos de macrohábitats de la zona.

Los resultados obtenidos muestran que el tamaño de un individuo está relacionado con el tamaño de su dominio vital, cuanto más grande es el individuo, más grande es su dominio vital. También, gracias a la introducción suave, que permite la aclimatación de los individuos antes de la liberación, los individuos una vez liberados siguen su patrón fenológico normal de actividad, es decir, no hay un efecto post-liberación. Finalmente, los resultados del uso de hábitat mostraron que esta especie prefiere zonas medianamente abiertas con una vegetación arbustiva y que evita zonas más húmedas o con una vegetación arbórea muy desarrollada. En conclusión, este estudio muestra que se puede incrementar el éxito de proyectos de introducción de tortuga mediterránea atendiendo al momento del año en el que se realiza la suelta, el tipo de hábitat en el que se liberan los individuos y el tamaño de los individuos liberados. Además, considerando que se ha podido observar la reproducción exitosa de la especie en la zona de estudio, se puede afirmar que el proyecto de reintroducción de la tortuga mediterránea en el Parque Natural de la Albufera de Valencia fue exitoso.

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Conclusiones

1. El modelo de distribución predictivo basado en la habitabilidad y la disponibilidad de los hábitats mostró que las zonas más favorables para los reptiles en los límites del Parque Natural de la Albufera de Valencia son la Devesa de El Saler (para las especies terrestres) y el perímetro de la laguna central, junto con las reservas biológicas (para las especies acuáticas).
2. Un gran problema para las poblaciones de reptiles es el grado de aislamiento y la falta de conectividad entre las zonas favorables. Este aislamiento es especialmente marcado para las poblaciones de lagartijas.
3. La competencia inter- e intraespecífica que se da en las poblaciones de lagartijas podría alterar la dinámica poblacional de las especies, adelantando la época reproductiva, acelerando la tasa de crecimiento y aumentando la proporción de machos.
4. Parece que la competencia entre las lagartijas se da principalmente a nivel trófico y la fuerza de mordedura parece ser un factor importante a la hora de determinar el nivel de competencia.
5. La lagartija colirroja es la lagartija con la dieta más específica de las tres estudiadas.
6. Existe una separación de nicho trófico entre la lagartija colirroja y la colilarga, al igual que un cambio ontogénico de la dieta en todas las especies.
7. Las reservas biológicas tienen un efecto muy positivo sobre las poblaciones de culebras, permitiendo el desarrollo de poblaciones más complejas y mejorando la condición corporal de los individuos.
8. Las características de las reservas biológicas, como su tamaño y su localización, influyen en su capacidad de favorecer las poblaciones de culebras.
9. El proyecto de conservación del galápago europeo realizado en el Tancat de la Pipa parece tener éxito. Siendo el hábitat más adecuado para la especie caracterizado por una vegetación palustre densa de diferentes especies de vegetales y una profundidad del agua de unos 15-20 cm.
10. El proyecto de reintroducción de la tortuga mediterránea realizado en la Devesa de El Saler es un éxito, habiéndose detectado incluso la reproducción de los individuos.
11. El éxito de un proyecto de reintroducción de la tortuga mediterránea se puede potenciar ajustando el momento

Conclusiones

de suelta, el hábitat de suelta y el tamaño de los individuos a soltar.

12. Es sumamente importante realizar un seguimiento de la fauna reptiliana en el Parque Natural, aunque sea a nivel básico, para poder detectar patrones negativos en las poblaciones y tomar medidas apropiadas a tiempo.

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Esto no es el final, solo es el principio de un camino mucho más largo. Es momento de poner un punto y final a este capítulo y seguir, trabajar para hacer este mundo un poco mejor.