Estudios sobre los efectos de perturbaciones ambientales en poblaciones animales mediante métodos analíticos y de simulación:

Testudo graeca como sistema de estudio

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Testudo graeca como sistema de estudio

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Studies on the effects of environmental disturbances in animal populations using analytical and simulation methods:
Testudo graeca as study system

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que da su conformidad a la lectura de la tesis doctoral presentada por Don Roberto Carlos Rodríguez Caro, titulada "Estudios sobre los efectos de perturbaciones ambientales en poblaciones animales mediante métodos analíticos y de simulación: *Testudo graeca* como sistema de estudio", que se ha desarrollado dentro del Programa de Doctorado en Análisis y Gestión Ambiental de este Departamento, bajo la dirección de Dr. Andrés Giménez Casalduero, Dr. José Daniel Anadón Herrera y la Dra. Eva Graciá Martínez.

Lo que firmo en Elche, a instancias de la interesada y a los efectos oportunos, a siete de julio de dos mil diecisiete.

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1. Resumen

Carmen López. Cuevas de Almanzora (Almería). 2014

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Las perturbaciones ambientales son uno de los principales motores de cambio de poblaciones, comunidades y ecosistemas. Aunque tales cambios son inherentes al funcionamiento de los sistemas naturales, el ser humano los ha incrementado y acelerado. En el contexto actual de cambio global, comprender los efectos de las perturbaciones naturales o antrópicas en la dinámica poblacional es fundamental para poner en marcha medidas adecuadas de protección de la biodiversidad.

Los ecólogos desarrollamos y aplicamos modelos para entender mejor el mundo que nos rodea. Esta modelización supone una simplificación y formalización matemática de la realidad observada, una manera de *traducir* en números los procesos y fenómenos que suceden en la naturaleza. Diferentes autores han propuesto un amplio abanico de criterios para la clasificación de los modelos ecológicos que, entre otros, pueden ser: estocásticos o deterministas, estacionarios o tempo-dependientes, a tiempo pasado o a tiempo futuro. También pueden ser clasificados como analíticos y de simulación. Los modelos analíticos están determinados por ecuaciones que utilizan datos empíricos para obtener parámetros que cuantifican el funcionamiento de los sistemas ecológicos. Los modelos de simulación generan sistemas artificiales que emulan sistemas reales y que pueden ser sometidos a experimentos de simulación.

Esta tesis comienza utilizando modelos analíticos y culmina empleando modelos de simulación de propio desarrollo. Con ellos se analizan los efectos de dos de las principales perturbaciones para las poblaciones animales en ambientes mediterráneos: los incendios, y la pérdida y fragmentación de hábitat. Se ha utilizado como sistema de estudio la población de tortuga mora (*Testudo graeca* L.) del sureste ibérico. La tortuga mora es representativa de especies amenazadas, de vida larga y baja dispersión. Está vinculada al paisaje tradicional mediterráneo, donde la estructura de los usos del suelo en mosaico favorece sus necesidades de termorregulación, refugio y alimento. Estos paisajes están muy amenazados por la pérdida y fragmentación de hábitat y, al mismo tiempo, por el incremento en la frecuencia de los incendios forestales. En concreto, en esta tesis se ha estudiado: i) la dinámica poblacional y la influencia de los factores endógenos de las poblaciones de tortuga mora (densodependencia), así como de factores exógenos (clima o incendios) (*Capítulos 1, 2 y 3*); ii) los efectos de los incendios en el crecimiento individual (*Capítulo 2*); iii) la estructura de la densidad de individuos en función del hábitat (*Capítulo 4*); y iv) la viabilidad poblacional en paisajes fragmentados con densidad baja y su relación con los patrones de movimiento y comportamiento (*Capítulo 5*). A nivel metodológico: v) se ha diseñado una aproximación basada en simulación inversa que permite estimar parámetros demográficos reduciendo los costes de muestreo (*Capítulo 3*); y vi) se ha desarrollado y aplicado un modelo de simulación basado en el individuo espacialmente explicito, para predecir la dinámica de las poblaciones bajo diferentes escenarios de cambio (*Capítulo 5*).

En el *Capítulo 1*, contenido en esta tesis, se ha estudiado la dinámica poblacional y la influencia de los factores endógenos de las poblaciones de tortuga mora (densodependencia), así como de factores exógenos (clima o incendios). Mediante modelos poblacionales clásicos de dinámica poblacional se ha determinado que los procesos densodependientes son muy relevantes en la dinámica de *T. graeca*. Además, en segundo orden, los factores exógenos como temperaturas extremadamente bajas durante el invierno y perturbaciones catastróficas como los incendios también influyen en la dinámica poblacional de la especie. Los procesos de densodependencia no se habían descrito anteriormente en otras especies del género *Testudo*. Trabajos previos sugieren que la densodependencia está regulada por desviaciones en el sex-ratio, pero este capítulo es el primer estudio que discute otros procesos como la competencia intraespecífica en relación a la regulación endógena de poblaciones de tortugas. Por su parte, aunque las temperaturas extremas durante el invierno modifican las tasas de crecimiento poblacional, no se puede llegar a concretar si afectan a las tasas de crecimiento poblacional máximo, o si están afectando a recursos esenciales como la comida o el refugio (capacidad de carga). Estudios previos señalan que la mortalidad de los individuos juveniles puede estar directamente relacionada con los inviernos muy fríos, y por lo tanto las tasas de reclutamiento y supervivencia de juveniles pueden disminuir notablemente durante hibernaciones a temperaturas muy bajas. Como la población de tortuga mora estudiada se encuentra en el límite norte del área de distribución, las temperaturas extremas del invierno podrían estar restringiendo el crecimiento poblacional o incluso la expansión de la especie. Un incendio ocurrido en el área de estudio, el otro factor exógeno analizado, tuvo un efecto negativo, directo y mantenido en el tiempo que redujo la capacidad de carga del sistema durante 9 años.

Con el fin de esclarecer el efecto de los incendios a escala de individuo, en el *Capítulo 2* se analizaron los patrones de crecimiento individual antes y después de la perturbación anteriormente analizada. Se observó una reducción en la tasa de crecimiento de los adultos, especialmente en los machos. Esto puede ser debido a que los requerimientos energéticos y físicos de machos y hembras son distintos, las hembras necesitan alcanzar un determinado tamaño para poder desarrollar las puestas de huevos. Por su parte, los machos no necesitan alcanzar un tamaño mínimo y son más pequeños que las hembras. A raíz de estos resultados se hipotetiza que los machos pueden comprometer su crecimiento en favor de otras demandas energéticas como mantener la actividad de campeo en la búsqueda de hembras. Por otro lado, mediante el análisis poblacional del crecimiento individual se pudieron obtener estimas de las tasas de supervivencia de los adultos antes y después del incendio. Tanto machos como hembras sufrieron un descenso en las tasas de supervivencia posteriores al incendio y que se mantuvo 4 años. Este descenso fue más pronunciado en hembras que en machos. Utilizando esta metodología solo se pudieron estimar las tasas de supervivencia de adultos, pero no las de juveniles y subadultos.

Para poder obtener estimas de todas las clases de edad antes y después del incendio, en el *Capítulo 3* se desarrolla una aproximación metodológica novedosa basada en simulación orientada a patrón. A partir de la estructura de edad de la población (el patrón observado) se estimaron los valores de supervivencia que mejor explicasen esa estructura estadísticamente. Los resultados son consistentes con los obtenidos por métodos clásicos, destacando valores muy altos en los adultos y subadultos, mientras que la supervivencia de los juveniles y las tortugas recién nacidas son bajos. Los efectos del incendio son mucho más acusados en los juveniles.

Por otro lado, también se han estudiado los efectos de la pérdida y fragmentación del hábitat. Para ello, en el *Capítulo 4* se ha calculado la densidad en función del hábitat a partir de muestreos utilizando las distancias de encuentros con el programa *Distance Sampling*. Tal y como planteaban trabajos previos, las densidades más altas de tortugas se encuentran en paisajes con una estructura en mosaico porque contienen lugares óptimos para la termorregulación, alimento y el refugio. Sin embargo, los pinares mostraron los índices más bajos de densidad debida a la elevada densidad de vegetación. Además, las diferencias entre los distintos pinares estudiados demostraron que los bosques maduros (con un mayor sotobosque y más denso) presentaban densidades próximas a cero, mientras que en los pinares claros la densidad de tortugas era mayor. Estos resultados parecen constituir un ejemplo paradigmático de como las reforestaciones en ecosistemas de matorrales mediterráneos semiáridos pueden tener un efecto negativo en la conservación de su biodiversidad.

Finalmente, en el *Capítulo 5* se ha integrado la información obtenida en los estudios anteriores y se ha desarrollado un modelo de simulación propio para obtener estimas de la viabilidad poblacional en paisajes fragmentados y su relación con los patrones de movimiento y comportamiento. Mediante este modelo basado en el individuo espacialmente explícito se ha determinado que tanto la fragmentación y pérdida de hábitat como las pautas de movimiento de los animales son determinantes en la viabilidad de las poblaciones de *T. graeca*. Estos resultados sugieren que los hábitats fragmentados amenazan la conservación de las poblaciones de la tortuga mora por efecto *Allee* en poblaciones de baja densidad. Además, se encontró que la dinámica poblacional es especialmente sensible a los patrones de movimiento y comportamiento. Las estrategias de búsqueda de conespecíficos para el apareamiento fue uno de los factores clave para la extinción de las poblaciones. La edad en la que los individuos juveniles empiezan a dispersarse también está directamente relacionada con la viabilidad poblacional. Las dispersiones tardías favorecen que los individuos se mantengan en áreas donde coexisten con otras tortugas, favoreciendo la reproducción. Por otra parte, se ha evidenciado que la plasticidad en los patrones de movimiento compensa los problemas que pueden encontrar las tortugas en los hábitats fragmentados. Los patrones de movimiento fijos a lo largo del tiempo acumulan efectos negativos como la sobredispersión de los individuos o el exceso de fidelidad a una determinada zona impidiendo la interacción con otros conespecíficos.

Los resultados de esta tesis muestran que perturbaciones como los incendios y la pérdida y fragmentación de hábitat afectan negativamente a la viabilidad de poblaciones de tortuga mora. Concretamente, los incendios tienen efectos directos y mantenidos en el tiempo. Los incendios son perturbaciones habituales en el sureste ibérico, pero el aumento en su intensidad o recurrencia podría aumentar la probabilidad de extinciones locales, especialmente en un contexto actual de cambio climático. Por otro lado, las principales causas de pérdida y fragmentación de hábitat se deben al desarrollo de infraestructuras, la intensificación agrícola y a las reforestaciones con pinar. Estos cambios de uso implican un descenso en la densidad de individuos. Además, la disminución de la conectividad entre las diferentes manchas del paisaje conlleva una reducción de las tasas reproductivas y, consecuentemente, la pérdida

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de la viabilidad poblacional. Especialmente destacada en las poblaciones de baja densidad.

Las aproximaciones metodológicas empleadas evidencian la idoneidad de los planteamientos integrados que combinan modelos analíticos y de simulación en la resolución de problemas ecológicos y de conservación. Además, este trabajo pretende ser punto de partida para futuras investigaciones. La aproximación propuesta para la estima de parámetros demográficos reduciendo los costes de muestreo, debe ser explorada en otros sistemas y con otros procesos. Por su parte, el modelo de simulación basado en el individuo servirá, entre otros, para evaluar el papel del cambio climático en la viabilidad poblacional, el efecto de cambios en la recurrencia e intensidad de los incendios a medio y largo plazo, o las consecuencias en la dinámica poblacional que pueden tener la creación de nuevas infraestructuras.

Esta tesis constituye una contribución notable para la comprensión de los efectos de las perturbaciones en poblaciones animales y para el desarrollo de metodologías novedosas que permitan abordar problemas ecológicos complejos. Además, desde un punto de vista de la conservación, evidencia la importancia de aplicar estrategias enfocadas a la protección del hábitat, conservando los paisajes tradicionales y su conectividad. De la misma forma, destaca la importancia de la gestión forestal por sus implicaciones para la conservación de la fauna (control de incendios y de reforestaciones).

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2. SUMMARY

Carmen López. Cuevas de Almanzora (Almería). 2014

Environmental disturbances are one of the main drivers of change in populations, communities and ecosystems. Although such changes are inherent in natural systems, humans have increased and accelerated them. In the current context of global change, understanding the effects of natural or anthropogenic disturbances on population dynamics is essential to develop appropriate biodiversity protection measures.

Ecologists develop and apply statistical models to understand the world. This modelling is a simplification and mathematical formalization of the reality, a way to *translate* the natural processes and patterns to numbers. Scientists have proposed a wide range of criteria for the classification of models, which may be stochastic or deterministic, stationary or time-dependent or focused on a future or past time. Models can also follow an analytical or simulation approach. Analytical models are determined by equations that use empirical data to obtain parameters to quantify populations. Simulation models generate artificial systems to emulate real ones and to develop simulation experiments.

In this thesis, I start using analytical models and, in the end, I use simulation models. The thesis analyses the effects of two of the main disturbances for Mediterranean animal populations: a) fires, and b) habitat loss and fragmentation. The selected study system is the spur-thighed tortoise population (*Testudo graeca*) in southeastern Spain. The spur-thighed tortoise is representative of endangered, long-lived and low dispersal species. *T. graeca* inhabits in the traditional Mediterranean landscape, where the configuration of the land use conforms mosaic landscapes. This habitat provides tortoises with the resources to cover their needs: thermoregulation, shelter and food. These mosaic-like landscapes are threatened by habitat loss and fragmentation, and by recurrent fires.

This thesis aims to assess: i) the role of the endogenous (density dependence) and exogenous factors (climate or fire) in the population dynamics of the spur-thighed tortoise (*Chapters 1, 2, 3*); ii) the effects of fires on individual growth (*Chapter 2*); iii) the role of different land-use type on the density of tortoises (*Chapter 4*); and iv) the changes in population viability in fragmented landscapes with low density and its relation with movement and behavior patterns (*Chapter 5*). To do so, this thesis develop v) a new approach based on inverse simulation to estimate demographic parameters reducing sampling costs (*Chapter 4*); and vi) a spatially explicit individual-based simulation model to predict the dynamics of populations under different scenarios (*Chapter 5*).

Chapter 1 shows the influence of endogenous factors of spur-thighed tortoise populations (density dependence), as well as exogenous factors (climate or fires) on the population dynamics. On the one hand, density-dependent processes are very relevant in the dynamics of *T. graeca*. These processes have not been previously described for other species of the genus *Testudo*. Previous works suggest that density dependence is regulated by deviations in the sex ratio, but this study is the first one to discuss other processes such as intraspecific competition in relation to the endogenous regulation of turtle populations. On the other hand, exogenous factors such as extremely low temperatures during winter and disturbances such as fires also influence the population dynamics of the species. Although extreme winter temperatures change population growth rates of the spur-thighed tortoise population, the effects are unknown. Extreme temperatures may affect the maximum population growth rates, or maybe, essential resources such as food or shelter (i.e. carrying capacity). Previous studies indicate that the mortality of juvenile individuals may be directly related to very cold winters, and therefore, juvenile recruitment and survival rates can be reduced during hibernation with very low temperature. The studied spur-thighed tortoise population is at the northern boundary of its range, thus, extreme winter temperatures may be restricting population growth or even species expansion. A fire event, the other exogenous factor analyzed, that eventually occurred in the study area had a negative, direct and maintained effect. One of its consequences was the reduction of the carrying capacity of the system during 9 years.

In order to clarify the effect of fires at the individual level, in *Chapter 2* the individual growth patterns were analyzed before and after the previously analyzed disturbance. There was a reduction in the growth rate of adults, especially in males. The energetic and physical requirements of males and females are different, as females need to reach a certain size in order to lay clutches. On their side, males do not need to reach a minimum size and are smaller than females. According to the results, we hypothesized that males can compromise their growth in favor of other energy demands such as maintaining the home range to search for females. Moreover, adult survival rates before and after the fire were estimated by means of the population analysis of the individual growth. Both males and females suffered a reduction in post-fire survival rates that was maintained for about 4 years. This decrease was larger for females than for males. Using this methodology, it was only possible to estimate the survival rates of adults, but not those of juveniles and subadults.

In order to obtain survival estimations of all age classes before and after the fire, in *Chapter 3* a novel methodological approach based on pattern-oriented simulation was developed. From the age structure of the population (the observed pattern), the survival values that best explained this structure were estimated statistically. The results are consistent with those obtained by classical methods, highlighting very high survival values in adults and subadults, while the survival of juveniles and newborn tortoises was low. The effects of the fire were much stronger for juveniles.

On the other hand, the effects of habitat loss and fragmentation were also studied in the thesis. In *Chapter 4*, the density of tortoises was calculated according to the habitat with the program Distance Sampling, by using the distances to encounters. The highest densities of tortoises were found in landscapes with a mosaic structure. These landscapes contain optimal locations for thermoregulation, food and shelter. However, the pine forests showed the lowest density values due to the high vegetation density. The different pine forests studied showed that mature forests (with greater and denser understory) presented densities close to zero, while in the clear pine forests the density of tortoises was higher. These results seem to be a paradigmatic example of how reforestation in semi-arid Mediterranean shrubland ecosystems can have a negative effect on the biodiversity conservation.

Finally, *Chapter 5* integrates the information obtained in the previous studies and uses a simulation model to obtain estimations of population viability in fragmented landscapes and

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their relationship with patterns of movement and behavior. By means of a spatially explicit individual model, both habitat fragmentation and loss and animal movement patterns were determinant in the viability of *T. graeca* populations. These results suggest that fragmented habitats threaten the conservation of spur-thighed tortoise populations by an *Allee effect* in low density populations. Population dynamics were especially sensitive to patterns of movement and behavior. Conspecific search strategies for mating were one of the key factors for the extinction of populations. The age at juvenile dispersal was also directly related to population viability. Late dispersions drove individuals to remain in areas where they already coexisted with other tortoises, favoring reproduction. On the other hand, it was evidenced that the plasticity in the movement patterns may compensate the problems that tortoises can find in the fragmented habitats. The fixed patterns of movement over time accumulate negative effects such as overdispersion of individuals or excessed fidelity to a given area preventing interaction with other tortoises.

The results of this thesis show that disturbances such as fires and habitat loss and fragmentation affect negatively the populations of the spur-thighed tortoise. Specifically, fires have direct and maintained effects over time. Fires are common disturbances in the Iberian Southeast, but in the current context of climate change, the increase in intensity or recurrence may drive tortoise populations to local extinctions.

The main causes of habitat loss and fragmentation in the study area are the development of infrastructures, the agricultural intensification, and pine plantations over the last century. These changes in land use seem to drive a decrease in the density of individuals. Moreover, the reduction in the connectivity between patches in the landscape entails a decrease in reproduction rates and a loss of population viability, especially in populations with low density.

The methodological approaches used in this thesis support the suitability of using integrated methods, which combine analytical and simulation models to solve ecological and conservation issues. These studies are a starting point for further research. The proposed approach to estimate demographic parameters reducing sampling costs should be explored in other systems and other processes. The individual based model can be useful to assess, among others, the role of climate change in population viability, the effect of changes in the recurrence and intensity of fires, or the consequences creating new infrastructures in the dynamics of animal populations.

This thesis constitutes a significant contribution to the understanding of the effect of disturbances in animal populations such as the spur-thighed tortoise, and for the development of novel methodologies to address ecological problems. It highlights the importance of developing conservation strategies focused on habitat protection, conserving traditional landscapes and their connectivity. The results of the thesis emphasize the importance of forest management (fires control and reforestations policies) and its implications for the conservation of the fauna.

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3. INTRODUCCIÓN

Instituto Geográfico Nacional. Lorca (Murcia). 2014

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Introduction

La Ecología (del latín “oikos” que significa casa y “logos” que hace referencia al estudio científico) se basa en el estudio de “la casa” en su concepto más amplio. Los ecólogos estudian el medio ambiente, que es casa y hogar de las diferentes especies y comunidades que conforman el planeta. Pero vivimos en un mundo cambiante, tanto el clima, como la tierra que pisamos o el océano que baña nuestras costas han cambiado a lo largo de los años y seguirán cambiando en el futuro (Dansgaard *et al.* 1993, Petit *et al.* 1999). Estos cambios ocurren de manera natural, pero durante los últimos siglos se han visto incrementados por la actividad del ser humano (Crowley 2000). Una especie que rápidamente colonizó el planeta, explotando los recursos disponibles hasta llegar a unos límites que cuestionan su propia persistencia (Hibbard *et al.* 2006).

Las nuevas corrientes científicas llaman a nuestra época el Antropoceno (Crutzen y Stoener 2000; CUADRO 1). Un periodo donde el ser humano ha modificado y sigue modificando drásticamente el medio ambiente a una velocidad inusitada (Hibbard *et al.* 2006). Los cambios antrópicos han dado lugar a una grave crisis ambiental con consecuencias como la desaparición de bosques (Foley *et al.* 2005), la acidificación de océanos (Fabry *et al.* 2008), el cambio climático (IPCC 2013) o la pérdida de biodiversidad, conocida como “la sexta extinción” (Barnosky *et al.* 2011).

Si bien es cierto que las extinciones se han ido produciendo a lo largo de la historia de nuestro planeta (Stanley 1986), el ser humano es el mayor responsable de los actuales procesos de extinción (Burney y Flannery 2005). La trasformación del hábitat, la contaminación y la sobreexplotación de especies y de los recursos, son las principales causas de la pérdida de biodiversidad (Millennium Ecosystem Assessment 2005, Malcolm *et al.* 20006, Root y Scheider 2006).

Para poner en marcha medidas que mitiguen esta pérdida de biodiversidad necesitamos comprender qué huella histórica ha tenido la humanidad (Fischer y Lindenmayer 2007). En el entorno Mediterráneo, catalogado como uno de los 25 puntos calientes de biodiversidad a nivel mundial (Myers *et al.* 2000, Cuttelod *et al.* 2009), las actividades humanas han transformando los paisajes desde la aparición de la agricultura en el Neolítico (Bottema *et al.* 1990, Mercuri *et al.* 2011). Técnicas como la quema, el corte, la limpieza, la construcción de terrazas y el pastoreo han sido desde entonces

CUADRO 1 – EL ANTROPOCENO

El concepto Antropoceno fue propuesto hace más de una década por Crutzen y Stoermer (2000) para identificar una nueva época geológica donde la influencia del ser humano en el medio ambiente era indiscutible. El término Antropoceno sugiere que 1) la Tierra se encuentra en las últimas etapas del Holoceno, y 2) las actividades humanas son, en gran medida, responsables de ese cambio.

El origen de este concepto se remonta a varias décadas atrás. Ya desde los años 70 surge cierta preocupación medioambiental tal y como se refleja en el libro *The Limits To Growth* (Meadows *et al.* 1972). Determinar el inicio del cambio de época es difícil, especialmente por las diferencias en la industrialización de los distintos países. Algunos autores marcan 1800 d.C. como inicio de este periodo. Mucho se ha discutido sobre esto, y no fue hasta 2016, en el 35º Congreso Internacional de Geología en Sudáfrica, cuando se acordó reconocer oficialmente el Antropoceno como una época geológica en la historia de La Tierra (Anthopocene Working Group; AWG)

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utilizadas para cultivar, y con el fin de establecer y mantener los pastizales (Barbero *et al.* 1987, Blondel y Aronson 1999). Estas actividades alteraron el paisaje natural y muchas especies se vieron amenazadas tanto por la pérdida de hábitat, como por la persecución directa (McClure 2013). Pero también sirvió para crear un paisaje en mosaico que ha provocado una reconfiguración de las comunidades biológicas, en muchos casos dando lugar a puntos calientes de biodiversidad asociados a estos paisajes manejados (Bignal y McCracken 1996). Sin embargo, por la velocidad y la magnitud de los cambios que vivimos actualemente en el Antropoceno, incluso estos mosaicos y las especies que los habitan peligran (Naveh 1998, Farina 2000, Underwood *et al.* 2009, Plieninger 2014). La urbanización, la creación de infraestructuras lineales, la intensificación y el abandono agrícola, las reforestaciones, o grandes catástrofes ecológicas como los incendios o las fuertes sequias comprometen cada vez más la conservación de la biodiversidad en todo el planeta (Puigdefábregas y Mendizabal 1998, Antrop 2000, Tscharntke *et al.* 2005, Lundström-Gilliéron y Schlaepfer 2003, Moreira y Russo 2007, Alrababah *et al.* 2007, Ruiz-Labourdette *et al.* 2012, Palombo *et al.* 2013). En esta tesis abordo el estudio de los efectos de las perturbaciones ambientales en la fauna. Concretamente, estudiaré los efectos de los incendios forestales (*Capítulos 1, 2 y 3*) y de los cambios de usos de suelo (*Capítulos 4 y 5*), que fragmentan y destruyen el hábitat, en la historia de vida y la demografía de las poblaciones de tortuga mora (*Testudo graeca Linnaeus,* 1758) en el sureste ibérico.

Sistema de estudio

La tortuga mora en el sureste ibérico

Los reptiles son considerados uno de los grupos taxonómicos más vulnerables. Las tendencias poblacionales indican su declive a escala global (Gibbon *et al.* 2000), siendo su principal amenaza la perdida de hábitat (Cuttelod *et al.* 2009). Concretamente, las tortugas de tierra, son especialmente vulnerables a perturbaciones en el hábitat por ser especies de vida larga y presentar bajas tasas de dispersión (Huey 1982). De hecho, de las 43 especies de tortugas terrestres existentes, 31 están amenazadas (UICN 2017). Además, otros problemas como el comercio ilegal o la tenencia en cautividad actúan de manera sinérgica afectando a la viabilidad de las poblaciones silvestres (Thorbjarnarson *et al.* 2000, Ljubisavljević *et al.* 2011).

La tortuga mora es una de estas especies amenazadas, se encuentra en regresión a escala mundial en la categoría de vulnerable (UICN 2017, CUADRO 2). *T. graeca* es una tortuga terrestre de mediano tamaño que habita paisajes áridos y semiáridos (Anadón *et al.* 2015). Aunque su área de distribución abarca principalmente el norte de África, buena parte de Oriente Medio y parte del este de Europa, también presenta poblaciones pequeñas y aisladas en el oeste de Europa (Graciá *et al.* 2017, Fig. 1). Entre éstas últimas, la población de mayor entidad se encuentra en el sureste ibérico, entre las provincias de Almería y Murcia (aprox. 4000km2; Anadón *et al.* 2007, 2010). Estudios genéticos sugieren que la especie colonizó el sureste de España desde el norte de África hace unos 20.000-30.000 años (Graciá *et al.* 2013a).

Las poblaciones del sureste ibérico se encuentran

CUADRO 2 – LA TORTUGA MORA, UNA ESPECIE AMENAZADA

A nivel europeo, la tortuga mora está incluida en los Anexos II y IV de la Directiva Hábitats (92/43/CEE), relativa a la conservación de los hábitats naturales y de la fauna y la flora silvestres. La directiva prescribe la declaración de Zonas Especiales de Conservación (ZEC), el desarrollo de planes de conservación, diagnósticos periódicos de su estado y fomento de la investigación (arts. 3, 17 y 18). A nivel nacional, el Catálogo Español de Especies Amenazadas también considera a la especie como ***vulnerable***. La legislación autonómica de Andalucía cataloga a la especie como ***en peligro***, mientras que La Región de Murcia y Baleares la consideran ***vulnerable***. Cabe apuntar que se trata de una especie bandera de los ecosistemas semiáridos litorales y prelitorales que habita, y que, además, actúa como especie paraguas ya que por su consideración en la Directiva Hábitats se han designado Lugares de Interés Comunitario (LICs) ligados a su conservación.

Especie bandera – Son especies carismáticas, que atraen la atención del conjunto de la sociedad (Noss 1990) y que sirven como símbolo de un lugar concreto obteniendo apoyo gubernamental o del público en general para el desarrollo de acciones de conservación (Isasi-Catalá 2011)

Especie paraguas – Especies características de un lugar que, con la conservación de su hábitat, ayudan a proteger a otras especies (Roberge y Angelstam 2004). Preservando paisajes que de otra manera no estarían bajo políticas de conservación. Estas especies también se usan para el establecimiento de corredores ecológicos entre áreas naturales separadas entre sí (Fleishman 2000).

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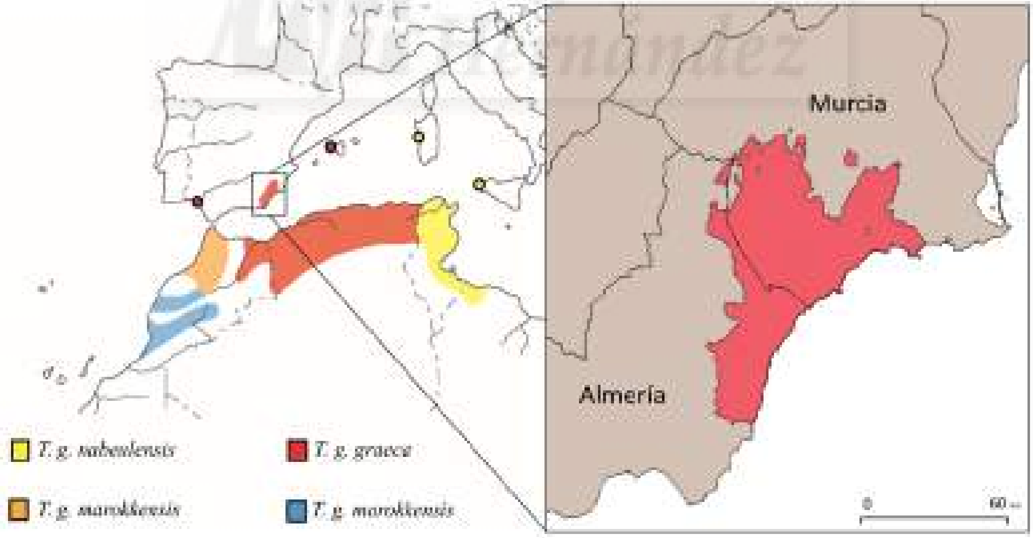

Figure 1. Distribución aproximada de las subespecies de tortuga mora (*Testudo graeca*), que habitan en el Mediterráneo Occidental y distribución de la subespecie (*T. g. graeca*) en el sureste ibérico.

asociadas a paisajes que presentan una estructura de vegetación abierta. Estos paisajes muestran una composición en especies muy variable en el área de distribución de la tortuga. En un extremo del gradiente ambiental aparecen zonas propias del límite del bosque, es el caso de pinares de pino carrasco (*Pinus halepensis*). En el otro extremo hay matorrales termófilos con influencia marítima como los cornicales *(Periploca angustifolia),* con especies como *Launaea arborescens*. En situaciones ambientales intermedias aparecen matorrales de composición variable, predominando los espartales (*Stipa tenacissima*) intercalados, por una parte, con matorrales más densos con una mayor representación del estrato arbustivo con espino negro (*Rhamnus lycioides*), lentisco (*Pistacia lentiscus*) o palmito (*Chamaerops humilis*) y, por otra parte, con matorrales menos densos representativos de estadios sucesionales intermedios como albaidares (*Anthyllis cytisoides*), acompañados de arbustos como romero (*Rosmarinus officinalis*) o jara (*Cistus sp*) y de caméfitos como (*Helianthemum almeriensis*, *Artemisia sp*., etc). También aparecen pequeñas manchas de cultivo de secano tradicional, principalmente almendro, olivo y cereal (Giménez *et al*. 2004). Estas manchas pueden constituir puntos de atracción, probablemente por contener abundancia de herbáceas y por ser un lugar adecuado para asolearse o realizar las puestas (Swingland y Stubbs 1985). Este tipo de paisajes representan un mosaico heterogéneo de usos de suelo al cual se asocian, a menudo, las densidades más altas de tortugas porque ofrecen refugio, alimento y lugares abiertos para la termorregulación (Anadón *et al*. 2005, 2006a, 2006b).

La población de tortugas del sureste ibérico ha sido estudiada a largo plazo con objetivos científicos y de conservación, principalmente por el Área de Ecología de la Universidad Miguel Hernández. Desde 1999 se han estudiado más de 100 lugares de muestreo repartidos por toda el área de distribución. Este seguimiento ha sido continuado en el tiempo en algunas localidades como en las “Cumbres de La Galera” en Lorca (Murcia), pero también se han realizado estudios puntuales cubriendo diferentes lugares durante distintos años que han servido para abordar diversos aspectos como su distribución y abundancia (Anadón *et al*. 2005, 2006b, 2009, 2010), selección de hábitat (Anadón *et al*. 2006a, 2007), patrones de crecimiento, actividad o de movimiento (Pérez *et al*. 2002, Anadón *et al*. 2012, Rodríguez-Caro *et al*. 2015), patrones genéticos (Graciá *et al*. 2011, 2013a, 2013b, 2017), problemas asociados a la tenencia en cautividad (Pérez *et al*. 2004, 2012, Anadón *et al*. 2007, Chávarri *et al*. 2012), o el efecto de los incendios (Sanz-Aguilar *et al*. 2011)

Las principales amenazas que afectan a esta especie y que están causando el declive de las poblaciones son: i) la modificación de los usos del suelo como la creación de nuevos regadíos o el desarrollo de infraestructuras urbano-turísticas (Giménez *et al*. 2001, 2006); ii) el incremento de la recurrencia de perturbaciones como incendios (Sanz-Aguilar *et al*. 2011); iii) los cambios en el clima y la aparición de condiciones climáticas adversas (como describieron Fernández-Chacón y colaboradores para *T. hermanni*; 2011); y iv) a la extracción de individuos silvestres por su consideración como animal doméstico (Pérez *et al*. 2004, 2012).

Incendios forestales

Los incendios forestales, tanto originados por causas

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antrópicas como naturales, son perturbaciones características de las regiones de clima mediterráneo (Pausas *et al.* 2008). Concretamente, el área de distribución de la tortuga mora se encuentra en uno de los climas más áridos de la península ibérica y es especialmente sensible a sufrir pequeños incendios forestales. Por ejemplo, según los datos del Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente del Gobierno de España, en la Región de Murcia, durante el periodo entre 1995-2015 han ocurrido 2764 incendios que han quemado 4598 ha. de superficie forestal, dando lugar a un bajo promedio de hectáreas quemadas por incendio (1.7 ha/incendio). La respuesta al fuego de las poblaciones animales es compleja (Russell *et al.* 1999), según Whelan y colaboradores (2012) los efectos de los incendios en la fauna se pueden clasificar en tres niveles. (a) De primer orden: efectos directos en la supervivencia de los individuos; (b) de segundo orden: efectos indirectos, mantenidos en los años posteriores debidos a las modificaciones que sufre el hábitat; y (c) de tercer orden: efectos evolutivos, que implican procesos de adaptación a la recurrencia de incendios.

En un contexto de cambio global donde se prevén cambios en la recurrencia o intensidad de los incendios (Pausas 2004), las consecuencias que estas perturbaciones pueden tener en especies como la tortuga mora pueden ser muy graves (Sanz-Aguilar *et al.* 2012, Couturier *et al.* 2014). Se han descrito efectos en la supervivencia, la reproducción, las capacidades de movimiento y en el *fitness* de las poblaciones de tortuga (Hailey 2000, Esque *et al.* 2003, Couturier *et al.* 2011,2014, Sanz-Aguilar *et al.* 2012, Santos y Cheylan 2013, Badiane *et al.* 2017).

Pérdida y fragmentación de hábitat

La pérdida de hábitat ha sido descrita como la principal amenaza para la biodiversidad (Brooks *et al.* 2002). En especies animales puede implicar mortalidad directa de individuos en el área afectada (Goss-Curtard *et al.* 2006), variaciones en sus tasas reproductivas (Pulliam y Danielson 1991), reducción del *fitness* (Garel *et al.* 2007), pérdida de diversidad genética (Dixo *et al.* 2009), o incluso alteración de los patrones de comportamiento (Anadón *et al.* 2012). Los efectos de la fragmentación son, sin embargo, menos evidentes. Se entiende como fragmentación la división del paisaje en manchas de hábitat de menor tamaño. Las consecuencias de los cambios en la estructura del hábitat pueden modificar los patrones de movimiento, afectando a la conectividad funcional de las poblaciones (Tischendorf y Fahrig 2000, Schooley y Wiens 2003) y aumentar probabilidad de entrar en vórtices de extinción (Wilcox 1985; Turner 1996, Fahrig 2003). Además, las poblaciones que se encuentran en paisajes perturbados son más vulnerables a otros factores de riesgo como puede ser el cambio climático (Opdam y Wascher 2004). La gravedad de las consecuencias de la pérdida y la fragmentación del hábitat depende en gran medida de la distribución de la población (Collinge 2009). La tortuga mora en el sureste ibérico, al encontrarse dentro de un rango de distribución reducido, resulta mucho más sensible a estos procesos que aquellas especies o poblaciones con rangos de distribución amplios (Lande 1993, Brown *et al.* 1996).

Durante las últimas décadas, en el sureste ibérico se está produciendo una notable intensificación del territorio debido a la creación de nuevos regadíos y al desarrollo urbano-turístico, principalmente en

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CUADRO 3 – CAMBIOS EN LOS USOS DEL SUELO

Usos del suelo en el área de distribución de la tortuga mora en el sureste ibérico según el CORINE (Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente) en 1990 y 2012. De su comparación se extrae que se han perdido zonas naturales, se han intensificado los cultivos de secano y se ha incrementado la urbanización especialmente en las zonas costeras y las zonas próximas a las autovías.

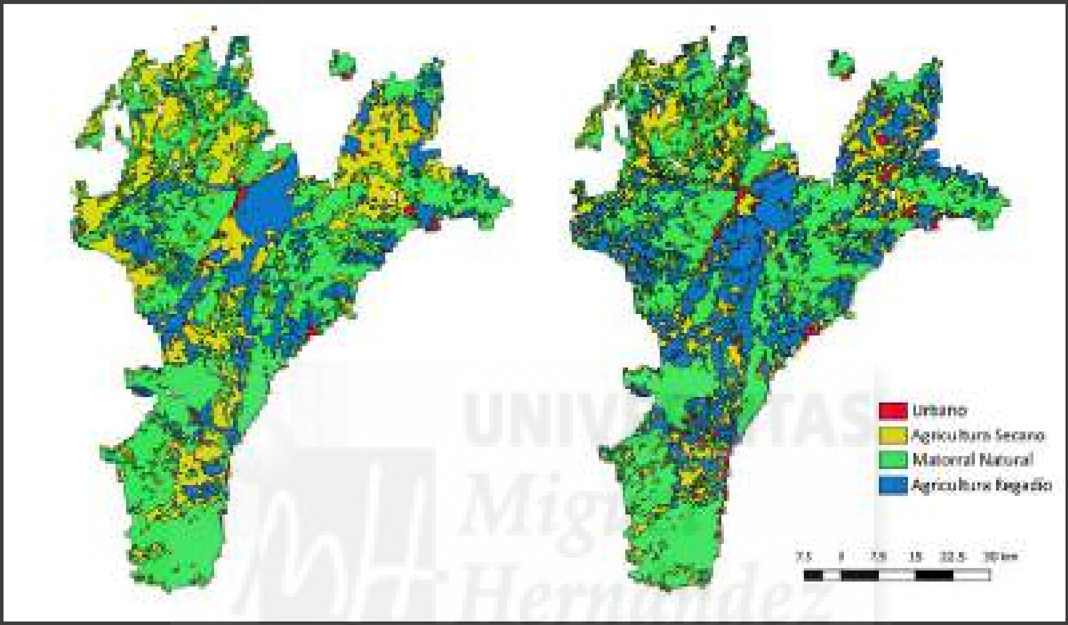

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Figura C3a. Mapa de usos del suelo de 1990 a la izquierda y de 2012 a la derecha.

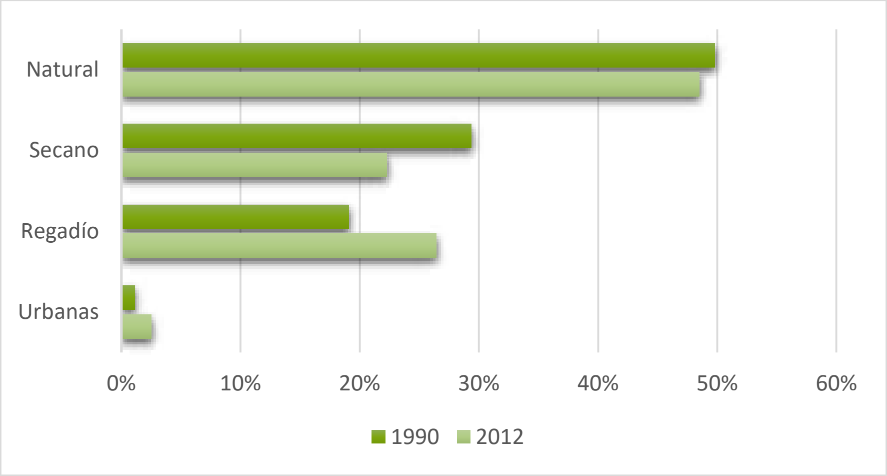

Figura C3b. Porcentaje de uso de suelo correspondiente a los dos años.

piedemontes y llanos (Giménez *et al.* 2001, 2006). Paralelamente, en las sierras y relieves del área de distribución se ha producido un fuerte proceso de éxodo y abandono rural, lo que ha generado la perdida de paisajes agrícolas mixtos. Sólo durante el periodo entre 1990 – 2012, los cambios de uso del suelo en el área de distribución de la tortuga mora en el sureste ibérico han supuesto una pérdida de 355 km^2 de hábitat. Este área equivale a casi un 8.7 % del total de la superficie de distribución de la tortuga en el sureste ibérico (CUADRO 3). Estos procesos son especialmente relevantes si se entienden dentro de una dinámica de intensificación del territorio creciente, sin previsiones de ralentización.

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El estudio de la historia de vida

La historia de vida de una especie comprende el conjunto de procesos relacionados con el desarrollo de los individuos desde su nacimiento hasta su muerte, y que determinan su dinámica poblacional (Stearns 1992). En ecología, el estudio de la historia de vida es una disciplina básica que permite desarrollar estrategias de conservación dirigidas a favorecer la viabilidad de las poblaciones (Lande 1988, Stearns 1992, Gibbon *et al.* 2000, Morris y Doak 2002, Williams *et al.* 2002, Sinclair *et al.* 2006).

Las variaciones en la dinámica poblacional están determinadas por las respuestas a factores ambientales (Stearns 1976, Congdon y Gibbons 1990, Roff 1992, Hellgren 2000). Identificar estos factores, ya sean de naturaleza biótica (interacciones intra o interespecíficas) o abiótica (perturbaciones, catástrofes o procesos climáticos) es esencial para estimar los parámetros clave que determinan el estado de una población, como las tasas de supervivencia, reproducción o índices de abundancia (Begon *et al.* 1996). Estas estimas permiten inferir dinámicas poblacionales, descifrar su pasado y predecir su futuro (Krebs 2001).

En el actual panorama científico, los trabajos sobre historia de vida de especies han sido relegados (McCallum y McCallum 2006) por otros que estudian los efectos del cambio global y las perturbaciones ambientales (CUADRO 4). Esto puede ser debido a que el conocimiento sobre historias de vida está muy avanzado o, por otro lado, a que el interés que suscitan los problemas relacionados con la actual crisis global es mayor. Cabe entonces preguntarse qué repercusión tendrá este cambio de enfoque que va en detrimento del conocimiento biológico de las especies, y cómo esto afectará a las políticas de conservación. La investigación básica debería, de algún modo, seguir siendo apoyada, porque brinda información en la que se soportan los estudios aplicados.

Esta tesis plantea la necesidad de fundamentar los análisis de los problemas derivados del cambio global mediante investigación en ecología básica. Este tipo de trabajos exigen la creación de marcos conceptuales adecuados, esfuerzo en trabajo de campo (seguimientos a medio-largo plazo) y el desarrollo de modelos. El coste de la realización y ejecución de estas tareas es muy variable y los recursos en conservación son siempre limitados. Los gestores deben optimizarlos en actuaciones que garanticen resultados (Myers *et al.* 2000). Grandes esfuerzos de muestreo para incrementar el número de individuos, problemas de detectabilidad imperfecta, especies crípticas o la necesidad de extensos periodos de monitoreo para especies de vida larga son algunos de los costes a los que hacer frente para obtener datos representativos (Congdon *et al.* 1994, Heppell 1998). La búsqueda de nuevos métodos para obtener información sobre la historia de vida es clave para la conservación de especies amenazadas, para entender su dinámica de cambio y para plantear medidas de gestión (Rossmanith *et al.* 2007, Wiegand *et al.* 2003, 2004).

CUADRO 4 – HISTORIA DE VIDA & CAMBIO GLOBAL

Busqueda en Scopus de conceptos claves relativos a la historia de vida, concretamente “*life history traits*” y “*survival rates*”. Se ha comparado la evolución de la aparición de estos conceptos frente a otros relacionados con perturbaciones, como pueden ser “*habitat disturbance*” o “*landscape fragmentation*” (estudiados en esta tesis). Para hacer esta comparativa se han usado los artículos indexados en *Agricultural and Biological Science* y en *Environmental Science*. La búsqueda de estos conceptos se ha efectuado en el título, resumen y palabras clave. Esta exploración evidencia un interés decreciente de las disciplinas relacionadas con el estudio de la historia de vida de los individuos.

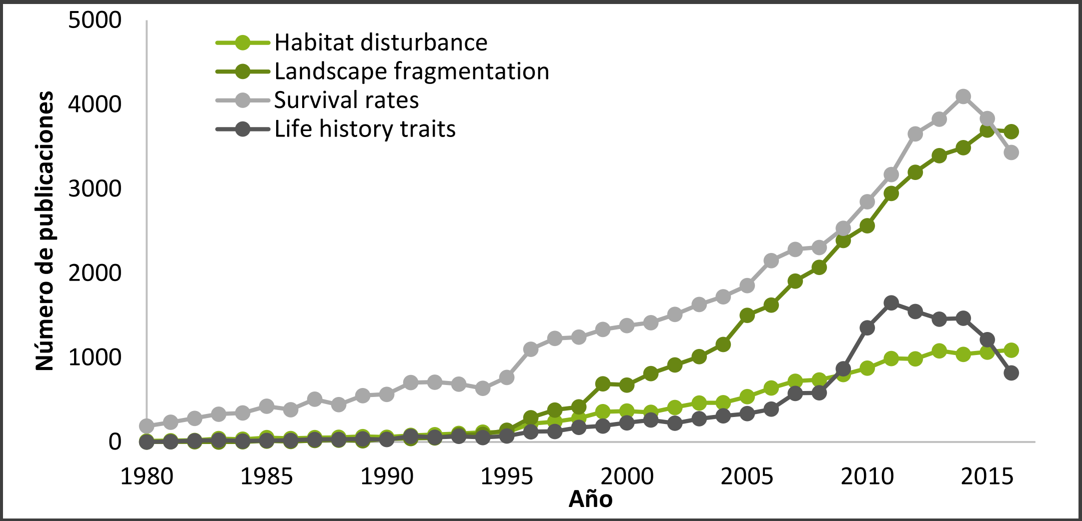

Figura C4. Número de publicaciones en el periodo 1980-2016, en las que aparecen las palabras clave identificadas en la leyenda (búsqueda realizada en mayo-2017 en la base de datos www.scopus.com.)

Integración de métodos analíticos y de simulación

Los modelos matemáticos permiten conocer, entender y predecir problemas en estudios ecológicos (Jorgensen, 1994, 2002, Blanco 2014). Son representaciones de la realidad mediante relaciones matemáticas y de cuantificación de los procesos o patrones observados en la naturaleza (Gertsev y Gertseva 2004). Como herramientas científicas permiten diagnosticar el estado de las poblaciones e identificar los parámetros clave para establecer medidas apropiadas de gestión (Morris y Doak, 2002; Norris 2004). Algunos de estos modelos necesitan mucha información de partida (Beissinger y Westphal 1998) y su grado de complejidad depende del objetivo para el cual se ha desarrollado el mismo (Kimmins *et al.* 2008). Debemos entender los modelos como una simplificación de la realidad para hacerla medible y comparable, porque como dijo Box y Draper (1987): "*Essentially, all models are wrong, but some are useful*"[1].

Existen diferentes criterios de clasificación de los modelos (Jørgensen y Bendorricchio 2001, Gertsev y Gertseva 2004). Según la temporalidad de las variables estudiadas podemos definir modelos estacionarios o tempo-dependientes. Pueden ser enfocados a entender el pasado o para realizar proyecciones futuras. Según su distribución en el espacio podemos clasificarlos según sean agrupados o distribuidos. En función de cómo ocurren los cambios en el tiempo podemos definirlos como discretos o continuos. Cuando los parámetros y variables de entrada de un modelo producen siempre el mismo conjunto de valores hablamos de modelos deterministas, mientras que cuando se incluye una componente aleatoria son modelos estocásticos. Si planteamos un modelo teórico y después se obtiene la información a partir de observaciones para validar el modelo se clasifican como dominantes o, por otro lado, si los datos observados se ajustan al modelo se identifican como modelos subdominantes. Finalmente, pueden clasificarse como analíticos y de simulación. Los modelos analíticos están determinados por ecuaciones que utilizan datos empíricos para obtener parámetros que cuantifican el funcionamiento del sistema. Los modelos de simulación, que también pueden ser llamados numéricos (Gertsev y Gertseva 2004), desarrollan sistemas artificiales que emulen situaciones reales y que pueden ser sometidos a experimentos de simulación. Estos modelos tienen una estructura más abierta y compleja, que permite representar procesos biológicos.

Modelos analíticos

Los modelos analíticos en esta tesis han sido utilizados para la descripción asuntos tan diversos como el crecimiento individual, calcular estimas de densidad, conocer los factores que afectan a la dinámica poblacional o calcular estimas de supervivencia. A continuación, detallo las particularidades de los modelos aquí empleados, siguiendo un orden creciente en términos de organización ecológica (de individuos a poblaciones).

Patrones de crecimiento individual: Aportan información sobre el estado físico de las poblaciones y sobre el *fitness* individual. Evalúan, en definitiva, la velocidad de crecimiento y el tamaño alcanzado. Existen diversas funciones para inferir patrones de crecimiento, pero todas derivan de la función de Richards (1959).

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[1] "Básicamente, todos los modelos son erróneos, pero algunos son útiles". Box, G.E., Draper, N.R. (1987). Empirical model-building and response surfaces (Vol. 424). New York: Wiley.

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$$S_t = S_\infty (1 - b e^{-kt})^{1/n}$$

El parámetro S_t es el tamaño individual a un tiempo *t*, S_∞ es el tamaño asintótico que alcanzan los individuos de esa población, *k* es la tasa de crecimiento constante, *b* es un parámetro asociado al patrón de crecimiento y finalmente *n* es el parámetro que determina la forma de la curva de crecimiento. Además, estos modelos no sólo describen el crecimiento de los individuos de una población, sino que además pueden ser utilizados para calcular estimas de supervivencia (Beverton y Holt 1956). Este método utiliza la media de los tamaños de los individuos de una población y los parámetros obtenidos en la ecuación de Richards (1959) para estimar las tasas de mortalidad.

$$Z = \frac{k(S_\infty^{-\frac{1}{n}} - \bar{X})}{\bar{X} - S_R^{-\frac{1}{n}}}$$

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El coeficiente *Z* es la tasa de mortalidad, $\bar{X}$ representa el promedio de tamaño de los adultos y S_R es el tamaño medio de edad de reclutamiento.

Estimas de abundancias o de densidad de poblaciones: Para la estima de la abundancia o de la densidad de las poblaciones de esta tesis, se ha utilizado Distance Sampling 6.2 (Thomas *et al.* 2010). Este modelo estima densidades en base a información de transectos lineales o puntuales. La clave radica en la estimación de la probabilidad de detección de los individuos en función de la distancia de encuentro de los mismos (CUADRO 5), teniendo en cuenta variables metodológicas, ambientales o estacionales (Marques y Buckland 2003). El método asume, entre otros, que los individuos a una distancia cero del observador son siempre detectados, y que los transectos deben ser realizados de manera aleatoria en el lugar de muestreo (Burham *et al.* 1980, Buckland *et al.* 2001). Posteriores mejoras del modelo han permitido aumentar la precisión en las estimas y flexibilizar algunas de las asunciones de partida (Marques *et al.* 2010, Buckland *et al.* 2009, Borchers *et al.* 1998).

Dinámica poblacional: Con información sobre la abundancia obtenida durante una serie temporal se pueden calcular estimas de la dinámica poblacional. Los modelos basados en la teoría de las dinámicas poblacionales son herramientas analíticas que

CUADRO 5 – PROBABILIDAD DE DETECCIÓN CON DISTANCE SAMPLING

La probabilidad de detección se obtiene utilizando la frecuencia de encuentros en función de la distancia perpendicular entre el observador y los animales encontrados. De esta manera la frecuencia de encuentros a distancias más largas va disminuyendo. Estas observaciones se ajustan a una curva de detección (línea roja). A partir del área bajo esta curva y el área total del máximo de encuentros que se obtendría con un cien por cien de detectabilidad, se calcula la probabilidad de detectar individuos en cada muestreo.

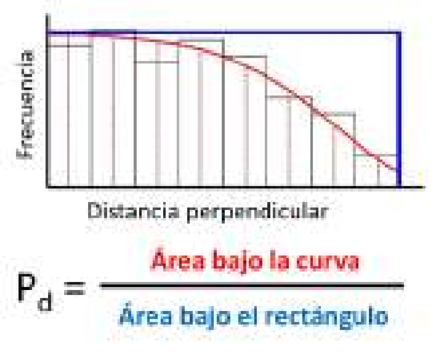

Figura C5. Ejemplo de curva de detección en función de la frecuencia de animales observados para el calculo de P_d (probabilidad de detección).

pueden ayudar a identificar las principales causas que condicionan las fluctuaciones de las poblaciones (Royama 1992, Berryman 1999). Reconocer el papel de los procesos endógenos (densodependencia) y exógenos (como el clima o las perturbaciones) en las tendencias poblacionales es uno de los principales objetivos de la ecología de poblaciones (Andrewartha y Birch 1954; Turchin 2003).

El estudio de las dinámicas poblacionales es esencial para construir y diseñar los análisis de viabilidad poblacional (PVA, Bessinger y Wetphal 1998, Noss, 1999, Morris y Doak 2002). A partir de los años 90 empezaron a utilizarse PVAs como herramientas para predecir el tamaño poblacional futuro, establecer las probabilidades de extinción y determinar el efecto de las perturbaciones (Leslie 1945, Boyce 1992, Beissinger y Westphal 1998, Coulson *et al.* 2001, Caswell 1989, 2001). Las aproximaciones para realizar los PVAs han evolucionado desde los tradicionales estudios que utilizaban como base las matrices de transición (Ferrière y Baron 1996, Caswell 2001) hasta los más novedosos modelos de simulación espacialmente explícitos basados en el individuo, donde la demografía interacciona con el movimiento, el paisaje o incluso los rasgos genéticos de las poblaciones (Hare y Deadman 2004, DeAngelis y Mooij 2005, Currat *et al.* 2004, Revilla y Wiegand 2008, Bodeci *et al.* 2014).

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Modelos de simulación

En esta tesis se ha desarrollado un modelo orientado a patrón para la obtención de parámetros demográficos y un modelo espacialmente explícito basado en el individuo para analizar la viabilidad de las poblaciones.

Modelos orientados a patrón: Tradicionalmente, para estimar los rasgos de vida se han diseñado estudios sobre el terreno que dan lugar a estimas directas de los parámetros poblacionales de interés. Pero también se pueden utilizar los patrones observados en la naturaleza para estimar de forma indirecta qué parámetros o procesos han generado esas observaciones. Este tipo de aproximaciones se conoce como modelos orientados a patrón (CUADRO 6). El uso de patrones para seleccionar parámetros y procesos se ha utilizado ampliamente en varias áreas de la ciencia como hidrología, geología, oceanografía o climatología (Tarentola 1987, Gottlieb y DuChateau 1996; Wunsch 1996; Bennett 2002) y durante los últimos años también en los estudios de ecología (e.g., Wiegand *et al.* 1998, 2004, Revilla *et al.* 2004, Kramer-Schadt *et al.* 2007, Hartig *et al.* 2011; Martínez *et al.* 2011, 2016, Anadón *et al.* 2012, May *et al.* 2015).

Grimm y colaboradores (1996) expusieron que "*the most successful models were those that took their orientation from [such] distinct patterns in nature*"[1]. Estos autores definieron el "patrón" como una clara e identificable estructura en la naturaleza. Los patrones son el resultado de la interacción de diferentes procesos ecológicos que integran factores endógenos, como la dispersión o supervivencia, y factores exógenos, como las variaciones climáticas o perturbaciones (Wiegand *et al.* 2003). Por este motivo, se puede concluir que los patrones contienen una gran cantidad de información aparentemente "oculta" del sistema de estudio (Wiegand *et al.* 2003). El modelado inverso o modelo orientado a patrón optimiza la relación entre los datos observados en la naturaleza y los resultados obtenidos por simulaciones. Por un lado,

---

[1] "Los mejores modelos son aquellos que toman su orientación de [semejante a] los diferentes patrones de la naturaleza". Grimm, V, *et al.* (1996). Pattern-oriented modelling in population ecology. Science of the Total Environment, 183(1-2), 151-166.

todas las combinaciones posibles de parámetros son simuladas hasta encontrar la parametrización que mejor representa los patrones observados en la realidad (Wiegand *et al.* 2004). Por otro lado, los modelos alternativos con distintos procesos pueden ser comparados para determinar qué proceso es capaz de representar mejor la realidad observada (Railsback 2001, Railsback y Harvey 2003). De esta manera, los parámetros y procesos que obtengan los resultados más similares a los patrones observados serán los se utilicen para representar ese sistema.

Trabajos recientes proponen nuevas aproximaciones utilizando esta metodología para calcular parámetros demográficos. Por ejemplo, Zipkin y colaboradores (2014) integran modelos basados en simulación inversa u orientado a patrón (Kramer-Schadt *et al.* 2007) y estructuras poblacionales a través de *N-mixture* models (Carroll y Lombard 1985, Royle 2004).

Modelos basados en el individuo espacialmente explícitos: Otro tipo de modelado de simulación que está

CUADRO 6 – MODELOS ORIENTADOS A PATRÓN

(A). Los modelos convencionales (aquellos que no están orientados a patrón) basan su trabajo en estudios sobre el terreno y apoyo bibliográfico para construir un modelo que nos ofrecerá unas estimas que describan el funcionamiento del sistema. Pero esta aproximación es unidireccional y favorece que los errores se acumulen a lo largo de la investigación de una manera difícil de evitar. (B) En el modelado orientado a patrón las hipótesis sobre los parámetros y los procesos están directamente vinculadas al patrón inferido de los datos observados. Este patrón es comparado con todos los datos simulados a través de diferentes hipótesis, seleccionando finalmente los parámetros y procesos que generan datos similares a los datos observados. De esta manera se minimiza la propagación de errores a través del diseño de estudio.

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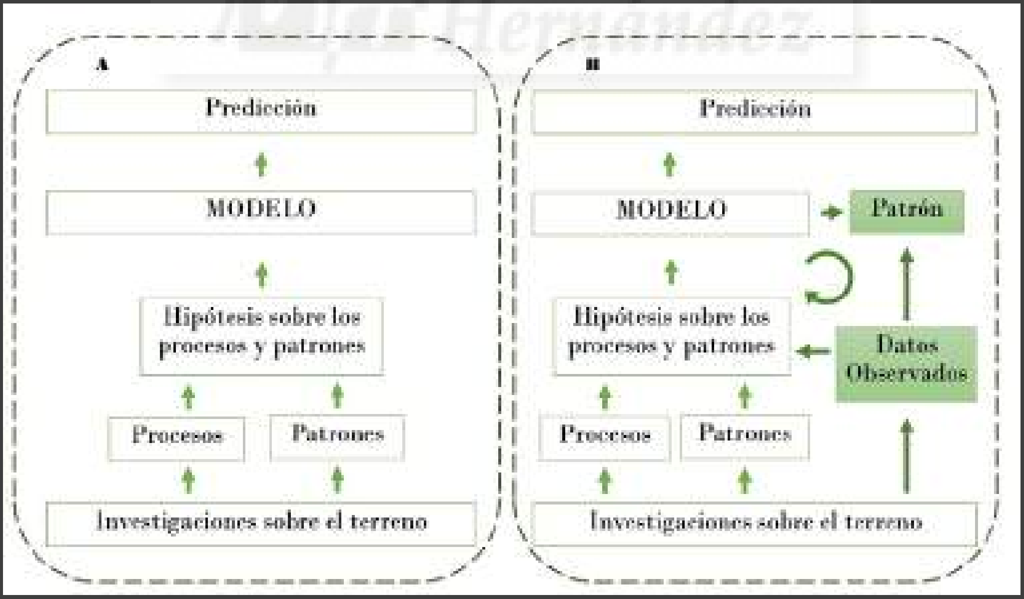

Figura C6. Figura extraída y modificada del trabajo de Wiegand y colaboradores (2003), donde se hace una comparación entre la propagación de errores que se pueden dar en un modelo tradicional (A) y en otro modelo orientado a patrón (B).

teniendo mucho éxito para abordar la dinámica poblacional y su relación con el paisaje es la fundada en los modelos espacialmente explícitos basados en el individuo (IBM; Wiegand *et al.* 1999, Wiegand *et al.* 2005, Grimm y Railsback 2005). Los IBMs simulan variabilidad individual en demografía y dispersión, que puede incluso llegar a ser heredable o dependiente del ambiente que le rodea. Estos modelos permiten también modelar escenarios donde los censos sobre el terreno no son posibles (p.e. tienen baja capacidad de detección o el número de individuos es demasiado bajo para obtener muestras representativas). Además, ofrecen la posibilidad de estudiar el efecto que puede tener el comportamiento y los movimientos de los individuos en la viabilidad de las poblaciones. Este hecho es muy importante para evitar la sobreestimación que podrían dar lugar los modelos demográficos clásicos (Clark *et al.* 2001). En estos modelos clásicos, una población con una tasa de crecimiento positiva siempre va a crecer. No obstante, en las poblaciones reales (al igual que en ejercicios de simulación) puede que no ocurra así. Por ejemplo, si no suceden eventos reproductivos por la falta de interacción entre los individuos (debida a otras causas como la fragmentación del hábitat), si hay cambios en las tasas de supervivencia en función del espacio (lugar con mayor riesgo a ser depredados o fuentes de recursos) o si los patrones de movimientos alteran las tasas de supervivencia o reproducción.

Desde un punto de vista teórico, esta aproximación está permitiendo un mejor entendimiento de las consecuencias de la pérdida y fragmentación del hábitat (Grimm y Railsback 2005, Wiegand *et al.* 2005). Estos modelos permiten conectar procesos ecológicos esenciales como pueden ser demografía, genética y movimiento con el hábitat en el que se encuentran. Además, son especialmente adecuados para evaluar las tasas de dispersión o conectividad entre diferentes tipos de paisajes (Revilla *et al.* 2004, Nathan *et al.* 2008, Kramer-Schadt *et al.* 2011, Clobert *et al.* 2012).

El estudio de los patrones de movimiento en función del hábitat mediante modelos de simulación espacialmente explícitos ha sido reconocido como un factor clave para entender la estructura espacial de las poblaciones y metapoblaciones (Revilla *et al.* 2004, Revilla y Wiegand 2008), así como para comprender el efecto de las expansiones o contracciones de las especies (Kramer-Schadt *et al.* 2004, 2011), el patrón de infección de enfermedades en las poblaciones (Kramer-Schadt *et al.* 2009), los efectos de las perturbaciones en las estrategias de movimiento (Anadon *et al.* 2012) o la efectividad de corredores ecológicos para conectar poblaciones en paisajes fragmentados (Kanagaraj *et al.* 2013).

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Objetivos y estructura de la tesis

El objetivo de la tesis doctoral es analizar los efectos de los incendios, así como de la pérdida y fragmentación de hábitat en poblaciones animales, utilizando como sistema de estudio la tortuga mora en el sureste ibérico. Con el fin de llevar a cabo este objetivo general se han planteado los siguientes objetivos específicos:

i. Analizar la tendencia poblacional para determinar los factores endógenos y exógenos que condicionan la dinámica poblacional.

ii. Evaluar los efectos de los incendios en el crecimiento individual.

iii. Estudiar la densidad de los individuos en función del hábitat.

iv. Analizar la viabilidad poblacional en paisajes fragmentados con densidad baja y su relación con los patrones de movimiento y comportamiento.

Además, esta tesis pretende aportar nuevas herramientas para el estudio de especies amenazadas. Por ello, a nivel metodológico se ha planteado los siguiente objetivos:

v. Proponer una aproximación basada en simulación inversa que permita estimar parámetros demográficos reduciendo los costes de muestreo.

vi. Desarrollar un modelo de simulación basado en el individuo espacialmente explicito para predecir la dinámica de las poblaciones bajo diferentes escenarios de cambio.

Esta tesis se estructura en cinco capítulos que abordan los objetivos planteados utilizando diferentes aproximaciones metodológicas (Tabla 1). Para ello se han utilizado datos del seguimiento de diferentes poblaciones al norte del área de distribución (Figura 2), obtenidos desde 1999 hasta 2013 e información bibliográfica sobre esta población derivada de estudios anteriores.

Tabla 1. Características de cada uno de los capítulos de esta tesis identificando: perturbación estudiada, tipo de modelo, objetivo específico que aborda y origen de los datos utilizados. *N* = número de individuos. Las localidades de estudio están representadas en la Figura 2.

Capítulo	Método	Perturbación	Tipo de modelo	Objetivos	*N*	Serie temporal	Localidades de estudio
1	Modelo de crecimiento poblacional	Incendio	Analítico	i	593	1999 - 2013	Galera
2	Modelos de crecimiento individual	Incendio	Analítico	i y ii	168	2000 - 2009	Galera
3	Matrices de transición y modelos orientados a patrón	Incendios	Simulación	i y v	270	2003 y 2009	Galera
4	Muestreo por distancias	Fragmentación	Analítico	iii	251	2012	Galera, Madroñales y Palomera
5	Modelo espacialmente explicito basado en el individuo	Fragmentación	Simulación	iv y vi	-	Predicción futuro	Galera, Bas Sur*

*Galera y Bas Sur fueron utilizadas para realizar las simulaciones en un paisaje natural y otro fragmentado, respectivamente. Para obtener la parametrización del modelo se usaron 5 localidades para el movimiento (Anadón *et al.* 2012) y 14 para el estudio de los parámetros reproductivos (Rodríguez-Caro *et al.* 2014).

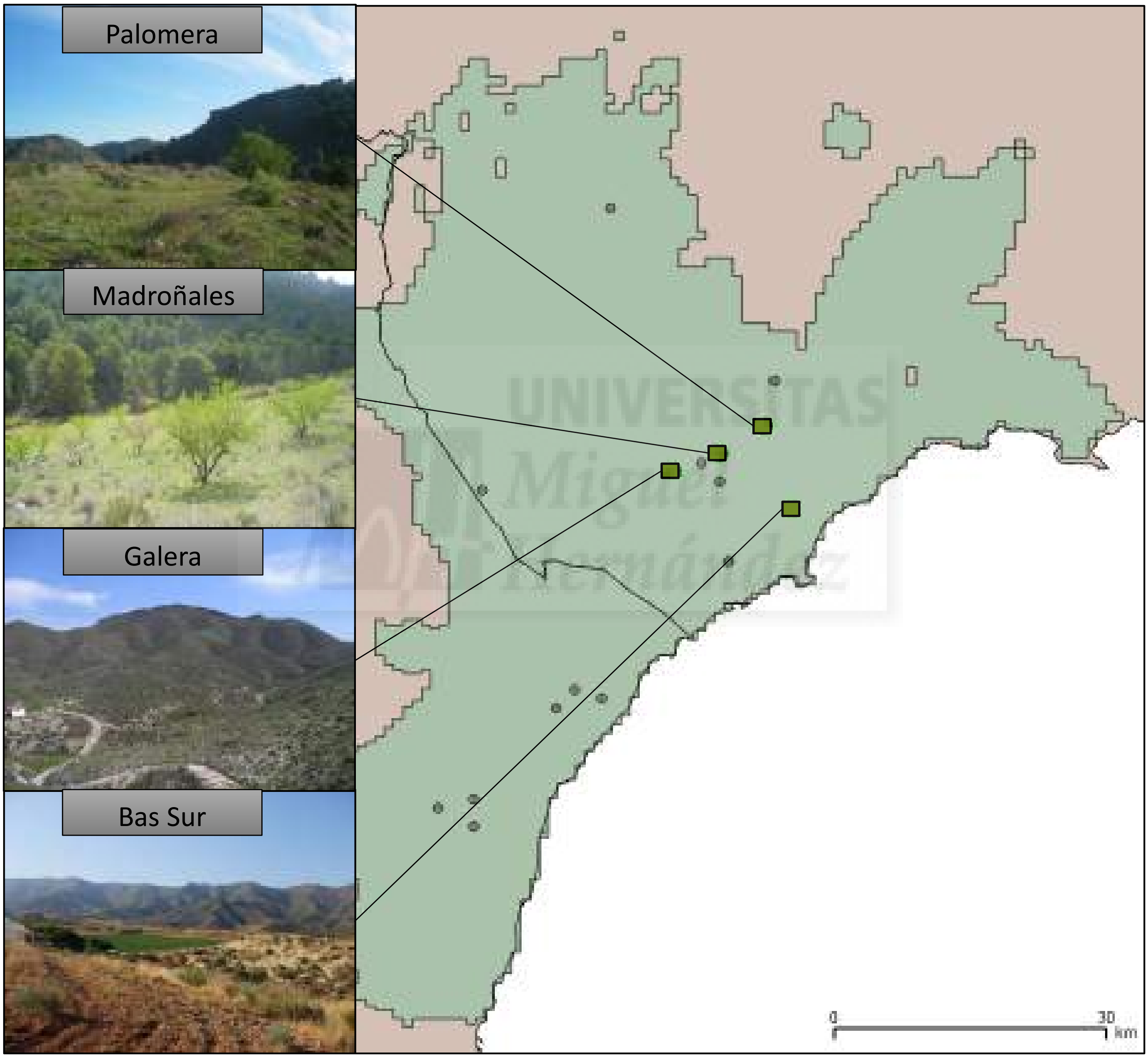

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Figura 2. Los cuadros verdes identifican la posición dentro del área de distribución de las localidades utilizadas en los capítulos de esta tesis. Los puntos grises corresponden a las localidades analizadas en trabajos previos para parametrizar movimiento y reproducción en el capítulo 5 (Anadón *et al.* 2012 para el movimiento y Rodríguez-Caro *et al.* 2014 para la reproducción)

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4. Capítulos

Carmen López. Cuevas de Almanzora (Almería). 2014

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Density dependence, climate and fires determine population fluctuations of the spur-thighed tortoise *Testudo graeca**

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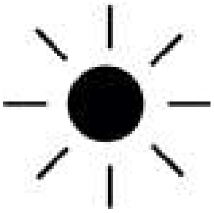

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Abstract

Population fluctuations are driven by a combination of multiple factors, which can be classified into endogenous and exogenous. Endogenous factors are directly related to density-dependent forces, whereas exogenous factors are environmental drivers (e.g. climate). Several studies have reported the effects of endogenous and exogenous factors using exponential population models in mammals, birds or insects, but few works have explored the effects on reptiles, specifically in tortoises. In this study, we developed logistic population growth models to decipher the role of these factors on the population dynamics of the spur-thighed tortoise *Testudo graeca*. The role of environmental drivers in the distribution, movement, survival, reproduction or individual growth has been described for this species in previous works, but no studies have examined the effects of both endogenous and exogenous factors in population growth rates. Using long-term data of *T. graeca* in southeastern Iberian Peninsula (1999–2013), we fitted non-linear logistic models with endogenous and exogenous effects. The results showed that endogenous processes are important drivers of the population dynamics of this species, and that exogenous factors, such as freezing hours in winter, also directly affect the population growth rate. Intolerance of extreme winter temperatures may especially affect hatchlings and juvenile tortoises. Our models also showed that perturbations (i.e. a fire occurred during the monitoring period) have a lasting impact by reducing the carrying capacity of the population. This study shows that simple quantitative approaches based on population dynamic theory are useful for deciphering the ecological mechanisms underlying dynamics of tortoise populations.

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Keywords: non-linear logistic models, *Testudo graeca,* endogenous, exogenous, disturbance, population density, climate, temperature.

Introduction

Models based on population dynamic theory are simple tools to decipher the causes of population change and can provide reasonably accurate predictions (Royama, 1992; Berryman, 1999). These models, constructed from classical ecological principles, are helpful to develop conservation and management policies (Berryman, 1999; Saether *et al.*, 2000; Coulson *et al.*, 2001; Stenseth *et al.*, 2002; Lima & Naya, 2011). Recognizing the role of endogenous (i.e. density dependence) and exogenous factors (i.e. climate or disturbances) in the dynamics of natural populations is a central subject within the field of population ecology (Nicholson, 1933; Andrewartha & Birch, 1954; Royama, 1992). Endogenous factors are density dependent, and they cause changes in dynamic variables (e.g. the per capita growth rate). Consequently, these factors are affected by those changes. In contrast, exogenous factors are density independent and may influence the per capita growth rate, but are not affected in turn by those changes (Royama, 1992; Berryman, 1999; Turchin, 2003). Many authors have studied the effects of endogenous and exogenous factors using exponential or logistic growth models (Berryman, 1999). Studies with birds (Furness & Greenwood, 1993; Lima & Estay, 2013), mammals (Lima & Berryman, 2006; Lima, Previtali & Meserve, 2006; Previtali *et al.*, 2009) and insects (Estay & Lima, 2010) support this classical approach. Although previous studies analyze population trends of several species of reptiles (i.e. Reading *et al.*, 2010; Luiselli *et al.*, 2014), to the best of our knowledge, there are no previous studies using this approach within this group.

In this study, we developed population dynamic models to decipher the role of endogenous and exogenous factors on the population dynamics of the spur-thighed tortoise, *Testudo graeca*, a threatened terrestrial tortoise inhabiting Mediterranean landscapes. The strongest evidence of density-dependent factors (i.e. endogenous) in shaping population dynamics in tortoises is from giant tortoises in oceanic islands (Swingland & Coe, 1979; Gibson & Hamilton, 1984). However, the very particular nature of these case studies may limit any generalization. For *T. graeca* there are no works describing densitydependent processes regulating its population dynamics, and only one work suggests density-dependent processes in the genus *Testudo* (Hailey & Willemsen, 2000; for *T. hermanni*). In contrast to endogenous factors, there is much more evidence for the role of exogenous factors in the population dynamics of tortoises. Specifically, for the *Testudo* genus, most works indicate a key role of positive effect of winter and autumn precipitation in the survival of the younger individuals (Díaz-Paniagua, Keller & Andreu, 2001; Fernández-Chacón *et al.*, 2011 for *T. graeca* and *T. hermanni*, respectively). Our work was carried out in the population of *T. graeca* in south-eastern Iberian Peninsula. In this population, previous studies have shown the effects of climate or other habitat disturbances (such as fire) on the species' distribution and abundance (Anadón *et al.*, 2006a,b, 2012a), on individual movement patterns (Anadón, Wiegand & Giménez, 2012b) and on individual growth, survival and reproduction rates (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013). Specifically, climate has been described as the most important factor shaping the species' distribution (Anadón *et al.*, 2006a). Main climate constraints are related to autumn rainfall and the number of freezing days in winter. These two

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factors could be related to limitations imposed by the length of the annual activity period (Anadón *et al.*, 2006a). Fires have also been described as a factor that causes direct and delayed reductions in local survival in the years after the fire (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013).

According to previous works, we expect both endogenous and exogenous factors to affect the population dynamics of *T. graeca* in south-east Iberian Peninsula. Due to the scarcity of studies on endogenous factors, the relative weight of this driver remains an unknown a priori. We hypothesize that exogenous forces could play an important role, specifically the rainfall in autumn could have a direct effect on abundance and the extreme temperatures in winter could affect negatively the abundance of tortoises. We also hypothesize that as a consequence of fire, the density of tortoises may be reduced in the years after the disturbance.

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Materials and methods

Study system

The spur-thighed tortoise, *T. graeca*, is a long-lived species inhabiting multi-successional Mediterranean shrublands (Anadón *et al.*, 2006a,b). Like other *Testudo* species, its population dynamics are characterized by delayed reproductive maturity and high and constant adult survival (Hailey & Loumbourdis, 1988; Díaz-Paniagua *et al.*, 2001; Sanz-Aguilar *et al.*, 2011). This study was carried out in a natural reserve 'Cumbres de la Galera' in the Region of Murcia in south-eastern Spain (37°320N, 1°390W). The area is a typical coastal semiarid Mediterranean shrubland. The reserve (70 ha) is surrounded by continuous and suitable habitat for the species (Anadón *et al.*, 2006a). Our study area within the reserve covered 35 ha. The mean annual rainfall and temperature are 295 mm and 18–19°C, respectively. According to regional models based on climate, relief and lithology, the reserve contains the optimum habitat for the species (Anadón *et al.*, 2006a). In summer of 2004, a fire affected approximately 31% of the study area (10.8 ha). Although fire events in this region are quite common (232 recorded fires between 1995 and 2005), most fire events, around 76%, burned less than 1 ha (Sanz-Aguilar *et al.*, 2011). However, the 2004 fire burned more than 250 ha and was one of the most extensive fires recorded in south-east Spain within the last decade.

Data collection

The tortoise population at the reserve 'Cumbres de la Galera' was monitored annually from 1999 to 2013. Tortoises were sampled in the spring, according to their annual activity patterns (Díaz-Paniagua, Keller & Andreu, 1995; Pérez *et al.*, 2002) and under adequate weather conditions (i.e. not with rain or with temperature below 18°C). The same area was evenly covered by walking along annual line transects through the habitat. Relative abundance of the species was estimated from the number of tortoises found per hour and per person, although the sampling effort was variable over the years. The minimum sampling effort in a year was 40 h. We could not assume that detection was the same in different months during spring because the activity of tortoises assumes a seasonal pattern. For this reason, we used data from a previous radiotelemetry study to obtain an estimate of the percentage of surface-active tortoises during the sample months (March = 38.1%; April = 52.9%; May = 48.5%; using the per cent of active tortoises from the total of radiotelemetry tortoises, data from Pérez *et al*., 2002). Detection might also vary with the year, size and stage of the individuals, with the experience of the observer, or sampling effort (e.g. Anderson *et al*., 2001). To quantify these effects and correct for these potential biases, we performed a distance sampling analysis (Buckland *et al*., 2001) using the software Distance 6.0 (Thomas *et al*., 2010). Our results indicated that, out of these potential confounding factors, only size (adults vs. non-adults) had an effect on the detectability of tortoises in our population (see Appendix S1 for further details). Accordingly, relative abundance of adults and non-adults was corrected according to their detection probabilities (adults: 0.452, non-adults = 0.215).

Environmental data

Climatic data for our study period (1998–2013) were provided by the Agricultural Information System of Murcia from the Research Institute of Agricultural and Alimentary Development of Murcia (siam.imida.es). We used the two climate factors directly associated with our hypothesis (e.g. temperature and precipitation), as well as potential evapotranspiration. Precipitation and potential evapotranspiration were described by their cumulated values, whereas temperature was described by four different metrics (total mean, means of the maximum and minimum monthly temperatures and extreme temperatures were described as the number of hours below 0°C; Table 1). In turn, each one of these six climatic descriptors was calculated for six different time frameworks: current spring (spr), previous year (py), previous spring (pspr), previous summer (psum), previous autumn (paut) and previous winter (pwin). In total, we tested 36 variables describing climate.

Diagnosis

We modeled endogenous and exogenous influences based on the R-function (Berryman, 1999). The R-function represents the realized per capita population growth rates (R_t) which reflects the processes of individual survival and reproduction (Berryman, 1999). Defining R_t = log (N_t)log (N_t-1), where N_t is the relative abundance of tortoise at time *t*, we can express it as (Berryman, 1999):

$$R_t = \ln\left(\frac{N_t}{N_{t-1}}\right) = f\,(N_t, N_{t-1}, \dots, N_{t-i}, \varepsilon_t) \qquad (1)$$

Where ε_t is a random normally distributed variable and *i* represents the lag in years (1–8). This model represents the density-dependent population dynamics.

Table 1. Climatic variables used in this study. These six variables were used in six temporal frameworks [current spring (spr), previous year (py), previous spring (pspr), previous summer (psum), previous autumn (paut) and previous winter (pwin)]

Climatic Variables	Value of variable	ID
Temperature	Mean	*Tmean*
	Mean minimum	*Tmin*
	Mean maximum	*Tmax*
	Hours below 0ºC	*H*
Precipitation	Cumulated	*P*
Potential Evotranspiration	Cumulated	*PET*

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To understand the endogenous structure of our tortoise population, we first determined the time delay in density-dependent effects of this time series. Following Berryman & Turchin (2001), we carried out an autoregressive analysis using the partial rate correlation function (PRCF). We fitted a multiple regression between the per capita growth rates (R_t) and lagged population density (X_{t-i} = ln *Nt-i*) to estimate the PRCF$_{t-d}$ coefficients at each lag (*i* = 1,2,. . .), for statistical convenience we assumed a linear relationship (Royama, 1977). The population was dominated by first-order density-dependent effects (see below Results, Fig. 1); therefore, we used a non-linear version of the simple Ricker's (1954) equation as a starting point to model the R-function (Berryman, 1999).

Models of population dynamics

Assuming that population dynamics of tortoises are influenced by endogenous process, we used the non-linear logistic population model proposed by Royama (1992), derived from the logistic equation of Ricker (1954).

$$R_t = R_m - e^{(aX_{t-1} + c)} \qquad (2)$$

where R_t is the realized per capita population growth rate, R_m is a positive constant representing the maximum finite reproductive rate (related to the maximum growth rate), X_{t-1} is the logarithmic population density in time t_1, *c* is a constant representing competition and resource depletion and *a* indicates the effect of interference on each individual as density increases (Royama, 1992); $a > 1$ indicates that interference intensifies with density and $a < 1$ indicates habituation to interference. As the three parameters R_m, *a* and *c* have an explicit biological interpretation, we can include environmental perturbations in each parameter using the framework of Royama (1992). To model the effects of exogenous factors (climate) on the endogenous model (Equation 2), we added extra terms representing vertical and/or lateral effects (Royama, 1992). Simple additive environmental changes can be represented as vertical effects, which deflect vertically with proportional alterations in R_m. Vertical perturbations may affect survival and reproduction directly, causing changes in the maximum finite growth rate and can be expressed as:

$$R_t = R_m + d\,(Z_t) - e^{(aX_{t-1} + c)} \qquad (3)$$

where *d* is a simple linear function (positive or negative) of the different climatic lateral or non-additive effects (Royama, 1992). variables (Z_t).

An alternative process occurs when exogenous factors influence certain limiting resources, called lateral. Lateral perturbations are normally expected from changes in an essential resource such as food or nesting sites (Berryman 1999) and can only be evaluated jointly with the effect of population density. It can be expressed as:

$$R_t = R_m - e^{(aX_{t-1} + c + d\,(Z_t))} \qquad (4)$$

Parameters were estimated by non-linear convergence (i.e. Marquardt/Newton-Raphson algorithm) using non-linear regression from the nls library in the program R (Bates & Watts, 1988). We calculated the Akaike information criterion corrected for small-sample bias (AICc), and differences in AICc (ΔAICc) for each model (Burnham & Anderson, 2004). In addition, for each model we calculated the Akaike weights, w_i, as an index of its relative plausibility (Burnham &

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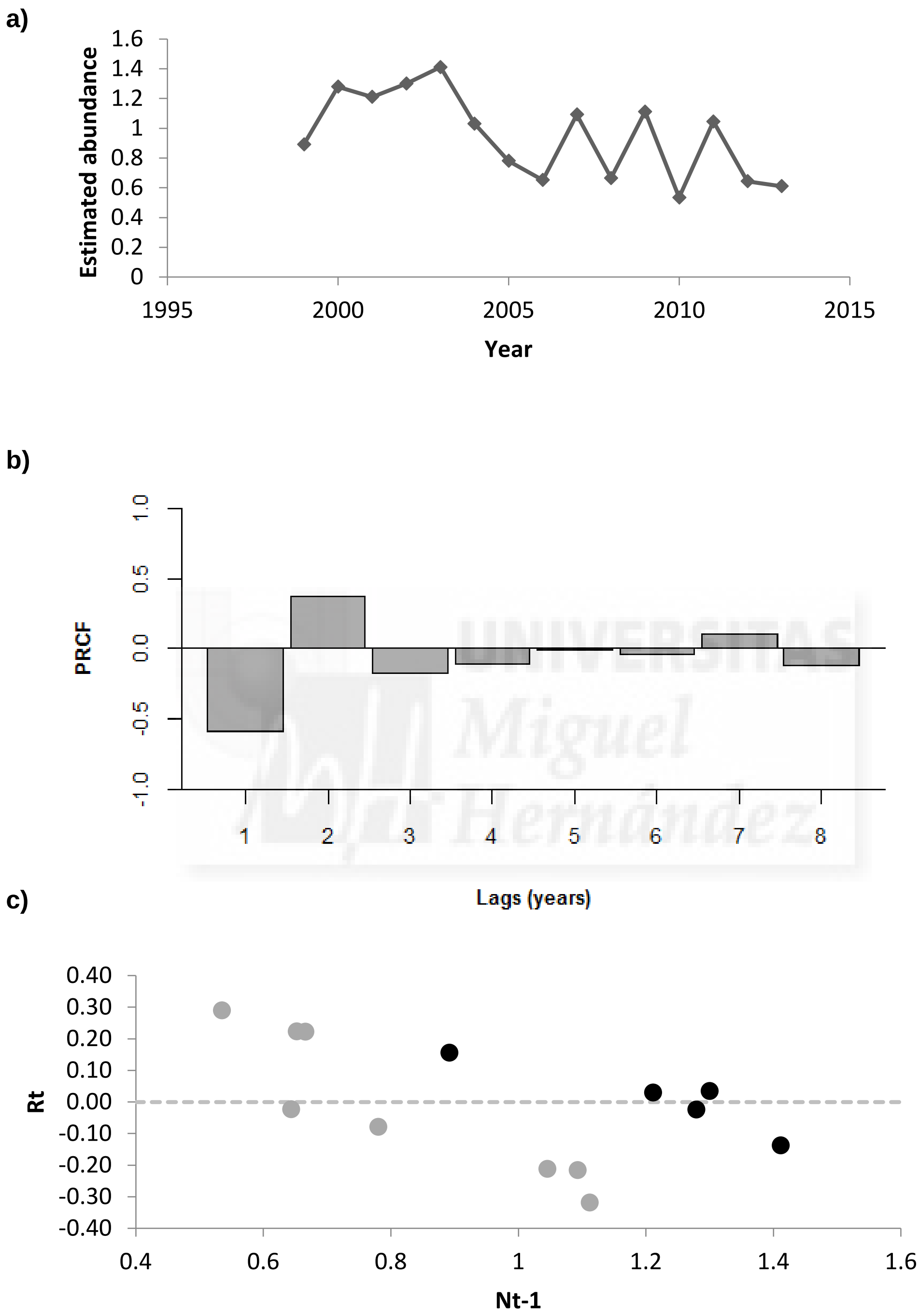

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Figure 1. (a) Annual estimate abundance of spur-thighed tortoises, (b) partial rate correlation function (PRCF) and (c) relationship between the logarithmic annual per capita rate of change (Rt) and population abundance (Nt-1). In black and gray are the years before and after the fire, respectively.

Anderson, 2002). Predictive performance of the models was also assessed by means of root-mean-square error values (rmse; Sheiner & Beal, 1981). Rmse represents the standard deviation of the residual values (i.e. the difference between the observed and the values predicted by the model) and thus smaller rmse values represent better predictive performance. In addition, we used Pearson's correlation coefficient between the observed and predicted values. The best model, as assessed from the AIC values, was selected to draw inferences and run deterministic predictions. We used total trajectory (annual predictions calculated by the information of the exogenous variable using the best model) and one-step-ahead deterministic predictions (annual prediction calculated by the information of the exogenous variable and the abundance of the previous year using the best model) to simulate the dynamic behavior of the fitted models and correlations between observed and predicted values of population abundance to assess the performance of each of them.

Results

Population dynamics showed numerical fluctuations with a sudden decrease after the fire, which happened in 2004 (Fig. 1a). Results from the PRCF

Table 2. Optimal population dynamic models for spur-thighed tortoise using the exponential form of logistic growth (Royama, 1992).

ID	Model	Parameters Estimates				AICc	ΔAICc	w_i	rmse	r_p
		a	b	C	d					
A1	$R_t = b – \exp (a X_{t-1} + c)$	3.73	0.43	-1.1583		-33.80	5.54	0.02	0.0536	0.9046
	Endogenous + climatic effects									
A2	$R_t = b – \exp (a X_{t-1} + c) + d H_{pwin}$	4.93	0.43	-1.4882	-0.0003	-39.34	0.00	0.25	0.0381	0.9531
A3	$R_t = b – \exp (a X_{t-1} + c + d H_{pwin})$	3.89	0.43	-1.3537	0.0007	-38.57	0.76	0.17	0.0391	0.9504
A4	$R_t = b – \exp (a X_{t-1} + c) + d Tmax_{spr}$	1.39	0.43	-0.0009	0.0323	-37.40	1.94	0.10	0.0401	0.9491
A5	$R_t = b – \exp (a X_{t-1} + c) + d Tmax_{spr})$	3.59	0.43	0.3699	-0.0719	-36.79	2.55	0.07	0.0417	0.9435
A6	$R_t = b – \exp (a X_{t-1} + c) + d PET_{pspr}$	1.74	0.43	-0.1402	0.0015	-36.13	3.21	0.05	0.0427	0.9406
A7	$R_t = b – \exp (a X_{t-1} + c + d Tmin_{pwin})$	3.73	0.43	-0.8648	-0.0434	-34.96	4.37	0.03	0.0445	0.9353
A8	$R_t = b – \exp (a X_{t-1} + c) + d Tmin_{pwin}$	2.93	0.43	-0.8237	0.0190	-34.55	4.79	0.02	0.0452	0.9333
A9	$R_t = b – \exp (a X_{t-1} + c) + d PET_{pyear}$	0.94	0.43	0.4647	0.0009	-34.16	5.18	0.02	0.0458	0.9313
A10	$R_t = b – \exp (a X_{t-1} + c + d Tmean_{pwin})$	4.04	0.43	-0.1552	0.0923	-34.08	5.26	0.02	0.0459	0.9309
A11	$R_t = b – \exp (a X_{t-1} + c + d PET_{pspr})$	3.39	0.43	-0.1315	-0.0028	-33.90	5.44	0.02	0.0462	0.9301

Parameters values were estimated by non-linear regression analysis. The best model was chosen by using Akaike information criteria for small sample size AICc. ΔAICc = increments of AICc, w_i = Akaike weights, rmse = represents the standard deviation of the residual values, r_p = Pearson's correlation coefficient between the observed and predicted values. The model notations are as follows: R_t, per capita population growth rate; b, maximum per capita growth rate; a, effect of interference on each individual as population size increases; c, d, f constants for the model; X_{t-1} = ln population abundance at time t-1.

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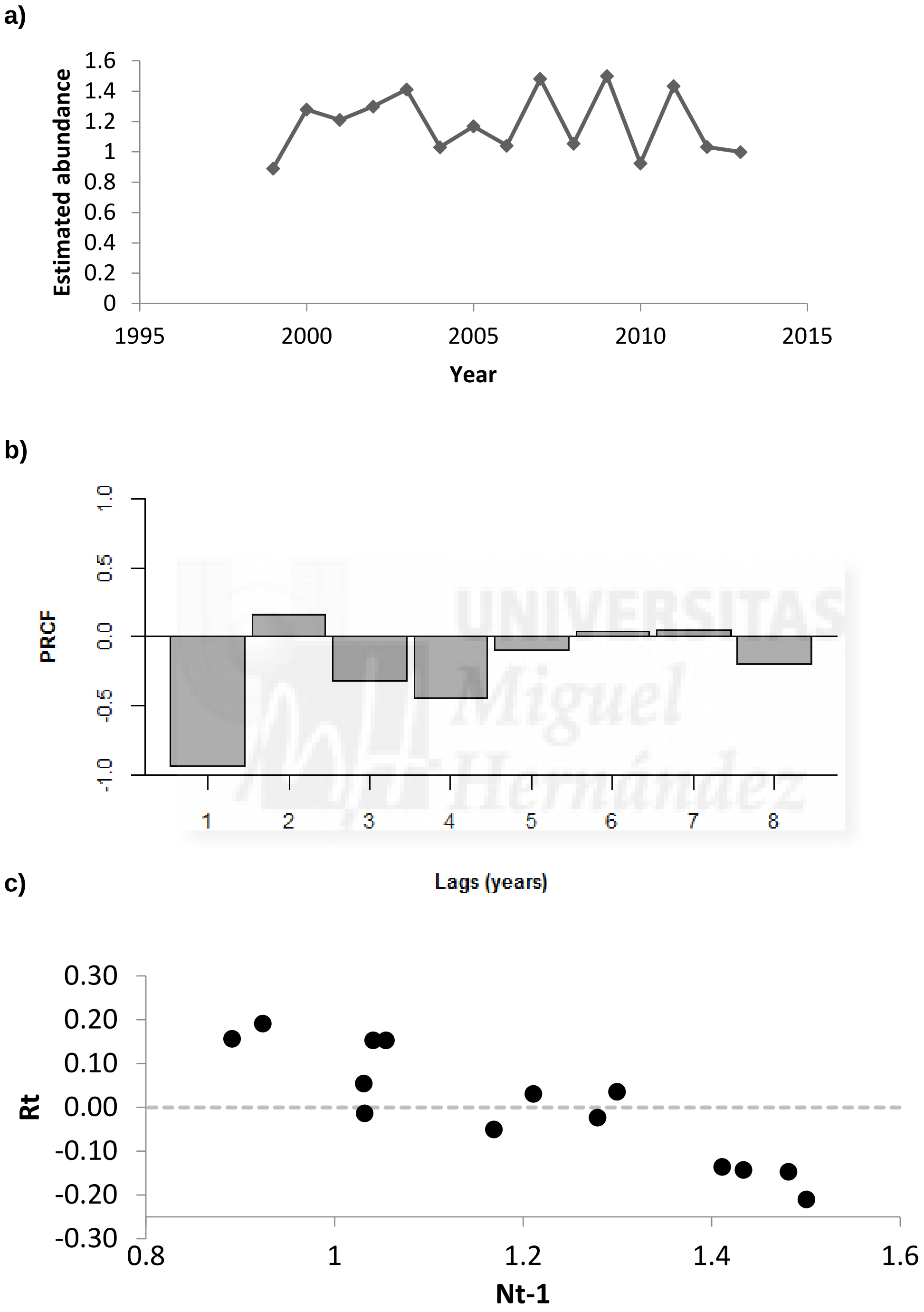

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Figure 2. Data corrected by effects of fire. (a) Annual estimate abundance of spur-thighed tortoises, (b) partial rate correlation function (PRCF) and (c) relationship between the logarithmic annual per capita rate of change (Rt) and population abundance (Nt-1).

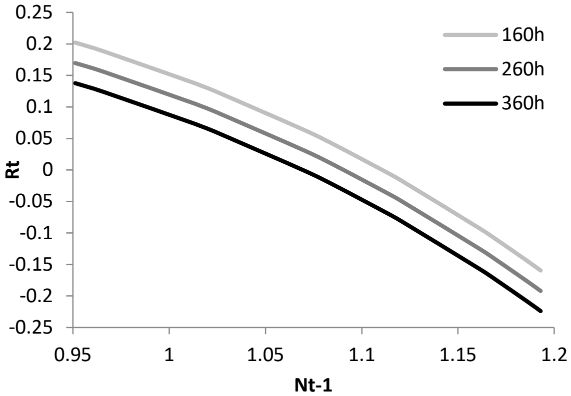

Figure 3. Relationship between the logarithmic annual per-capita rate of change (Rt), population abundance (Nt-1) and number of hours below 0°C in winter, according to the model with vertical effects (A2), The mean of hours below 0°C was 266 hours during the study.

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strongly suggested a first order dynamics (Fig. 1b), which was also evident from the observer Rfunction (Fig. 1c). As there is a shift in the Rfunction before and after the fire (Fig 1c), we corrected these effects calculating the difference between the average of N_t before and after the disturbance (1.19 and 0.80 tortoises per hour, respectively). The difference (0.39) was added to the relative abundance after the disturbance to remove fire effects, the results are shown in Fig. 2a. It should be noted that including the fire effects into the model (i.e. as a dummy variable) would yield the same results. The PRCF after the correction also indicated strong density-dependent effects (Fig. 2b) and the R-function showed a clear relationship between the relative abundance and the per capita population growth.

Of the 72 candidate climatic models (36 variables with lateral and vertical effects), 10 improved the AICc of the endogenous model (Table 2). The model with the largest support included the endogenous effects and the number of hours below 0°C in winter with an additive negative effect (Table 2, model A2). The rmse was very low (0.0381) and the Pearson correlation was very high (0.9531) and the predicted effects in R_t are showed in Fig 3. This model seems to capture the observed dynamics effectively (Fig. 4). Correlations between observed and predicted values of density were 0.54 for total trajectory predictions and 0.73 for one-step-ahead predictions, respectively (Fig. 4). Two models had a similar statistical support than model A2, as their difference in AIC values was less than 2 units (Burnham & Anderson, 2002). These models included the number of hours below 0°C as lateral effects and $Tmax_{spr}$ with vertical effects (Table 2). The two models with the largest support, vertical and lateral effects of the number of hours below 0°C (Table 2, A2 and A3) actually yielded very similar predictions, as shown by the similarity in their response curves (Appendix Fig. S1).

Discussion

Our results indicate that endogenous processes are relevant forces in the dynamics of *Testudo graeca* and that climate factors also help account for variability in species population dynamics. To the best of our knowledge this is one of the few, and the most direct, evidence of intrinsic population regulation in continental tortoises (i.e. not in oceanic islands). With regards to exogenous factors, although the influence of climate in tortoises has been widely reported elsewhere (Díaz-Paniagua *et al.*, 2001; Anadón *et al.*, 2006a,b, 2012a; Attum *et al.*, 2011), most of these studies are based on statistical correlation between estimates of population size and environmental variables. Here, we deduced the structure of the population processes, which is a central issue in population dynamics (Royama, 1992).

Our work indicates that the population dynamics of *T. graeca* in south-eastern Iberian Peninsula show fluctuations that are largely associated with density-dependent processes. These results show that the species' dynamics are regulated by intra-specific mechanisms, such as intra-specific competition (Berryman, 1999). Mechanisms put forward to explain this pattern are territoriality, aggressive behavior and nutrient limitation at carrying capacity (Berryman, 1999). As in most terrestrial tortoises, the studied populations of *T. graeca* present a promiscuous mating system with overlapping home ranges (Anadón *et al.*, 2006b) and, unlike other *Testudo* populations, male–male combats are extremely rare (R. Rodríguez-Caro & E. Graciá; pers. obs.). Thus, resource limitation at carrying capacity is the most plausible mechanism driving intra-specific competition in this population. Interestingly, this density-dependent mechanism is different from the only previous work reporting intrinsic population regulation (Hailey & Willemsen, 2000). These authors suggested that population regulation in a studied population of *T. hermanni* occurs via sex ratio, with population with high densities showing a sex ratio strongly biased toward males. In any case, further studies are needed to identify the density-dependent mechanisms acting in the studied population in south-east Spain.

Our results indicate that temperature, and not rainfall, is the most important climatic factor determining the dynamic of the spur-thighed tortoise. Our models indicate that the number of freezing hours during winter (extreme temperatures) is the climate variable with the largest impact on the dynamics of the studied tortoise population; extreme cold winters reduce the population growth rates. Main climate effects for this variable are vertical, which indicates that they induce changes in the maximum per capita growth rate (*Rm*). However, the model with the same variable as a lateral affect also fitted the data very well, which means that, alternatively, differences in temperature might promote changes in the availability of essential resources, such as food or nesting sites. Regarding the role of temperature, the ability of reptiles to cope with lower temperatures remains limited. Reports of widespread mortality among

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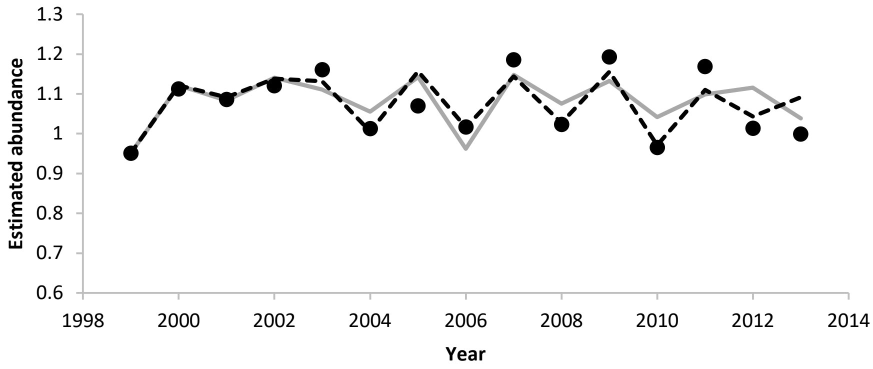

Figure 4. Comparisons between observed abundances (points) and deterministic predictions (lines) for the best model (A2). Total trajectory prediction is represented by the grey solid line and one-step-ahead prediction by the black dotted line. Estimated abundances (tortoises per hour searching) were adjusted by detection probability without fire effects.

hatchlings due to extreme minimum temperatures are common (St. Clair & Gregory, 1990; Lindeman, 1991; Packard, 1997; Packard *et al.*, 1997; Andreas & Paul, 1998; Nagle *et al.*, 2000) and demographic studies have shown that winterkill may contribute significantly to mortality in the first age classes (Tinkle, Congdon & Rosen, 1981). In cold temperate regions, winter mortality may significantly constrain recruitment and limit population size (e.g. Tinkle *et al.*, 1981; MacCulloch & Secoy, 1983; St. Clair & Gregory, 1990; Rozycki, 1998; Schneeweiss, Andreas & Jendretzke, 1998). The population of *T. graeca graeca* in south-eastern Spain inhabits in the northern limit of the distribution of this species in the western Mediterranean (Graciá *et al.*, 2013). This subspecies is widely distributed in the north of Africa, where the climate is warmer. Thus, in the Spanish population, colder winters may constrain the growth of the population.

According to Anadón *et al.* (2006a, 2012a) the distribution and abundance of *T. graeca* in south-eastern Iberian Peninsula and North Africa is largely controlled by rainfall variables, especially winter and autumn precipitation, followed by the number of freezing days in winter. The key role of rainfall before the active season of tortoises (i.e. spring, Pérez *et al.*, 2002) has been also indicated in demographic studies for *Testudo* species (Díaz-Paniagua *et al.*, 2001 for *T. graeca*, Fernández-Chacón *et al.*, 2011 for *T. hermanni*). However, rainfall variables did not show effects in our models. As such, the relative role of rainfall versus temperature factors on the population dynamics of the species remains to be clarified.

Fire events also had a clear effect on the dynamics of the studied population, as it has been described in previous works (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013). Previous works show that although reproduction rates were not affected, survival rates decrease in the years after the fire (Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013). Accordingly, our results indicate that fire disturbance reduces abundance of tortoises and this effect is prolonged because the species is long lived. The models show that disturbance also reduces the carrying capacity of the system. Fire may alter food availability or cause loss of shelters from predators and thermal refugia after the disturbance (Esque *et al.*, 2003). The studied tortoise population seems to be trapped in a low equilibrium density point after the fire event, suggesting that the changes in the ecosystem structure and function cause a large impact on this reptile population.

Our approach supports the notion that simple models based on population dynamics can be used to disentangle the effect of different environmental variables. Current studies provided examples where these simple models are helpful to understand the causes of population fluctuations and make accurate predictions (Berryman & Lima, 2006; Lima & Berryman, 2006; Lima *et al.*, 2008a,b; Previtali *et al.*, 2009; Lima & Naya, 2011; Lima & Estay, 2013). This study also supports their accuracy for long-lived reptiles, as our results are consistent with previous studies on the species, and shed light into the relative role of endogenous and exogenous factors in the population dynamics.

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Supporting Information

Appendix S1. Factors that affect the detection of tortoises.

Appendix Table S1. Models with the possible variables which affect detectability.

Appendix Figure S1. Effects of abundance of tortoises (N_{t-1}) and number of hours below 0°C in winter according to (a) the model with vertical effects (effects in the maximum growth rate, R_m) in population growth (R_t); and (b) the model with lateral effects (exogenous factors influence some limiting resources).

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Maintained effects of fire on individual growth and survival rates in a spur-thighed tortoise population*

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Abstract

Fires strongly influence the ecology of reptiles and have both direct and indirect effects on population dynamics as they affect life history traits. Here, we examine the effects of fire on individual growth patterns and on the survival rates of a tortoise *Testudo graeca* population in south-eastern Spain. We compare the biometric data from recaptures 4 years before and after a fire which burned 31 % of our study area. The Von Bertalanffy and Gompertz growth models best describe the individual growth patterns for males and females. In males, but not females, fire significantly decreased the time required to reach their asymptotic size (k parameter). However, adult survival analyses reveal that the local survival rates lowered for both sexes after fire. Our work evidences that the effects of fire can be complex and maintained over time, affecting different life history traits.

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Keywords: Disturbance, Fire effects, Growth models, Survival rates, *Testudo graeca*

Introduction

Stochastic disturbances are of particular importance in conservation and ecology inasmuch as habitat perturbations may result in significant changes in population extinction probabilities (Greenberg 2001). Fire is one of the commonest disturbances that operates across multiple landscape scales to alter habitat structure and diversity (Russell *et al.* 1999; Esque *et al.* 2003). Three levels at which fires affect wildlife have been identified (Whelan *et al.* 2002): (1) direct or first-order effects that occur over a short time period lasting days or weeks; (2) second-order effects, indirect effects of fires that occur over a longer term which may affect key life history traits of individuals, such as growth, survival or reproduction; and (3) third-order effects, as evolutionary effects.

Reptile species are expected to be fire-sensitive species due to their low escape capabilities. In several regions, fires are one of their main threats (Couturier *et al.* 2011). In this study, we analysed fire effects on a population of the spur-thighed tortoise *Testudo graeca* in south-eastern (SE) Spain. In particular, we assessed second-order effects on individual growth and first- and second-order effects on survival by comparing population life traits before and after fire.

Materials and methods

Study system and data collection

The spur-thighed tortoise is a long-lived threatened species that lives in multi-successional Mediterranean shrublands with home ranges 2.56 ± 3.02 and 1.15 ± 0.15 ha for males and females respectively (Anadón *et al.* 2006). This study was carried out in the biological reserve "Las Cumbres de la Galera" (Murcia, Spain; 34 ha). In the summer of 2004, a fire due to human activities burned approximately 250 ha. Although it started outside the reserve and was rapidly extinguished, 31 % of the study area was affected. This fire was one of the most extensive fires occurred in SE Spain in the last decade.

The tortoise population in the reserve was sampled visually, through captures–recaptures of individuals between 2000 and 2009. Sex was determined according to external secondary characters. Unsexable immature individuals were classified as subadults. Individuals were measured for straight-line carapace length (CL) and marked by notching the marginal scutes. This sampling scheme included a 4-year period before the fire (females = 16, males = 20 and subadults = 3) and another 4-year period after the fire (2005–2009, females = 68, males = 56 and subadults = 5). Although the same area was sampled annually, the efforts made were more intensive after the fire.

Individual growth and survival

The effects of fire on individual growth were assessed using growth models from changes in individual sizes through time. To determine if the overall growth rates of either sex differed before and after fire, nonlinear regressions were used with four commonly used growth models (von Bertalanffy, Gompertz, Richards and a logistic model, as in Dodd and Dreslik 2007; see Electronic supplementary material 1). Having selected the most likely model, we formulate sex-specific growth curves for pre- and post-disturbance.

These growth models were defined by two constant parameters, asymptotic size S_∞ (millimetres) and parameter *k* (per year), in relation to the time required to reach their asymptotic size. The overall differences in growth curves were assessed using an *F* test (as in Lindeman 1999). The estimates of the parameters in the models (*k* and S_∞) were tested using a *t* test. Statistical analyses were performed using the R software (R Core Team 2012).

As previous studies have suggested, population viability in tortoises is sensitive to the survival of adults (Sanz-Aguilar *et al.* 2011). Consequently, we addressed their survival rates by using the method described by Beverton and Holt (1956). This method employs the mean of a size distribution and S_∞ calculated previously (see ESM 2). We used a bootstrap to calculate the confidence interval (as in Oedekoven *et al.* 2013) and a *t* test to calculate the difference.

Results

The models that best described tortoises' population growth were the von Bertalanffy model and the Gompertz model, when considering the whole study period (see ESM 1). For further analyses, we selected the von Bertalanffy model as it is the most widely used model to describe chelonians population growth.

Differences in growth curves between sexes were observed, which were due to the asymptotic size parameter S_∞ (t_{40} = 9.380, P < 0.001); females had a larger S∞ than males (161.84 ± 8.23 and 121.17 ± 2.83 mm, respectively). In relation to fire effects, growth curves were depressed in females and males, but significantly so in the latter (females, $F_{2,\ 76}$ = 1.83; *P* = 0.167; males, $F_{2,\ 96}$ = 5.79, *P* = 0.004). After the fire, the differences were located in parameter *k* (t_{94}=3.002, *P*=0.003; Fig. 1), which decreased for the male population from 0.23 to 0.11 year^{-1}.

Survival rates lowered for both sexes after the fire from 98.43±2.67 to 95.10±1.09 for males and from 94.65±2.27 to 90.09±2.95 for females (*P* <0.001 in both cases).

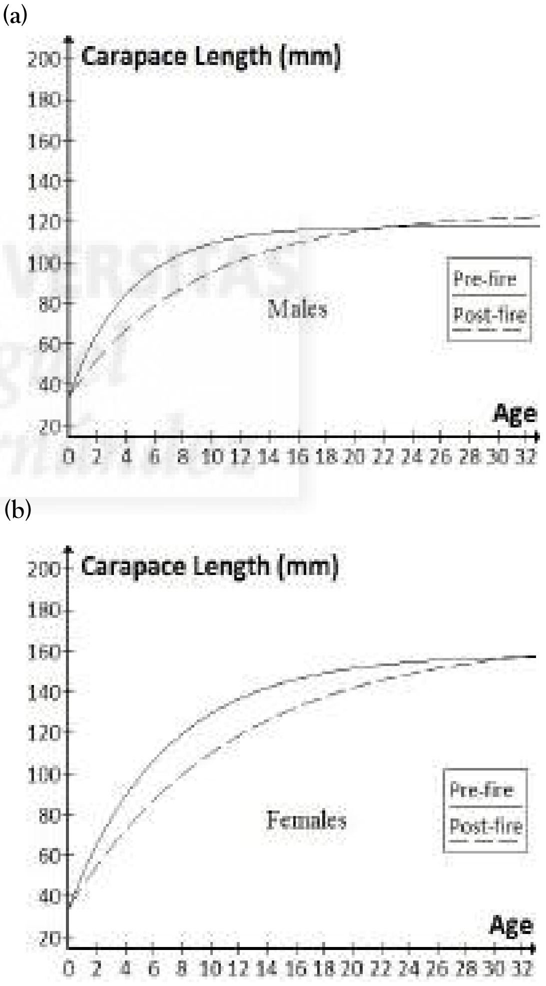

Figure 1. Von Bertalanffy's growth curves for males (a) and females (b) by disturbance, relating individual sizes and the inferred age from the model

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Discussion

There have been many studies which have addressed the effects of fire on herpetofauna (e.g. Russell *et al.* 1999; Lindenmayer *et al.* 2008), and Mediterranean tortoises are specially sensible to this disturbance affecting important traits as mortality or small-scale movements (Hailey 2000; Couturier *et al.* 2011). However, due to the unpredictability of such events, there are very few works that compare the same population before and after disturbance (Sanz-Aguilar *et al.* 2011; Dodd *et al.* 2012).

Fire may alter food availability or may cause loss of shelter from predators and thermal refugia after the disturbance (Esque *et al.* 2003). After the fire, growth was slower in both males and females, although with a difference only significant in males (Fig. 1). These results were supported by a posterior correlation between weight (W) and CL before and after the fire, revealing a significant decrease intheW of males (MANOVA;W=FIRE+CL; females, P=0.347; males, P=0.0118). Sex-specific reproductive traits could be responsible of differences in energy requirements (i.e. males spend energy in bigger home ranges as a consequence of active search of females; Anadón *et al.* 2006).

Very few studies have focused on how the second-order effects of fires affect survival rates of animal populations. Sanz-Aguilar *et al.* (2011) studied first- and second-order effects on the survival of *T. graeca* by considering our same study system, but they employed capture–recapture models. Their work revealed that the survival probabilities of adults lowered from 98 % before fire to 86 % during the first year after fire, 95 % in year 2, 96 % in year 3 and 97 % in years 4 and 5 (an average of 4 % over the 5-year period). Our results report similar reductions in this population's survival rates (4% for females and 3% for males) using a different approach. From an applied and methodological point of view, our work demonstrates that the study of individual growth patterns can yield similar survival estimates to those offered by capture–recapture techniques.

For terrestrial tortoises, the effects of fires strongly depend on species and population and also on fire characteristics. Several studies have shown that fire can even have beneficial repercussions for tortoise populations (Russell *et al.* 1999; Yager *et al.* 2007). However, as shown by Sanz-Aguilar *et al.* (2011), despite some populations being able to coexist with fires, high recurrences or small population sizes can lead to local extinctions of spur-thighed tortoises.

In this sense, our work provides complementary results to current knowledge of the effects of fires on *T. graeca*. We did not only find effects on the survival rates of individuals but also detected that fire has relevant effects on their growth, which have consequences for population dynamics (i.e. number of eggs or clutches, size at maturity or even changes in survival). For this reason, we suggest that the effects of disturbance are complex and variable because they affect several life history traits.

Acknowledgments We thank Dr. F. Botella and S. Quiñones. Besides, we also thank all the people who participated in the fieldwork. The Spanish Ministry of Science funded this work through the project CGL2009-08251 and CGL2012-33536. We also wish to thank the "Delegación General de Medio Natural de la Comunidad Autónoma de la Región de Murcia" and ACUDE for allowing us to work in its reserve. R. Rodriguez and E. Graciá were

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Supporting Information

Appendix ESM1. Growth models.

Appendix ESM 2. Survival rates.

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A low cost approach to estimate demographic rates using inverse modelling*

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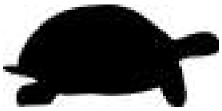

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Abstract

1. Management and conservation of species depends on estimation of demographic parameters. Current methods for estimating survival require time series data and large sample sizes, which are usually not available for species of conservation concern.
2. We propose and evaluate a new approach to estimate demographic parameters and to test alternative hypothesis on the drivers of temporal variation in demographic rates. Our “inverse” approach is less data hungry than current methods and combines matrix population models and inverse modeling within a statistical model selection framework. In short, we search parameterizations for which the age distribution predicted by the matrix model best matches the observed population age distribution.
3. To illustrate and test our approach, we (i) estimated the survival rates in a population of the tortoise *Testudo graeca* based on one year of data, (ii) assessed the impact of sample size on the accuracy of our approach, and (iii) tested alternative hypotheses on the impact of fire disturbance on the survival rates of the population. We then compared the results with those obtained by capture-recapture (CRC) estimates based on long-term monitoring.
4. Using the age distribution of 153 tortoises captured within a single year, our approach yielded estimates of the survival rates that were reasonably accurate when compared to CRC estimates based on 11 years of data and more than 1009 observations of 675 individuals. Simulation experiments showed that our method provided robust estimates if sample size is above 100 individuals. The best models describing the impact of perturbations on the temporal variations of survival identified by our approach included the model identified by previous CRC analyses.
5. Our approach allows for estimation of survival rates using relatively small sample sizes that can be obtained within one field season. This is a substantial advance in wildlife conservation because it decreases the cost for estimating demographic rates, especially for rare or elusive species. Further studies are needed to assess the robustness of our approach under more general scenarios.

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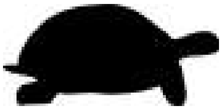

Keywords: Pattern-oriented model, survival rates, demography, tortoise, disturbance, fire, *Testudo graeca*

Introduction

The estimation of demographic parameters such as survival and reproduction rates is key for accurate forecasting of the fate of wildlife populations and for evaluating alternative management actions (Boyce 1992; Williams, Nichols & Conroy 2002; Beisinger & McCullogh 2002). In ecology, several approaches have been developed to estimate demographic parameters of wild animal and plant populations (Williams, Nichols & Conroy 2002; Thomson, Cooch & Conroy 2009). The estimation of age dependent survival (especially for long-lived species) is particularly difficult because current methods typically require long-term monitoring of individuals, which involves intensive field effort. An additional complication in monitoring of animal populations is imperfect detection (Lebreton *et al.* 2002; Thomas *et al.* 2010; Sanz-Aguilar *et al.* 2016). Two main approaches have been developed to overcome this problem. First, the survival of animals can be directly estimated based on telemetry data that provide an accurate monitoring of individuals over time (Kaplan-Meier 1958; Millspaugh and Marzluff 2001). Alternatively, a capture-recapture (CRC) framework allows for dealing with imperfect detection and is now commonly used to estimate animal survival rates (Lebreton *et al.* 1992; Lebreton & Pradel 2002; Cohen 2004; Giménez *et al.* 2007; Thomson, Cooch & Conroy 2009; Sanz-Aguilar *et al.* 2016). However, although both methods proved to be accurate and useful they can often not be applied for species of conservation concern where long-term studies would be very costly or infeasible (Williams, Nichols & Conroy 2002). Additionally, the marking technology may have negative effects on individuals' survival (Calvo & Furness 1992; Dugger *et al.* 2006).

Alternative "low cost" methods to obtain accurate estimates of demographic parameters are therefore needed, especially for the conservation of endangered, rare, or elusive species for which detailed demographic data is typically scarce but urgent diagnosis needed. One recently proposed low cost approach is the *N-mixture* model framework that allows estimation of demographic parameters (i.e. survival and reproduction) using stage-structured count data of unmarked individuals (Chandler & King 2011; Dail & Madsen 2011; Zipkin *et al.* 2014a, b). However, *N-mixture* models still require repeated counts of individuals over time.

Here, we present a novel approach to estimate age-dependent demographic rates based on pattern-oriented modeling (Wiegand *et al.* 2003; Grimm *et al.* 2005). Pattern-oriented modeling is essentially an inverse modeling approach where the outputs of a population model called "patterns" (e.g., the emerging stable age structure of a population) are used to estimate the model inputs (e.g., the unknown demographic parameters; Wiegand *et al.* 2003). In other words, inverse modeling estimates parameter values by optimizing the match between observed patterns and the corresponding simulated model outputs. Here we used an information theoretical approach (Burnham & Anderson 2002) to identify the model parameterization with the highest likelihood, given the observed patterns and the given population model, and to distinguish among competing model structures. Inverse modeling has been traditionally used in several scientific areas like hydrology, oceanography, soil science or climatology (Tarantola 1987; Gottlieb & DuChateau 1996; Wunsch 1996; Benner 2002), but only more recently in ecological studies (e.g.,

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Wiegand *et al.* 1998, Wiegand, Revilla & Knauer 2004; Revilla *et al.* 2004; Kramer-Schadt *et al.* 2007; Hartig *et al.* 2011; Martínez *et al.* 2011, 2016; Anadón, Wiegand & Giménez 2012; White *et al.* 2014; May, Huth & Wiegand 2015).

The objective of this study is to present and evaluate a new approach to estimate demographic parameters and to test alternative hypothesis on the drivers of temporal variation in demographic rates. Our approach to estimate demographic parameters uses the age distribution of the population that can be obtained by short-term studies and age-structured population projection matrix models (Caswell 2001). We illustrate our approach using long-term monitoring data from a population of the spur-thighed tortoise (*Testudo graeca*) in the southeastern Spain.

Our specific goals were threefold. First, we compare estimates of survival rates of *T. graeca* from our novel approach using only age-distribution data of one year with estimates obtained by means of capture-recapture methods using the entire long term monitoring data (11 years, 1009 individual captured, Sanz-Aguilar *et al.* 2011). Second, we simulated data sets to explore how sample size impacts the accuracy and precision of the estimates of survival rates. Third, to illustrate model selection with our approach we test alternative hypothesis on the impact of fire disturbance on the survival rates of the population.

Materials and methods

General methodology

Our framework relies the assumptions that a) the sampled population is stable and closed (i.e., no dispersal in or out of the study area), b) the observed population age structure during sampling contains signal of the demographic rates and detectability processes, and c) demographic stochasticity is relatively unimportant.

Demographic processes

First, an age-structured Leslie projection matrix (Caswell 2001; Fig. 1b) is used to generate the expected stable age distribution (Fig. 1c) of hypothetical populations under different combinations of demographic parameters such as age-dependent S_i survival rates and fecundity F (Fig. 1a). To find the demographic parameters that best match the observed age structure (Fig. 1e), we varied them systematically over the entire parameter space (Fig. 1a) (Wiegand, Revilla & Knauer 2004).

The age-structured Leslie transition matrix (A) takes the form:

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & F & F & \dots \\ S_1 & 0 & 0 & 0 & 0 & 0 & 0 & \dots \\ 0 & S_2 & 0 & 0 & 0 & 0 & 0 & \dots \\ 0 & 0 & S_3 & 0 & 0 & 0 & 0 & \dots \\ 0 & 0 & 0 & S_4 & 0 & 0 & 0 & \dots \\ 0 & 0 & 0 & 0 & S_5 & 0 & 0 & \dots \\ 0 & 0 & 0 & 0 & 0 & S_6 & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & S_m \end{bmatrix} \quad (1).$$

where the S_i represent the survival rates for age i = 1 to m, with m being the largest age class and F the fecundity rate. Usually, the population is divided into m different age classes and the same survival rates S_i (i = 1,.., m) are assumed within each age class i. The fecundity term varies depending on timing of the census: pre- and post-breading census. In the case of pre-breeding matrices, we obtain:

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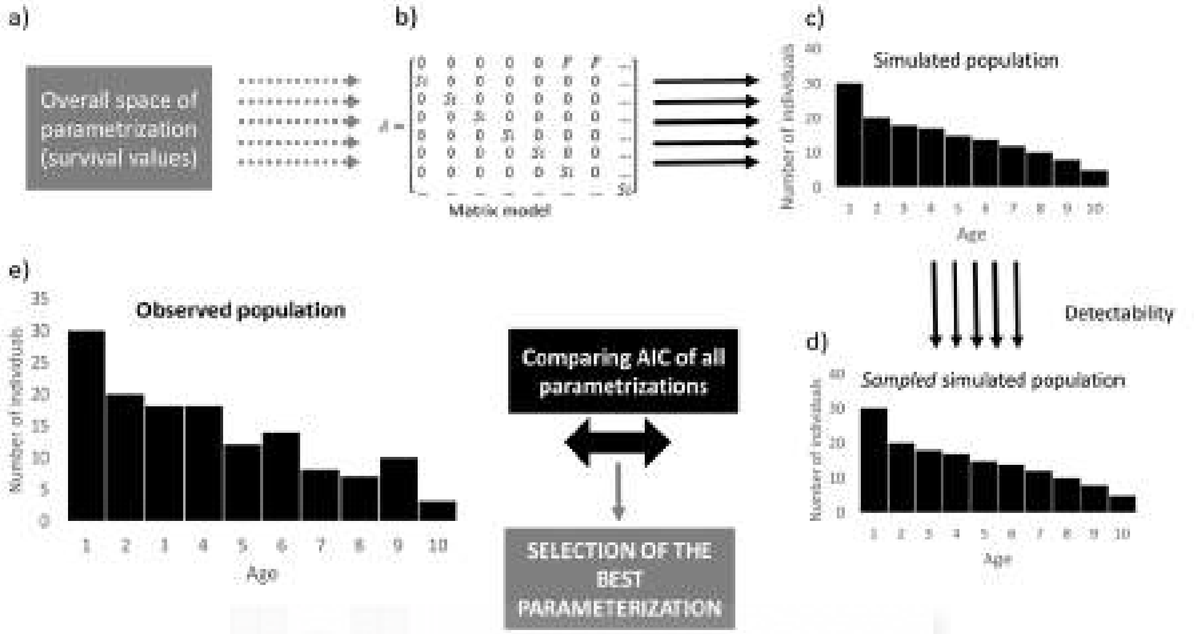

Figure 1. Summary of general framework of the model.

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$$F = SR^{*}\ BS^{*}S_1 \qquad (2)$$

and in the case of post-breeding matrices we obtain:

$$F = SR^{*}\ BS^{*}Sb \qquad (3)$$

where SR is the female sex ratio (note that the Leslie matrix is calculated only for females), BS the breeding success, S_1 first-year survival and S_b the survival of the breeder age class.

Detection processes

If individuals of the different age classes (e.g., juveniles vs. adults) differ in their detectability, the predicted stable age distributions must be corrected. For example, the simulated age distributions can be multiplied by the detection probabilities of each age class to obtain the “observable age distribution” of the simulated populations.

Estimating demographic parameters

Our general framework can be applied for any combination of the parameters $\theta = (S_1, \ldots, S_m, SR, BS, \ldots)$ of the age -structured Leslie transition matrix (eq. 1) that are unknown whereas the values of the other parameters must be known. We identified the vector θ of unknown model parameters that fitted the observed age distribution data best by using a likelihood approach (Hilborn & Mangel 1997, Burnham & Anderson 2002). To define the match between observed and predicted age distributions, we calculated the likelihood of observing the observed age frequencies (x_1, x_2, x_3, x_4,..., x_m, where m is the number of age-classes) given the simulated age structure (p_1, p_2, p_3, p_4,..., p_m) that emerged from the different parameterizations θ of the population model. Given the multinomial nature of our variable, the log-likelihood function is given by:

$$l(p_1, p_2, ..., p_m) = \log(\frac{n!}{\Pi x_i!}) + \sum_{i=1}^{m} x_i \log(p_i) \qquad (4)$$

where n is the total number of individuals, x_i (i = 1 ...m) is the observed number of individuals in age class i and p_i (i = 1 ...m) is the model prediction of the proportion of individuals in age class i.

To find the most likely parameter vector $\theta = (\theta_1, ., \theta_l, ..., \theta_o)$, we evaluated the model for all possible combination of parameters values with ranges covering the biologically plausible ranges. There are different possibilities to cover the entire parameter space; we used here an equidistant grid with k values for each of the o parameters to be determined. For each of the resulting k^o parameterization θ_j we then calculated the AIC value and the corresponding Akaike weights w_j. In theory we could just use the parameterization with the smallest AIC value, but many parameterizations may receive similar support (i.e., their distance to the smallest AIC value is below 2; Burnham & Anderson 2002). We therefore used an alternative approach based on model averaging that yields for each of the k tested values Θ of parameter θ_l an associated probability. To this end we selected all k^{o-1} parameterizations that contain the given value Θ of θ_l and estimated the sum of the Akaike weights w_j of these model parameterizations j. Thus,

$$w + (\Theta, l) = \sum_{j=1}^{k^o} w_j I(\boldsymbol{\theta}_j, \Theta, l) \qquad (5)$$

where the function $I()$ takes a value of one if parameterization θ_j contains the value Θ of the lth parameter and zero otherwise. Plotting $w+(\Theta, l)$ for each parameter θ_i over its k values Θ shows us how the likelihood for each parameter changes with its value. Finally, the best estimate for each parameters was the value with the largest $w+(\Theta, l)$ and the confidence interval at 95%.

Model selection

Our approach can be extended to test alternative hypothesis on the drivers of temporal variation in demographic rates. To this end different model structures are implemented that correspond to these hypotheses. For each alternative model structure, we determined the best estimate of the parameter vector θ and compared competing models structures based on their corresponding AIC values. Model structures with $\Delta AIC < 2$ receive similar support (Burnham & Anderson 2002).

Case study

We applied our framework to estimate survival rates of a long-term monitored population of the spur-thighed tortoise *Testudo graeca*. The spur-thighed tortoise is a small long-lived chelonian widely distributed in the Mediterranean basin. The "Cumbres de la Galera" population has been monitored during the last 15 years (Sanz-Aguilar *et al.* 2011; Anadón, Wigand & Giménez 2012; Rodríguez-Caro *et al.* 2013; 2016). In summer of 2004, a fire burned 31% of the study area. Sanz-Aguilar *et al.* (2011) and Rodríguez-Caro *et al.* (2013) estimated survival and the effect of fire on survival rates by means of multistate capture-

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recapture models and, by comparing the size of tortoises with the asymptotic size, respectively. These survival estimates were used to validate that resulting from our method.

We examined the observed age structure of the population in two different years: just before the fire event (year 2003; Fig. 2) and 5 years after (year 2009; Fig 2) when the cumulative effects of fire over time are expected to be ceased (Sanz-Aguilar *et al.* 2011). We approximated individual age using growth rings and the carapace length (see details in Supporting Information 1). We distinguished twenty-five age classes, the oldest one including all individuals older than 25 years because the accuracy of age estimations for the older individuals in our population is low (Rodríguez-Caro *et al.* 2015). To compare our estimates of survival rates with those obtained by classical capture-recapture methods, we classified the tortoises aged 1 to 4 years old as juveniles, those aged 5 to 8 as subadults, and older individuals as adults, thus having four age classes (Sanz-Aguilar *et al.* 2011), we also include the survival from hatching to one-year-old. Thus, our task is to find the best parameterization for the vector $S = (S_1, S_2, S_3, S_4)$ of survival rates.

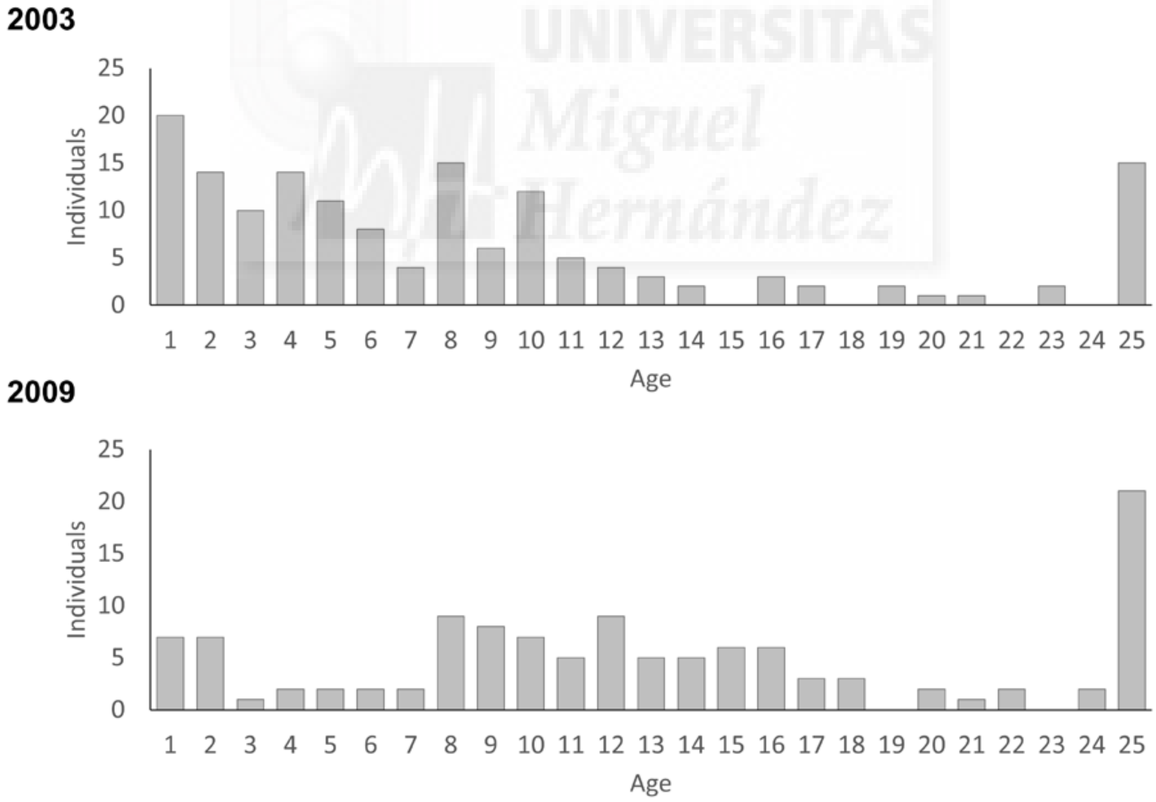

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Figure 2. Age distribution of the population in 2003 and 2009, before and after the disturbance. *N* = 153 and *N* = 117, respectively

Application 1: Estimating survival

We first estimated the survival in our population using one year of monitoring (before the fire, 2003; N=154, Fig. 2). In a first step, we generated all possible parameterizations $S = (S_1, S_2, S_3, S_4)$ where the ranges of each of survival rate S_i varied between 0.01 and 0.99 with steps of 0.02. For each S_i we therefore tested 50 alternative values. This resulted in a total of 50^4 = 6,250,000 parameterizations (Fig. 1a). In a second step we generated the stable age distribution predicted by the Leslie matrix model for each parameterization j (Fig. 1b). We used a pre-breeding Leslie matrix with 25 age-classes (eq. 1), but survival rates were the same within each size class. Thus, our goal is to determine the values for the vector $S = (S_1, S_2, S_3, S_4)$ of survival rates which yield the lowest error. The fecundity parameter of the Leslie matrix was defined by equation 2, where first-year survival (S_1) was inversely determined by our approach, the sex ratio (*SR*) in this population was 1:1 (Rodríguez-Caro *et al.* 2010), breeding success $BS = NC*CS*HS$ = 5.21. We obtained the number of clutches (NC = 2), clutch size (CS = 3.16, Rodríguez-Caro *et al.* 2014) and hatching success (HS = 0.824) from the population in southwestern Spain (Doñana National Park, Díaz-Paniagua, Keller & Andreu 1997).

In a third step, we converted the predicted age distribution into an age distribution that considered the age-specific detectability (Fig. 1d). We obtained age-specific estimates of detectability by distance-sampling procedures (Thomas *et al.* 2010; see Supporting Information 2 for details). Detection probabilities were 0.27 for juveniles, 0.41 for subadults and 0.47 for adults.

In a fourth step, we calculated the likelihood (eq. 4) for each parameterization S_j using the corresponding detectability-corrected simulated age distribution (Fig. 1d) with the observed age distribution of the monitoring of 2003 (Fig. 1c) and estimated the most likely value for the vector $S = (S_1, S_2, S_3, S_4)$ based on the $w+(\Theta, l)$ for $l = 1,\ldots, 4$ (eq. 5). Finally, we compared our estimated survival rates with the mark-recapture estimates of Sanz-Aguilar *et al.* (2011).

We also performed a sensitivity and elasticity analysis to understand the role of the different parameters in the matrix model, using the *popbio* R package (Stuben & Milligan 2007). This analysis describes the consequences of small changes of model parameters on asymptotic growth rate that results from the Leslie matrix. The sensitivity and elasticity analysis contribute important information for management and conservation decisions about wildlife population. We explore the relative importance of each factor and we discuss the effects of the bias in each estimated parameter. This analysis is also important to know how accurate our estimates should be.

Application 2: Impact of sample size.

By means of simulation experiments, we assessed the impact of sample size on the precision and accuracy of the survival estimates obtained by our approach. Starting from stable age distribution resulting from a pre-breeding Leslie matrix with the values of $S = (S_1, S_2, S_3, S_4)$ selected in Application 1, we simulated a population of 1000 individuals. We used the observed detection probabilities to obtain samples of the simulated population with different sizes N. The sampled simulated data based on the known $S = (S_1, S_2, S_3, S_4)$ were used like the observed data in our inverse modeling approach presented in

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Application 1. We repeated this process for different sample sizes *N* (*N* = 500, 400, 300, 200,....50). For each sample size *N*, the process was repeated 20 times.

Application 3: Factors impacting survival

Our approach also allows for testing alternative hypotheses on temporal variation in the survival and fecundity parameters of the Leslie matrix. We applied this feature to our case study by assessing the impact of a fire disturbance (that occurred in our population in 2004) on the temporal variation of the survival rates. We then compared our results with a previous study that estimated survival rates after fire by means of capture-recapture approaches (Sanz-Aguilar *et al.* 2011) for the same population and disturbance. We tested four competing hypotheses (Fig. 3). The first hypothesis (H1) is our null hypothesis that represents no effects of fire on survival; in H2, survival rates decrease and do not recover in subsequent years after fire; in H3 the fire impacted survival only in the next year with a total recovery the subsequent years; and in H4, survival rates decreased after fire but show in the following years a progressive recovery (Fig. 3).

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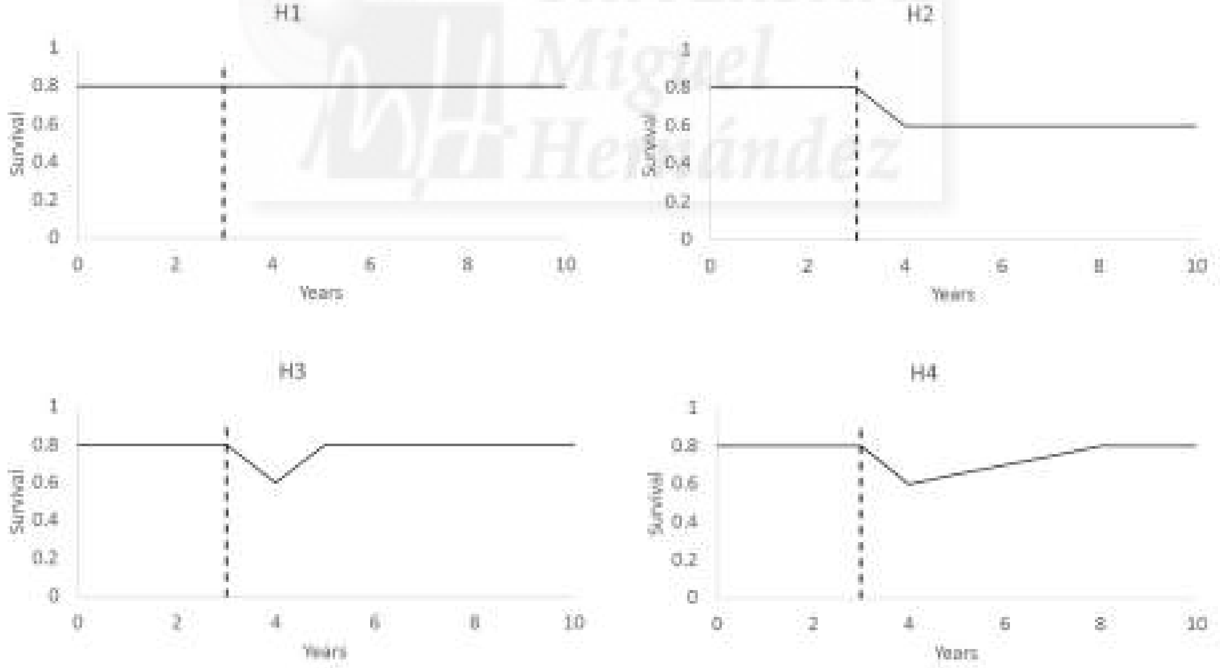

Figure 3. Hypothesis about the effects of the fire. H1 is non-effects of the fire perturbation, H2 is permanent decrease in the survival rates, H3 is just effect in the year of the fire with a total recovery the next year, and H4 is drop of survival in the year of the fire and a progressive recovery in the subsequent years.

We used the most likely model parameterization determined in Application 1 to generate the stable age distribution for the year 2004 of the fire. We then simulated the next 5 years using survival rates modified in accordance with the different hypotheses and compared the simulated age distribution to the observed distribution from 2009 (i.e. 5 years after the fire). For H1, the survivals parameters did not change, we had thus no parameter to determine. For H2, the population was simulated with constant new survival rates Sf for all five years after the fire, we had thus four parameters to estimate. For H3, population dynamics was simulated with new survival rates S_f only for the year after the fire whereas we applied the other years the pre-fire survival rates . Finally, H4 was tested by means of an additional parameter that described the rate of recovery in survival after the year of the fire (Fig. 3). Here we estimated therefore 5 parameters. We corrected the maximum survival after disturbance with the data of Application 1 to avoid that survival rates continue to increase. The fire disturbance did not have negative effects on fecundity (Sanz-Aguilar *et al.* 2011), so we assumed no change in fecundity. We finally compared our estimate survival rates and the most likely hypothesis with that obtained in the previous study of Sanz-Aguilar *et al.* (2011).

Results

Application 1

The survival rates estimated with our methods were Š = (0.23, 0.81, 0.83, 0.99) (Fig. 4). Sanz-Aguilar *et al.* (2011) estimated the survival rates of the population using 10 years of monitoring and obtained Š = (NA, 0.20, 0.79, 0.98) for juveniles, subadults and adults, respectively (Table 1). (Note that capture-recapture estimates did not consider first year survival). Our estimates based on just one year of monitoring yielded thus very similar estimates for adults and subadults, but not for juveniles.

Table 1. Survival rates estimated in this work (95% confidence interval) and the estimates calculated by Sanz-Aguilar. N is the number of tortoises found in the fieldwork, the effort is the number of hours searching tortoises by person, and finally the number of years monitoring to reach the estimates.

	Present Work	**San-Aguilar *et al.* 2011**
S1	0.23 (0.11 – 0.32)	-
S2	0.81 (0.41 – 0.92)	0.20 (0.08 – 0.42)
S3	0.83 (0.42 – 0.92)	0.79 (0.57 – 0.90)
S4	0.99 (0.48 – 0.99)	0.98 (0.92 – 0.99)
N	173*	1389 (675 recaptures)
Effort	196 hours searching	1600 hours searching
Years	2003	1999 - 2009

*173 tortoises found during the monitoring, but 20 were recaptures

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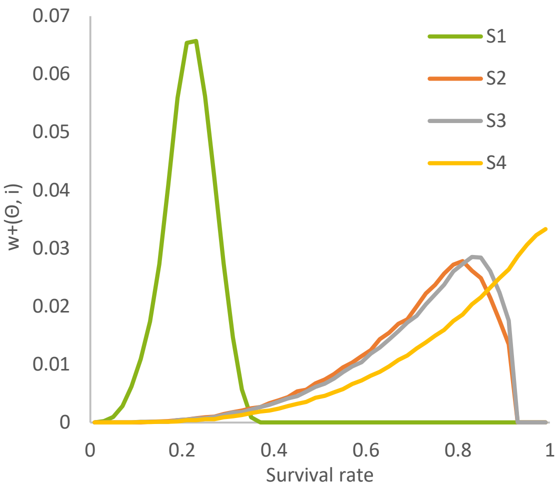

Figure 4. Values of likelihood for each estimate of survival *w*+(*Θ*, *i*). The most probably vales were 0.23 for S1, 0.81 for S2 0.83 for S3, and 0.99 for S4.

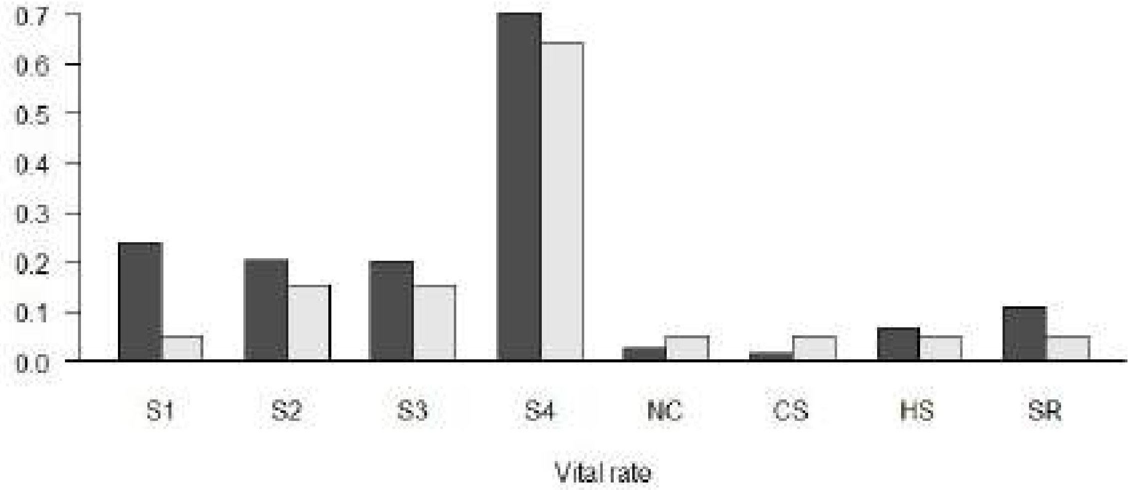

Figure 5. Sensitivity (black bars) and elasticity (grey bars) values for the parameters. S_1 is one-year-survival rate, S_2 is juvenile survival, S_3 subadult survival, S_4 adult survival, *NE* number of eggs, *NC* number of clutches, *SR* sex ratio and *HS* hatching success.

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Sensitivity analyses showed that adult survival was the key factor determining the growth rate the population most strongly (Fig. 5).

Application 2

We simulated size distribution data based on known survival rates and then applied our analysis to estimate the survival rates. We found that our estimates were robust for sample sizes larger than 100 individuals, but uncertainty increased for smaller sample sizes (Fig. 6), especially for S_1, S_2. Within this range, the obtained estimates were slightly biased from the original survival rates. However, estimates of adult survival, the most sensitive parameter of the sensitivity and elasticity analyses (Fig. 5), did not show any bias. Below 100 individuals the behavior of the estimates was more uncertain with larger bias and larger confidence intervals (Fig. 6).

Application 3

The observed age distribution after the fire was calculated with 117 tortoises corresponding to the year 2009 (Fig. 2). The hypotheses that received the least support were the null hypothesis H1 with no impact of fire on survival and hypothesis H3 where survival was only reduced the year after fire. Hypotheses H2 and H4 that assumed more long-lasting effects of fire on survival received similar support from the data (ΔAIC < 2, Table 2). Hypothesis H2 support a permanent reduction of the survival 5 years after the disturbance with a high reduction in one-year-old and juvenile survival Š = (0.07, 0.37, 0.81, 0.91). However H4, showed similar results in the decrease of survival Š = (0.05, 0.45, 0.83, 0.87) but with an additional parameter,

Table 2. Survival rates after the fire and AIC for each hypothesis. Hypothesis were explained in Methods - Application 3.

Hypothesis	S1	S2	S3	S4	AIC
H1	0.23	0.81	0.83	0.99	196.48
H2	0.07 (0.03 – 0.11)	0.37 (0.18 – 0.48)	0.81 (0.39 – 0.83)	0.91 (0.45 – 0.99)	141.73
H3	0.03 (0.01 – 0.09)	0.39 (0.19 – 0.66)	0.83 (0.37 – 0.83)	0.55 (0.27 – 0.81)	188.62
H4*	0.05 (0.02 – 0.07)	0.45 (0.33 – 0.57)	0.83 (0.59 - 0.83)	0.87 (0.64 – 0.96)	142.81
Sanz-Aguilar *et al.* 2011					
H4	NA	0.11 (0.04 – 0.31)	0.62 (0.39 - 0.84)	0.95 (0.83 – 0.99)	

*H4 has a slope of recovery = 0.01

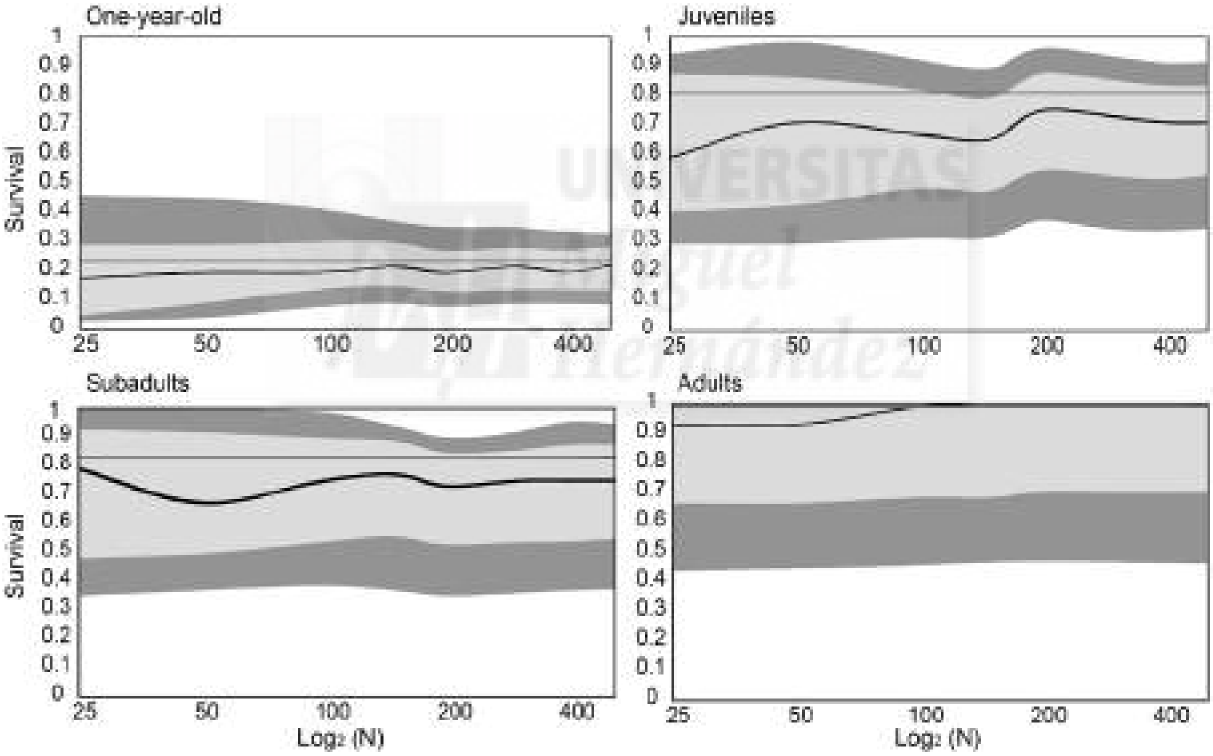

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Figure 6. Relation between the number of individuals (*N*) with the estimate survival rates (black lines) and their confidence intervals (75% light grey area and 95% dark grey area). Grey lines are the known survivals rates.

the recovery rate (slope = 0.01). With that slope, adult survival recovered completely within 5 years, subadults did not suffer a survival decrease, but juveniles and one-year-old needed more time to reach the pre-fire survival rates.

Our results partially match those obtained by Sanz-Aguilar *et al.* (2011). They identified hypothesis H4 as the one that best described the impact of the fire on survival. According to Sanz-Aguilar *et al.* (2011), after fire, survival rates were 0.95, 0.62 and 0.11 for adults, subadults and juveniles, respectively. They found a very fast recovery of adults and subadult, but a much slower recovery in juveniles (Sanz-Aguilar *et al.* 2011).

Discussion

We propose a novel low-cost approach based on inverse modeling and classical matrix models to estimate age-specific demographic rates of animal populations. Our approach does not need repeated counts of individuals over time as required for commonly used capture-recapture methods (Lebreton *et al.* 1992) or N-mixture models (Chandler & King 2011).Using simulated data, we showed that a population sample of the age structure for more than 100 individuals and estimates of detectability among different age classes are needed to obtain robust estimates of demographic rates. We applied our new approach to estimate of survival rates of the tortoise *T. graeca*. Using one year of monitoring with 153 individuals, our approach yielded similar estimates than capture-recapture methods using data from >10 years (> 1000 individuals). Additionally, we extended our approach to test alternative hypotheses on the impact of fire disturbance on the survival rates of the population and found evidence for a substantial decline of survival rates that lasted for several years after the fire.

Estimating survival

Our estimates agreed with capture-recapture estimates for subadults and particularly adults, the age classes for which the species demography is more sensible (Doak, Kareiva & Kleptka 1994; Walker *et al.* 2012; Pérez *et al.* 2012, see also Fig. 5). However, our estimate for juvenile survival (S_2 = 0.81) was substantially higher than the capture-recapture estimate (S_2 = 0.2). However, it must be noted that this difference could emerge to a large extent because of methodological differences. Our approach estimates survival of the first year that was very low (S_1 = 0.23), whereas capture-recapture analyses did not consider because hatchling were not marked (they have a soft carapace). Additionally, the capture-recapture estimate of juvenile survival may be low because of the low detectability and sample size of young individuals (Doak, Kareiva & Kleptka 1994; Hailey 2000; Tuberville *et al.* 2008; Pike *et al.* 2008); because recapture probabilities of juveniles were not modelled separately; or because some juveniles may also lose the marks when growing carapace. Moreover, the estimates for juveniles of our approach showed smaller confidence intervals than the CRC estimates.

A previous work by Fernández-Chacón *et al.* (2011) on the sister tortoise *T. hermanni* that modeled recapture probabilities including age effects found a first-year survival rate of 0.39 (0.22-0.59) and an average of juvenile survival from age 1 to 4 years old of 0.69. These estimates are very similar to the rates obtained here for *T. graeca*. Finally, regarding the first year survival, our estimate (0.24) was lower that the estimate by Keller, Díaz-Paniagua & Andreu (1998) for the population of the species in SW Spain (0.39). This difference could reflect actual differences between the two populations and suggest that overall survival of juveniles in our study

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area could be lower than in other populations. In the Doñana National Park, the predation of hatchlings has been described as very low (Keller, Díaz-Paniagua & Andreu 1998), whereas in our population in the southeastern Spain predation rates are higher (García *et al.* 2003).

Impact of sample size on robustness of survival estimates

Our simulation exercise (Application 2) showed that our survival estimates are robust, albeit slightly biased for the younger classes, provided samples sizes range are larger than 100 individuals. In our case study we observed a notable decrease in the precision and accuracy of the estimates if the sample size was below 100 individuals. A sample size of 100 individuals from a single count or year represents a very low sampling effort in comparison to the long-term monitoring effort usually needed in capture-recapture studies (in our case 15 years). Obviously, there is a trade-off represented in the slightly biased estimates obtained (in our case, around 10% for juveniles and subadults; Fig. 6). The bias did not appear for adults, which is the most sensitive parameter in the demography of the species. In what circumstances is this decrease in the accuracy of the estimate acceptable? For many conservation efforts, where long term monitoring programs are too expensive or infeasible, our proposed method will be extremely useful. In those rarer cases where funds are available and higher accuracy is necessary, a decision framework is needed that optimizes decision making by considering both the cost of long-term monitoring as well as their benefits in terms of reduction in conservation uncertainty (e.g. Field *et al.* 2004, Wildermuth, Anadón & Gerber 2013). Moreover, our estimates were rather stable even with a low number of individuals. Our approach would also be very useful to compare different population facing perturbations.

Model selection and impact of fire on survival

Our approach was also successful in testing alternative hypotheses on factors affecting survival. We found evidence for a substantial decline of survival rates after the fire that lasted for several years after the fire. Hypothesis H4 (that predicted a gradual recovery of survival rates during the 5 years after the fire) obtained a similar fit of the age distribution data than hypothesis H2 (that assumed a constantly reduced survival rate for the next 5 years), but the increased model complexity of H4 (one more parameter describing the rate of recovery) was not fully compensated. At the end, H2 and H4 received similar support (i.e., $\Delta AIC < 2$). Our results partially matched the results obtained by Sanz-Aguilar *et al.* (2011) based on mark-recapture. Both methods, with very different sampling efforts, identified the same general hypothesis to describe the impact of fire on the survivals. Adults and subadults survival showed only a weak decrease after the fire and they recovered relatively fast, taking between three to four years to return to the original survival values. In contrast, juveniles and one-year-old tortoises suffered after the fire a notable decrease in survival and their recovery was more slowly. However, as a consequence of the different predictions of juvenile survival, results of our method and of the capture-recapture estimates differed in the juvenile class. The ability of our method to test the support of alternative hypothesis on how different ecological processes impact the demography multiplies its usefulness and makes it more comparable to

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standard demographic estimation methods in ecology and conservation.

Although our example is based on an age-structured population, the proposed approach can also be used for stage-structured populations. In addition, our approach can estimate reproductive parameters using known survival rates. However, application of our approach requires that (i) individuals can be aged reliably (otherwise a stage matrix model should be used), (ii) the population should be close and stable, and (iii) the minimal number of individuals needed for this study is around 100. Future research should consider the effects of stochasticity, immigration and emigration, and non-equilibrium dynamics. Additionally, coupling of our method with an optimization framework could assist in the decision regarding the trade-off between reduced cost vs. increased reliability in the parameter estimates (Field *et al.* 2004, Wildermuth, Anadón & Gerber 2013).

Overall, our approach provides a framework for estimating demographic rates with much lower sampling efforts than conventional approaches. It attempts to broaden the toolbox of biodiversity conservation and provides tools that are likely to be useful when long-term monitoring is not feasible, or the assessment of impacts on survival is needed. Our approach opens up the possibility of estimating life history traits, such as survival, with information collected just during of one year of fieldwork.

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Supporting Information

Appendix SI 1. Age estimates.

Appendix SI 2. Detectability rates.

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Low tortoise abundances in pine forest plantations in forest-shrubland transition areas*

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Abstract

In the transition between Mediterranean forest and the arid subtropical shrublands of the southeastern Iberian Peninsula, humans have transformed habitat since ancient times. Understanding the role of the original mosaic landscapes in wildlife species and the effects of the current changes as pine forest plantations, performed even outside the forest ecological boundaries, are important conservation issues. We studied variation in the density of the endangered spur-thighed tortoise (*Testudo graeca*) in three areas that include the four most common land types within the species' range (pine forests, natural shrubs, dryland crop fields, and abandoned crop fields). Tortoise densities were estimated using a two-stage modeling approach with line transect distance sampling. Densities in dryland crop fields, abandoned crop fields and natural shrubs were higher (>6 individuals/ha) than in pine forests (1.25 individuals/ha). We also found large variation in density in the pine forests. Recent pine plantations showed higher densities than mature pine forests where shrub and herbaceous cover was taller and thicker. We hypothesize that mature pine forest might constrain tortoise activity by acting as partial barriers to movements. This issue is relevant for management purposes given that large areas in the tortoise's range have recently been converted to pine plantations.

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Ecotones are areas with relatively sharp environmental gradients that possess unique natural attributes [1 - 4]. The southeastern Iberian Peninsula constitutes a biogeographic ecotone between the Mediterranean and arid subtropical biomes, and is the distribution limit for about 350 plant species [5, 6]. There is a progressive change from Mediterranean Forest, with *Pinus halepensis* as a dominant species, to the arid subtropical shrublands. Agriculture, fires and overgrazing have affected this ecotone since the Neolithic [7], leading to the existence of seminatural or human landscapes characterized by habitat patches at different successional stages. These landscapes host a great biodiversity [8] and thus are key to conservation policies [9, 10]. In the last decades, however, these landscapes have suffered drastic changes due to crop abandonment, intensive agriculture, urbanization and reforestation [11].

Here we assess the effects of pine forests on a wildlife species in the forest-shrubland transition of the southeastern Iberian Peninsula. Reforestations in the Mediterranean have been based mostly on pine plantations to prevent erosion, floods, desertification, to assist or accelerate ecological succession from shrubs to original forest [12] and recently to mitigate anthropogenic carbon dioxide emissions [13]. In the Iberian Peninsula's Murcia province, approximately 94,000 hectares (8% of the province) have been reforested in the last 110 years [14, 15]. Since the sixties, reforestations have been done mainly in the ecotone between Mediterranean forests and the arid subtropical shrublands (i.e., in areas with precipitation values close to the precipitation limit of the forests) [14, 16]. In this ecotone, most reforestations with *P. halepensis* outside the forest's ecological boundaries (i.e., an afforestation) have frequently failed because the trees were in poor physiological condition, had poor growth, and had a high susceptibility to disease [17, 14, 15]. Pine plantations also have substantial negative consequences on other components of biodiversity, including a species-poor shrub understory [18]. Negative effects have also been described for birds [12, 19], insects [20, 21] and mammals [22]. However, studies addressing pine plantation effects on the herpetofauna are scarce (but see [23]).

The spur-thighed tortoise (*Testudo graeca*) is an endangered terrestrial tortoise inhabiting the ecotone between Mediterranean and arid subtropical areas [24]. The main threat to the species is habitat degradation, loss and fragmentation [25]. Within the distribution range of *T. graeca*, approximately 14% of available habitat has been the object of reforestation [14]. The main requirements of the species are sunny places for basking and shelters for protection from extreme temperatures and predators [9]. These two requirements are strongly dependent on the vegetation canopy which, in turn, could be affected by reforestation, so it is appropriate to evaluate *T. graeca* use of the landscape in the southeastern Iberian Peninsula [9]. In addition, *T. graeca*'s low mobility and dispersal abilities increase its vulnerability to local extinctions, which may be exacerbated by the impact of local changes in habitat quality [26 - 28].

The aim of this work is i) to understand the role of the different land-use types on the density of *T. graeca* and, in particular, ii) to study whether pine forests affect *T. graeca* population density. Density of tortoises have been widely estimated using line transect distance sampling methods [29 - 31]. For our study, we first used a two-stage modeling approach for distance sampling data [32] to estimate tortoise densities at the landscape scale in the principal habitat patches within the species' range (i.e., shrubs, dry crops, pine forest and abandoned crops). For the second step, we described the vegetation cover of the habitat types at the microhabitat scale.

Materials and methods

Ethics statement

Permits for the field work and animal handling were provided by "La Delegación General de Medio Natural de la Comunidad Autónoma de la Región de *Murcia*" *(AUT/ET/UND/48/2010)*.

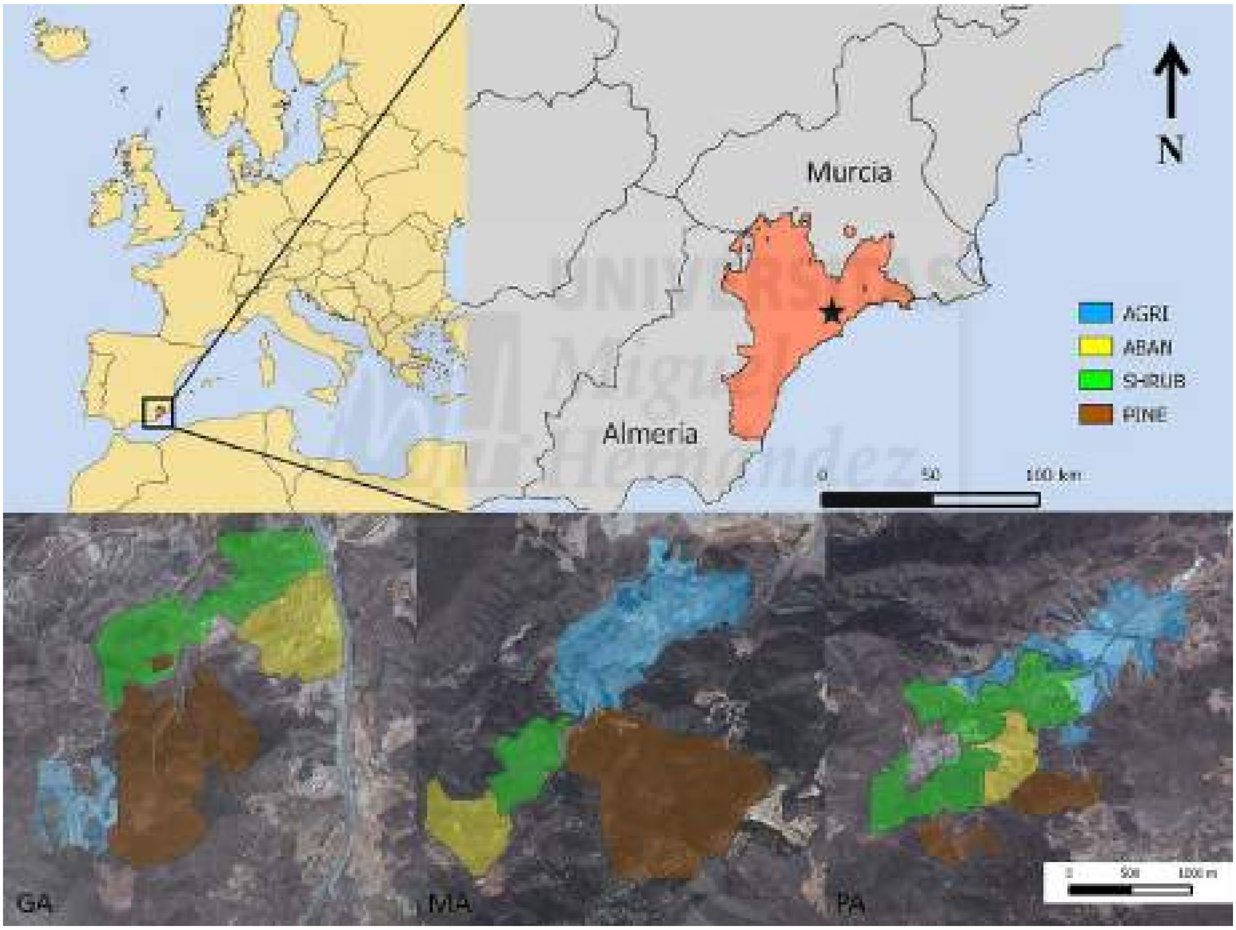

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Figure 1. Location of the study sites in the southeastern Iberian Peninsula and distribution of habitat types within the field sites. The transects were performed in GA (Galera), MA (Madroñales) and PA (Palomera). Down panels are orthophotos of the PNOA (National Aerial Orthophotography Plan) provided by the Centro Nacional de InformacioÂn GeograÂfica (http://centrodedescargas.cnig.es/CentroDescargas/index.jsp).

Study area and data collection

We estimated the abundance of *T. graeca* in different habitat types in the southeastern Iberian Peninsula. We chose three sample sites within the species' range (Fig 1): Galera (GA), Madroñales (MA) and Palomera (PA). Each site was surveyed three times during spring 2012. The three sites each contain the four most representative land uses or habitat patches within the species' distribution in the southeastern Iberian Peninsula [9, 33]. The four habitat patches were defined by their dominant land use or type of forest: pine forest (PINE, dominated by the Aleppo pine *P. halepensis*, one of the pine forests, GA, is the result of reforestation programs from the early 1980s); natural shrubs (NAT, with several species like *Anthillis cytisoides*, *Artemisia herba-alba*, *Rosmarinum officinalis*); dryland, tree-based crop fields (AGRI, such as olive *Olea euroapea* or almond tree *Prunus dulcis*); and abandoned crop fields (ABAND, where agricultural land has been abandoned and overgrown by bushes). The sampling effort was similar in each patch and each site; we covered around 0.33±0.19 km^2 in area on each survey.

We surveyed tortoises using line transect distance sampling method [34], in spring (April and May, 2012), as this is the most important period of activity for the tortoises in this area [35]. Surveys were performed under adequate weather conditions (i.e. not during rain or temperatures below 18°C). Tortoises were detected visually by surveying along predefined lines through each of the four habitat types (PINE, NAT, AGRI and ABAND). We determined the sex of the tortoise according to secondary sexual characteristics [36], young individuals with no sex associated were classified as a subadults. Transect lines, around 1521±160 m long and straight, were randomly placed among habitat patches, covering the whole study area. A group of eight observers executed the surveys, walking simultaneously in four pairs, one pair worked in each habitat. Each site was surveyed in three consecutive days and observer pairs rotated between transect to avoid bias. For each tortoise detection, observers recorded the perpendicular distance from the tortoise to the transect line.

Distance sampling analysis

For distance sampling calculations [34], we assumed detectability decreased as a function of perpendicular distance from the line and used the observed distances to model the detection function. In our study, we could not assume that the probability of detecting a tortoise on the line was certain, because the surface activity of tortoises has a strong seasonal pattern. For this purpose, we multiplied the data from a previously conducted radiotelemetry study to obtain an estimate of the percentage of surface-active tortoises during the monthly samples (April = 52.9%; May = 48.5%; using the percent of active tortoises from the total of tortoises with radio transmitters, [35]).

We adopted a two-stage modeling strategy to evaluate the relationship between tortoise densities and habitat [32, 37]. In the first stage, we fitted a detection function to the distance data using Distance 6.0 [38]. Upon preliminary inspection of the fit, we removed perpendicular distances beyond 4.25m (truncation distance, hereinafter ω) where detection probabilities generally fell to 0.1 or lower [34]. Due to the observers' tendencies to round distances, we grouped the detections into five distance intervals (cutpoints: 0, 0.75, 1.5, 2.25, 3.25,

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4.25 m; [34]). We evaluated the fit of the half-normal (HN) and hazard rate (HR) key functions with and without cosine series adjustments and explored covariate distance sampling techniques (MCDS) to model heterogeneity in detection probabilities. Covariates included were habitat patch (PINE, NAT, AGRI and ABAND), site (GA, MA and PA) and stage (ADULTS and SUBADULTS). Akaike's Information Criterion (AIC, [39]) was used for model selection.

The best fitting detection model was then used to estimate the effective area that we included in the second-stage count model as an offset to account for imperfect detection within the surveyed strip (adjusting these counts using the data of a radiotelemetry study, [35]). In the second stage, we related adjusted counts to the covariates that may influence tortoise densities. Here, we used generalized linear models (GLM) with a log-link and a quasipoisson error structure. We also included habitat patch (hereafter, patch), site and the interaction of both as independent variables, since tortoise densities may vary among the sites or habitat patches. As in the first stage, we compared candidate models and selected the best model based on minimum AIC [40]. We used MuMIn package in R-project (R Core Team, 2013) to calculate a modification of Akaike's Information Criterion for overdispersed count data (QuasiAIC, QAIC).

Vegetation structure analyses at microhabitat scale

Microhabitat structure was surveyed randomly around each transect (at 15-minute intervals), and at the location of each detected tortoise, in plots of diameter 3m. The cover of herbaceous vegetation, tree, shrub, perennial grasses and bare soil were noted visually and recorded for each plot (Table 1).

We characterized the four habitat patches according to the vegetation structure. Discriminant function analysis (DFA, SPSS statistics 21) was performed to identify the variables that influence the differences between patches at microhabitat scale (differences in vegetation coverage in plots of diameter 3 m between patches). When we found differences in tortoise density in the same habitat patch among the three sites, we used DFA to explore differences in vegetation structure between these sites.

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Results

Density model

We detected 251 tortoises but, after truncation at ω, we included 192 individuals in our analyses (S1

Table 1. Vegetation and soil categories assessed in the microhabitat analysis. Seven coverage categories were used for each variable: 1 = 0-1%; 2 = 2-10%; 3 = 11-33%; 4 = 34-50%; 5 = 51-66%; 6 = 67-90%; 7 = 91-100%.

Variable	*Description*
TREE	Coverage of trees
TALL	Coverage of tall shrub (> 150 cm height)
MEDIUM	Coverage of medium-sized shrub (between 50 cm – 150 cm height?
SMALL	Coverage of small shrub (< 50 cm height)
GRASSES	Coverage of perennial grasses
HERB	Coverage of herbaceous vegetation
BARE SOIL	Coverage of bare soil

Table). The detection model with stage as a covariate provided the best fit (Table 2). Average detection probabilities were lower in subadults than adults. The detection probabilities and 95% confidence intervals were 0.629 (0.529-0.747) for adults and 0.315 (0.164-0.604) for subadults.

Table 2. Detection function models (first stage) for tortoises. The variable sites (GA, PA, MA), patches (AGRI, ABAND, NAT, PINE) and stage (ADULTS, SUBADULTS) were used in the analysis.

Key function[a]	Covariates	K	AIC
HR	Stage[b]	3	573.84
HN	Stage[b]	2	574.23
HN		1	577.08
HR		2	578.25
HR	Patch[b]	5	579.90
HN	Patch[b]	4	580.15
HN	Site[b]	3	580.44
HR	Site[b]	4	582.00

K = Number of parameters in the model

[a] Key function models: hazard rate (HR) and half normal (HN)

[b] Factor covariates

Table 3. Factors affecting the density of tortoises (second stage). Results of generalized linear models (GLM) with a log-link and a quasipoisson error structure. QuasiAIC was used for model selection. Degrees of freedom (df) and percentage of explained deviance (Dev) are also shown.

Model	QAIC	ΔQAIC	df	Dev
Patch x site	207.7	0.0	12	58.5
Patch + site	259.2	51.5	6	30.8
Patch	270.3	62.6	4	24.4
Site	312.8	105.1	3	5.7
Intercept only	322.4	114.7	1	0

The regression model (second stage) indicated that tortoise abundance was affected by the interaction between patch and site (Table 3). Tortoise densities were greater in dryland, treebased crop fields, abandoned crop fields and natural shrub patches (d_{mean} = 7.97, 6.93 and 6.34 tortoises/ha, respectively) than in pine forest (d_{mean} = 1.25 tortoises/ha). We also detected tortoise density differences between sites in tree-based agriculture and pine forests (GLM results in S2 Table).

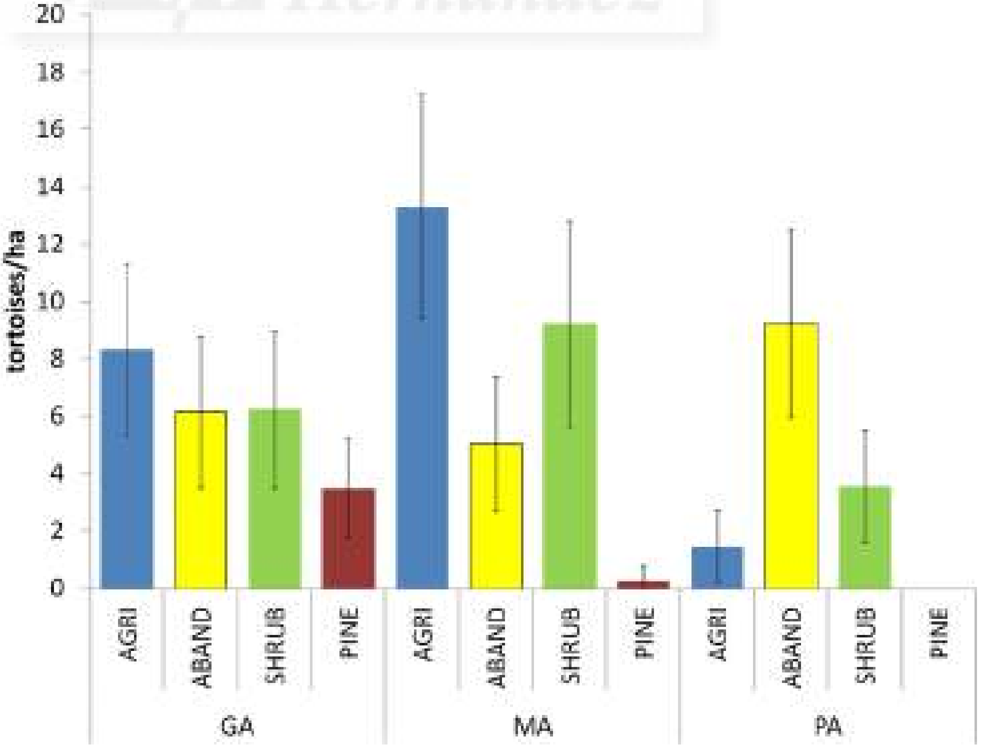

Figure 2. Density of tortoises (tortoises/ha ± CI) by site and patch type, derived from the best fitting quasipoisson count model (i.e., habitat x site).

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Densities in tree-based agriculture were lower in PA than in GA and MA (*P.value* < 0.001). Density in pine forests was higher in GA than in PA (no tortoises were found there) and MA (*P.value* = 0.029; Fig 2).

Vegetation structure analyses at microhabitat scale

We recorded 656 vegetation samples (we recorded 241 vegetation samples associated with tortoises encounters, and we randomly recorded 415 vegetation samples in each transect). At microhabitat scale, the DFA derived three discriminant functions. The first and second functions explained 97.7% of the variation. The pooled within-groups correlations to the first function are related positively with the cover of medium-sized and small shrubs and negatively to the coverage of bare soil. This function can be interpreted as a gradient from bare soil to dense shrub coverage. The second function indicated the influence of tall and thick vegetation because the coverage of trees and tall shrubs contributed positively. Using just the first two functions, we can describe the different patches (See S1 Fig). Dryland crop fields were described as areas with high values of bare soil and trees (Fig 3). Abandoned crop fields were characterized by a cover of shrubs without trees or tall shrub, and high cover of herbaceous vegetation. There was a high cover of plants in natural shrublands, in particular of medium and small-sized shrubs. In pine forest, trees and tall shrubs were dominant.

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Since we found site differences in tortoise densities in pine forest, we compared the vegetation coverage of pine forest in two groups, with high density of tortoises (GA) and low density of tortoises (MA and PA). The DFA created just one function, which was significant (χ^2 = 56.853, df = 4, *P* < 0.001). This function can be interpreted as a gradient of vegetation cover (with the discriminating variables: TALL = 0.704, HERB = 0.332, TREE = 0.144, see Table 1 for categories of vegetation cover). Both kinds of pine forest were characterized in different positions of the discriminant function, GA forest was negatively related to the function(- 0.981) and, MA and PA forests were positively related (0.818). According to these analyses, the mean amount of

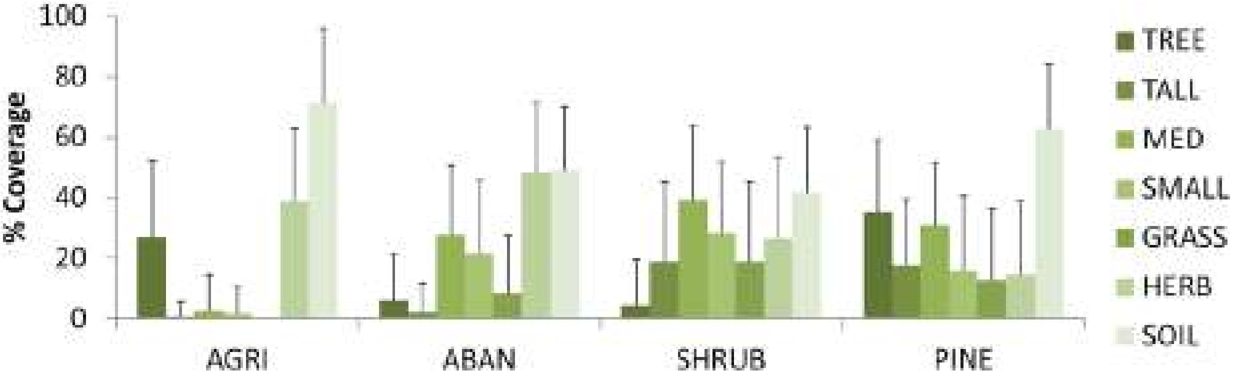
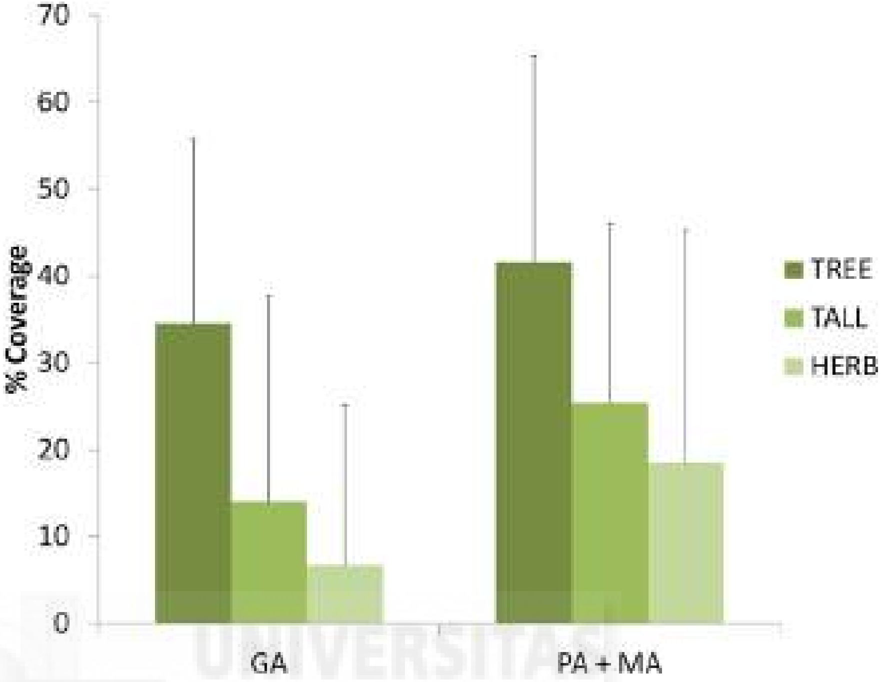


Figure 3. Mean cover of each environmental variable significant in the DFA per patch. Pine forest (PINE), natural shrubs (NAT), dryland tree-based crop fields (AGRI) and abandoned crop fields (ABAND). See Table 1 for categories of vegetation cover (TREE, TALL, etc.). AGRI = 216, ABAND = 155, NAT = 158 and PINE = 127 samples.

Figure 4. Comparison of microhabitat characteristics of pine forests between patches with high and low density of tortoises. MA and PA show lower density than site GA and thus are merged. See Table 1 for categories of vegetation cover.



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vegetation coverage (TALL, HERB and TREE) was higher in MA and PA than in GA (Fig 4a).

We also tested the differences in AGRI between the low density site (PA) and the other two sites (GA and MA). We did not find differences in the vegetation structure of AGRI patches among locations using DFA ($P > 0.05$).

Discussion

Two-stage modelling was a good approach to disentangle the factors affecting detectability and density of tortoises. As in previous works, we found that detectability was affected by individuals' age class: juveniles versus adults [29, 30, 41]. On the other hand, density was also affected by habitat patches and sites. According to abundance classes defined in a previous study [42], the density estimates of *T. graeca* found in this work for the three sites (GA = 6.35; MA = 6.95; PA = 3.56 ind/ha) showed high values within the southeastern Iberian Peninsula. As has been shown in previous studies, reptiles prefer landscapes with mosaic structure for thermoregulation because they contain basking places near shadier areas where animals can cool and find shelter [9, 43]. In our study, differences in the density of tortoises were found at two scales. Firstly, at a patch scale, the lowest tortoise densities were found in pine forest. Trees and dense vegetation cover in pine forest patches may explain the low tortoise abundance, since open areas are needed to fulfil the thermoregulation requirements of tortoises [44]. Previous studies [9, 33] showed that there is a positive relationship between the presence of *T. graeca* and shrubland cover when the shrubland cover is 75% or less. Those authors also showed that *T. graeca* prefer re-colonize shrublands and cropland rather than more complex mature shrublands. Our results accord with previous works showing that densely forested areas such as pine forest, have a negative effect on reptiles [45, 46] and that tortoises prefer open habitats [47, 48], such as dryland or abandoned crops fields and natural shrub. Secondly, at the microhabitat scale, differences in tree-based agriculture patches were not so evident. Only the cover of bare soil seemed to differ between sites (mean cover of bare soil in AGRI for PA was 82.05% and 63.70% in GA and MA). However, this relation could have resulted from excessive ploughing in the tree-based agriculture areas of PA (authors, pers. obs.). The high percentage of bare soil can influence other mechanism as predation by the absence of shelter.

In relation to pine forest, there were also important differences at the microhabitat scale. Forests of diverse origin (i.e. natural or as a result of reforestations) are common throughout the range of *T. graeca* in the southeastern Iberian Peninsula. Pine forest of GA is the result of reforestation programs from the early 1980s and, we found in our results that microhabitatcharacteristics in GA were different than in the other two sites (PA and MA). As we found in the discriminant analysis, early

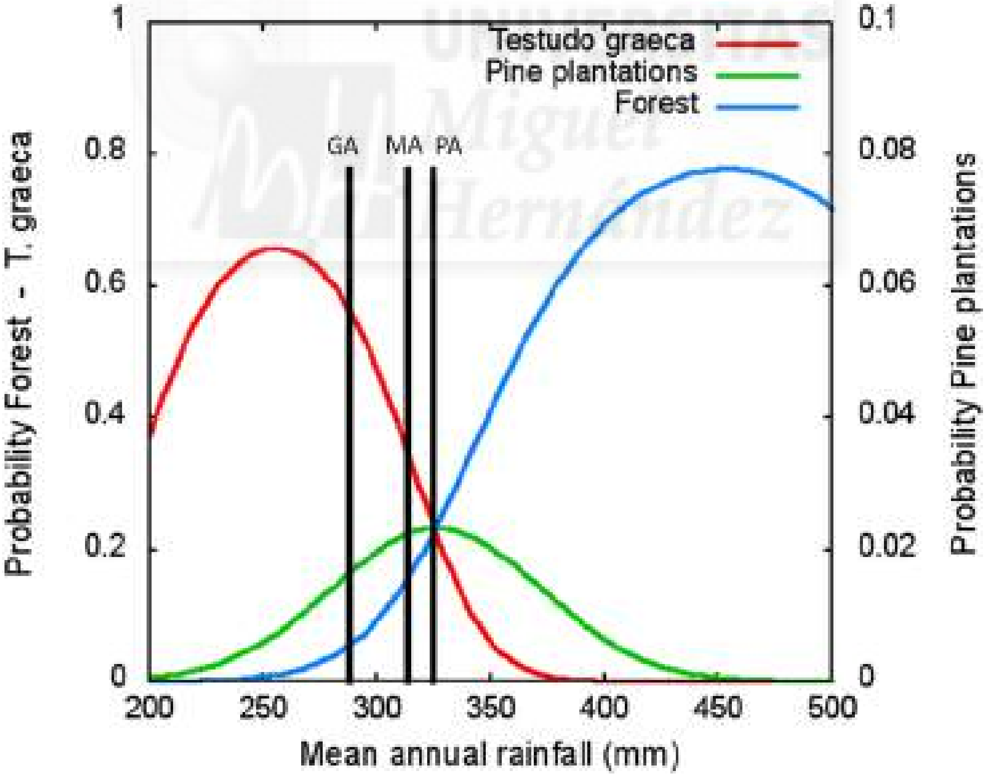

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Figure 5. Probability of presence of natural forests and pine plantations in southeastern Iberian Peninsula [14, 16] and, probability of presence of *T. graeca* [33] as a function of mean annual rainfall, according to statiscally significant distribution models. GA, MA and PA sites were represented according their annual rainfall.

reforested pine forest of GA showed lower shrub coverage compared to other sites. Besides the age of the reforestation, the structure of the vegetation between the pine plantations in GA and the pine forests in the other two sites may also be explained by the climate differences among the sites. GA is slightly dryer than the other two study sites (290 mm vs 310-320 mm of average annual rainfall). Because our study sites were located in a forest-shrubland transition area, this small difference in rainfall produces notable differences in the kind of forest and in the viability of pine plantations [14, 15]. According to regional climatic models (Fig 5, [14]), the probability of occurrence of pine forest is 5% in GA and ranges from 10 to 20% in the other two sites. Thus, pine plantations in GA are younger and pines have worse conditions than the other two study sites. These differences lead to lower canopy cover values, more open areas and a better habitat quality for thermoregulation purposes of *T. graeca* (i.e. [9, 33]).

From a conservation perspective, our results suggests that pine forest might act as a partial barrier for populations at a landscape scale. The impact of pine forest plantations on *T. graeca* distribution areas has the potential to be higher at higher precipitation levels due to the dense forest canopies. Forest conservation policies mainly aim to prevent deforestation [49], but there is an increasing awareness that an excess of forest cover may also be problematic, especially in human-altered landscapes in temperate regions [50], and particularly for some reptile species [45, 46]. Pine forest plantations are a low-quality habitat for different species of reptiles [51, 52]. Recent studies pointed the importance of consider thermal requirements of forest plantations for richness and abundance of reptiles [53]. Current conservation polices are not focused on preserving the mosaic structure of the landscape. However, maintaining the heterogeneity of these mosaic traditional landscapes is key to prevent the loss of biodiversity [10]. In this sense, results from this study should be considered in nature conservation plans, specifically in the management of the Natura-2000 network in the southeastern Iberian Peninsula (Directive 92/43/EEC, http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm). New policies should match the need of restoring forest in those areas where they have been historically replaced by shrubs, and the conservation of species like the spur-thighed tortoise that is linked to the current heterogeneous landscapes with patches of open habitats.

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Supporting information

S1 Table. Distribution of observation between sites and habitat patch. Tortoises found during the surveys.

S2 Table. Parameter estimates from the best approximating, generalized linear model with Standard Error (SE). We show the results of the

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GLM with model site-patch interaction. We found significant differences in the interaction between PA-AGRI and MA-PINE, in both the density is lower than in the other sites.

S1 Fig. Results of the DFA analysis. The first function (the gradient from bare soil to dense shrub coverage) is showed in the X axis, the second function (the influence of tall and thick vegetation) in the Y axis. The 656 samples are showed in different colors according habitat type and, finally, the centroids for each habitat are also showed.

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Movement and behavioural traits determine the population viability of a low-dispersal species in fragmented landscapes*

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Abstract

1. Assessing the role of animal movement and behaviour in buffering the viability of populations in human-altered habitats is one of the main challenges for ecological research.
2. We herein address the interacting effects of movement and behavioural traits, habitat fragmentation and population characteristics on the population viability of the spur-thighed tortoise (*Testudo graeca*). A previous study, based on individual-based modelling, found that land use intensification strongly impacts the movement and behaviour of non-dispersing spur-thighed tortoises.
3. We aimed to assess whether habitat fragmentation may reduce mating encounters, or if altered and more variable movement behaviour might counterbalance negative fragmentation effects. To this end, we explored the role of selected species spatial traits in supporting the viability of populations: effectiveness of mating search, juvenile dispersal capabilities, behavioural plasticity and philopatry.
4. We developed a spatially explicit individual-based model parameterised with empirical and bibliography data. The model includes movement, reproduction and mortality, and was used to calculate population extinction rates over 200 years.
5. Our results indicate that the combination of human-altered landscapes and the associated changes in movement patterns generally have negative effects on the viability of *T. graeca* populations.
6. A sensitivity analysis of the analysed traits showed that: i) the viability of *T. graeca* populations was very sensitive to changes in the effectiveness of mating search strategies; ii) increased dispersal capabilities of juveniles proved counterproductive; iii) variable movement behaviour was beneficial for *T. graeca* populations as it buffered habitat loss and fragmentation effects; but iv) temporal variation in the home range of tortoises had no effects on the simulated scenarios.
7. It is unknown how conspecific attraction underlies mating search strategies in *T. graeca*, but the effectiveness of such a biological mechanism is crucial to support the viability of low density populations in fragmented scenarios. We also found that *T. graeca* populations merely counterbalanced harmful fragmentation effects when behavioural plasticity was included in the model.
8. Our results are representative of long-lived species with low dispersal capabilities and suggest these taxa to be among the most vulnerable to habitat loss and fragmentation.

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Keywords: Idividual-based modelling, homing behaviour, philopatry, behavioural plasticity, Allee effect, long-lived species, *Testudo graeca*, sensitivity analysis

Introduction

Animal movement and behaviour have been recognised as key ecological traits for population ecology (Nathan *et al.*, 2008). The interaction between movement ability and landscape structure determines the realized movements in space and species' functional connectivity (Tischendorf & Fahrig, 2000; Schooley & Wiens, 2003). Understanding this interaction is especially relevant to conserve the populations impacted by habitat perturbances (Fahrig, 2007; Niebuhr *et al.*, 2015). In the 20th century, human activity has altered land use in many areas of the world and promoted habitat fragmentation for many species (Brooks *et al.*, 2002). Consequently, understanding how animal populations face habitat changes in today's global change scenario is one of the main challenges for ecological research (Sala *et al.*, 2000). Given the importance of animal movement and behaviour for population dynamics and species persistence, the emerging movement ecology field has considerably grown in the last decade (Getz & Saltz, 2008; Nathan *et al.*, 2008; Patterson *et al.*, 2008; Schick *et al.* 2008; Smouse *et al.* 2010). Several ecological theories deal with the role of movement and behaviour in a habitat loss and fragmentation scenario (Fahrig, 2007; Villard & Metzger, 2014; Niebuhr *et al.*, 2015), and taxon-specific studies have addressed how movement patterns change in real human-altered landscapes (e.g., Anadón, Wiegand & Giménez, 2012; Pittman & Semlitsch, 2013; Schüttler *et al.*, 2017). However, very few studies have assessed for natural systems the interaction between movement patterns in fragmented habitats and their effects on population viability (Morales *et al.*, 2010).

Animal movement and behaviour govern the search for resources, exchanges of individuals among subpopulations, colonisation processes and the maintenance of gene flow. Each individual movement involves a balance between potential benefits for survival or reproduction, and potential commitments in energy expenditure and mortality risk terms (Bélichon, Clobert & Massot 1996; Baker & Rao, 2004; Payo-Payo *et al.*, 2017). Correlated random walk models (Kareiva & Shigesada, 1983) are powerful tools to reproduce the inherent stochasticity of animal movements and behaviour (Kramer-Schadt *et al.*, 2004, Börger, Dalziel & Fryxell, 2008, Anadón, Wiegand & Giménez, 2012). These mechanistic models simulate random walk trajectories that emulate complex movement or behavioural processes, such us habitat selection (e.g., Moorcroft and Barnett, 2008) or philopatry (e.g., Cagnacci *et al.*, 2010). The comparison of simulated and empirical data may help to identify the biological processes that underlie the patterns observed in the field (e.g., Börger, Dalziel & Fryxell, 2008; Patterson *et al.*, 2008; Kie *et al.*, 2010). Integrating random walk models with individual based models that consider demographic processes may allow the identification of specific key biological traits for population viability, which are especially impacted by habitat alteration (Kramer-Schadt, Revilla & Wiegand, 2005, 2008).

This study addressed the effects of the interaction that links movement and behavioural traits of species (spatial traits), habitat fragmentation and population characteristics on the population viability of a long-lived species: the spur-thighed tortoise (*Testudo graeca*). A previous study, based on individual-based movement modelling that used radio-tracking data, found that land-use intensification in SE Spain strongly impacts the

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movement and behaviour of non-dispersing spur-thighed tortoises (Anadón, Wiegand & Giménez, 2012). While tortoises in natural landscapes showed strong site fidelity and slight individual variability, their movement and behaviour in altered landscapes greatly varied among individuals. A wide range of movement patterns was found particularly among females, which ranged from strong home behaviour to unbounded movements. When placed in the population dynamics context, this behaviour may reduce mating encounters in fragmented landscapes (Wosniack *et al.*, 2014), or alternatively, increased movement in fragmented landscapes may benefit mating search strategies and counterbalance negative fragmentation effects on population viability (Niebuhr *et al.*, 2015).

To assess whether habitat fragmentation reduces mating opportunities or not, we explored the role of four selected spatial traits in buffering fragmentation effects: mating search effectiveness, juvenile dispersal capabilities, behavioural plasticity and philopatry. To do so, we used a spatially explicit individual-based model that integrates the spatially explicit movements of individual tortoises with demographic processes. We assumed that tortoises maintained age-class transitions and survival rates in fragmented landscapes, but non-permeable linear barriers impeded mating encounters across them. We parameterised the model based on empirical and bibliographic data, and analysed a range of simulation scenarios that covered different habitat characteristics, population densities and adult survival rates.

To assess the relative importance of the four biological traits related to movement and behaviour for population viability, we used the generated simulation scenarios and conducted a sensitivity analysis to explore the sensitivity of the extinction rates of *T. graeca* over 200 years in relation to: i) mate searching effectiveness; ii) the age transition of juveniles to higher movement capacities; iii) behavioural plasticity; iv) tortoises' site fidelity. We further hypothesised that the effect of some of these parameters may differ among the simulated scenarios with distinct habitat characteristics, population densities and adult survival rates.

Methods

Study system

The spur-thighed tortoise *Testudo graeca* is a medium-sized tortoise whose main Western European population is found in SE Spain. This species inhabits mainly semiarid shrublands and traditional agricultural landscapes, and is heavily threatened by habitat fragmentation and loss (IUCN, 2002). *T. graeca* individuals are non-territorial, with overlapping home ranges ranging from 1 to 5 ha in SE Spain (Anadón *et al.*, 2006). As characteristic long-lived animals, they mature at the age of 8-10 years, and reach ages of 30-40 years (Díaz-Paniagua, Keller, & Andreu, 2001). *T. graeca* shows the particular sperm storage feature, a biological trait that allows clutches to be fertilised for several years after mating (Roques, Díaz-Paniagua, & Andreu, 2004). Clutch sizes vary mostly between 1 and 7 (the authors, unpublished data).

This species is ideally suited to study fragmentation effects on population dynamics. Firstly, radiotracking data, together with long-term capture-recapture studies, suggests that individuals show low-dispersal capacity and good site fidelity (Sanz-Aguilar, 2011; Anadón, Wiegand & Giménez, 2012). This makes low-density populations especially vulnerable to habitat disturbances (Sanz-Aguilar *et al.*, 2011). Secondly, basic demographic aspects of populations have already been addressed (e.g., Díaz-Paniagua, Keller, & Andreu, 2001; Sanz-Aguilar *et al.*, 2011; Rodríguez-Caro *et al.*, 2013), and the parameterisation of the movement behaviour of adult *T. graeca* males and females in natural and fragmented landscapes has already been implemented into a spatially explicit individual-based model (Anadón, Wiegand & Giménez, 2012).

STEPLAND: a spatially explicit individual-based model to simulate spur-thighed populations' viability

This model was specifically implemented in Python 2.7 and adds demographic processes to the individual-based model of tortoise movement developed by Anadón, Wiegand and Giménez (2012). For the model's description, we followed the Overview, Design concepts and Details protocol (ODD) proposed by Grimm *et al.* (2006, 2010). Figure 1 shows the model's general overview and its description is summarised in the paragraphs below (a full ODD version is shown in Appendix S1).

Entities, attributes and spatial scales. STEPLAND contains two types of entities: the landscape and tortoises. The 3 km × 3 km landscape is composed of a grid of 10 m × 10 m cells. Each grid cell is characterised by its position (x and y coordinates), and also by its assignment to one of the four habitat categories used by Anadón, Wiegand and Giménez (2012); intensive land use, traditional agriculture land, flat natural areas and natural areas on slope; or to the additional non-permeable infrastructures category. Each grid cell is also characterised by being assigned to a reproductive unit made up of landscape barriers. Landscapes are enclosed by a non-permeable border that represents discrete populations.

Tortoises have as attributes: sex, age, their location over time and the location of their focal-point attractor (that represents home behaviour). Additionally, eleven attributes govern the subprocesses of their movement (following Anadón, Wiegand & Giménez, 2012; see Appendix S1 for more information on movement parameterisation).

Input, initialisation and output. Model inputs include the initial population, the landscape and model parameterisation (Fig. 1). The initial number of individuals for the different age classes was established following a stable age distribution predicted by an age-stage structured deterministic matrix population model (Caswell, 2001) with the POPBIO package in the R software (Stubben and Milligan, 2007; R Core Team, 2014; Appendix S2). Then the tortoises of the initial population were randomly distributed across the landscape. These initial conditions were the same among the simulation scenarios that started with the same number of tortoises. Model parameterisations were based on the previous work of Anadón, Wiegand and Giménez (2012), empirical data and on a bibliographic review (Appendix S3). Data output consists of CSV files that comprise the surviving tortoises of the population and their attributes over time. Own scripts were developed in R (R Core Team; 2014) and in Python 2.7, and allowed such massive outputs to be processed.

Temporal scales, process overview and scheduling. Each time step represents 1 day, while outputs are summarised for periods of full years. All the simulations were run for 200 years and replicated 64 times. The model consists of submodels for movement, reproduction and mortality (Fig. 1).

Movement of tortoises is governed by their attributes, the time of the year (i.e., they exhibit a seasonal activity pattern) and the habitat characteristics of current and neighbouring cells. According to Anadón, Wiegand and Giménez (2012), each tortoise has the possibility of moving up to a certain number of steps per day, which depends on the time of the year. For each step, three normalised weights, which correspond to three movement subprocesses (i.e., homing behaviour, habitat dependency and autocorrelation; Fig. 1), are estimated for all eight neighbouring cells. The product of these three weights yields the

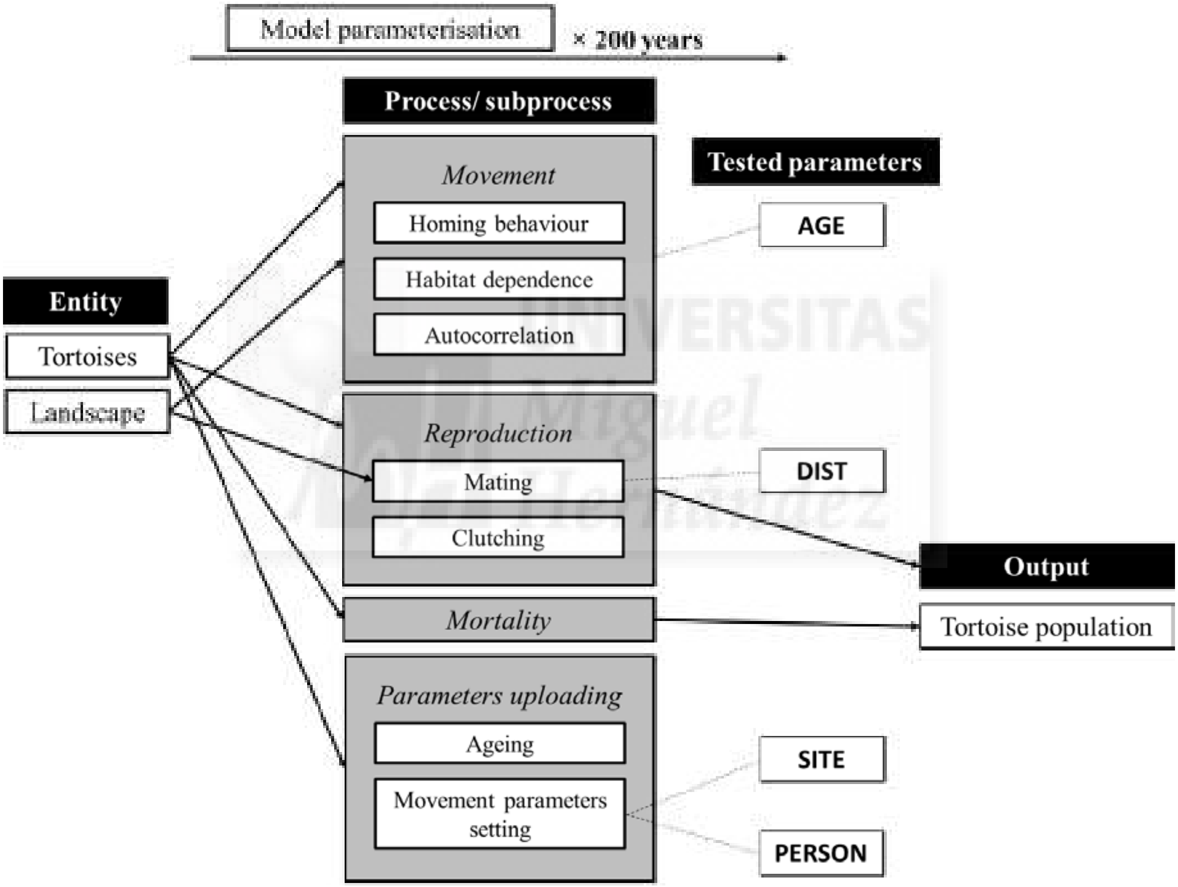

Figure 1. Main processes implemented into the spatially explicit individual based model STEPLAND to simulate the population dynamics of spur-thighed tortoise populations. Each simulation starts with an initial population of the tortoises that inhabit a landscape, which governed the specific parameterisation of the simulation. The output compresses the generated populations of tortoises after N years (here N = 200). Tortoises are subject to four basic processes: movement, reproduction, mortality and parameters uploading. Landscape characteristics influence tortoise movements, while spatial constraints influence reproduction (i.e.: long distances or barriers among males and females hinder matings). From the generated output, it is possible to obtain tortoise abundances. The effects of some parameters on population dynamics were assessed with a sensitivity analysis. See Table 1 and Fig. 2 for a description of the parameters and the simulation scenarios, respectively.

final probability of a neighbouring cell to be selected in the next step. Thus, movement is governed by (i) "Habitat dependence", in which the habitat categories of the eight neighbouring cells receive habitat-dependent weights; (ii) "autocorrelation", which describes the tendency to keep the previous direction; and (iii) "Homing behaviour", which describes an individual's tendency to maintain a stable home range around a focal point position.

The demographic submodel reflects the species' known biology. Reproduction consists of three processes: mating, sperm storage and clutching (Fig. 1). Matings between adult individuals occur once a year, at the beginning of the spring. Sperm storage and multiple paternity, which are specific traits of spur-thighed tortoises (Roques, Díaz-Paniagua & Andreu, 2004), were modelled as a temporal dissociation between multiple mating events and clutching. Some studies have found that sperm can be viable in the oviducts of females for as long as 3-4 years (e.g., Cutuli *et al.*, 2013). Therefore, we modelled sperm caducity, in which females lose the possibility of being reproductive if they do not find males after 3 years.

Adult females have the opportunity to lay up to three clutches a year (Díaz-Paniagua, Keller & Andreu, 1996). Mortality is considered a single mortality event implemented at the end of each simulated year. Annual mortality rates vary among age classes, including eggs, immature individuals, subadults, adult males and adult females. Appendix S2 shows the parameters values and an extended description of the criteria followed for their selection.

Simulation scenarios

The combination of three initial population density levels, two different adult survival rates and two distinct landscapes resulted in 12 different simulation scenarios.

Simulations started with 45, 90 and 180 tortoises (N_0), which covered very low to medium population densities, as found in the natural populations of the species in SE Spain (0.05, 0.1 and 0.2 tortoises/ha; Anadón *et al.*, 2009). These densities are representative of 42% of the species distribution range in SE Spain (Sanz-Aguilar *et al.*, 2011).

We selected two annual survival rates (S) of adults, which represented medium and high survivals rates (S_{MEDIUM} = 0.95 and S_{HIGH} = 0.98; calculated as 1 - adult mortalities in Appendix S3). The model's combination of demographic parameters resulted in theoretical growth rates of λ = 1.008 (for S_{MEDIUM}) and λ = 1.02 (for S_{HIGH}) (Appendix S3). These theoretical growth rates were calculated deterministically by using the POPBIO package in the R software (i.e., without considering demographic or environmental stochasticity; Appendix S2), and represent theoretically viable populations. However, in the simulated populations with our spatially explicit individual-based model, spatial constrains and demographic stochasticity may result in lower effective growth rates, and even in population extinctions.

Finally, we considered two 3 km × 3 km landscapes from Almenara's Mountains in SE Spain that currently host *T. graeca* populations: "Galera", representing natural landscapes with very low cover of intensive land uses or non-permeable infrastructures (1%); and "Bas", which represents altered landscapes with a much higher proportion of intensive land uses or non-permeable infrastructures (26%). In the former, which lacks internal barriers, we assumed the population to be potentially panmictic (i.e., in theory, all individuals are able to breed). Contrarily in the latter, we assumed the intensive land uses and non-permeable infrastructures to impose constraints for reproduction, and individuals were only able to mate if they were located in the same reproductive unit (Fig. 2).

Simulation analysis approach

We conducted a local sensitivity analysis of four model parameters to assess the effects of movement and behavioural traits, habitat fragmentation and population characteristics on extinction probabilities over 200 years. To do this, we first simulated all 12 scenarios (Table 1) by standard model parameterisation, which comprises plausible values taken from the bibliography and our own empirical data (Appendix S3). In the next step, we varied the value of one parameter at a time across its plausible range by maintaining the standard parameterisation for the other parameters (Table 1). This was repeated for all 12 scenarios and for the four parameters of interest (Table 1).

In order to assess the effect of differences on mate searching effectiveness, we assumed that mating occurred only if males and females were located in the same reproductive unit (i.e., there was no linear barrier between them; Fig. 2), and if the Euclidean distance between them was shorter than a certain threshold distance (the DIST parameter in Table 1). To model the differential movement capacities of juveniles, we varied the age threshold where tortoises started to move (the AGE parameter in Table 1). The tortoises below this age threshold did

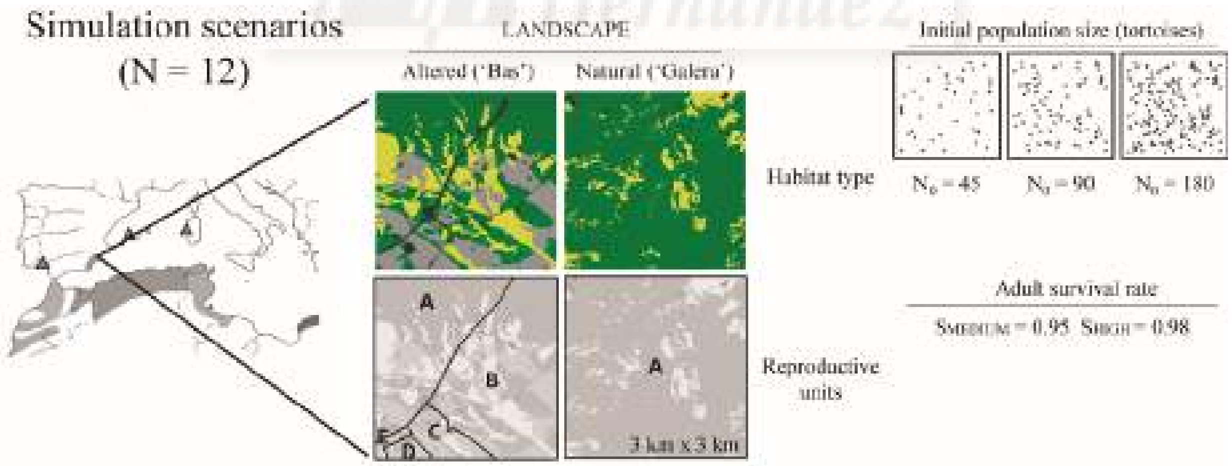

Figure 2. Components of the generated simulation scenarios. We generated 12 plausible *Testudo graeca* populations by combining two landscapes from SE Spain (natural and altered), three initial population sizes that represent low-density populations (N_0) and two adult survival rates (S). The grey areas in the first map show the approximate Western Mediterranean distribution range of *T. graeca* (triangles represent small populations). The two landscapes considered herein are located to the north of the species' distribution range in SE Spain.

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Table 1. Initial conditions and parameters considered in simulations with the spatially explicit individual-based model STEPLAND. To generate simulation scenarios, we combined all the values of initial population size, adult survival and landscape type, which gave 12 scenarios. For the sensitivity analysis, we individually varied the values of the tested parameters. The selected values for the parameterisation maintained across simulations ("standard parameterisation") are shown in bold. Appendix S3 describes the model's full parameterisation.

	Tested condition or process	**Model variable**	**Values**	**Description**
Initial conditions	Population size	N_0	45/90/180	Initial number of tortoises. Representing very low to medium densities.
	Adult survival rate	S	0.95/0.98	Annual survival rates of adults expressed as decimals.
	Landscape type	LANDSCAPE	Natural/Altered	Landscapes of 3km × 3 km that represent natural and altered conditions in which simulations take place (the "Galera" and the "Bas" SE Spanish site, respectively).
Parameters	Mate searching effectiveness	DIST	100/ 300/ **500**/700	Threshold of maximal distance between females and males that allows mating (in metres).
	Movement capacity of juveniles	AGE	3/**4**/5	Age when individuals start to move (years old).
	Behavioural plasticity	PERSON	**YES**/NO	Stable individual personalities are emulated by maintaining individual movement parameterisation throughout tortoises' lifetime ("YES"). Alternatively, variable personalities are emulated by reassigning individual movement parameterisation each year ("NO")
	Site fidelity or philopatry	SITE	**YES**/NO	Site fidelity among years is emulated by maintaining the location of the focal-point attractor of tortoises for their lifetime ("YES"). Alternatively, lack of site fidelity among years is emulated by reassigning this location to the last position reached each year ("NO")

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not change their location, while the older ones displayed increased movement capacity until they reached the reproductive age.

Furthermore, we assessed the effect of behavioural plasticity by randomly assigning to each tortoise a new movement parameterisation at the beginning of each year, against the case in which tortoises maintained their movement parameters throughout their life (the PERSON parameter in Table 1). Individual parameterisations for the movement process were taken from the identified by Anadón, Wiegand and Giménez (2012) (for more information on movement parameterisation, see Appendix S1). In the same vein, we simulated philopatry by maintaining the location of tortoises' focal point attractor for their whole lifetime, or alternatively, by reassigning this location to the individual's last position at the end of each year (the SITE parameter in Table 1).

The total number of independent model simulations was 8,448 (12 simulation scenarios × 11 movement parameterisations × 64 replicates). We tested for statistically significant differences among simulations using the Kruskal Wallis tests in the R software. Multivariate binomial GLM models were used to assess the sensitivity of the evaluated parameters for population extinction. The variables in relation with the initial conditions were treated as factors (N_0, S, LANDSCAPE), while model parameters were treated as numerical (DIST, AGE) or factor (PERSONALITY, SITE) variables. The selection of the best model was based on Akaike's information criterion (AIC; Burnham and Anderson, 2004) using a stepwise backward algorithm. We assumed model structures with ΔAIC < 2, as similarly supported (Hastie and Pregiborn, 1992). Posthoc analyses (ANOVA function) served to calculate the explained deviance of each parameter to the selected model.

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Results

Individual movement behaviour, habitat fragmentation and population characteristics

Our results showed that habitat loss and fragmentation strongly affected the viability of *Testudo graeca* populations. The initial conditions of the simulation scenarios had a strong impact on the population dynamics of *T. graeca* (Table 2). The extinction rates (EX) over a 200-year time horizon vastly differed among simulation scenarios with distinct initial densities of tortoises (EX = 0.43, when N_0 = 45 tortoises; EX = 0.2, when N_0 = 90 tortoises; and EX = 0.1, when N_0 = 180 tortoises; $\chi2$ = 870.93; df = 2; p < 0.01). Landscape type also influenced population viability, which revealed the relevance of the spatial constraints implemented into our model. The extinction rate was higher in the altered "Bas" landscape (mean EX = 0.28) than in the natural "Galera" landscape (mean EX = 0.21) ($\chi2$ = 55.8; df = 1; p < 0.01). Finally, the two different adult survival scenarios (0.95 and 0.98) presented major variations in the number of viable population trajectories (mean EX = 0.39, for S_{MEDIUM}; and mean EX = 0.1 for S_{HIGH}) ($\chi2$ = 940.84; df = 1; p < 0.01).

Table 2. Extinction rates (as decimals) of *Testudo graeca* populations over 200 years. Simulations were replicated 64 times using the standard parameterisation based on empirical data and on a bibliographic review (Appendix S3). The simulation scenarios combined different initial populations sizes (N_0), adult survival rates (S_{MEDIUM} = 95.4; S_{HIGH} = 97.5) and habitat characteristics (LANDSCAPE). Note that the deterministic growth rate, estimated from the demographic parameters, yields λ = 1.008 (for S_{MEDIUM}) and λ = 1.02 (for S_{HIGH}). Population extinction arises due to spatial constraints, and also due to demographic stochasticity, especially for N_0 = 45 and S_{MEDIUM}.

	Very-low density (N_0 = 45 tortoises)		Low density (N_0 = 90 tortoises)		Medium density (N_0 = 180 tortoises)	
LANDSCAPE	S_{MEDIUM}	S_{HIGH}	S_{MEDIUM}	S_{HIGH}	S_{MEDIUM}	S_{HIGH}
Natural	0.66	0.02	0.02	0	0	0
Altered	0.77	0.02	0.30	0	0	0

Mate searching effectiveness

Mate searching effectiveness, represented by the maximal distance DIST between males and females where mating occurred (within the 100-700 m range), strongly influenced the population dynamics of *T. graeca*. Extinction rates were very sensitive to changes in mate searching effectiveness. The best model to fit our simulated data included all four parameters: LANDSCAPE, N_0, S and DIST, and the interactions between N_0 and DIST, and LANDSCAPE and S. The DIST parameter explained 54.28% of deviance (the highest among the parameters), while the model's total explained deviance was 67.61% (Table 3).

For S_{MEDIUM}, all the simulations were extinct when DIST = 100 m, and most of them were when DIST = 300 m (Fig. 3a). However with DIST = 700 m, all the simulations were viable for S_{HIGH}, and also for S_{MEDIUM}. Only the simulations that started with N_0 = 45 individuals showed a low percentage of extinctions (Fig. 3a). Finally, intermediate DIST values (DIST = 300 m, when S_{HIGH}; and DIST = 500 m, when S_{MEDIUM}) produced a wide range of population dynamics (Fig. 3a). In these cases, extinction rates were related mostly with LANDSCAPE and N_0 values. See Table S1 (Supporting Information) to consult extinction rates.

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Table 3. GLM results that describe the sensitivity of the four tested parameters for population extinction over 200 years. The parameters govern processes in relation with movement and behaviour. The best model only included those variables or interactions with ΔAIC < 2. See Table 1 for the description of parameters and variables.

Process	Parameter	Variables included in the GLM model	% of explained deviance
Mate searching strategies	DIST	DIST	54.28
		S	6.66
		N_0	4.12
		N0:DIST	2.06
		LANDSCAPE:S	0.30
		LANDSCAPE	0.20
		Total model	**67.61**
Juvenile dispersal	AGE	S	29.08
		N_0	20.06
		LANDSCAPE	2.66
		AGE	1.00
		Total model	**52.75**
Behavioural plasticity	PERSON	S	27.75
		N_0	27.20
		PERSON	0.63
		LANDSCAPE	0.50
		LANDSCAPE: PERSON	0.44
		Total model	**56.53**
Philopatry	SITE	S	30.78
		N_0	25.44
		LANDSCAPE	0.92
		Total model	**57.14**

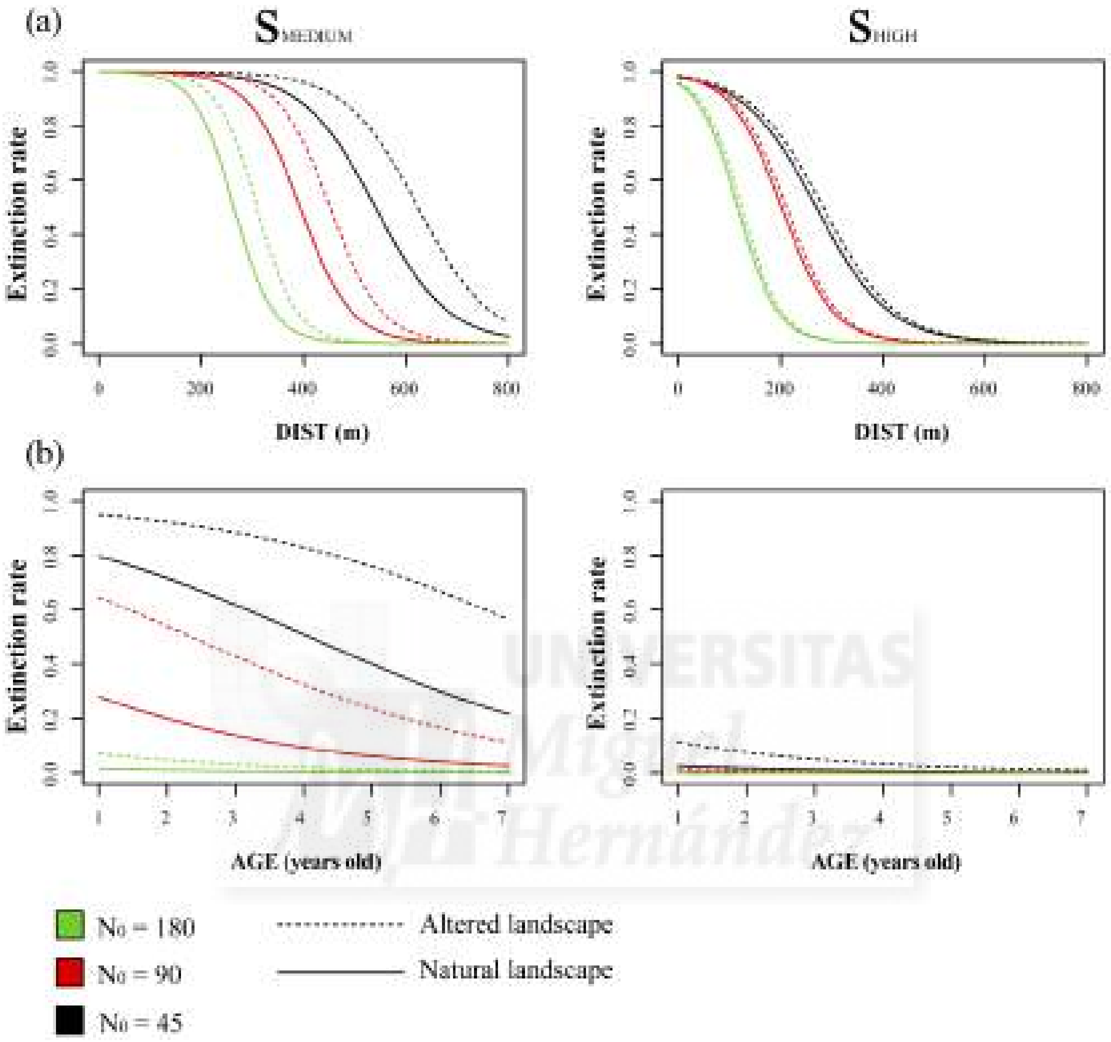

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Figure 3. Extinction rates (as decimals) predicted by GLMs, according to the model's standard parameterisation, with different values of the DIST (a) and AGE (b) parameters. The DIST parameter imposes a maximal distance threshold between females and males, and allowed mating (in metres). The AGE parameter represents the age when juveniles start to move (years old). Simulation scenarios included two different adult survival rates (S_{MEDIUM} = 0.95; S_{HIGH} = 0.98), habitat types and the initial population sizes. See Table 1 and Appendix S3 for further information on model parameterisation.

Movement capacity of juveniles

Allowing earlier movement of juveniles had a relatively low impact on the population viability of *T. graeca.* The selected model included all four parameters, LANDSCAPE, N_0, S and AGE, and there were no interactions among them. The model's total explained deviance was 52.75%, and the AGE parameter was the least explicative (around 1% of model deviance) (Table 3). The effects of AGE (with simulated values that ranged from 3 to 5 years) were only appreciable for the S_{MEDIUM} scenario, when initial population sizes were N_0 = 45 individuals, and N_0 = 90 individuals. In these simulation scenarios, delayed age transitions to adult movement resulted in lower extinction rates of populations (Fig. 3b). See Table S1 (Supporting Information) to consult extinction rates.

Behavioural plasticity

Behavioural plasticity, represented in our model through annually changing movement parameterisations with the Boolean PERSON parameter, had a limited influence on the population dynamics of *T. graeca*. The best model included all the variables: LANDSCAPE, N_0, S and PERSON, and the interaction between PERSON and LANDSCAPE. The model's total explained deviance was 56.53%, where PERSON was slightly explicative and contributed 0.63% of deviance (Table 3). The scenarios with S_{HIGH} or N_0 = 180 tortoises resulted in viable trajectories in almost all cases. However, extinction rates varied in the remaining scenarios, but only as a result of changes in the PERSON variable in the scenario with an altered LANDSCAPE. In particular, non-plasticity in movement behaviour increased extinction rates (Fig. 4). See Table S1 (Supporting Information) to consult extinction rates.

Site fidelity or philopatry

In our simulations, the maintenance, or not, of

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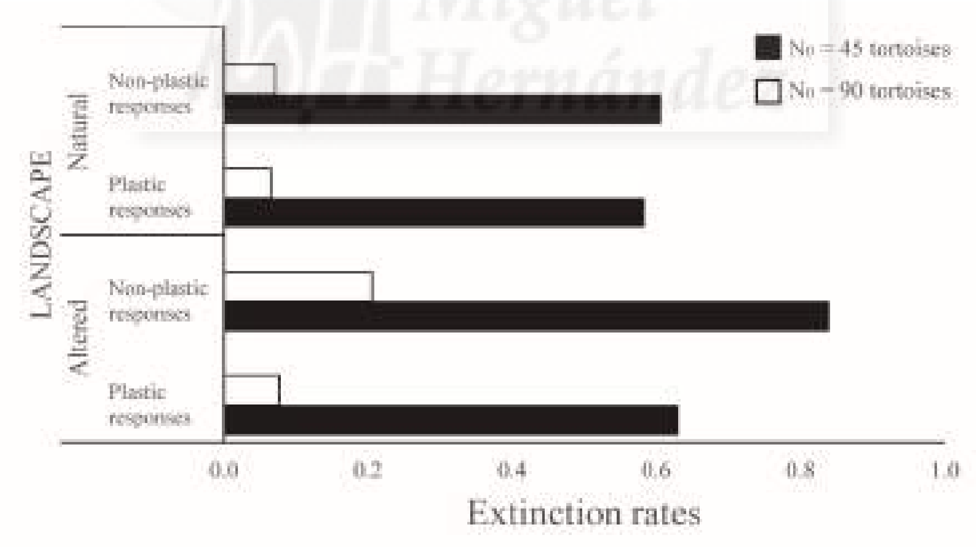

Figure 4. Extinction rates (as decimals) over 200 years for the simulation scenarios with adult survival rate S_{MEDIUM} (0.95) by considering variations in the Boolean PERSON parameter. This parameter emulates stable or instable personalities among years. We simulated natural and altered landscapes with different initial population sizes (N_0). Very few extinctions were produced in the scenarios with S_{HIGH} (0.98) or initial population sizes of N_0 = 180 tortoises. Each simulation was replicated 64 times.

stable home ranges had no effect on the extinction rates of *T. graeca* populations. The best fitting model only included those variables that related to the simulation scenarios: LANDSCAPE, N_0, S (Table 3). The SITE parameter, which governs the maintenance of the focal-point attractor location of tortoises among years, and its interaction with the other variables, was excluded from the model. See Table S1 (Supporting Information) to consult extinction rates.

Discussion

This study addressed the interacting effects of movement and behavioural traits, habitat fragmentation and population characteristics on the population viability of the spur-thighed tortoise (*Testudo graeca*). More specifically, we explored the role of selected spatial traits in buffering the effects of fragmentation: mating search strategies, juvenile dispersal capabilities, behavioural plasticity and philopatry. Our results showed that human-altered habitats strongly affect the viability of *T. graeca* populations. However, the extinction rates over 200 years were most sensitive to changes in population density, the survival rates of adults and mating search effectiveness.

Effects of human-altered habitats on Testudo graeca *populations.*

Our results indicated that the combination of human-altered landscapes and associated changes in movement patterns generally had negative effects on the viability of *T. graeca* populations (Table 2). The scenarios that combined low initial population densities and medium survival rates of adults were especially sensitive to landscape changes because here the theoretical population growth rate was only 0.8% (λ = 1.008). In contrast, the corresponding scenarios with 2% theoretical population growth did not become extinct, while the scenarios with very low initial population densities were quite likely to become extinct (Table 2). These results are in line with those of Pearson and collaborators (2014), who found for a broad context of climate change that species' vulnerability depends on interactions between life history and spatial traits, being occupied area, population size and population growth among the most important predictors.

In SE Spain, the transformation of shrublands or traditional crops into intensive lands, and the development of infrastructures and exurban areas, have affected around 10% of the spur-thighed tortoise population range since 1990 (Anadón *et al.*, 2007; unpub. data). Our simulation experiments suggest for this regional context that fragmented landscapes aggravate the conservation status of *T. graeca* by generating Allee effects in low-density populations (i.e. isolation between sexes) (Alharbi & Petrovskii, 2016). This was also shown by our sensitivity analysis, where the minimum distance between males and females that allowed mating was the main population viability factor. Consequently, low-density populations of tortoises may disappear in some tens of years. Their current presence in highly fragmented areas is probably the result of their high longevity, but not of population viability (Henle *et al.*, 2004).

Sensitivity of movement and behavioural traits for population viability

Changes in behaviour are among the first responses of animals to human-altered conditions (Sih, Ferrari & Harris, 2011). However, not all behavioural responses are beneficial (Igual *et al.*, 2007; Sih, Ferrari & Harris, 2011; Wong & Candonlin, 2015). Human-altered conditions can damage sensory systems (Rosenthal & Stuart-Fox, 2012) or affect physiological processes (Burchanan & Partecke, 2012), which results in inappropriate behavioural responses. Hence, the question that arises is if plastic responses suffice to keep pace with human-altered conditions (Sih, Ferrari & Harris, 2011). Surprisingly, only a handful of studies have explicitly addressed this question (see Wong & Candonlin, 2015 for a review). In this context, we found that the population dynamics of the spur-thighed tortoises was especially sensitive to mating search strategies, but also to the movement capacity of juveniles and behavioural plasticity in movement, but to a lesser extent.

Effectiveness of mating search strategies: The DIST parameter, the maximum distance of male and female individuals to allow for mating encounters, was a key factor for population dynamics and extinction. In spite of being a simplification of a complex biological process, the values of this parameter resulted in a lower extinction risk (300-500 m; Fig. 3a), which well fitted the mean maximal annual displacement distances reported for *T. graeca* males and females of 189-275 m and 148-271 m, respectively (Dmax in Table C3 of Anadón, Wiegand & Giménez, 2012). Clearly, unrealistically high parameter values (e.g., > 500 m) lead to additional reductions in the extinction risk because they counteract the Allee effect, which hinders finding mates in low-population densities. If and how conspecific attraction underlies mating search strategies in *T. graeca* remains unknown but, according to our results, such a biological mechanism would support the viability of low-density populations in fragmented scenarios. As the movement patterns of *T. graeca* males strongly pursue mating opportunities (Díaz-Paniagua, Keller & Andreu, 1995; Anadón, Wiegand & Giménez, 2012), we hypothesise that the size of their home ranges may vary inversely with the density of available females.

Movement capacity of juveniles: We assumed that juveniles started more extended movements (beyond their 100 m2 neighbourhood) at the age of 3, and that movement capabilities increased linearly until they reached maturity (see also Díaz-Paniagua, Keller & Andreu, 1995; Keller, Díaz-Paniagua & Andreu, 1997). For the critical circumstances of low initial population densities and low theoretical growth rates, starting movement later reduced the extinction risk (Fig. 3b). The explanation is simple: longer periods of movement imply a higher risk of ending up in areas without conspecifics. However, the likelihood of reproducing with relatives is inversely related to juvenile dispersal capabilities (Wolff, Lundy & Baccus, 1988), which thus creates a trade-off between two types of Allee effects on population viability: inbreeding depression and difficulties to find a mate.

Behavioural plasticity: Behavioural plasticity describes animals' tendency to adjust their behaviour to suit habitat conditions and to increase fitness (Van Buskirk, 2012). The "movement personalities" of the spur-thighed tortoises that inhabit human-altered landscapes show wider inter-individual variability, which ranges from strong site fidelity to unbounded movements (Anadón, Wiegand & Giménez, 2012). Our results indicated that maintaining personalities over time increased the

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extinction risk for *T. graeca* populations of inhabiting altered landscapes. The accumulation of negative effects of extreme behaviours (i.e., individuals that overdisperse or show extreme site fidelity) increased the stochasticity of the population trajectories, and thereby the extinction risk quite by chance. On the contrary, temporally variable personalities reduced the population extinction risk in human-altered landscapes to the levels of natural landscapes (Fig. 4). This result highlights the possible relevance of *T. graeca*'s behavioural plasticity to buffer habitat loss and fragmentation effects.

Philopatry: The maintenance of stable home ranges during their lifetime did not affect the population dynamics in our simulation experiments. It is well-known that tortoises show philopatry as a characteristic trait (e.g., Kaddour *et al.*, 2006; Anadón, Wiegand & Giménez, 2012; Lecq *et al*, 2014), and that stable home ranges offer individuals high quality feeding patches, refugee areas and, with females, places to lay their eggs. In addition, philopatry may prevent tortoises from wandering into low-density areas where mating encounters are rare. Lack of site fidelity effects is probably due to the moderate shifts in the focal point attractors in our simulations (to the last location in the year), which do not lead populations to drift apart. Nevertheless, philopatry could be relevant for low-dispersal organisms to prevent Allee effects in other contexts (e.g., during range expansions; Stiebens *et al.*, 2013).

Do altered T. graeca*'s movement patterns in human-altered habitats counterbalance habitat fragmentation effects on population viability?*

As this study did not consider the landscape to possess a carrying capacity, we assumed the same demographic parameters for the tortoises that inhabit human-altered and natural landscapes (except for movement parameterisations). Therefore, the population dynamics differences between the corresponding scenarios in natural and altered landscapes could arise due only to spatial mechanisms (reduced mating encounter rates due to barriers or altered movement).

Theoretical studies have predicted that fragmentation per se may lower mating encounter rates (Wosniack *et al.*, 2014) and, alternatively, movement patterns might counterbalance the effects on population viability (Niebuhr *et al.*, 2015). In general, habitat alterations worsen the quantity of high-quality habitats and increase border effects. Altered animal movement patterns may play an important role by avoiding these disturbances and maintaining the functional connectivity of systems (Mimet *et al.*, 2013; Niebuhr *et al.*, 2015).

Here we found that the movement patterns of *T. graeca* individuals merely counterbalanced the harmful effects of human-altered habitats when behavioural plasticity was included in the model (Fig. 4). In natural habitats, females exhibit high site fidelity and narrower home ranges than males (Díaz-Paniagua, Keller & Andreu, 1995; Anadón, Wiegand & Giménez, 2012). In altered habitats, individuals tend to avoid intensified patches (mainly new irrigated crops), and females show highly variable home range sizes (0.85±0.9 ha in natural landscapes, 3.5±4.46 ha in altered landscapes) (Anadón, Wiegand & Giménez, 2012). Such variability in the movements of the females that inhabit human-altered landscapes suggests that they do not provide basic conditions or resources for them on a fine-scale (Anadón, Wiegand & Giménez, 2012). Further research is needed to confirm our hypothesis, that of *T. graeca* populations being able to buffer certain levels of habitat changes thanks to behavioural plasticity, and to explore its consequences for the genetic patterns of populations (i.e., changes in gene flow).

Our approach, which integrates movement patterns and demography, allowed us to estimate the fate of populations and to identify processes or species characteristics that strongly influence population viability. The obtained results are representative of long-lived species with low-dispersal capabilities. We hypothesise that these taxa are particularly vulnerable to habitat loss and fragmentation effects. It is noteworthy that around half the freshwater turtle and tortoise species are considered threatened (van Dijk *et al.*, 2014). This is a high proportion compared with other vertebrates: 13% in birds, 21-25% in mammals, 30-41% in amphibians (Hoffmann *et al.*, 2010). Further efforts should be made to explore the consequences of landscape changes for population viability of such threatened taxa. Impacts on population connectivity may reduce gene flow on the landscape scale and might promote local endogamy. Consequently, low-dispersal species, like tortoises, could lose evolutionary potential in today's global change scenarios.

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Supporting Information

Appendix S1. Overview, Design concepts, and Details protocol of the individual-based model used in this work.

Appendix S2. Script in R for the calculation of stable age distribution and population growth rates.

Appendix S3. Model parameterisation based on empirical data and bibliographic review on *Testudo graeca* and *T. hermanni*. When more than three values were available, we discarded the extreme values and calculated the average. See Appendix S1 for a detailed description of the mortality, reproduction and movement processes.

Appendix Table S1. Extinction rates (as decimal) of *Testudo graeca* populations in year 200 at the simulation scenarios.

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5. CONCLUSIONES

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CONCLUSIONES GENERALES

1. Esta tesis constituye una contribución notable para la comprensión de los efectos de las perturbaciones ambientales en poblaciones animales y para el desarrollo de metodologías novedosas que permitan abordar problemas ecológicos.
2. Mediante estudios de historia de vida hemos podido obtener información sobre la dinámica poblacional, las consecuencias de los incendios, los efectos de la pérdida y fragmentación del hábitat, así como plantear estrategias de conservación para una especie amenazada.
3. El uso de métodos analíticos clásicos como los modelos de crecimiento poblacional, realizados con información obtenida en estudios de seguimiento a largo plazo, permiten entender los factores endógenos y exógenos que afectan a la dinámica poblacional.
4. En las poblaciones animales, los incendios tienen consecuencias directas (o inmediatas) y mantenidas en el tiempo. Estas perturbaciones modifican la dinámica poblacional, la capacidad de carga del sistema o incluso el *fitness* de los individuos.
5. La estructura heterogénea del hábitat, donde se alternan matorrales en diferentes estadios sucesionales y áreas agrícolas tradicionales de secano, favorece la presencia de animales ectodermos al ofrecer refugio, alimento y lugares de asoleamiento. Las especies de vida larga con bajas capacidades de dispersión y una tasa de respuesta lenta ante los cambios en el hábitat son especialmente sensibles a los procesos de pérdida y fragmentación de hábitat. Por este motivo, la modificación de este paisaje y la creación de barreras como infraestructuras lineales incrementan las probabilidades de extinción local de estas especies.
6. Los planes de conservación y recuperación de fauna deben incluir tanto el seguimiento a largo plazo, como la realización de estudios puntuales para responder preguntas concretas. Esta doble estrategia permitirá continuar con el estudio de la historia de vida de la especie y tener en cuenta los efectos de las perturbaciones ambientales que sufre.
7. Se ha presentado un método para estimar parámetros demográficos mediante modelado de simulación inversa con costes de monitoreo reducidos. Con sólo un año de muestreo se obtienen estimas de supervivencias similares a otros modelos que utilizan datos de más de 10 años. Por este motivo, esta aproximación es especialmente útil para especies amenazadas, con baja detectabilidad o bajo número de individuos.
8. Se ha desarrollado un modelo basado en el individuo espacialmente explicito que integra demografía, movimiento y la influencia del hábitat. Este modelo permitirá abordar preguntas sobre la conectividad entre las poblaciones, la necesidad de la creación de corredores ecológicos o el efecto de las grandes infraestructuras lineales en las poblaciones de tortuga.
9. Los resultados de esta tesis ponen de manifiesto la necesidad de integrar diferentes metodologías de trabajo tanto analíticas como de simulación para resolver preguntas sobre el estado de conservación de las especies, su persistencia en el futuro y los posibles efectos de las perturbaciones ambientales.

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CONCLUSIONES APLICADAS A LA TORTUGA MORA

Dinámica poblacional: A escala local, especies de vida larga como la tortuga mora están reguladas en primer orden por los procesos endógenos (densodependencia) y en segundo orden por procesos exógenos como el clima o los incendios. La variable climática más importante para predecir la abundancia de tortugas es el número de heladas durante el invierno. Los inviernos extremadamente fríos se relacionan con una disminución del número de individuos. Estos eventos extremos durante la época de hibernación pueden afectar a las tasas de supervivencia de especies ectotermas como las tortugas, especialmente de los juveniles.

Consecuencias de los incendios: Después del incendio, sucede una disminución de su capacidad de carga de sistema que se mantienen a medio plazo (aprox. una década). Además, las tasas de supervivencia disminuyen después de los incendios, especialmente en el caso de los juveniles. Aunque la reducción en las tasas de supervivencia de los individuos adultos es baja, puede comprometer la persistencia de la población porque, como la mayoría de especies de vida larga, la supervivencia adulta es el parámetro más sensible en la dinámica poblacional.

Perturbaciones como los incendios provocan una reducción del *fitness*. Concretamente se ha detectado una reducción en la velocidad de crecimiento, especialmente en los machos, que tardan más en alcanzar su tamaño asintótico después de la perturbación. Las consecuencias de esta ralentización deben ser exploradas para comprender si tiene implicaciones poblacionales como un retraso en la madurez sexual o la vulnerabilidad ante otras amenazas.

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Pérdida y fragmentación de hábitat: Los procesos de pérdida y fragmentación de hábitat influyen en el comportamiento y el movimiento de los individuos, además, reducen la viabilidad de sus poblaciones, especialmente en situaciones de baja densidad. Entre los rasgos espaciales de comportamiento estudiados, la efectividad de las estrategias de búsqueda de pareja es clave para la viabilidad poblacional. Además, la plasticidad en el comportamiento amortigua los efectos negativos de la fragmentación. Por el contrario, la dispersión temprana de los juveniles incrementa las probabilidades de extinción de las poblaciones.

Por otro lado, los pinares de reforestación presentan densidades muy bajas o total ausencia de tortugas. Estos resultados indican que los pinares maduros pueden actuar como barreras para la conectividad entre poblaciones.

Estrategias de conservación: Las políticas de control forestal como la prevención de incendios o las reforestaciones deben integrar la conservación de las especies amenazadas que están afectadas por alteraciones del hábitat a escala local, como la tortuga mora. Nuevas políticas de restauración de la cubierta vegetal en lugares donde históricamente se ha eliminado la vegetación natural deben incluir la conservación de especies vinculadas a los paisajes actuales.

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6. CONCLUSIONS

Carmen López. Cuevas de Almanzora (Almería). 2014

GENERAL CONCLUSIONS

1. This thesis constitutes a significant contribution to the understanding of the effect of human disturbances to animal populations such as the spur-thighed tortoise, and for the development of novel methodologies to address ecological problems.

2. Through life history studies, we have obtained information about population dynamics, the consequences of fires, the effects of habitat loss and fragmentation, as well as the development of conservation strategies for natural populations.

3. Classical analytical methods such as population growth models with information obtained from long-term follow-up studies allowed us to understand the endogenous and exogenous factors that affect population dynamics.

4. In animal populations, fires have direct (or immediate) and maintained consequences over time. These disturbances modify the population dynamics, the carrying capacity of the ecosystem or even the fitness of the individuals.

5. The heterogeneous structure of the habitat, with shrubs at different successional stages and traditional dryland agricultural areas, support the presence of ectothermal animals by offering shelter, food and basking places. Long-lived species with low dispersal capabilities and slow response rates to changes in habitat are especially sensitive to habitat loss and fragmentation processes. The modification of the landscape and the creation of barriers like linear infrastructures increase the probability of local extinctions of these species.

6. Wildlife conservation plans should include both long-term monitoring and timely surveys to answer specific questions. This double strategy will allow to continue the study of the life history of the species and the effects of the environmental disturbances.

7. That thesis shows an approach to estimate demographic parameters reducing monitoring costs by inverse simulation model. With just one year of sampling, survival estimates were similar to those from other models that use data from more than 10 years. For this reason, this model may be especially useful for threatened species with low detectability or a low number of individuals.

8. A spatially explicit individual-based model integrating demography, movement, and habitat influence has been developed. This model could address questions about connectivity between populations, the need to develop ecological corridors or the effect of large linear infrastructures on tortoise populations.

9. The results of this thesis show that the integration of analytical and simulation models is useful to solve questions about the conservation status of the species, their persistence in the future and the effects of environmental disturbances.

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APPLIED CONCLUSIONS TO *TESTUDO GRAECA*

Population dynamics: At local scale, long-lived species as the spur-thighed tortoise are regulated in the first order by the endogenous processes (density-dependence) and in the second order by exogenous processes such as climate or fires. The most important climatic variable to predict the abundance of tortoises is the number of freezing days during winter. Extreme cold winters are directly related to a decrease in the number of individuals. This extreme events during the hibernation season may affect the survival rates of ectothermal species such as tortoises, especially juveniles.

Effects of fire: After fire events, there is a reduction in the carrying capacity that is maintained in the medium term (about a decade). Moreover, survival rates are reduced after fires. This decline is especially pronounced for both hatchling and juvenile individuals. Although adult survival rates are only marginally reduced, it may compromise population persistence because, as for most long-lived species, adult survival is the most sensitive parameter in tortoise population dynamics.

Disturbances such as fires cause a reduction in fitness. A reduction in growth rate has been detected, especially in males, which take longer to reach their asymptotic size after the disturbance. This slowdown should be explored to understand the possible consequences, such as delayed sexual maturity or vulnerability to other disturbances.

Habitat loss and fragmentation: Habitat loss and fragmentation processes influence the behavior and movement patterns of individuals and reduce the viability of the populations, especially for populations with low density. Among the analyzed behavior traits, the viability of *T. graeca* populations was very sensitive to changes in the effectiveness of mating search strategies. Behaviour plasticity buffers the negative effects of fragmentation. On the contrary, early dispersion in juveniles increases the probability of extinction.

In addition, pine plantations showed very low densities or total absence of tortoises. This result indicates that mature pine forests can act as partial barriers to population connectivity. Forest policies to prevent deforestation should take into account the species of fauna associated with traditional landscapes in order not to compromise the conservation of these species.

Conservation strategies: Forest control strategies such as fire prevention or reforestation should integrate the conservation programs for threatened species such as the spur-thighed tortoise. New policies about restoration of vegetation cover in places where natural vegetation has historically been removed should include the conservation of species linked to current landscapes.

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8. ANEXOS

Carmen Cañizares. Lorca (Murcia). 2012

Appendix S1

To understand the factors that affect the detection of tortoises, we used the Distance Sampling method (Thomas *et al.*, 2010). This method assumes that detectability decreases as a function of the perpendicular distance from the line and it uses the observed distances to model the detection function. Therefore, we can use this method in the years where we recorded the distance of the encounters (6 out of the 14 years of the study). The detection function was fitted to the distance data using Distance 6.0 (Thomas *et al.* 2010). Upon preliminary inspection of the fit, we removed perpendicular distances beyond 4.25m (truncation distance, hereinafter ω) where detection probabilities generally fell to 0.1 or lower (Buckland *et al.* 2001). Due to the observers' tendencies to round distances, we grouped the detections into five distance intervals (cutpoints: 0, 0.75, 1.5, 2.25, 3.25, 4.25 m). We evaluated the fits of the half-normal (HN) and hazard rate (HR) key functions with and without cosine series adjustments and explored multiple covariate distance sampling techniques (MCDS) to model potential heterogeneity in detection probabilities. Covariates included here were ADULTS (two factors: adults and juvenile), STAGE (three factors: juvenile, males and females), EXP (two factors: experienced and novel observers), YEAR (factor with 6 different years) and EFFORT (continuous variable with the number of hours searching for tortoises). Akaike's Information Criterion (AIC, Akaike 1973) was used for model selection.

The results are shown in Appendix Table S1. Only the variables ADULTS and STAGE improved the model without covariates. Specifically ADULT with HR as key function was the best model. We found that the detection probability was 0.452 for adults and 0.216 for juveniles. Thus, the probability of finding a juvenile is 0.478 lower than finding an adult. We used that probability to correct the observed data.

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Appendix Table S1

Table S1. Models with the possible variables which affect detectability. HR is hazard rate model and HN is Half Normal. ADULTS (two factors: adults and juvenile), STAGE (three factors: juvenile, males and females), EXP (two factors: experienced and novel observers), YEAR (factor with 6 different years) and EFFORT (numerical factor with the number of hours searching for tortoises).

Model	Covariable	AIC	ΔAIC
HR	ADULTS	716.89	0
HR	STAGE	717.27	0.38
HN	ADULTS	727.76	10.87
HN		728.22	11.33
HN	STAGE	728.52	11.63
HR		729.15	12.26
HR	EXP	729.92	13.03
HR	EFFORT	730.12	13.23
HR	YEAR	733.91	17.02
HN	EXP	737.41	20.52
HN	EFFORT	739.35	22.46
HN	YEAR	741.80	24.91

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Appendix Figure S1

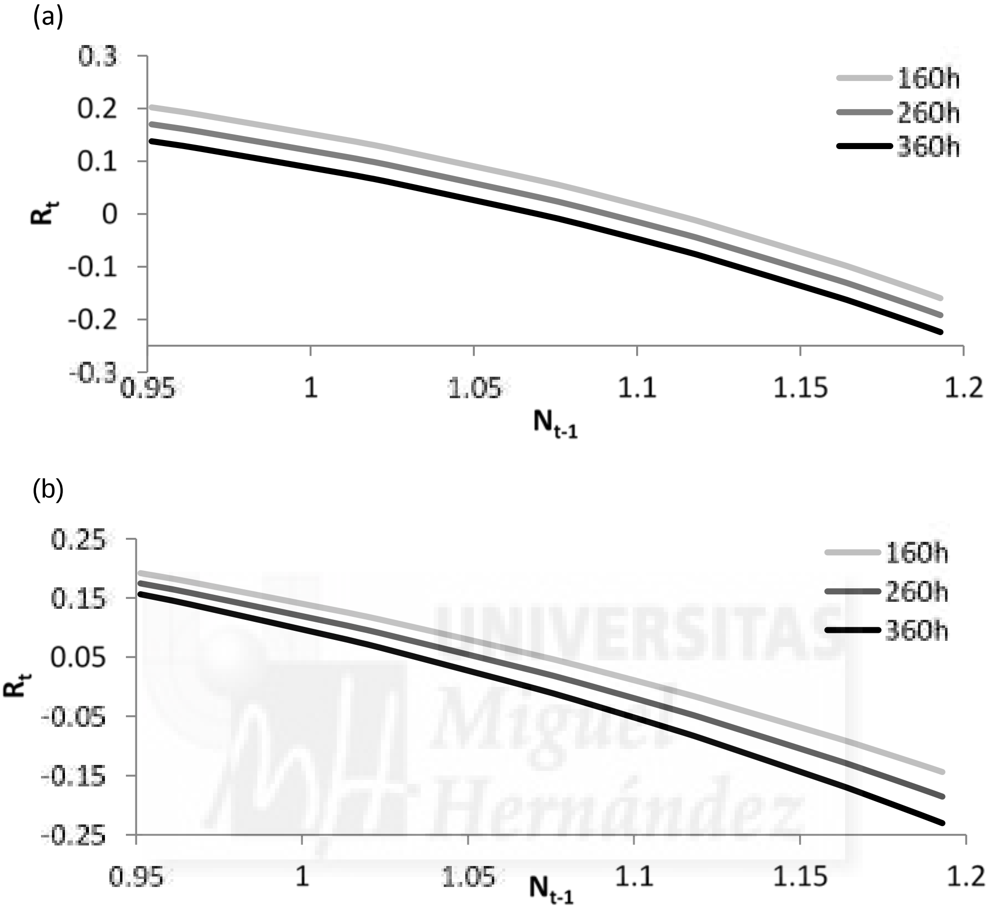

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Figure S1. Effects of abundance of tortoises (N_{t-1}) and number of hours below 0ºC in winter according to (a) the model with vertical effects A2 (effects in the maximum growth rate, R_m) in population growth (R_t); and, (b) the model with lateral effects A3 (exogenous factors influence some limiting resources). 160h is that in 160 hours the temperature was 0ºC or less, the same for 260h and 360h. In our dataset, the mean of hours below 0ºC was 266 hours. The predictions of the effects in these models are quite similar, but we select the model A2 using the Akaike's Information Criterion (AIC, Akaike 1973).

Appendix ESM1

Non-linear regression was used with four commonly used growth models (von Bertalanffy; Gompertz; Richards; a Logistic model; Table S1). The best growth model was firstly identified for males and females separately by considering the entire sampling period (8 years). Starting with the AICc values (i.e., the AIC values corrected for small sample size), we calculated the Akaike weights (w_i), which indicated the probability of each model being the best model among the four model candidates (Burnham and Anderson 2002).

The model that best described males' population growth when considering the whole study period was the von Bertalanffy model (48%), followed by the Gompertz model (29%). Conversely, females showed the opposite result as the Gompertz model was the most supported (43% probability), followed by the von Bertalanffy model (30%; Table S2). Comparisons between the growth patterns of males and females were made using the von Bertalanffy model since this model obtained the highest mean probability for both males and females (averaged probability: Bertalanffy = 39%, Gompertz = 36%). Additionally, selection of the von Bertalanffy model enhanced the comparability of the results of our work as it is the most widely used model to describe chelonians population growth (Zivkov *et al.* 2007; Macale *et al.* 2009). The calculated parameters using the growth curves between sexes appear in Table S3.

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Table S1. For known age models, the dependent variable is carapace length at age t (CL), S_∞ is asymptotic size, b is a parameter associated with the amount of growth remaining, and k is the growth rate. For the Richard's model, n is a curve shape parameter. For the interval analogues, the parameters are the same, although the dependent variable is carapace length at recapture (CL2), CL1 is carapace length at the initial capture, and t is the interval between captures in years. This table has been created with modifications from Dodd and Dreslik (2007).

Model	Known age	Interval analogue
Von Bertalanffy[1]	$S_\infty(1 - be^{-kt})$	$CL2=S_\infty - (S_\infty - CL1)\, e^{-kt}$
Gompertz	$S_\infty e^{be^{-kt}}$	$CL2=S_\infty\, e^{\log(CL1/S_\infty)\, e^{-kt}}$
Richards	$S_\infty(1 - be^{-kt})^{1/n}$	$CL2=S_\infty\ (1 + ((CL1/S_\infty)^{1/n} - 1)\, e^{-kt})^n$
Logistic[2]	$S_\infty/(1 - be^{-kt})$	$CL2 = CL1\, S_\infty/(CL1 + (S_\infty - CL1)e^{-kt})$

1 - Interval analogue derived by Fabens (1965).

2 - Interval analogue derived by Schoener and Schoener (1978).

Appendix ESM1

Table S2. Growth model parameters and inter-model comparisons using an information-theoretic approach for females (n=80) and males (n=96). *n* = shape parameter of the growth model; S_∞ = asymptotic size; *k* = growth rate; AICc = Akaike information criterion corrected for small sample size; ΔAICc = AICc differences; w_i =model probability;

Model	n	S_∞	k	AICc	ΔAICc	w_i
Females						
Betarlanffy		161.84	0.106	475.55	0.71	0.30
Gompertz		158.01	0.147	474.84	0	0.43
Richards	2.455*	159.15	0.131	476.43	1.59	0.19
Logistic		156.54	0.178	478.41	3.57	0.07
Males						
Betarlanffy		121.27	0.155	485.84	0	0.48
Gompertz		120.52	0.195	486.89	1.05	0.29
Richards	1.48*	120.96	0.168	487.48	1.64	0.21
Logistic		120.21	0.227	492.64	6.8	0.02

(*) Calculated from the model as appears in the Table S1.

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Table S3. Fire-related changes in von Bertalanffy growth parameters for males and female *Testudo graeca*. S_∞ = asymptotic size; *k* = growth rate

	Females				Males			
	S_∞	CI	k	CI	S_∞	CI	k	CI
Global	161.84	±8.23	0.106	±0.032	121.27	±2.83	0.156	±0.034
Pre-fire	158.26	±7.66	0.145	±0.048	118.23	±4.24	0.228	±0.078
Post-fire	165.61	±14.86	0.086	±0.040	125.04	±4.45	0.112	±0.032

Appendix ESM1

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Appendix ESM2

We addressed the survival rates of adults by using the method described by Beverton and Holt (1956). This method employs the mean of a size distribution, and assumes constant and continuous recruitment to the population by following this formula:

$$Z = \frac{k(S_\infty^{-\frac{1}{n}} - \bar{X})}{\bar{X} - S_R^{-\frac{1}{n}}}$$

where Z is the mortality coefficient, $\bar{X}$ represents the mean size of adults, and S_R is the mean size upon recruitment. Parameters S_∞ (asymptotic size), parameter k (year-1), and n (curve shape) were obtained by the growth models (see Online Resource 1). Having calculated Z, it was possible to assess the annual mortality rate ($1-e^z$) and annual survival rates (e^z).

As only adults were considered, S_R was the equivalent to their mean size upon maturity, which can be inferred from the carapace and scute length measures. To carry on this analysis, two measures of the third costal scute on the right side of the carapace (Germano 1988; Fig. S1), the total scute length (TSL) and the maturity scute length (MSL) were also taken. The first one, from the natal scute to the last ring, describes the length of the scute at the present time. MSL, from the natal scute to the last wide ring, describes the TSL when the individual reaches maturity (Fig. S1). All the lengths were measured to the nearest millimetre using a digital caliper.

The growth rates of the tortoises dramatically lowered when reaching maturity, and as this growth pattern is reflected precisely in the width of the deposited rings on scutes, wide growth scute rings corresponded to large growth rates (Lagarde *et al.* 2001). The scute measure MSL is, thus, the length of the scute when an individual reached maturity. We first estimated the mean MSL for males and females separately. Then we transformed this MSL measure into total body length (CL) by plotting the current CL and TSL measures (Fig. S2).

Although this method requires constant and continuous recruitment, this restriction can be overcome because S_R is defined by the study. If recruitment size is sufficiently large, the actual ages at recruitment can be considered (Ebert 1999). As a general rule, the greater the difference between sizes at birth and recruitment, the closer one comes to continuous recruitment (Ebert 1999).

Note that the survival rates obtained by this method include both the direct effects of fire and the long-term effects which occurred during the 4-year period after the fire. In this sense, our survival rates jointly inform about the first- and second-order effects.

For the survival analysis, the inferred sizes at recruitment values (defined in this work as the mean size at maturity) were S_R = 135.34 mm for females and S_R = 103.62 mm for males (considering that females and males reached maturity with a mean SL = 35.52 mm and SL = 25.05 mm, respectively, using regressions CL = 3.1147*SL + 24.8704, R^2 = 0.70 for females and CL = 3.0068*SL + 28.2822, R^2 = 0.61 for males).

The results of survival rates are shown in Table S1.

Appendix ESM2

Table S1. Fire effects on survival rates and standard errors by sex for the population after and before the fire.

	Females		Males	
	Survival (%)	SD	Survival (%)	SD
Global	91.31	1.905	96.71	1.308
Pre-fire	94.65	2.271	98.43	2.671
Post-fire	90.09	2.95	95.07	1.089

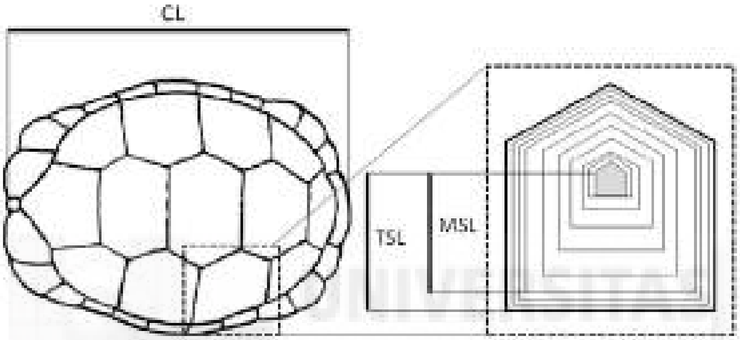

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Figure S1. Measures of tortoise carapace length (CL), total scute length (TSL), and maturity scute length (MSL) in adult individuals. When subadults become adults their growth rates dramatically lower and, consequently, the width of their new rings also narrows. .

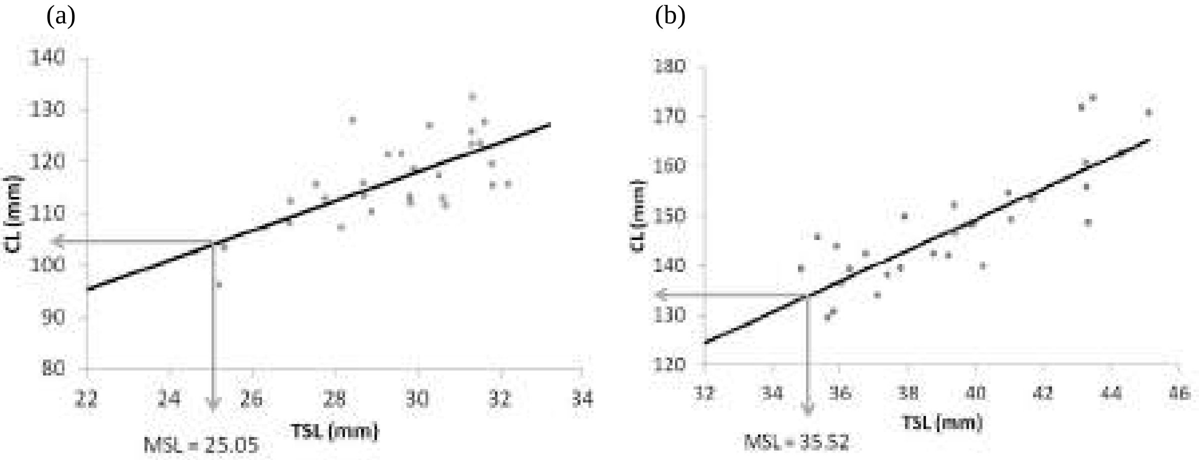

Figure S2. Relation between total scute length (TSL) and carapace length (CL) for (a) male and (b) female *Testudo graeca*. Mean estimated CL at maturity extrapolated from mean maturtity scule lenght.

Appendix ESM2

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Appendix SI 1

We estimate the age of the individuals using two methods; 1) counting de number of rings (Rodríguez-Caro *et al.*, 2015) and measuring the carapace length (Rodríguez-Caro *et al.*, 2013).

The method of counting growth rings was described in Rodríguez-Caro *et al.*, (2015). We used this method for tortoises aged up to 10 years old, the period in which counting growth rings is plausible.

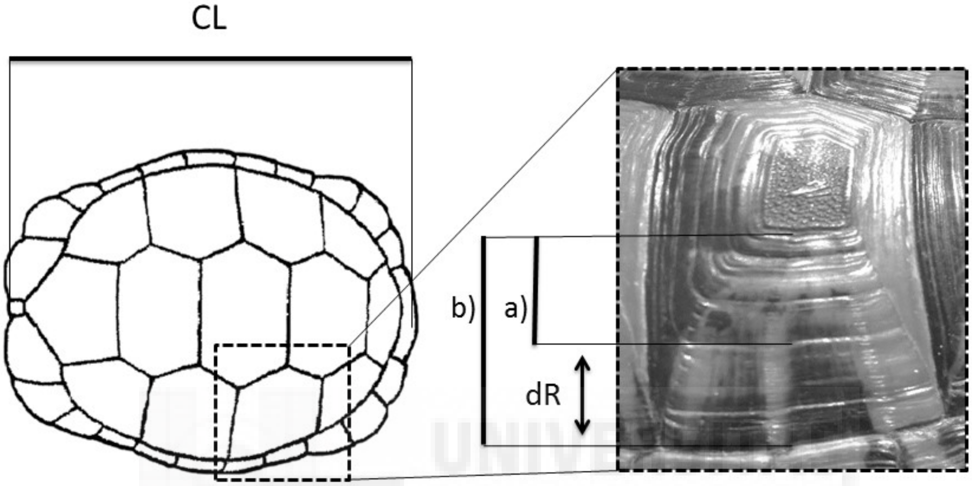

Figure S1.1. Example of number of rings and measure of the carapace length (CL) from Rodríguez-Caro *et al.*, (2015)

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For tortoises older than 10 years old, we calculate their age using an inverse regression by the equation 1 of Von Bertalanffy Model (Fabens, 1965) from Rodríguez-Caro *et al* (2013).

$$S_\infty(1 - be^{-kt}) = CL \qquad \text{eq. 1}$$

S_∞ is asymptotic size, b is a parameter associated with the amount of growth remaining, k is the growth rate, t is the age of the individual and CL is the size (carapace length). We used the inverse of eq. 1 to calculate t (age of the tortoises) using CL. We used the data calculated in Rodriguez-Caro *et al.*, 2013 (table S1.1)

Table S1.1. Values of the parameters of Von Bertalanffy model according to Rodriguez-Caro *et al.*, 2015 for males and females.

Sex	S_∞	b	k
Females	156.26	-0.7843	0.145
Males	118.23	-0.7112	0.228

Appendix SI 1

REFERENCES

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Appendix SI 2

We used the Distance Sampling method (Thomas *et al.*, 2010) to calculate the detectability of the individuals. This method assumes that detectability decreases as a function of the perpendicular distance from the line and it uses the observed distances to model the detection function. We use the same 153 individuals captured in 2003. The detection function was fitted to the distance data using Distance 6.0 (Thomas *et al.*, 2010). Upon preliminary inspection of the fit, we removed perpendicular distances beyond 4.25m (truncation distance, hereinafter ω) where detection probabilities generally fell to 0.1 or lower (Buckland *et al.*, 2001). Due to the observers' tendencies to round distances, we grouped the detections into five distance intervals (cutpoints: 0, 0.75, 1.5, 2.25, 3.25, 4.25 m), similar to other studies (Rodríguez-Caro *et al.*, 2017). We evaluated the fits of the half-normal (HN) with multiple covariate distance sampling techniques (MCDS) including STAGE as a covariate (three factors: juvenile, subadults and adults). We found that the detection probability was 0.47 for adults, 0.41 for subadults and 0.27 for juveniles. Our results are similar to previous studies (Rodriguez-Caro *et al.*, 2016, 2017)

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S1 Table

Table S1. Distribution of observation between sites and habitat patch

Site	AGRI	ABAND	SHRUB	PINE	TOTAL
Galera	34	23	24	20	101
Madroñales	67	20	17	1	105
Palomera	5	32	8		45
Total	**106**	**75**	**49**	**21**	**251**

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S2 Table

Table S2. Parameter estimates from the best approximating, generalized linear model with standard error (SE). Interaction effects between variables (*) are also shown.

	Estimate	SE	p.value
Intercept	-7.3319	0.21816	<0.001
MA	-0.3026	0.3323	n.s.
PA	0.3895	0.2854	n.s.
AGRI	0.337	0.2834	n.s.
PINE	-0.4696	0.3255	n.s.
NAT	-0.4096	0.3513	n.s.
MA*AGRI	0.7485	0.4067	0.069
PA*AGRI	-2.2318	0.5647	**<0.001**
MA*PINE	-2.4534	1.1094	**0.029**
PA*PINE[1]	NA	NA	**NA**
MA*NAT	0.8163	0.4893	n.s.
PA*NAT	-0.7581	0.5084	n.s.

1. No tortoises were found in the pine forest (PINE) of Palomera (PA), so we excluded PA's pine forest from the analysis.

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S1 Figure

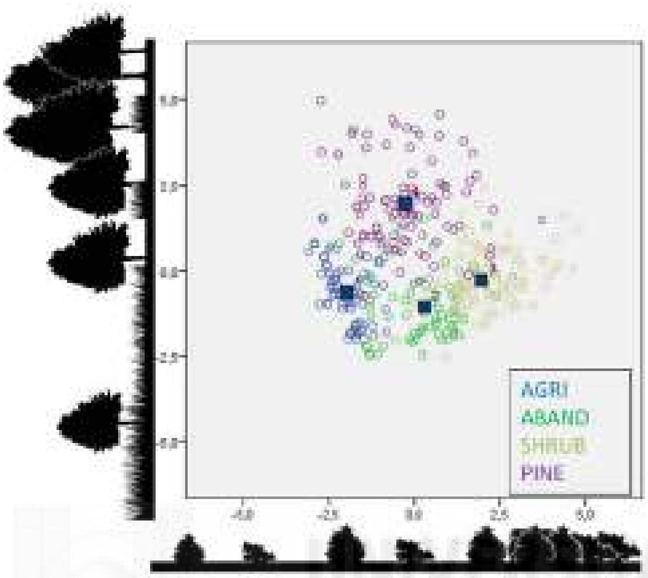

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Figure S1. Results of the DFA analysis. The first function (the gradient from bare soil to dense shrub coverage) is showed in the X axis, the second function (the influence of tall and thick vegetation) in the Y axis.

Appendix S1

Overview, Design concepts, and Details protocol of the individual-based model used in this work

STEPLAND: a spatially explicit individual-based model to simulate spur-thighed populations' viability

Purpose

The main objective of STEPLAND is to evaluate the viability of spur-thighed tortoise populations that inhabit natural or human-altered landscapes in SE Spain in short or medium terms (some hundreds of years). The model was implemented into Python 2.7 and its code is available in XXX.

Entities, attributes and spatial scales

In STEPLAND there are two different entities: landscapes and tortoises.

Landscapes comprise an area of 3 km × 3 km (although other areas are also possible) and are composed of a grid of cells of 10 m × 10 m. Each cell is characterised by its position (x and y coordinates) and its habitat category:

- intensive land use
- traditional agriculture land
- flat natural areas and natural areas on slopes
- non-permeable infrastructures

These categories were used in a previous study that addressed the effects of habitat fragmentation on tortoise movements (Anadón, Wiegand & Giménez, 2012). Moreover, each grid cell is characterised by its assignment to a reproductive unit that include all cells not separated by a landscape barrier, such as highways of dense human infrastructures. Landscapes host discrete populations if they are enclosed by a non-permeable border or, alternatively, open habitats in which individuals are equally likely to enter and go out (Fig. 1A).

Tortoises are characterised by the following attributes: sex, age, time for stored sperm caducity, their actual location and past locations. Additionally, the nine parameters AU1, AU2, dHB, rHB, H1W, H2W, H3W, H4W and H5W govern their movement and the location of their focal-point attractor. All except H5W, these parameters were taken from the movement analysis of Anadón, Wiegand & Giménez (2012). See the description of the movement process for further information.

Input, initialisation and temporal scales

Inputs include the landscape, the initial population and model parameterisation; they are all included in a SQL database that is directly read by the model. Initially, 45, 90 and 180 tortoises are randomly distributed across the space (N_0), which represents three very low and low densities, as found in the natural populations of species in SE Spain (Anadón *et al.*, 2009). The different age classes are established following the stable age distribution predicted by an age-stage structured deterministic matrix population model (Caswell, 2001) using the POPBIO package in the R software (Stubben & Milligan, 2007; R Core Team, 2014; R scripts are shown in Appendix S2). The demographic parameters of the age-stage structured deterministic matrix population model are the same as the demographic parameters of the simulation model (Appendix S2). These initial conditions were conserved between simulations and replicates. The complete model parameterisation is shown in Appendix S3.

Appendix S1

In our model each time step represents 1 day, while outputs are summarised for periods of full years. Simulations are run for 200 years and replicated 64 times. For operational reasons, the simulation stopped if the total number of tortoises in the landscape exceeded 4,500.

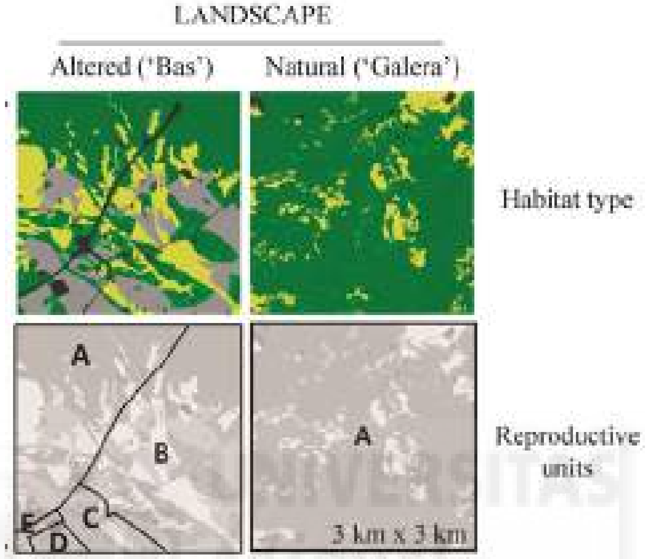

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Figure A1. Examples of landscapes that may be used in STEPLAND. Habitat categories include: non-permeable infrastructures (black), intensive lands use (grey), traditional agriculture lands (yellow), flat natural areas (light green) and natural areas on slopes (dark green). Reproductive units are made up of cells not separated by landscape

Process overview and scheduling

In STEPLAND, tortoises are subject to three basic processes, movement, reproduction and mortality, and their parameters are updated across simulations. They move up to 4 times a day according to their attributes and movement parameters, the time of the year and the habitat category of the surrounding cells (as modelled and parameterised by Anadón, Wiegand & Giménez; 2012). Adult females can reproduce up to 3 times a year, as evidenced by own data and previous studies that have addressed the reproduction of this species (Díaz-Paniagua, Keller & Andreu, 1996, 1997). However, spatial issues may hinder mating, like an excessive distance between females and their nearest adult males, or presence of non-permeable barriers between them. Annual mortality rates are implemented through a single event of mortality, placed at the end of the year. The age of the alive tortoises is then updated, and their movement attributes may also be uploaded. Data output is obtained in periods of year, and consists in compressed CSV files with the alive tortoises of the population and their attributes. Own scripts, developed in R (R Core Team, 2014) and Python 2.7, allow these massive outputs to be processed. Figure A2 shows a general overview of the model and the following paragraphs describe the main processes in more detail.

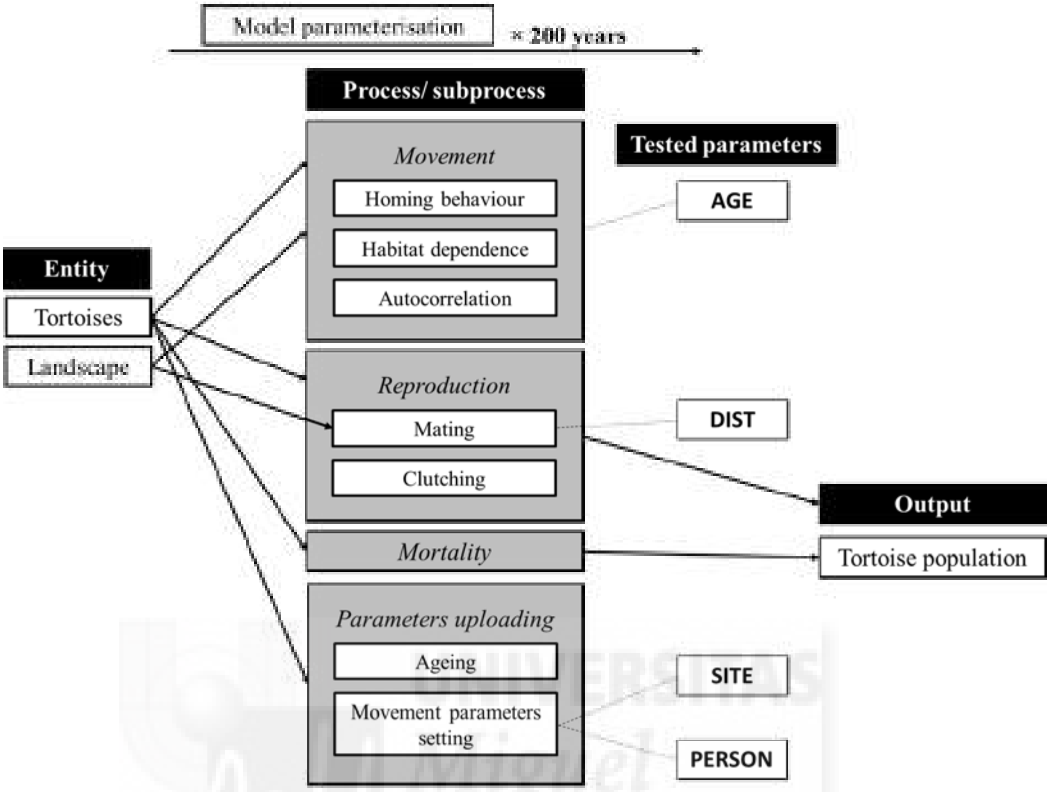

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Figure A2. Main processes implemented into STEPLAND that connect tortoises' inhabiting landscapes and final tortoise abundances after 200 years. Tortoises are subject to the four basic processes: movement, reproduction, mortality and parameters uploading. Landscape characteristics influence tortoise movements. Final tortoise abundances are directly dependent on reproduction and mortality processes. The number of times that processes or subprocesses occur a year are shown in brackets.

Movement

This process was modelled and parameterised according to Anadón, Wiegand and Giménez (2012). This previous work was based on individual-based modelling and pattern-oriented modelling using radio-tracking data, and found that land-use intensification in SE Spain had a strong impact on the movement and behaviour of non-dispersing spur-thighed tortoises. While tortoises showed high site fidelity and slight individual variability in natural landscapes, movement and behaviour greatly varied among individuals in altered landscapes. Particularly for females, a wide range of movement patterns was found, which ranged from strong home behaviour to unbounded movements. Anadón, Wiegand and Giménez (2012) determined 5,627 individual parameterisations of annual movements that were compatible with empirical movement data. The females that inhabited altered landscapes formed the largest set of individual profiles (Table A1).

Appendix S1

Table A1. Number of individual parameterisations for the movement process, as determined by Anadón, Wiegand and Giménez (2012).

	Natural landscape	Altered landscape
Males	139	51
Females	155	5,282

Tortoises whose age is over the parameter age_first_mov, have the possibility of changing their location up to 4 times q day (i.e., four movement steps; Fig. A3). The PMOV parameter is the probability of moving during a given day, and is dependent on the month and sex of the tortoise. Hibernation and aestivation periods, when tortoises are inactive, are well-represented by the distribution of PMOV probabilities throughout the year (Fig. A4a). Subsequently, the DMOV parameter is the discrete probability to move s cell steps in each movement step (Fig. A3). DMOV varies between adult males and females (Fig. A4b). We also assumed that subadults had a lower movement capability than adults. To implement this, we assumed the number of cell steps s to increase linearly with age until the reproductive age:

$$s_{subadult} = round(s_{adult} \times \frac{subadult's\ age}{reproductive\ age})$$

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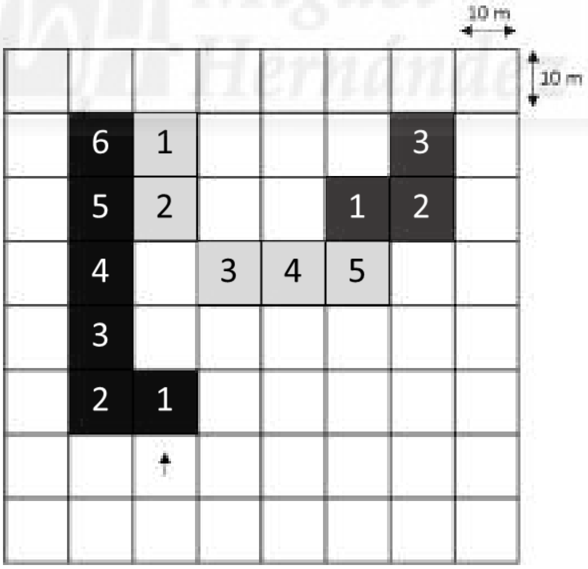

Figure A3. Exemplification of the movement of a simulated tortoise in a given day. Starting from the arrow, the tortoise makes three movement steps during the day (represented by different colours), with six, five and three cell steps each (movement directions are represented by numbers).

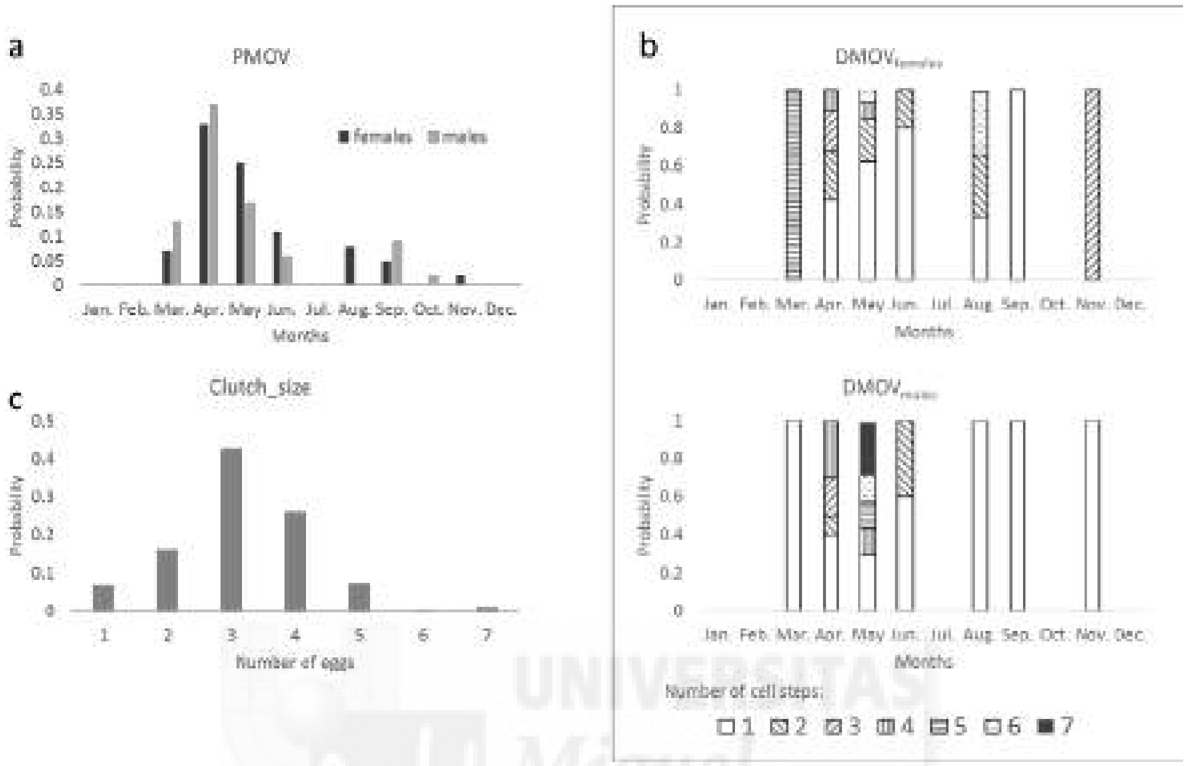

Figure A4. Discrete probability distributions of parameters PMOV (a); DMOV of females and males (b) and clutch_size (c).

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In each cell step, three subprocesses interact in the selection of one of the eight neighbouring cells of the tortoise. Through the following subprocesses, each cell acquires three normalised weights, which are multiplied to calculate its final probability to be occupied:

i) **Autocorrelation**: it describes the tendency of keeping the previous direction. The eight cells surrounding the present location are numbered from *i* = 1, …, 8, where index *i* = 1 indicates the cell step following exactly the previous direction. Then *i* = 2, …, 8 were numbered clockwise. The weights di to enter the neighbouring cells with indices *i* = 1, …, 5 (movement to the right) were calculated as:

$$d_i = \max[0, \frac{1.5+(0.5-i)\times AU}{1.5-0.5\times AU}]$$

and for the remaining weights representing movement to the left, we assumed isotropic movement (i.e., $d_6 = d_4$, $d_7 = d_3$, $d_8 = d_2$). Finally, weights di were normalised to add up to 1. As cell steps are nested inside movement steps, we used two parameters to describe autocorrelation in movement. The AU1 parameter represents the autocorrelation between consecutive movement steps and affects only the first cell step of each movement step. The AU2 parameter is the autocorrelation between the following cell steps. Thus for the first cell step, we used AU1, and AU2 for the other cell steps (Fig. A5).

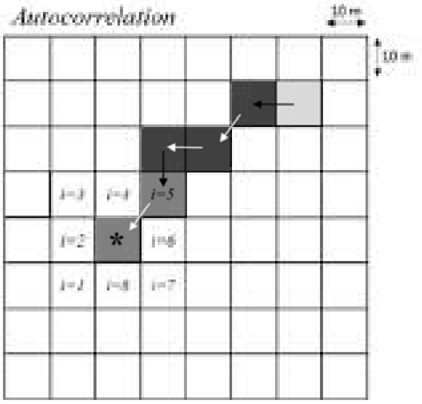

Figure A5. Schematic representation of the autocorrelation subprocess. Arrows differentiate steps or cell step transitions using parameters AU1 (in black) or AU2 (in white).

ii. Homing behaviour: modelling an individual's tendency to maintain a stable home range around a focal point position. Weights bi are numbered in the same way as the weights for autocorrelation. We arbitrarily considered the individual's first location as the focal-point attractor. To model homing behaviour, we assumed that two critical distances existed around the focal point. Firstly, if the individual is located close to the focal point, it will not show homing behaviour (i.e., bi = 1/8 for all i = 1,.. 8). The dHB parameter is the distance threshold below which no homing behaviour occurs. Secondly, if the individual is located at a distance D longer than 2*dHB, the bias towards the focal point is maximal and the cell j closest to the focal-point attractor has probability bj = 1 to be occupied, while the remaining seven cells have probability bi = 0. In intermediate situations in which dHB < D < 2dHB, the bias of bj increases proportionally with distance D up to 2*dHB with the formulas:

$$b_j = (D\text{-}dHB)/(dHB) \text{ and } b_j = (1 - b_i)/7 \text{ for } i \neq j$$

In order to enhance the biological realism of the model, we consider a temporal delay to put homing behaviour in force after the distance threshold dHB from the focal point has been exceeded. This allows tortoises to temporally leave their most regularly used areas to meet specific needs, such as egg-laying in females or mate-searching in males (Díaz-Paniagua, Keller & Andreu 1995; Pérez *et al.*, 2002). The rHB parameter is the temporal delay (in days) of homing behaviour since dHB was exceeded (R) (Fig. A6).

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iii. Habitat dependence: in which relating to habitat quality, the eight neighbouring cells received habitat-dependent weights to be occupied through parameters H1W (intensive land use), H2W (traditional agriculture), H3W (flat natural areas), H4W (natural areas on slopes) and H5W (non-permeable infrastructures). The weights of the eight cells are subsequently normalised to add up to 1 (Fig. A7).

Appendix S1

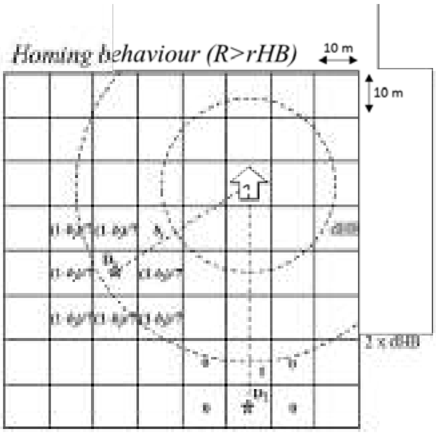

Figure A6. Schematic representation of the homing behaviour subprocess. Asterisks indicate the location of tortoises, with distances D_1 and D_2 to the focal point attractor. Note that dHB < D_1 < 2dHB and that D_2 > 2dHB.

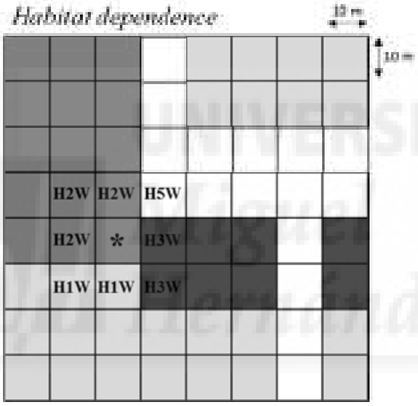

Figure A7. Schematic representation of the habitat dependence subprocess. Cell colours represent habitat categories.

Reproduction

Sperm storage, a vital trait of spur-thighed tortoises (Roques, Díaz-Paniagua & Andreu, 2004), was modelled as a temporal dissociation between mating and clutching.

i. **Mating**: once a year, at the beginning of spring, mature females localise mature males in their surroundings. Given the spatial constraints to meet males, we assumed that mating occurred only if their Euclidean distance was below a minimal distance given by the DIST parameter. Moreover, both males and females should be located in the same reproductive unit of the landscape and, therefore, there should be no barriers effect between them. Some studies have evidenced that sperm can be viable in the oviducts of females for as long as 3-4 years (Cutuli *et al.*, 2013), but no long-term studies have addressed in depth the drop of sperm viability over time. Therefore, we modelled sperm caducity simply: the females that find males are able to be, for the same probability, reproductive for 3 years (represented by the sperm_cad parameter). If females find mates, then the stored sperm caducity timer is reset to zero; otherwise, a sum of 1 is assigned to the sperm caducity timer. Females no longer have the possibility of being reproductive if their sperm caducity timer reaches 3.

ii. **Clutching**: after matings, the repro_female parameter simulates the probability of females with available sperm to be gravid for all 3 times that clutching can take place in spring (Díaz-Paniagua, Keller & Andreu, 1996, 1997; unpublished data). The number of eggs that gravid females lay is determined from a discrete probability distribution clutch_size (Fig. A4c). Clutch viability is later simulated by applying mortality rates over each egg (Díaz-Paniagua, Keller & Andreu, 1997; Díaz-Paniagua, Andreu & Keller, 2006; see the next paragraph for more details).

Mortality

There is a single mortality event implemented at the end of each simulated year. Annual mortality rates vary among age classes: eggs, immature individuals, subadults, adult males and adult females (M_0, $M_{immatures}$, $M_{subadults}$, M_{adults}, respectively; Díaz-Paniagua, Keller & Andreu 2001, 2002; Sanz-Aguilar *et al.*, 2011). Eggs are identified as individuals whose age equals 0, while age cuttings apply (subadult_age, female_adut_age and male_adult_age) for the transition among the remaining classes. The individuals that died and their attributes disappear from the population.

Parameters uploading

i. **Ageing**: the age of each alive individual sums 1 at the end of the year.

ii. **Temporal** changes in movement characteristics: In our model all individuals may maintain the same movement parameterisation (and/or the same focal point attractor) for their whole lifetime, or may change it each year. At the beginning of simulation, the parameters of tortoises related with movement, these being AU1, AU2, dHB, rHB, H1W, H2W, H3W, H4W and H5W, are randomly assigned to the initial individuals from a data set that contains the previous parametrisation. At the beginning of each year, these parameters are also assigned to newborns. These parameters can be maintained for their whole lifetimes by simulating individual personalities, or can alternatively be randomly reassigned to all the individuals at the beginning of each year by representing non-stable behaviours. In the same vein, the spatial location of the focal point attractor is assigned at the beginning of simulation to individuals as their initial coordinates, and at the beginning of each year to newborns as the location of their clutches. To simulate philopatry, the location of the focal point attractor can be maintained for tortoises' whole lifetime, or can be alternatively reassigned to their last locations at the end of the year by representing lesser stable ranges.

Design concepts

Basic principles: the model assumes that: i) tortoises maintain age-class transitions and survival rates in fragmented landscapes; ii) habitat fragmentation causes changes in their movement and behaviour (as reported by Anadón, Wiegand & Giménez 2012); iii) non-permeable linear barriers hinder tortoise mating across them.

Appendix S1

Emergence: simulations may result in different population dynamics due to variations in tortoises' reproductive success.

Adaptation: tortoises face fragmentation by modifying their movement decisions. They avoid intensive land uses and non-permeable infrastructures.

Objective: tortoises do not have any particular objective implemented into simulation but, as previously mentioned, they modify their movement decisions according to habitat characteristics.

Sensing: tortoises are able to detect habitat fragmentation in landscapes of 3 km × 3 km. They also recognise their surrounding habitat in 30 m × 30 m (the eight adjacent grid cells).

Interaction: Tortoises are able to mate if they are separated by a shorter Euclidean distance than the distance introduced by the max_dist_male_female parameter and inhabit the same reproductive unit.

Learning: tortoises do not change their behaviour according to their experience.

Prediction: tortoises do not have the capacity to predict future conditions.

Stochasticity: tortoises' initial location and assigning movement parameters to them are purely stochastic processes. The remaining "reproduction", "movement", "mortality" processes become semi-stochastic by implementing discrete probability distributions.

Collectives: there are not defined collectives in the model.

Observation: the output serves to calculate the number of alive individuals of a population at a given time and, consequently, population viability over time.

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Appendix S2

Script in R for the calculation of stable age distribution and population growth rates.

```
rm(list=ls(all=TRUE))

####################################################################################
FEMALE based Matrix Model for Testudo graeca: PVA for Testudo graeca
###################################################################################
library(MASS)
library(popbio)
# demographic parameters
s1 <- 0.497        #  Juvenile survival (1-4yrs)
s2 <- 0.863        #  subadult survival (4-7 years)
s3 <- 0.954     #  Adult survival (>7years)
NC<-2           ### Number of clutches
CS<-3.0482      ### Number of eggs.
ES<-0.2802       ### Hatching success*1st winter survival
SR<-0.5        ### Sex ratio

# Pre birth-pulse matrix model for Testudo graeca
A <- matrix(c(0,   0,   0,   0,   0,   0,   0,   0,   0,   NC*CS*ES*SR,
s1,   0,   0,   0,   0,   0,   0,   0,   0,   0,
0,   s1,   0,   0,   0,   0,   0,   0,   0,   0,
0,   0,   s1,   0,   0,   0,   0,   0,   0,   0,
0,   0,   0,   s2,   0,   0,   0,   0,   0,   0,
0,   0,   0,   0,   s2,   0,   0,   0,   0,   0,
0,   0,   0,   0,   0,   s2,   0,   0,   0,   0,
0,   0,   0,   0,   0,   0,   s3,   0,   0,   0,
0,   0,   0,   0,   0,   0,   0,   s3,   0,   0,
0,   0,   0,   0,   0,   0,   0,   0,   s3,   s3),nrow = 10, byrow = TRUE)


# Lambda

lambda(A)

stable.stage(A)
```

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Appendix S3

Model parameterisation based on empirical data and bibliographic review on *Testudo graeca* and *T. hermanni*. When more than three values were available, we discarded the extreme values and calculated the average. See Appendix S1 for a detailed description of the mortality, reproduction and movement processes.

Movement

Parameter	Description	Values	Observations	References
AGE	Age transition to achieve home ranges over 100m^2	3,4,5 years	Tested process: "Movement capacity of juveniles" in Table 1"	Keller, Díaz-Paniagua & Andreu 1997. Evaluated in this work by a sensitivity analysis.
SITE	Stability of home ranges. Site fidelity among years is emulated maintaining the location of the focal-point attractor of tortoises for their whole life ("YES"). Alternatively, the lack of site fidelity among years is emulated reassigning this location to the last position reached each year ("NO")	YES/NO	Tested process: "Site fidelity" or "philopatry" in Table 1"	Evaluated in this work by a sensitivity analysis.
PERSON	Behavioural plasticity. Stable individual personalities are emulated maintaining individual movement parameterisation through the whole life of tortoises ("YES"). Alternatively, instable personalities are emulated reassigning individual movement parameterisation each year ("NO").	YES/NO	Stable individual personalities are emulated maintaining individual movement parameterisation through the whole life of tortoises ("YES"). Alternatively, instable personalities are emulated reassigning individual movement parameterisation each year ("NO")	Evaluated in this work by a sensitivity analysis.
PMOV	Probability of moving during a given day, being dependent of the month and the sex of the tortoise	See Supporting Information Appendix S1	See Figure A4 in Appendix S1	Anadón, Wiegand & Giménez 2012
DMOV	Discrete probability to move *s* cell steps during each movement step	See Supporting Information Appendix S1	See Figure A4 in Appendix S1	Anadón, Wiegand & Giménez 2012
AU1	Autocorrelation between consecutive movement steps, affecting only the first cell step of each movement step	See Supporting Information Appendix S1	See Figure A5 in Appendix S1	Anadón, Wiegand & Giménez 2012
AU2	Autocorrelation between cell steps	See Supporting Information Appendix S1	See Figure A5 in Appendix S1	Anadón, Wiegand & Giménez 2012
dHB	Distance threshold below which no homing behaviour occurs	See Supporting Information Appendix S1	See Figure A6 in Appendix S1	Anadón, Wiegand & Giménez 2012
rHB	Temporal delay (in days) of the homing behaviour since *dHB* was exceeded	See Supporting Information Appendix S1	See Figure A6 in Appendix S1	Anadón, Wiegand & Giménez 2012
H1W	Habitat-dependent weights of each cell to be occupied of intensive land uses	See Supporting Information Appendix S1	See Figure A7 in Appendix S1	Anadón, Wiegand & Giménez 2012
H2W	Habitat-dependent weights of each cell to be occupied of traditional agriculture	See Supporting Information Appendix S1	See Figure A7 in Appendix S1	Anadón, Wiegand & Giménez 2012
H3W	Habitat-dependent weights of each cell to be occupied of flat natural areas	See Supporting Information Appendix S1	See Figure A7 in Appendix S1	Anadón, Wiegand & Giménez 2012
H4W	Habitat-dependent weights of each cell to be occupied of natural areas on slope	See Supporting Information Appendix S1	See Figure A7 in Appendix S1	Anadón, Wiegand & Giménez 2012
H5W	Habitat-dependent weights of each cell to be occupied of non-permeable infrastructures	See Supporting Information Appendix S1	See Figure A7 in Appendix S1	Anadón, Wiegand & Giménez 2012

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Appendix S3

Mortality

Parameter	Description	Values	Observations	References
subadult_age	Age transition from immature to juvenile classes	4 years old		Sanz-Aguilar *et al.*, 2011; Ben Kaddour *et al.*, 2005
male_adult_age	Age transition of males from juvenile to adult classes	7 years old		
female_adut_age	Age transition of females from juvenile to adult classes	7 years old		
M_0	Survival rates of individuals with less than a year. Representing hatching rate and newborn survival. Calculated as their product.	0.72	Hatching rates: 0.824[1] , 0.613[2] Newborn survival rate: 0.39[3]	[1]Díaz-Paniagua, Keller & Andreu 1997; [2]Díaz-Paniagua, Andreu & Keller 2006; [3]Keller, Díaz-Paniagua & Andreu 1998
$M_{immatures}$	Mortality rates of juvenile tortoises.	0.503	*T. graeca:* 0.80[1], 0.28[4], 0.945[5], *T. hermanni:* 0.31[6], 0.48[7].	[1]Sanz-Aguilar *et al.*, 2011; [2]Rodriguez-Caro *et al.*, 2013; [3]Rodríguez-Caro *et al.*, under review; [4]Díaz-Paniagua, Keller & Andreu 2001; [5]Rouag *et al.*, 2007; [6]Fernandez-Chacón *et al.*, 2011 [7]Henry *et al.*, 1998
$M_{subadults}$	Mortality rates of subadult tortoises	0.137	*T. graeca:* 0.21[1], 0.155[2] *T. hermanni*: 0.12[6], 0.12[7]	
M_{adults}	Mortality rates of adult tortoises.	0.046	*T. graeca:* 0.02[1], 0.0157[2], 0.0535[2], 0.08[3], 0.091[4], 0.0394[5] *T. hermanni:* 0.02[6], 0.05[7].	

Reproduction

Parameter	Description	Values	Observations	References
female_repro_age	Age at maturity of females	10 years old		Rodríguez-Caro *et al.*, 2013
male_repro_age	Age at maturity of males	7 years old		Rodríguez-Caro *et al.*, 2013
repro_female	Probability to lay eggs each clutching date	0.66		Rodríguez-Caro *et al.*, 2014
DIST	Threshold of maximal distance among females and males that allows mating.	100, 300, 500, 700 m	Tested process: "Effectiveness of mate searching" in Table 1"	Evaluated in this work by a sensitivity analysis.
sperm_cad	Time of caducity of the stored sperm.	3 years		Cutuli *et al.*, 2013
clutch_size	Probability of the number of eggs per clutch in each clutching date.	1 egg = 0.0677 2 eggs = 0.1594 3 eggs = 0.4262 4 eggs = 0.2590 5 eggs = 0.0717 6 eggs = 0.0040 7 eggs = 0.0120	Calculated from more than 500 radiographs in field. See Figure A4 in Appendix S1.	Rodríguez-Caro *et al.*, 2014

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Appendix Table S1

Extinction rates (as decimal) of *Testudo graeca* populations in year 200 at the simulation scenarios. Simulations were replicated 64 times using the standard parameterization based on empirical data and on a bibliographic review (Appendix S3) and individual variations of the tested parameters. Simulation scenarios combined different initial populations sizes (N_0), adult survival rates (S_{MEDIUM} = 95.4; S_{HIGH} = 97.5) and habitat characteristics (landscape).

			S_{Low}						S_{High}					
			Natural landscape			Altered landscape			Natural landscape			Altered landscape		
Process	Parameter	Parameter value	N_0=45	N_0=90	N_0=180	N_0=45	N_0=90	N_0=180	N_0=45	N_0=90	N_0=180	N_0=45	N_0=90	N_0=18
Mate searching strategies	DIST	100	1.00	1.00	1.00	1.00	1.00	1.00	0.94	0.88	0.61	0.95	0.88	0.61
		300	0.94	0.89	0.30	0.98	0.94	0.58	0.41	0.13	0.00	0.45	0.22	0.00
		500	0.66	0.02	0.00	0.77	0.30	0.00	0.02	0.00	0.00	0.02	0.00	0.00
		700	0.14	0.00	0.00	0.30	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juvenile dispersal	AGE	3	0.67	0.02	0.00	0.83	0.55	0.05	0.05	0.00	0.00	0.05	0.00	0.00
		4	0.66	0.02	0.00	0.77	0.30	0.00	0.02	0.00	0.00	0.02	0.00	0.00
		5	0.39	0.05	0.00	0.67	0.38	0.03	0.00	0.00	0.00	0.02	0.00	0.00
Behavioural plasticity	PERSON	Non-plastic responses	0.66	0.02	0.00	0.77	0.30	0.00	0.02	0.00	0.00	0.02	0.00	0.00
		Plastic responses	0.61	0.03	0.00	0.63	0.08	0.00	0.02	0.00	0.00	0.02	0.00	0.00
Philopatry	SITE	With site fidelity	0.66	0.02	0.00	0.77	0.30	0.00	0.02	0.00	0.00	0.02	0.00	0.00
		Without site fidelity	0.70	0.05	0.00	0.77	0.25	0.02	0.02	0.00	0.00	0.02	0.00	0.00

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9. AGRADECIMIENTOS

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Para terminar, me he dejado una de las partes de la tesis con más responsabilidad porque sé que es lo primero que se lee. Además, tengo a mucha gente en la mente a la que se lo quiero agradecer y espero no dejarme a nadie.

Pero vamos a empezar por el principio, a la primera persona a la que le tengo que agradecer haber llegado hasta aquí es a Andrés. Él fue quien me introdujo en el mundo de la ciencia; desde nuestra primera charla sobre investigación, allá por 2009, hasta ahora ha pasado bastante tiempo, muchas reuniones, muchas "vueltas", pero sobre todo buenos momentos que recordaré siempre y que me hacen estarle muy agradecido desde que me dijo: "¿Tú te has planteado algún día hacer un doctorado?"

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Roberto C. Rodríguez Caro

Tesis Doctoral