

UNIVERSIDAD COMPLUTENSE DE MADRID
FACULTAD DE CIENCIAS BIOLÓGICAS



TESIS DOCTORAL

**Distribución de los murciélagos de España Central
determinada por muestreos acústicos: aplicaciones para su
conservación**

**Bat distribution in Central Spain determined by acoustic
surveys: applications for conservation**

MEMORIA PARA OPTAR AL GRADO DE DOCTORA

PRESENTADA POR

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Universidad Complutense de Madrid
Facultad de Ciencias Biológicas
Departamento de Biodiversidad, Ecología y Evolución



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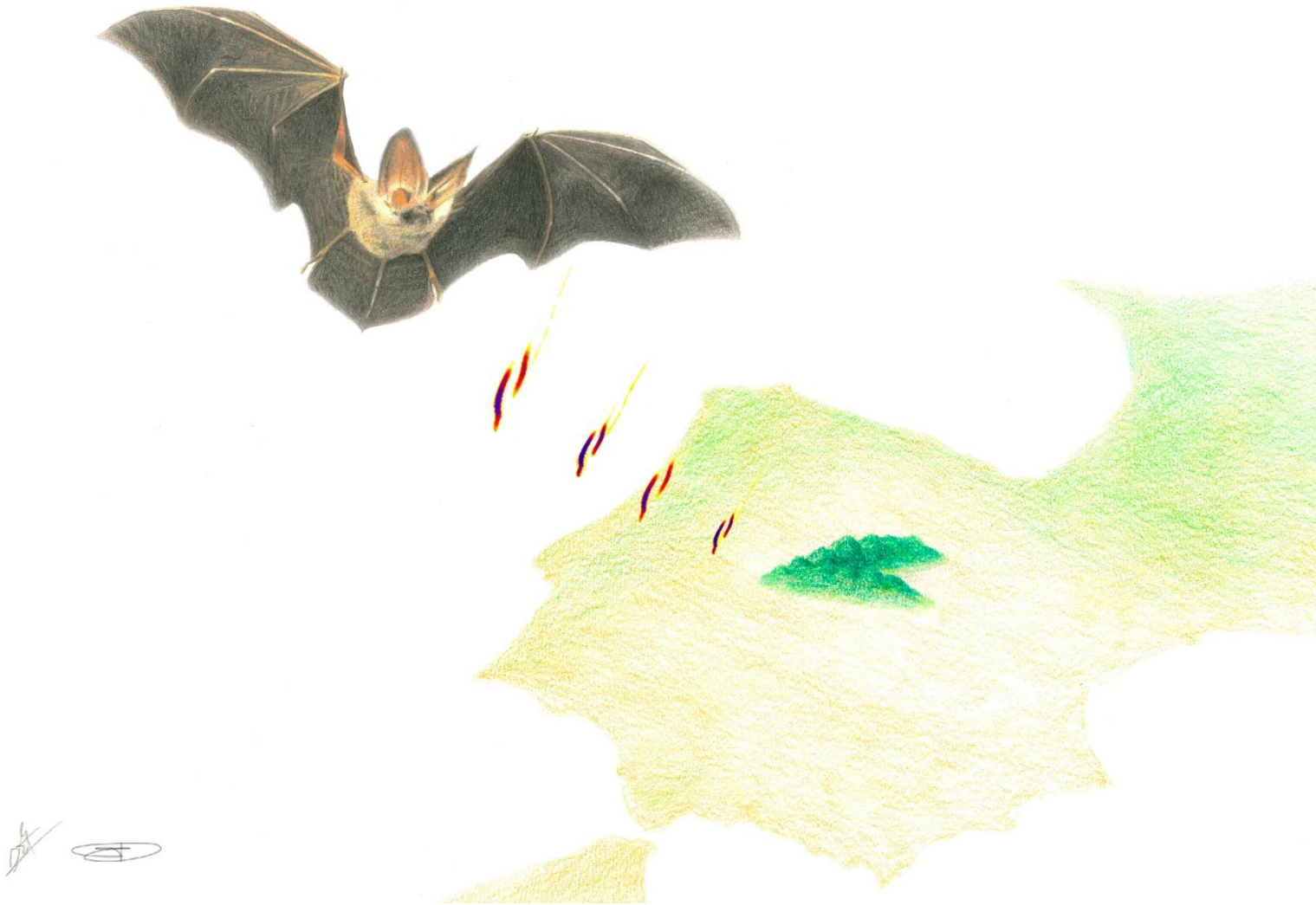
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APLICACIONES PARA SU CONSERVACIÓN.**

**BAT DISTRIBUTION IN CENTRAL SPAIN DETERMINED BY
ACOUSTIC SURVEYS: APPLICATIONS FOR CONSERVATION.**



**ELENA TENA LÓPEZ
TESIS DOCTORAL 2020**

**DIRECTORES:
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**DEPARTAMENTO DE BIODIVERSIDAD, ECOLOGÍA Y EVOLUCIÓN
FACULTAD DE CIENCIAS BIOLÓGICAS
UNIVERSIDAD COMPLUTENSE DE MADRID**

Financial support

This thesis was supported by the research assistant contract of Garantía Juvenil from the Council for Culture, Education and Sport in the Autonomous Community of Madrid and the European Social Fund.

A mi familia y amigos.

*Todas las ilustraciones de esta tesis son autoría de
Daniel A. Truchado y David A. Oropesa-Olmedo.*



“I think of a scientific naturalist as a person who is inexhaustibly fascinated by biological diversity, and who does not view organisms merely as models, or vehicles for theory but, rather, as the *raison d’être* for biological investigation, as the *Ding an sich*, the thing in itself, that excites our admiration and our desire for knowledge, understanding, and preservation.”

D. J. Futuyma, 1998.

Wherefore and whither the naturalist?

The American Naturalist, 151(1), 1-6.

AGRADECIMIENTOS

Si escribir la tesis ha sido un proceso bonito pero complicado, los agradecimientos no se quedan atrás. Lo primero de todo, quería expresar mi gratitud y admiración a mis dos directores, sin los cuales esta tesis no hubiera sido posible. Echo la vista atrás, desde que empecé allá en el 2014, y me siento orgullosa de esta evolución, cuando empecé sin saber nada de murciélagos, y ahora, aunque siempre quedan cosas por aprender de estas fascinantes criaturas, creo que “algo” más sé. Y todo ha sido gracias a vosotros. Gracias a ti, Telle. Desde que empecé la carrera e iba cada año a tu despacho y me decías que estudiara, y volviera más tarde, hasta que por fin fuiste mi profe en el último año. Nunca olvidaré ese día en las prácticas de campo de Navacerrada con las cámaras trampa. Ahí empezó todo, un trabajo exitoso en equipo con el TFG que derivó en que me brindaras una oportunidad maravillosa para empezar una línea de investigación con este grupo de animales. Gracias por tu paciencia y por tu apoyo incondicional, por todo lo que me has enseñado: desde saber diseñar un buen protocolo de muestreo en campo, a el correcto análisis de datos, redacción del trabajo y enfoque para su publicación. Nunca te estaré lo suficientemente agradecida. Incluido no solo en el aspecto científico, sino también en el académico y humano. Ha sido un privilegio haber podido impartir docencia en la universidad a tu lado y en las prácticas de campo, así como disfrutar aprendiendo en nuestros viajes de proyecto. Espero que esto solo sea el principio. Óscar, gracias por abrirme las puertas al maravilloso mundo de los murcis por la puerta grande. Valoro mucho que me aceptaras cuando aún ni me conocías. No olvidaré esa primera noche con Loreto y el quesito de mi pueblo, censando nada más y nada menos que un refugio de *Rhinolophus mehelyi*! Han sido muchas las noches compartidas juntos en el campo, experiencias que unen a unos niveles inexplicables. Gracias porque la mayoría de lo que sé de aspectos murcielaguiles te lo debo a ti. Gracias por formarme en el genial mundo de la bioacústica. Gracias por enseñarme a ser autosuficiente para trabajar con murciélagos y darme el relevo. Siempre nos uniré nuestra fascinación en común por estas criaturas únicas... Y no solo eso, sino que, gracias a esa pasión, he podido superar retos contigo como el de la las cuevas y la espeleología. Gracias por disfrutar en días como el de la torre humana en la “cueva del parto” ... Espero las siguientes aventuras juntos. ¡Deseando celebrar esta tesis con Rober y una mirinda los tres! Y ya no sigo porque como buenos directores sabéis que no sé escribir sin enrollarme y que soy muy moñas. A los dos, ¡GRACIAS!

Thanks also to the English reviewers of this thesis, Stewart, Tyson, Roger, Sarah and especially, to Jasper, for your fast and great advice. Gracias también a Dani Truchado y David Oropesa, por las maravillosas ilustraciones personalizadas de esta tesis que tanto os habéis currado, que tan bien supisteis plasmar y que mejoran tanto la tesis.

Como este recorrido ha sido largo, quiero dar las gracias a todas las personas que han intervenido en este proceso de una u otra forma. En especial y de una manera constante, lo han hecho todos lo que hemos compartido trabajo juntos en “el templo”, el despacho de Telle: Roberto, Germán, Antón Álvarez, Rafa y Juanolas (¡a ver esa productividad del departamento! jaja), Tomás, Javi Pérez- Tris, Pepe, Carlos, Chechu, Pelusa, Diego Batallas... Y de una manera muy especial, gracias al “Equipo Marroquino”. Gracias Chusa, por sus constructivos consejos y su amistad “de parcelas”. Gracias Luisón, por ser como eres, hace falta más gente como tú. Gracias a Iván, porque eres para mí el ejemplo del científico perfecto. Gracias a Onrubia, mi “Bracitos” (lo tenía que decir), por tantas risas y buenos momentos aprendiendo juntos. El final de estos agradecimientos

está inspirado en los tuyos. Gracias Álvaro, por todo lo aprendido en la uni y en el campo. Pero, sobre todo, gracias a “los Sardinillas”, Javi y Guille. Nunca olvidaré desde el primero momento que entré en el despacho de Telle y estabais del otro lado de las mesas. Me acogisteis como una más del equipo y me enseñasteis en lo académico y en personal. Javi, este recorrido lo acabamos juntos, pero es solo una etapa más. Ánimo en el siguiente paso y que lo disfrutemos juntos. Guille, esta tesis en parte es tuya. Los días en el despacho juntos debatiendo horas son irremplazables. Como decías en tu tesis, por más momentos así y lo que tenemos pendiente.

Así mismo, quiero dar las gracias a doctorandos de la planta 9, que hemos compartido este intenso camino de la tesis juntos. Gracias a los doctorandos que leyeron delante de mí, ya mis doctores, de los que tanto aprendí: Alex y Antón, ejemplos a seguir; Jasper, gracias por estar ahí, pase lo que pase y para bailar Azúcar Moreno; Sheila, amenizando las comidas; Michael y Melinda, mis padres adoptivos; Bea, hermana mayor y esos muestreos de la perdicera memorables, sobre todo, ¡las minas de Tierga! jaja; Ampí y Javi, nunca os estaré lo suficientemente agradecida con vuestro apoyo moral y logístico de campo, sois una pareja estupenda; y a María, mi Loti, mi compañera de tesis... lo que diga me quedo corta, quiero ser como tú de mayor. Sigue así y espero poder volver a hacer cuevas juntas. Y a los nuevos doctorandos, espero haberos sabido enseñar yo también: Gabri, sigue sin aburrirte en tus muestreos de campo; Héctor, ánimo en este recorrido y que echamos más partidas de pádel; Pablo, sigue así con una tesis tan interesante y que yo lo vea; y el “equipo Abantos”... no sé ni qué deciros. Luci (ya sabes que yo soy la única que puede llamarte así), gracias por todo tu apoyo, eres una chica modelo y que llegarás lejos y espero poder verlo contigo. David, mi Daivis, el viaje a México fue un antes y un después para mí y lo viví de tu mano, eres un ejemplo y estoy muy orgullosa de ti, gracias por enseñarme que, con esfuerzo y dedicación, todo se consigue. Y por último a Dani, mi alma gemela en esta tesis, con quien creo que he compartido todas mis alegrías y penas, mis risas y lloros. Tengo presión de leer tus agradecimientos de la tesis jaja pero te diré que eres mi modelo a seguir, como persona y como científico. Gracias por días de lloros, como la tesis en 3 minutos, y de risas, como el de Paco Pastel, que nos hacen sentir vivos...

Otros compañeros que compartieron mis días en la uni previamente a la tesis son mis compis de máster de “conversación con la fauna”. Gracias Marta, Lobón, Iván, Alfon gemelo de tesis, José mi canario favorito, y en especial, a Vir por todo lo compartido juntas en esos años de máster y Wild Madrid que siempre recordaré con mucho cariño. Pero por supuesto, este recorrido comenzó con mis amigos de la carrera de bio, con los que compartí mi emoción por la ciencia de la vida, y la vida en general. Gracias a todos, sois muchos, pero sobre todo, gracias a Dani Bustillo (¡y tu super dibu del lasiopterus!), a Sancho, a Nacho por todo lo que aprendí a tu lado y a mis gotitas, con las que formamos un mar: Anichurri, Saavi, Dani, Fon, Marti, Vir y Noush. ¡Sigamos moviendo olas juntas! Dentro de la UCM, también quería dar las gracias a los profes, alumnos y técnicos que han contribuido en algún momento de mi carrera académica, sobre todo, a Jesús, Palá Paul, Juan Zaballos, Sergio Pérez, Ana García Moreno y Lorena García. Y muy en especial, a Mariano Padilla, por alegrarme los días por los pasillos, ya sabes, ¡sé muy malo! Y al grupo de seguimiento de fauna, por alimentar la semilla de campo en la uni, sobre todo, a Pelao y Almu.

También quería agradecer a todos los que han amenizado mis días en lo que más nos gusta, el trabajo de campo y el bicherío. Gracias a Honorio, por poder disfrutar con él en los Montes de Valsaín, deberías ser el lord de esos terrenos... Y a Miguel, por tu

pasión y por tu generosidad, por ser tan buen fotógrafo y porque cada día disfrutamos más juntos y que siga siendo así. Gracias a Alberto Buhillo, por estar siempre ahí y aunque nos vemos poco, cada oportunidad que tenemos ocasión es una gran aventura. Sobre todo, *sierpegracias* a Raulophis, por todo su apoyo constante y ánimos en nuestra tesis de la vida... escribo esto escuchando Tash Sultana gracias a ti y a la que también le debo horas de concentración en la tesis. Ahora que esta etapa se cierra, estoy deseando llevar a cabo todos los planes futuros que tenemos juntos y viva ¡Dinaminatural! Gracias también a Octavio, por toda tu ayuda en la tesis y por los buenos momentos vividos juntos. Sigue cuidando el verde bosque. Gracias a Unai, por esos días sin dormir censando plantillas de vegetación y la “Plecosuerte”. Gracias a Xabi, por estar siempre ahí, por esas noches de pacharán y zorros y porque estoy deseando realizar trabajos juntos como doctores, empezando por nuestras becas. Gracias a Mario, por enseñarme tanto de campo desde un punto de vista diferente. Sabes que eres un gran amigo con el que quiero seguir viviendo aventuras juntos siempre con nuestros peludos. Siempre recordaré con cariño la noche de tormenta bailando bajo la lluvia con ranas... Pero, sobre todo, y el agradecimiento más importante de esta tesis es a todos y cada uno de los que me acompañasteis en los muestreos de esta tesis. Sin vosotros, no habría podido tomar los datos de murcis, y nada habría sido posible. Me habría encantado poner los nombres de todos, fuisteis muchos, a todos gracias porque me ayudasteis en lo más difícil, en los muestreos de campo en plena noche. Sabéis que tengo pendiente escribir una tesis de extraños fenómenos de la noche. Gracias Fer por aguantar el tipo la famosa y primera noche de muestreo ya sola sin Telle con el “dogging”, es algo que ha quedado como batallita de la tesis para los restos. Y gracias a todos, pero quería hacer una mención especial por tantas noches con su compañía a Carmen Soria, a Carmen Román, a Santi y, sobre todo, a Javi Pineda y a Cris, los que más noches me aguantasteis, llamadas de última hora y muestreos interminables... Os estaré eternamente agradecida. Javi, ya subo el brazo con la ¡Game Boy! Y Cris, eres la mejor prima.

Gracias a todos los que me habéis acompañado en el maravilloso mundo de los murcis en el que espero seguir mucho tiempo. Desde que empecé en mi formación de la bioacústica en los cursos de Drosera, gracias a Roberto y Rafa Márquez; de Cea Explora la Noche; de Biolearn, gracias Laura, Adrián y sobre todo, Xosé; y de DEST, gracias a Danilo y Leonardo por tantísima sabiduría. Pipistrello è bello! Gracias al equipo de Alcalá, Gonzalo y Susana, por ayudarme en los inicios. Gracias también al equipo salmantino, Wild Spain, a Miguel y Diego Lizana, pero sobre todo, a Luis por enseñarme mis primeros murciélagos en mano y ser tan feliz y halagador. To Sally and especially to Roger, for being my shoulder when I needed support and for teaching me in the bat world. To the Gib- Bats team, Clive, Geraldine, James, and for sure, Tyson and Stewart, you are an example of the bat team I would like to have, thanks for taking me in as a member too. Gracias a Rodrigo Medellín, el batman mexicano, por atenderme tan bien en México y enseñarme mi primer polinizador. Espero brindar con ¡más mezcal bat friendly! Thanks to the Nietoperek team, to Tomek, to Àngel and Laura for such an amazing experience. Gracias al Grupo de Espeleo Flash al que me introdujo Óscar, sois como una gran familia que me habéis adentrado en un mundo de paisajes subterráneos inigualables... gracias en especial al Cordi, Velén con V, Hevia, Desi y Migue (este canto último de agradecimientos va en tu honor...). Gracias a todos los que me ayudasteis y colaborasteis con las Bat Nights, en especial, a Vir y a Sara, de Brutal. Gracias a SECEMU y a todos sus socios, muchos me habéis aportado de una manera u otra. Quería dar las gracias de manera especial a Dani Fernández, a Pedro, a Félix, a Joxerra, a Maria, a Xabi, a Adrià, a Ricardo Rocha, a Sandra, a Juan Emilio, nuestra charla juntos en la UCM de la rabia en los medios fue genial; a Javier Juste, desde aquel primer correo emotivo que nos unió; al

presi, Juan Tomás, por todos sus sabios consejos; y a Carlos Ibáñez, mi admiración hacia tu trabajo y agradecimiento por lo enseñado son enormes. A ver si conseguimos lo de la biodetección. Pero, sobre todo, y a los que más tengo que agradecer, es a Catu, como primera alumna a la que le dirigí el TFG, fue un placer. A Santi, eres un alumno ejemplar, fue un gusto trabajar a tu lado con el TFM y espero que podamos trabajar más veces juntos. Y como broche final, gracias por recordarme la pasión con la que empezamos todos, por tu constancia y esfuerzo. Enhorabuena por lo que tienes, te lo mereces y disfruta de tu experiencia y que la compartas conmigo como sigues haciendo hasta ahora. Gracias al BaTeam, jamás olvidaré mis días de trabajo en Valsaín y todo es gracias a ti, Marisol. Aún recuerdo la primera noche de redes, con ver un lasiopterus en todo el verano nos dábamos por satisfechos y ¡cayeron 14! Ojalá hubiera una técnico como tú en cada parque, el mundo iría mucho mejor. Soy fan de ti y espero poder seguir con nuestros proyectos y que la próxima tesis sea la tuya. Y todo esto, no lo podía cerrar de otra forma que con el Murciequipo. Rober, gracias por enseñarme a trabajar desde una perspectiva diferente y muy necesaria como es la de la consultoría. Sigo admirada por tu forma de trabajar, tan profesional y a la vez, siempre con unas risas. No cambiaría ni una de las jornadas de campo los tres juntos, espero que sean muchas más, y con mirindas como las del Alto del León o Rosquillas del Albero. Chicos, ya puedo decir ¡que he escrito una tesis! Queda pendiente el Zalacaín.

Y gracias a ella, a mi compañera de viaje... A mi Chus, tú has recorrido prácticamente todas mis vivencias del mundo de los quirópteros conmigo, de Galicia a Gibraltar, ¡hasta a Italia! Me has aguantado en lo bueno y en lo malo, me has cuidado como una madre, como una amiga, como una hermana, como una compañera, como asistente Schuss... Mejor que yo a mí misma. Gracias por la lección de vida que me das día a día, esforzándote y trabajando, ayudando a los demás, pero sin olvidarnos de disfrutar. Estoy deseando celebrarlo con un heladito en los Alpes y, sobre todo, quiero ver qué próximas aventuras nos depara la vida juntas ya como doctora...

Como en este recorrido, el apoyo personal es fundamental, quiero dar las gracias al resto de mis amigos. Gracias a la “perripandi”, por alegrar mis mañanas. A Caballo Amigo, por llenar un aspecto muy importante de mi vida personal. A Claudia, mi sistah, por nuestros audios interminables, que inyectan energía. Gracias a Letes, por tu entusiasmo y amistad. A Luisma, por luchar juntos en el día a día frente al qué dirán. Gracias a Lau Tejedor, porque eres la mejor profe, me enseñas con tu ejemplo, superando retos y cuidando de tus amigos. Gracias a Pili, por siempre preguntarme cosas de murcis y por ayudarme a desconectar con temas perrunos que me cargan las pilas. A mi equipo de la cuadrilla asturiana, Mino, Servan, Juancho, y sobre todo, Pablo, Aritz, Nieves, Fer, Mario y Carli. Gracias por vuestro apoyo incondicional. Aún recuerdo cuando decidí empezar la tesis, las fuerzas y ánimos que me disteis para empezar y que me dais ahora para acabar. En cuanto termine, me tenéis ahí de nuevo para celebrarlo. Y gracias a Víctor, aunque te haya tocado vivir conmigo la recta final y quizá más angustiante, tú has hecho que haya sido mucho más fácil y la he acabado a tu lado. Eres el rey de la burbuja... Gracias y ya estoy deseando vivir las siguientes maravillosas etapas juntos, como guardia y doctora.

Y, sobre todo, gracias a mi familia, por apoyarme y darme fuerzas, por la paciencia, y por superar conmigo estos años de tesis. Gracias a mis tíos y a mis primos. Gracias a Eli, por cuidarme como a una hija. Gracias a mis peludos, Zar, Tula y Perla, porque sois miembros de la familia y porque me habéis ayudado a olvidarme de hasta de la tesis cuando estaba con vosotros. Espero Zar, que puedas ser un futuro perro ecodetector que ayude en el mundo de la conservación. Gracias a ti, tía Amparo, me

encantaría que pudieras estar aquí con tu alegría para celebrarlo. Y a ti, tío Jose. No olvidaré el día de recogida de los detectores en Navafría porque me dejó tirada el coche... como lo acabamos pasando de bien en los campos de girasoles... Que sigamos viviendo juntos experiencias como las de Valsaín, tío. Gracias, prima Laury por estar ahí siempre, tan cerca a pesar de la distancia física que nos separa. Estoy muy orgullosa de ti y espero que sigamos creciendo juntas. Gracias Luisi, Ángel y Cris, por esos días en el Esco. Cris, no sé ni como agradecerte todo lo que has hecho por mí, en la tesis, con tanta ayuda en los muestreos; y en lo que no es la tesis, no contando los días, sino haciendo que los días cuenten. Ya sabes que lo que sea por verte sonreír... Siempre Criel. Clemi, sabes lo que te quiero, mi segunda madre, qué paciencia tienes siempre conmigo y como me ayudas. No sé qué haría sin ti...Estabas deseando que acabara la tesis y parece que por fin podremos celebrarlo y ojalá estás orgullosa. Solo de ver tu cara cuando te he dicho que había puesto el punto y final, ha merecido la pena. Y gracias a mis padres, Carmen y Eduardo, por apoyarme en esta aventura de la tesis, y de la biología, a veces desconocida para vosotros, y que, a pesar de ello, siempre me habéis apoyado y animado. Gracias porque soy quien soy y he llegado hasta aquí por vosotros. Mamá, eres una campeona, luchadora nata, comprensiva y muy buena divulgadora... Solo con haber sacado la mitad de ti, me siento una privilegiada. Papá, con tu ejemplo como padre, amigo y buen trabajador has hecho la persona en la que me he convertido hoy, quizá por eso nos dicen que nos parecemos tanto. Sé que este camino que he elegido no es fácil y no siempre de buen gusto, pero gracias por apoyarme siempre. Desde pequeña esos días de caza juntos en el campo, me marcaron y avivaron mi pasión por la naturaleza. Me alegro de haberlos compartido juntos y espero poder disfrutar de más paseos juntos como doctora. Os estoy por siempre agradecida.

Por último, gracias a ellos, a los murcis. Por mostrarme un mundo hasta entonces desconocido para mí y que ha resultado ser fascinante... Porque me han enseñado a que no hay que juzgar a pesar de los prejuicios, a que lo estético es secundario y que todo tiene su función, por brindarme luz en la oscuridad, por enseñarme que se puede ser flexible y a la vez frágil, que no todo depende de un solo sentido, que en momentos de más actividad hay que comer más, y que en ausencia de alimento hay que hibernar, que hay que beber para no deshidratarse, que hay que cambiarse de refugio cuando las condiciones del entorno no son favorables, incluso con la familia acuestas, que se pueden volar grandes distancias en búsqueda de nuestros recursos, que ser sociable ayuda a una comunidad y hay que saber formar piña con los demás. Estoy deseando seguir aprendiendo con vosotros... ¡Vivan los murcis!

Gracias a todos,

Elena.

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SUMMARY

Bats are the second largest mammalian order and they have an important role in the ecosystem. However, their taxon is seriously threatened and difficult to sample. Nowadays, the development of bat detectors offers a way to explore bat richness and activity patterns in different environmental settings to aid bat conservation. Mountains are an important target for conservation actions as they depict altitudinal gradients where variation in climate and vegetation occurs which produces changes in species richness. In this context, the Guadarrama Mountains represent an elevation gradient in the Mediterranean region under the strong effect of climate and global change. The area is considered the richest hotspot for bats on the Iberian Peninsula, but information in bat distribution is still scarce. Consequently, the aim of this Doctoral Thesis is to disentangle the main drivers of bat richness and distribution in Central Spain to aid in developing more effective conservation and management strategies.

In chapter 1, we explored if there are similarities between birds and bats concerning their environmental requirements and the way the species richness is linked to environmental changes along the elevational gradient. Results showed that during the breeding period, bird and bat distributions in the Guadarrama Mountains have very different constraints in the search for resources. Passerines are linked to a small home range at a local scale while bats can move long distances from the roost to the foraging areas at a regional scale.

In chapter 2, we sampled the distribution of bat species in the Guadarrama Mountains to compare whether sectors with higher mean suitability and rarity indices overlap with protected areas and if they have lower human impact. The distribution of protected areas in the Guadarrama Mountains overlaps with most of the best sectors for bats which are located outside the most urbanized sectors.

In chapter 3, we evaluated whether bat species richness and activity are higher in gaps inside the forest than in the adjacent Scot pine forest. We also tested these differences in forest specialists since this group is particularly sensitive to forest management. Species richness and bat activity, as well as some individual species activity, increased more in gaps than they did in the adjacent control site.

In chapter 4, we decided to compare the occurrence of bats in urban parks in the city of Madrid with the presence of individual species registered in the surrounding Guadarrama Mountains. Urban parks were not particularly attractive for the regional pool of bat species as their occurrence was limited by the regional occurrence and with lower occupancies than in the Guadarrama Mountains. We also studied the way some geographical and environmental traits affected bat richness and composition in urban parks and whether the resulting bat richness distribution showed a nested pattern. Park size was the main driver for bat species richness distribution in urban parks. And this species richness distribution presented a nested pattern, where species within smaller parks are subsets of the pool of species occurring in the existing natural habitat.

This thesis provides support to the value of acoustic sampling in bat conservation. An extensive acoustic sampling program of bats was carried out along an altitudinal gradient and fragmented landscapes of the Guadarrama Mountains and the city of Madrid. Variations within species richness distribution of birds and bats along the altitudinal gradient should be taken into consideration to preserve biodiversity within the same geographical area. The network of protected areas along this gradient is appropriate, although bats were not considered in its creation nor in its follow-up projects. In the future, global change might cause disturbances occurring within this network, so specific approaches must be taken to anticipate and to mitigate the potential effects on bat assemblages. The centre of the peninsula is also composed by a heterogenous landscape, such as gaps that were used more intensely by bats than the adjacent forest matrix, including the most sensitive tree dwelling species. Gaps generate ecotones in landscapes that can be used by bats as corridors for commuting and foraging. Therefore, any forest and bat friendly management guideline should maintain gaps already created inside a homogenous forest in support of forest species conservation. Other fragmented landscapes are the parks of Madrid. To reverse the decrease of bat richness in urban areas, a proactive approach to bat conservation would be required by improving the attractiveness of biodiversity with the increase of park size and the connection of urban parks with the existing natural habitat. In addition, bat richness distribution was poorly nested in the elevational gradient but nevertheless it was strongly nested in urban parks. It can be concluded that distribution of bat species suggests a random sampling by parks of the regional availability of species. This is important to be considered since processes

occurring at a regional scale might be determinant for species richness in fragmented areas.

RESUMEN

Los murciélagos son el segundo orden de mamíferos más diverso, con un papel fundamental en el ecosistema. Sin embargo, suponen un grupo seriamente amenazado y difícil de muestrear. Actualmente, el desarrollo de detectores de ultrasonidos ofrece la posibilidad de explorar la riqueza y los patrones de actividad de los murciélagos en diferentes entornos ambientales para poder contribuir a su conservación de murciélagos. Las montañas son un objetivo importante para la conservación pues representan gradientes altitudinales con variaciones en factores climáticos y de vegetación que producen cambios en la riqueza de especies. En este contexto, la Sierra de Guadarrama representa dentro de la región Mediterránea, un gradiente altitudinal que se encuentra bajo el fuerte efecto del cambio climático y del cambio global. Es una zona considerada como el punto más diverso de murciélagos de la Península Ibérica, pero donde la información sobre la distribución de los murciélagos es aún escasa. Por ello, el objetivo de esta Tesis Doctoral es conocer los principales factores de la riqueza y distribución de murciélagos en el centro de España para ayudar en el desarrollo y mejora de las estrategias de conservación y gestión de murciélagos.

En el capítulo 1, exploramos si son similares los requerimientos ambientales por aves y murciélagos y la forma en que la riqueza de especies está relacionada con los cambios ambientales a lo largo del gradiente altitudinal. Los resultados demostraron que, durante el período de reproducción, la distribución de aves y murciélagos de la Sierra de Guadarrama mostraron limitaciones muy diferentes en la búsqueda de recursos. Los paseriformes están vinculados a una pequeña área de distribución a escala local, mientras que los murciélagos pueden moverse largas distancias desde el refugio hasta las áreas de alimentación a escala regional.

En el capítulo 2, muestreamos las presencias de murciélagos de la Sierra de Guadarrama para comparar si los sectores con mayor idoneidad y rareza coinciden con las áreas protegidas y con las que tienen menor impacto humano. La distribución de áreas protegidas en la Sierra de Guadarrama se superpone con la mayoría de los mejores sectores para murciélagos, que se encuentran fuera de los sectores más urbanizados.

En el capítulo 3, evaluamos si la riqueza y la actividad de las especies de murciélagos eran mayores en los claros de bosque que en el propio bosque adyacente de pino silvestre. También estudiamos estas diferencias en los murciélagos forestales, ya que este grupo es particularmente sensible al manejo forestal. La riqueza de especies y la actividad de los murciélagos, así como la actividad de algunas especies, aumentaron más en los claros de bosque que en el propio bosque adyacente.

En el capítulo 4, decidimos comparar la frecuencia de aparición de murciélagos en los parques urbanos de la ciudad de Madrid con la registrada en la Sierra de Guadarrama circundante. Los parques urbanos no fueron particularmente atractivos para el grupo regional de especies de murciélagos, cuya presencia estaba limitada por la presencia regional y con frecuencias de aparición menores que en la Sierra de Guadarrama. También estudiamos la forma en que algunos rasgos geográficos y ambientales afectaron a la riqueza y composición de murciélagos en los parques urbanos y si la distribución de la riqueza de murciélagos resultante mostró un patrón encajado. El tamaño del parque fue el principal factor limitante de la distribución de la riqueza de especies de murciélagos en los parques urbanos. Y esta distribución de la riqueza presentó un patrón encajado, donde las especies de dentro de los parques pequeños son subconjuntos del grupo de especies que se encuentra en el hábitat natural existente.

Esta tesis apoya el valor de los muestreos acústicos en la conservación de murciélagos. En ella, se llevó a cabo un extenso programa de muestreo de murciélagos a lo largo de un gradiente altitudinal y de paisajes fragmentados de la Sierra de Guadarrama y la ciudad de Madrid. Los cambios en la distribución de la riqueza de especies de aves y murciélagos a lo largo del gradiente altitudinal deben tenerse en cuenta para preservar la biodiversidad dentro de una misma área geográfica. La red de áreas protegidas a lo largo de este gradiente es adecuada, pero los murciélagos no fueron considerados ni en su creación ni en su gestión. En el futuro, el cambio global podría causar perturbaciones dentro de esta red, por lo que se deben tomar medidas específicas para anticipar y mitigar los posibles efectos potenciales sobre las comunidades de murciélagos. El centro peninsular también está compuesto por un paisaje heterogéneo como por ejemplo los claros de bosque, que los murciélagos utilizaron con mayor intensidad que la matriz de bosque adyacente, incluidas las especies forestales. Los claros de bosque generan ecotonos en el paisaje que los murciélagos pueden utilizar como corredores para desplazarse y buscar alimento. Por lo tanto, en cualquier medida de gestión forestal se

debe mantener los claros de un bosque homogéneo para favorecer la conservación de las especies forestales. Otros paisajes fragmentados son los parques de Madrid. Para revertir la disminución de riqueza en zonas urbanas, se requeriría un enfoque proactivo para la conservación de murciélagos mejorando el atractivo de la biodiversidad con un aumento del tamaño de los parques y la conexión de los parques urbanos con el hábitat natural existente. Asimismo, la distribución de la riqueza de murciélagos está pobremente encajada en el gradiente altitudinal, pero sin embargo sí está muy encajada en los parques urbanos. Se puede concluir que la distribución de especies de murciélagos sugiere un muestreo aleatorio por parte de los parques según la disponibilidad regional de especies. Es importante considerar esto, ya que los procesos que ocurran a escala regional pueden ser determinantes para la riqueza de especies en áreas fragmentadas.

GENERAL INTRODUCTION

“I have always found small mammals enough like ourselves to feel that I could understand what their lives would be like, and yet different enough to make it a sort of adventure and exploration to see what they were doing.”

Donald R. Griffin.

Echoes of Bats and Men, 1959.

INTRODUCTION

Bats (order Chiroptera) are the second largest mammalian order including over 1400 species (Simmons & Cirranello 2020). They are the only mammals capable of powered flight and they currently occur in all continents and are especially abundant in the tropics, but can't be found on some islands and the Poles (Altringham 2011). Moreover, they have an important role in the ecosystem as they contribute to biological pest control, seed dispersal or plant genetic diversity, among others (Kunz et al. 2011). Bat diversity makes this group an interesting target for conservation, especially because they are increasingly threatened by habitat loss and modification, alteration of roosting areas, pesticides and wind turbines (Mickleburgh et al. 2002, Voigt & Kingston 2016). Many bat species are included on the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN, <http://www.iucn.org>). However, due to their nocturnal behaviour, bats are difficult to sample. Although bat communities from many geographic areas have been studied, they remain poorly understood in aspects such as habitat selection or activity areas.

This situation is changing rapidly because there are increasing possibilities of exploring their distribution with new, useful technical and analytical approaches. Recently, the ultrasonic identification of bat calls represents an efficient, complementary and non-invasive method to verify the occurrence in the field of these species (Vaughan et al. 1997, Flaquer et al. 2007). All European bat species use echolocation for moving around and foraging (Dietz & Kiefer 2016). They use their sounds to navigate, ultrasounds called echolocation or bat calls. An echolocation call is produced on a frequency range from 8 to 200 kHz, and the range frequency between 20- 200 kHz is generally inaudible to the human ear. The calls can be characterized by different sound parameters as their frequency, their duration and their inter-pulse interval. Nowadays, recordings of the bat calls are performed with special equipment known as bat detectors. This methodology makes the study of bats possible without handling them in diverse habitats with different variables (Russo & Jones 2002, Barataud 2015). It is a consolidated methodology used in bat sampling that has proven to be useful for the research of many individual bat species. This methodology can improve the development of different fields in bat conservation and management, such as the study and the monitoring of populations (Flaquer et al. 2007), habitat use (Vaughan et al. 1997) and activity (Russo & Jones 2003).

Therefore, acoustic monitoring can provide a way to explore bat richness and activity patterns in different environmental settings (Flaquer et al. 2007).

Despite these improvements, bat detectors have some limitations that must be taken into account before carrying out bioacoustic studies with these animals. Bat detectors show, for instance, different results according to the use of different microphones and detection algorithms (Adams et al. 2012, Perea & Tena 2020). In addition, echolocation calls of individual species can be variable influencing in the efficacy of bat species detection (Adams et al. 2012, Russo & Voigt 2016) as echolocation calls are influenced by several factors (habitat, presence of conspecifics, environmental noise; Walters et al. 2012, Barataud 2015, Russo et al. 2018). All these shortcomings can affect the identification of some species such as those of genus *Myotis*, which have very similar echolocation calls (Parsons & Jones 2000). In the case of calls emitted by species of the genera *Plecotus* and *Rhinolophus*, ultrasounds are biased by their low power (Rydell et al. 2017) and strong directionality of their sound emissions (Schnitzler & Grinnell 1977).

Roost location and protection have been used as the most frequent approach for bat conservation (Medellín et al. 2018) but foraging sites are also important sectors to be considered (Russo & Jones 2003). This approach to the study of bat distribution can today be easily improved by using bat detectors. It is commonly acknowledged that there is a lack of cartographic approaches designed to detect the most important habitats and sectors for the conservation of bats (Razgour et al. 2016). Bat detectors allow to sample active bats over large areas and to use the resulting occurrences to disentangle the main drivers of species richness and activity and to produce species distribution models (Elith & Leathwick 2009, Razgour et al. 2016).

In this context, it is interesting to study the way bats are distributed along elevation ranges as they show sharp variations in biotic and abiotic factors. These environmental changes shape the distribution of individual species in mountain ranges and produce concomitant changes in species richness along elevation (McCain & Grytnes 2010). As a result, mountains are in addition an important target for conservation of bats and other species (Tellería 2020).

The Guadarrama Mountains represent an elevation gradient at the Mediterranean region, an area under the strong effect of climate and land use changes (Giorgi & Lionello 2008). These mountains induce an upwards decrease of temperature and an increase of

precipitation if compared to the surrounding lowlands (Gonzalez-Hidalgo et al. 2016). This climate turnover produces an altitudinal succession of vegetation belts and a concomitant change of animal assemblages (Ruiz-Labourdette et al. 2012, Flores et al. 2018).

The Guadarrama Mountains are located within the highly biodiverse Mediterranean region (Myers et al. 2000), where bat distribution is poorly known (Palomo et al. 2007, Paz et al. 2015). However, the centre of the Iberian Peninsula has a wide variety of bats, with 28 species (Paz et al. 2015). Interestingly, the Guadarrama Mountains harbor the richest bat hotspot (22 species) of the Iberian Peninsula, an important site for bat conservation in Spain (Paz et al. 2016, 2017). Despite this, information on bat distribution in the Guadarrama Mountains continue to be scarce (Palomo et al. 2007, Paz et al. 2015). Consequently, it seems interesting to increase the sampling effort of bat assemblages inhabiting the Guadarrama Mountains to disentangle the main drivers of bat richness and distribution to know more about conservation and management strategies. This is the aim of this Doctoral Thesis, carried out along the following chapters.

In chapter 1, we have tried to understand how changes in some environmental traits affect bats and birds. We decided to explore bird and bat requirements as they are both endothermic, insectivorous, flying vertebrates experiencing their breeding season in the Guadarrama Mountains. Former studies have reported similar and dissimilar responses in the way they track habitat structure and food availability (Lund & Rahbek 2002, Willig & Preseley 2016, Barbaro et al. 2019). Thus, despite the reported similitude between the two groups, the way birds and bats perceive the same environmental gradients remains highly controversial. Hence, we will try to approach this question within the geographical setting of the Guadarrama Mountains.

The Guadarrama Mountains harbor several protected areas for biodiversity conservation: A National Park, buffer areas of the National Park, natural parks, reserves, Special Protection Areas for birds, Sites of Community Importance and Special Areas of Conservation resulting from Natura 2000 European Union directives. In addition, a main part of the region is densely populated by humans (6.5 million inhabitants, Cincotta et al. 2000) so that urban encroachment and the connecting infrastructures constitute a main threat for nature conservation. Therefore, in chapter 2 we explore if the best areas for bats defined by species distribution models (Elith & Leathwick 2009, Razgour et al. 2016) are

within or outside the protected areas. More explicitly, we will carry out a gap analysis (Scott et al. 1993) to detect if the best areas for bat conservation are included in the regional network of protected areas (Buckman-Sewald et al. 2014, Bosso et al. 2016, Kerbiriou et al. 2018) in an area particularly stressed by urban encroachment (Tena et al. 2020a).

The structure of bat species assemblages is also constrained by landscape heterogeneity (Voigt & Kingston 2016). In this context, small patches of different habitats inside a matrix of homogenous landscape are frequently considered local hotspots for biodiversity (Pardini 2010). Gaps inside a large homogeneous forest extension (Schnitzer & Carson 2001) or parks inside an urban matrix (Baker & Harris 2007) are two examples of these local drivers of species diversity that we will explore in the study area.

Gaps are open areas produced by natural or human-induced disturbances (Muscolo et al. 2014) within the matrix of forest canopy. They can be very attractive for bat species richness as they promote habitat heterogeneity and border effects (Schnitzer & Carson 2001). Several studies have displayed greater bat activity in openings than in the nearby canopy forest (Menzel et al. 2002, Wood et al. 2017). Since bat assemblages are sensitive to forest structure and composition, especially tree dwelling bat species, it is commonly agreed that forest management will strongly influence the potential of these habitats to conserve bats (Charbonnier et al. 2016). Therefore, in chapter 3 we will assess the actual relationship between gaps and bats to improve management strategies designed to preserve bat forest species.

Other effect constraining biodiversity distribution in the Guadarrama Mountains and their piedmont is the metropolitan area of Madrid, which has experienced this strong process of urban encroachment (Goddard et al. 2010, Hewitt & Escobar 2011). Thus, it is interesting to evaluate the effect of urbanization on biodiversity and the way it can be managed for conservation (McKinney 2002). This can be particularly interesting because information on the way bats cope with urban landscapes is still poor (Avila-Flores & Fenton 2005, Scanlon & Petit 2009, Ancillotto et al. 2016, Krauel & LeBuhn 2016). In this context, urban parks are key areas for biodiversity conservation as they represent patches of semi-natural habitats used by species inhabiting the urban matrix (Baker & Harris 2007). To approach this issue in the study area, we will explore the way bats are distributed among the parks of Madrid city in chapter 4.

AIMS AND STRUCTURE OF THE THESIS

In this thesis, we study the main drivers affecting bat distribution and habitat selection in the Guadarrama Mountains and its surroundings using a multi-scale approach for application in bat conservation. Therefore, we update the information from bat assemblages of the study area (chapters 1, 2, 3, and 4) to answer the main questions of the thesis, which are: a) To disentangle the main climatic and vegetation drivers affecting bat assemblages in an altitudinal mountain gradient (chapter 1 and 2), b) to compare bat and bird richness distribution along this gradient (chapter 1), c) to generate bat species distribution models and to perform gap analysis with the network of protected and urban areas (chapter 2), d) to uncover the factors concerning bat assemblages in fragmented landscapes at a local scale for gaps inside the forest canopy (chapter 3) and for urban parks within an urban matrix (chapter 4), e) to compare bat occurrence at a local scale with the registered at a regional scale and to see if this distribution shows a nested pattern (chapters 2 and 4).

This thesis is structured in four chapters to address the following objectives:

- **Chapter 1.** Requirements of different taxonomic groups and the way species richness is influenced by environmental changes might be dissimilar. Here, we studied whether bird and bat species richness show similar patterns along the contrasting elevation gradient of Guadarrama Mountains. We performed a multi-scale approach to disentangle the potential effect of environmental drivers: climate effect, landscape structure and fine-grained habitat traits.
- **Chapter 2.** Sectors of bat activity (e.g. feeding) other than roosts have been rarely considered in the delimitation of protected areas for these mammals. Therefore, in this study we used bat detectors to sample the distribution of bat activity in the Guadarrama Mountains. We performed a gap analysis to explore whether the sectors most commonly used by active bats are covered by the current network of protected areas. We used bat occurrences to produce species distribution models and the resulting layers were used to produce mean suitability and rarity indices to detect the most suitable sectors for conservation. We also tested the relationship of the most suitable sectors for bat suitability and rarity with the urban encroachment of the city of Madrid.

- **Chapter 3.** Gaps inside the forest seem to play a major role in local species richness as they increase habitat heterogeneity and border effects. These clearings might be important also for bats as foraging and commuting sites. Therefore, we explored whether bat species richness and activity were higher in gaps within a large Scot pine (*Pinus sylvestris*) forest than in the adjacent tree covered control sites. We also tested these differences in the forest specialists since this group is particularly sensitive to forest management.
- **Chapter 4.** Urbanization is spreading rapidly at a global scale, a trend that affects biodiversity conservation in many areas. Because of this, we decided to analyse the occurrence of bats in urban parks in the city of Madrid. We compared the presence of individual species in urban parks with the presence of individual species registered in the surrounding Guadarrama Mountains. We also studied the way some geographical and environmental traits (park area, park distance to the edge of the town and vegetation structure) affected bat richness and composition in urban parks and whether the resulting bat richness distribution showed a nested pattern.

From all chapters of this thesis, two have already been published, one is currently under revision and last one is ready to be submitted to SCI journals:

CHAPTER	PAPER	STATUS
1	Tena, E. & Tellería, J. L. <i>Non coincident distribution of bird and bat species richness in a Mediterranean mountain range.</i>	Ready to be submitted
2	Tena, E. & Tellería, J. L. (2020). <i>Modelling bat distribution for conservation in a Mediterranean mountain range.</i> Animal Conservation.	Under a second revision
3	Tena, E., Paz, Ó. De, Peña, R. De la, Fandos, G., Redondo, M., & Tellería, J. L. (2020). <i>Mind the gap: Effects of canopy clearings on temperate forest bat assemblages.</i> Forest Ecology and Management, 474, 118341. https://doi.org/10.1016/j.foreco.2020.118341	Published
4	Tena, E., Fandos, G., Paz, Ó. De, Peña, R. De la, & Tellería, J. L. (2020). <i>Size does matter: Passive sampling in urban parks of a regional bat assemblage.</i> Urban Ecosystems, 23(2), 227-234. https://doi.org/10.1007/s11252-019-00913-2	Published

GENERAL METHODS

"In the end we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught."

Baba Dioum, 1968.

GENERAL METHODS

- STUDY AREA

The study area is located in the Guadarrama Mountains and the nearby city of Madrid, in Central Spain, a region of around 10,000 km² divided from NE to SW (Fig. 1). The flora of the Guadarrama Mountains is characterized in the higher elevation by an Atlantic vegetation region with juniper groves (*Juniperus communis*), montane grasslands (*Genista florida*, *Cytisus oromediterraneus*), Spanish broom (*Spartium junceum*) thickets, Scot pine (*Pinus sylvestris*) and Pyrenean oak (*Quercus pyrenaica*) forests; and in the lower elevation, by a Mediterranean vegetation region by Holm oak (*Quercus ilex*) forests, while the pastures around the summits are fringed by juniper (*Juniperus oxycedrus*) and Spanish broom (*Spartium junceum*) shrubs. The highest area is considered a National Park since 2013 (BOE 26/6/2013). Although, a main part of the region is densely populated by humans (6.5 million inhabitants) and occupied by a dense network of infrastructures (roads, railways, power lines.) and residential areas. As a result, a marked NW-SE gradient is defined between the less urbanized mountain areas and the lowland areas intensely occupied by humans around the city of Madrid. To analyse the wide variation at a local and at a regional scale, we register 338 sampling points that include different habitats along the elevational gradient of the mountains and urban environments (Fig. 1).

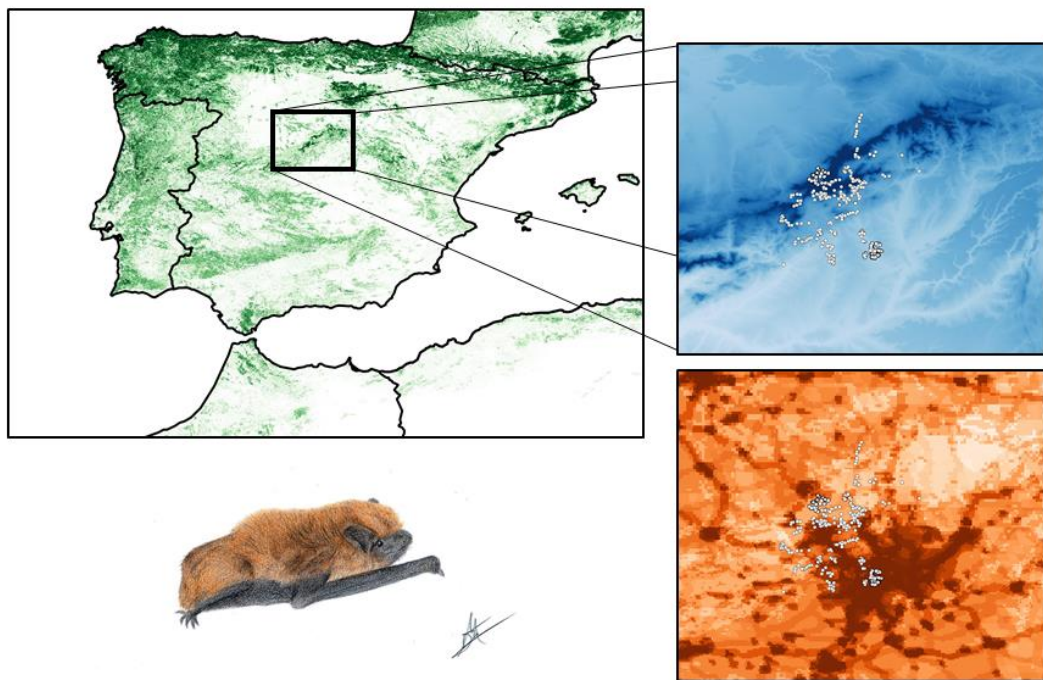


Figure 1. Left: Tree cover in the Iberian Peninsula with the study area located inside the square. Right: elevation (above) and human foot print (below) distribution in the study area. The white dots are the sampling locations in the study area.

- ACOUSTIC SAMPLING

All bat occurrence data collected for this thesis were sampled by bat detectors during the activity season (May- October) of 2014-2017. In many cases, each bat species emits calls with specific parameters that make them distinctive from the rest (Russo & Jones 2002, Barataud 2012, Russ 2012, Walters et al. 2012). Based on this, we registered 338 sampling points in the Guadarrama Mountains and its surroundings (Fig.1) and we obtained hundreds of thousands of recordings (in .wav format) with qualified bat detectors (Echo Meter 3, Echo Meter Touch, Echo Meter Touch Pro 1, Song Meter 2 and Song Meter 4 from Wildlife Acoustics). To filter and manually analyse all the recording data, we used specific software (Audacity 2.0.6, Bat Explorer 1.10, Kaleidoscope 4.5.4, Sonobat 3.1.2 p, Sonochiro, Bat Sound 4 and iBats ID 4.2). In our case, seven main parameters of the echolocation call were considered for the identification of the bat species (Russo & Jones 2002, Barataud 2012): the call structure, the frequency of maximum energy, the start frequency, the end frequency, the middle frequency, the duration and the inter- pulse interval (Fig. 2). However, this type of analysis does not always allow a specific identification, so the identifications

of the *Plecotus* and *Myotis* genera were grouped into *Plecotus* sp. (*P. auritus*/ *P. austriacus*) and *Myotis* sp. *Nyctalus leisleri*/ *Eptesicus serotinus* species were separated just when it was possible.

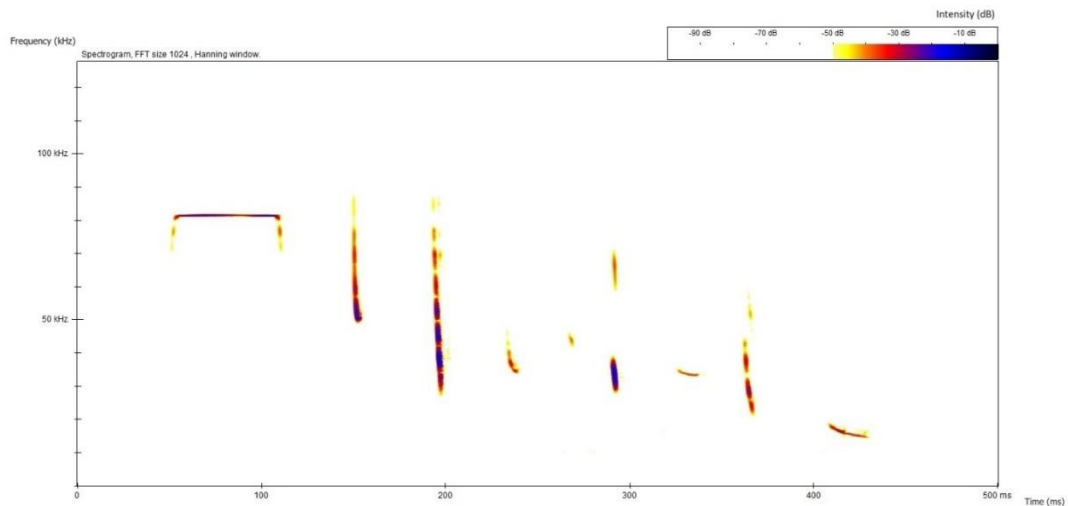


Figure 2. Echolocation calls of different bat species recorded during the thesis in the Guadarrama Mountains as visualized in Bat Sound 4. One call per species, except for *Barbastella barbastellus* which is composed of two calls. From left to right: *Rhinolophus ferrumequinum*, *Pipistrellus pipistrellus*, *Myotis* sp., *Pipistrellus kuhlii*, *Barbastella barbastellus*, *Hypsugo savii*, *Plecotus* sp. and *Nyctalus lasiopterus*.

- ENVIRONMENTAL TRAITS

For each sampling point, we assessed habitat structure in a 25 metres (m) radius. Cover (percentage) of grass, shrub (vegetation <0.5 m and between 0.5 and 2 m height) and tree (vegetation >2 m height) layers were visually assessed. In addition, we counted the number of shrub and tree species over 0.5 m height. Covers were used to perform a Principal Component Analysis (PCA, Abdi et al. 2010) to obtain latent variables able to describe the habitat structure at a local scale.

Moreover, other regional variables were measured by layers or rasters georeferenced with information from the environment. Climate rasters were obtained from Chelsa V1.2 for the period 2006-2015 (Karger et al. 2017) and vegetation rasters were downloaded from the Vegetation Continuous Fields MOD44B (GlobCover 2.2). Elevation was considered as a complementary indicator of certain meteorological events and as a topographical feature. And the potential effect of urbanization was

provided by the Human Footprint (Sanderson et al. 2002) as an index of population density, human land use and infrastructure.

- ANALYTICAL APPROACHES

To obtain all the results, different analytical approaches were applied in each chapter.

We explored the effect of the explanatory variables on bat and bird richness by controlling the potential effects of spatial autocorrelation (Diniz-Filho et al. 2003). Therefore, we used Generalized Least Squares (GLS) models with different spatial correlation structures (Dormann et al. 2007) that were evaluated by the Akaike information criterion (AICc, Burnham & Anderson 2002). These analyses were conducted in R 3.1.2 (R Development Core Team 2017) using the ‘MuMIn’ (Bartoń 2018) and ‘nlme’ (Pinheiro 2009) libraries.

QGIS 2. 18. 11 (QGIS Development Team 2016) was used to handle the cartographic information. For Species Distribution models (Elith & Leathwick 2009), we used Maxent software (Phillips et al. 2005), based on a maximum entropy approach to model species distributions (Phillips et al. 2006, Elith et al. 2011). We averaged the occurrence probabilities of species to map a multi-specific index of mean suitability and rarity for bats (Calabrese et al. 2014) so that we performed gap analyses (Scott et al. 1993) with these two indices and the network of protected areas. The potential effect of urbanization on the bats was analysed by a correlation between the mean suitability and rarity indices and the scores provided by the Human Footprint.

We used Generalized Linear Mixed-Effects Models (GLMM, Bolker et al. 2009) to compare species richness and bat activity trends in gaps and in the tree covered control points. The resulting models were compared to the null model by Akaike’s information criterion (AICc, Burnham & Anderson 2002). GLMM analyses were conducted with ‘lme4’ (Bates et al. 2014) package in R (R Core Team 2017, version 3.4.1).

To test if bat richness distribution registered a nested pattern in urban parks, we calculated the rate of nestedness. It is a measure that tries to analyse how species distribute within a fragmented habitat (Patterson & Atmar 1986). There is a nested pattern when the species are not distributed randomly within a matrix, but are arranged in order according to certain variables. The most common species are found

in all the fragments, while the rarer species are found in few of them. We studied whether bat assemblages are nested along an altitudinal gradient or between different urban parks of Madrid city. This measure can be calculated with the (Oksanen et al. 2011) in R (R Core Team 2017).

For bat distribution in urban parks, we tested by simple regressions whether the occurrence of individual species in urban parks was related to their regional occurrence and to roosting preferences. Moreover, we used a Wilcoxon Matched Pairs Test to assess whether the occurrence of species in urban parks was higher or lower than in the countryside. In addition, we used General Linear Models (GLM, Kim & Timm 2006) to explore the effect of park size, park distance to the edge of the town and vegetation structure on the number of bat species and on the rank of nestedness. We also used Generalized Linear Mixed-Effects Models (GLMM, McCulloch & Neuhaus 2014) to study the conjoint effects of the explanatory variables on species richness and nested rank. We conducted a Multi-Model Inference approach to select the best models (we used all top-ranked models summing to 0.95 AICc and that were better than the null model, Anderson & Burnham 2002). In all cases, models were adjusted to normality and heteroscedasticity of the resulting residuals. GLMM analyses and Multi-Model Inference analyses were conducted with ‘lm4’ (Bates et al. 2014) and ‘MuMIn’ (Bartoń 2018) R (R Core Team 2017) packages, respectively.

CHAPTER 1

Non-coincident distribution of bird and bat species richness in a Mediterranean mountain range.



“In nature nothing exists alone.”

Rachel Carson, *Silent Spring*.

This chapter is based on the manuscript:

Tena, E. & Tellería, J. L. Non-coincident distribution of bird and bat species richness in a Mediterranean mountain range. *Ready for submission*.

Non-coincident distribution of bird and bat species richness in a Mediterranean mountain range

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Abstract

Birds and bats are endothermic, flying vertebrates that feed on invertebrates in temperate areas. This could suggest a similar response to environmental gradients related to habitat structure and food availability. We tested if bird and bat species richness show similar patterns along a contrasting elevation gradient within the Mediterranean region (Guadarrama Mountains, Spain). To do this, we established a number of sampling points from 550 to 2000 m a.s.l. and recorded the number of bat and bird species. In addition, we assessed habitat structure and shrub richness, forest and farmland cover, temperature, and precipitation. We explored the altitudinal distribution of species richness and if it displayed a nested pattern. We used Generalized Least Square Mixed models with different correlation structures to account for spatial autocorrelation. Bird richness followed a unimodal distribution along the elevation gradient, with highest richness at mid elevations from where displayed a nested loss of species upwards and downwards. In addition, bird richness was positively related to habitat complexity and shrub richness. Bat richness was negatively related to temperature and reported a low but significant nested pattern of species distribution with elevation. These results suggest that bird richness was shaped by local changes in habitat structure while bat richness was driven by changes in temperature, probably related to the regional distribution of productivity and food resources. These differences in bird and bat species richness distribution in the environmental setting of the Guadarrama Mountains could be explained because bats may track for food regionally while passerines move locally around the nests. These biological differences could produce different distribution patterns in these endothermic, flying vertebrates, with birds tracking resources at smaller spatial scales than bats.

Key words: bat assemblage, bird assemblage, elevation, resource tracking, spatial scale.

Introduction

In the context of global change, it is interesting to assess the distribution of species richness and to unravel the factors shaping their spatial distribution in order to propose preventive or proactive conservation measures (Tilman et al. 2017). However, the idiosyncratic requirements of different taxonomic groups and the concomitant differences in the way they track the environment make it difficult to design common management guidelines aimed to protect the species within the same geographical settings (Wolters et al. 2006). Thus, it is necessary to perform approaches designed to unravel the way different groups react to environmental drivers within the study regions (Prendergast et al. 1993, Lund & Rahbek 2002).

Here we explore the potential effect of some environmental drivers on bird and bat species richness distribution along an elevation gradient at the Mediterranean region, an area under the strong effect of climate and land use changes (Giorgi & Lionello 2008). In this context, mountain ranges are important areas for conservation because low temperatures and high precipitation related to elevation allow the occurrence of northern and mountain species that, in addition to the Mediterranean ones typical of the piedmont, produce regional hotspots of biodiversity (Molina-Vanegas et al. 2016, Tellería 2020). Birds and bats are endothermic, flying vertebrates that feed on invertebrates during the breeding period in temperate areas. Because of these similarities, it could be conjectured that both groups will show similar distribution patterns of species richness. However, this proposal could be rejected because, despite some studies reporting that both birds and bats track food availability at local scales (Buler et al. 2007, Mendes et al. 2017), others have displayed different reactions to fine-grained habitat changes (Renner et al. 2018). In addition, large scale approaches have revealed similar and dissimilar distribution patterns of bird and bat richness within the same areas (Lund & Rahbek 2002, Willig & Preseley 2016, Barbaro et al. 2019). Thus, according to previous approaches, it seems difficult to predict how bird and bat richness distribute within a particular environmental and geographical setting.

Here we explore the distribution of bird and bat species richness within the Guadarrama Mountains (Spain) and the surrounding piedmont. First, we will try to know if species richness distributes along the elevation gradient according to a positive-negative relationship with elevation or, alternatively, show a monotonic, bell-shaped

pattern as has been previously reported in other areas and taxonomic groups (McCain 2009). In addition, we will explore if bird and bat species richness distribution fits to a nested pattern along the elevation gradient (Patterson & Atmar 1986). That is, if the turnover of species along the gradient displays a pattern in which most species are present at a given elevation level from where they disappear orderly upwards and downwards. Second, we will try to know if the observed trends of species richness are shaped by the same environmental drivers. To do this, since it is commonly agreed that species assemblages are shaped by a combination of climate, landscape and fine-grained habitat features (Ricklefs 2004), we will perform a multi-scale approach to disentangle the potential effect on species richness of the following environmental drivers:

Climate effect. Climate is a large-scale main predictor of species richness because of its effect on productivity (Cusens et al. 2012). As productivity changes with elevation (Rahbek 2005, McCain 2009), we will consider the effect of *precipitation* and *temperature* on bird and bat species richness. We assume here that increasing precipitations and decreasing temperatures will attenuate the pervasive effects of Mediterranean summer drought on productivity and will increase bird and bat species richness along the elevation gradient (McCain 2009).

Landscape structure. The occurrence of species within a given sampling point is a scale-dependent process strongly related to the surrounding landscape (Seoane et al. 2004). To account for this potential effect, we will assess *tree* and *farmland cover* around the study sites. As in the following set of variables, we assume that habitat diversification related to tree cover will increase richness while habitat simplification related to intensive farming will reduce the number of bird and bat species.

Fine-grained habitat traits. It has been suggested that habitat structure may have a strong effect on bat and bird species richness (Bradbury et al. 2005, Jung et al. 2012, Charbonnier et al. 2016, Renner et al. 2018). As flight allows birds and bats to freely exploit a three-dimensional space, it can be suggested that increasingly complex *habitat structure* will allow more species to occur in a given point. It can be also suggested that *plant richness* is usually related to a higher richness of primary consumers (invertebrates) that will increase in turn species richness of insectivorous birds and bats.

Material and methods

Study area

The Guadarrama Mountains are located in the Iberian Peninsula (Fig. 1) and range from around 550 m a.s.l. in the piedmont to 2428 m a.s.l. at the highest peak of Mount Peñalara (40.85°N -3.96°W). Along the elevation range, the area is covered by a succession of vegetation belts from dry and hot lowlands to rainy, cold highlands. Cereal fields, grasslands, and sclerophyllous trees and shrubs (*Quercus ilex*, *Cistus ladanifer*) occur in the piedmont (under 1000 m). Scrublands (*Cistus laurifolius*) and less drought-tolerant wooded pasturelands (*Quercus pyrenaica*) and mowing meadows covered by ash (*Fraxinus excelsior*) occur at mid elevations. Mountain pasturelands, shrublands (*Juniperus communis*, *Cytisus oromediterraneus*) and Scots pine (*Pinus sylvestris*) forests distribute at the highest elevations (above 1500 m). These mountains are managed for extensive cattle breeding except in the case of pinewoods, which are managed for timber production. Since 2013, the most elevated areas of these mountains (33,960 ha) have been declared a National Park.

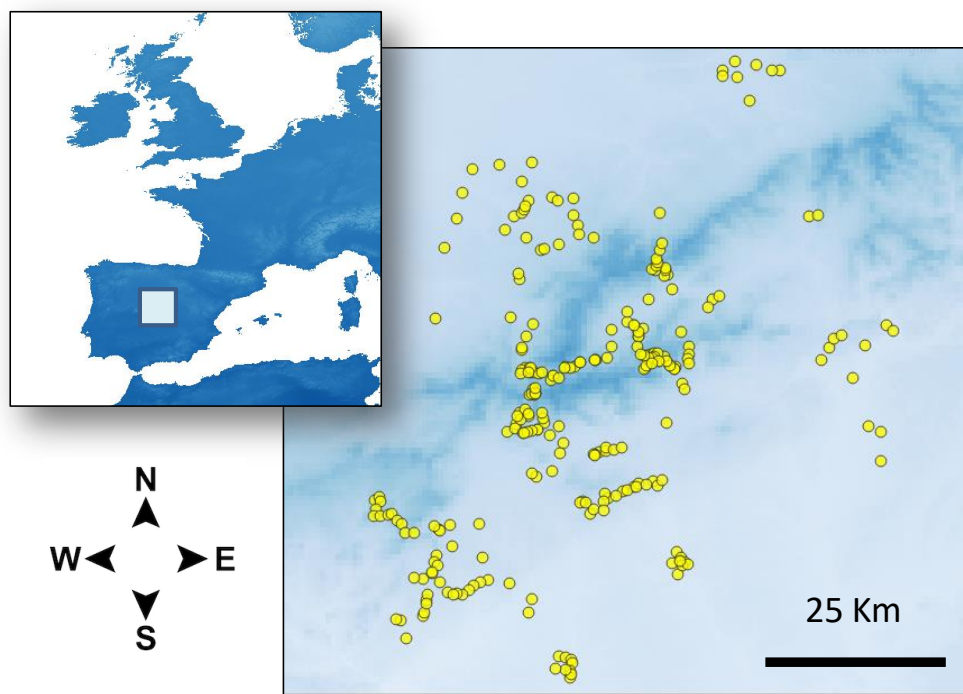


Figure 1. Distribution of the study area within the Western Palearctic and location of the sampling points within the area. Dark area shows the distribution of Guadarrama Mountain.

Bird and bat sampling

During May and June of 2014, 2015, and 2019, we counted birds in 166 circular sampling points distributed among different elevations (550 to 1900 m a.s.l.; Fig. 1) and habitats (we excluded urban areas). The number of species detected per sampling point during 10 minutes within a 100-m radius were recorded in each sampling point. We only considered the presence of passerines (O. Passeriformes) and other bird species (e.g. woodpeckers and doves) usually counted by this method (Bibby et al. 2000). This provides the species density (Lomolino 2001), an index of species richness, free of the effect of sampled area (Gotelli & Colwell 2001). The same sampling protocol was carried out for bats in 99 sampling points recorded during the breeding season (June and July) of 2014 and 2015 (Fig. 1). In this case, as the number of species recorded in 10 minutes sampling periods was small, we repeated the counts three times to increase the number of detected bat species. Since bat activity varies throughout the night (Vaughan et al. 2007), we only sampled this group during three hours after dark. In addition, each sampling point was distributed evenly along these three hours to prevent any systematic effect of sampling time. All sampling points were geo-referenced (latitude and longitude) with GPS devices during field work.

Birds were identified by visual and sound cues by one of the authors (JLT). Bats were recorded by ultrasound bat detectors (Echo Meter 3, Wildlife Acoustics) by the other author (ET). All sequences were recorded as full-spectrum in WAV format and filtered using Kaleidoscope (Wildlife Acoustics, Inc.). The filter settings were specified between 8 and 120 kHz and 2 to 500 ms and each sequence during 5 seconds. We then analysed the WAV files by using Bat-Sound 4 (Pettersson Elektronik AB, Uppsala). The sequences were analysed using a sampling frequency of 44.1 kHz, with 16 bits/ sample and a 512 pt. Power spectrum (Fast Fourier Transform) was analysed with a Hamming window. At least, two bat calls were analysed at random from each sequence. The resulting spectrograms were explored manually after (Rydell et al. 2017) by assessing a set of parameters (call structure, start frequency, end frequency, frequency of maximum energy, duration, and inter-pulse interval) currently used to identify bat species (Russo & Jones 2002, Barataud 2012). It is commonly agreed, however, that spectrograms do not provide enough information to identify some individual species (Rydell et al. 2017). Thus, we ascribed the calls to different sonotypes in the case of *Nyctalus-Eptesicus* and two different groups in *Myotis* and *Plecotus* genera, respectively.

Environmental traits

We assessed habitat structure in 25-m-radius circles around each sampling point. Cover (percentage) of grass, shrub (vegetation <0.5 m and between 0.5 and 2 m height), and tree (vegetation >2 m height) layers were visually assessed. In addition, we counted the number of shrub and tree species over 0.5 m height as an index of *plant richness*. Covers were used to perform a principal component analysis to obtain a latent variable able to describe habitat structure. We selected one component related to an increasing gradient of tree development (PC1, eigenvalue: 1.03; explained variance: 25.86 %; factor loadings, grass layer: -0.329; shrub cover under 0.5m: -0.491; shrub cover 0.5–2 m: 0.010; tree cover >2 m: 0.828). The factor scores of sampling points within this component were used as comprehensive indices of *habitat structure*. This index of plant richness was not correlated at all (r : 0.07).

We recorded landscape structure and climate from two different cartographic data banks. The regional farmland and forest cover were obtained from EarthEnv (<https://www.earthenv.org/>, Tuanmu & Jeyz 2014). Forest cover results were obtained by adding the covers of Deciduous Broadleaf Trees, Evergreen Deciduous Needle-leaf Trees, Evergreen Broadleaf Trees and Mixed Other Trees provided by this databank. We used Chelsa 1.2 (<http://chelsa-climate.org/>, Karger et al. 2017) to download Annual Mean Temperature (Bio1), Mean Temperature of Warmest Quarter (Bio10), Annual Precipitation (Bio12) and Precipitation of Driest Month (Bio17). Because of the high correlation between the two temperatures and precipitations ($r > 0.7$ in both cases), we selected Annual Precipitation (Bio12) as a comprehensive index of water availability and Mean Temperature of Warmest Quarter (Bio10), as an index of summer stress. Despite both indices being correlated ($r=-0.74$, $p<0.001$), we used them because they depict well the hot/dry to cold/moist gradient to Mediterranean mountains (both were related to elevation, temperature r : -0.98, $p<0.001$; precipitation r : 0.78, $p<0.001$). All these cartographic data, provided at a 1 km resolution, were managed with QGIS 3.4.15 (<https://qgis.org/>, QGIS Development Team 2020).

Data analysis

Bird and bat richness were not studied in the same sampling points by logistic problems (bat sampling at night was very difficult in some mountain sectors). Thus, we tested if the environmental setting studied in both cases were the same. To this end, we eliminated

some bird sampling points taken over 1900 m. In this way, the variables considered in this study did not present differences between the bird and bat sampling points (Table 1). After, the study variables were arranged in altitudinal levels (200 m intervals except in the lowest and in the highest that encompassed an elevation range of 300 m) to have a plain comparison of how they distributed within the mountains (Fig. 2).

Table 1. Scores of the explanatory variable recorded in bird and bat sampling points. Results of t-tests to compare the differences are also shown.

	Birds (n:166)	Bats (n:99)	
	Mean \pm SD (min-max)	Mean \pm SD (min-max)	t (P)
Habitat complexity	-0.02 \pm 0.94 (-2.42-2.58)	0.02 \pm 1.08 (-2.65-2.37)	0.353 (0.724)
Plant species (n)	3.62 \pm 1.98 (0.00-10.00)	3.26 \pm 2.05 (0.00-9.00)	-1.415 (0.157)
Forest cover (%)	30.58 \pm 29.76 (0.00-100.00)	33.75 \pm 36.28 (0.00-100.00)	0.772 (0.440)
Farmland cover (%)	34.70 \pm 28.11 (0.00-100.00)	35.61 \pm 29.88 (0.00-100.00)	0.247 (0.804)
Temperature (°C)	21.50 \pm 2.48 (16.30-26.00)	20.92 \pm 2.56 (15.50-26.10)	-1.827 (0.069)
Precipitation (mm)	670.2 \pm 116.0 (442.0-972.0)	692.3 \pm 126.3 (437.0- 963.0)	1.448 (0.148)

Nestedness of bird and bat assemblages were assessed on the two matrixes in which the presence/absence for birds and bats were arranged according to altitude levels (Patterson & Atmar 1986). We estimated nestedness by using the matrix Temperature (T, Ulrich et al. 2009) and Nestedness Overlap and Decreasing Fill (NODF, Rodríguez-Gironés & Santamaría 2006, Almeida-Neto et al. 2008). The significance of these indices was estimated by comparing them with one hundred random rearrangements of the original presence/absence matrix.

Finally, we explored the effect of the explanatory variables on bat and bird richness by controlling the potential effects of spatial autocorrelation (Diniz-Filho et al. 2003). To do this, we used Generalized Least Squares (GLS) models with different spatial correlation structures (Dormann et al. 2007) that were evaluated by the Akaike information criterion (AICc, Burnham & Anderson 2002). These analyses were conducted in R 3.1.2 using the ‘MuMIN’ (Bartoń 2015) and ‘nlme’ (Pinheiro 2009) libraries for the standardized explanatory variables and ‘Vegan’ library (Oksanen et al. 2011) for the nestedness (R Development Core Team 2017).

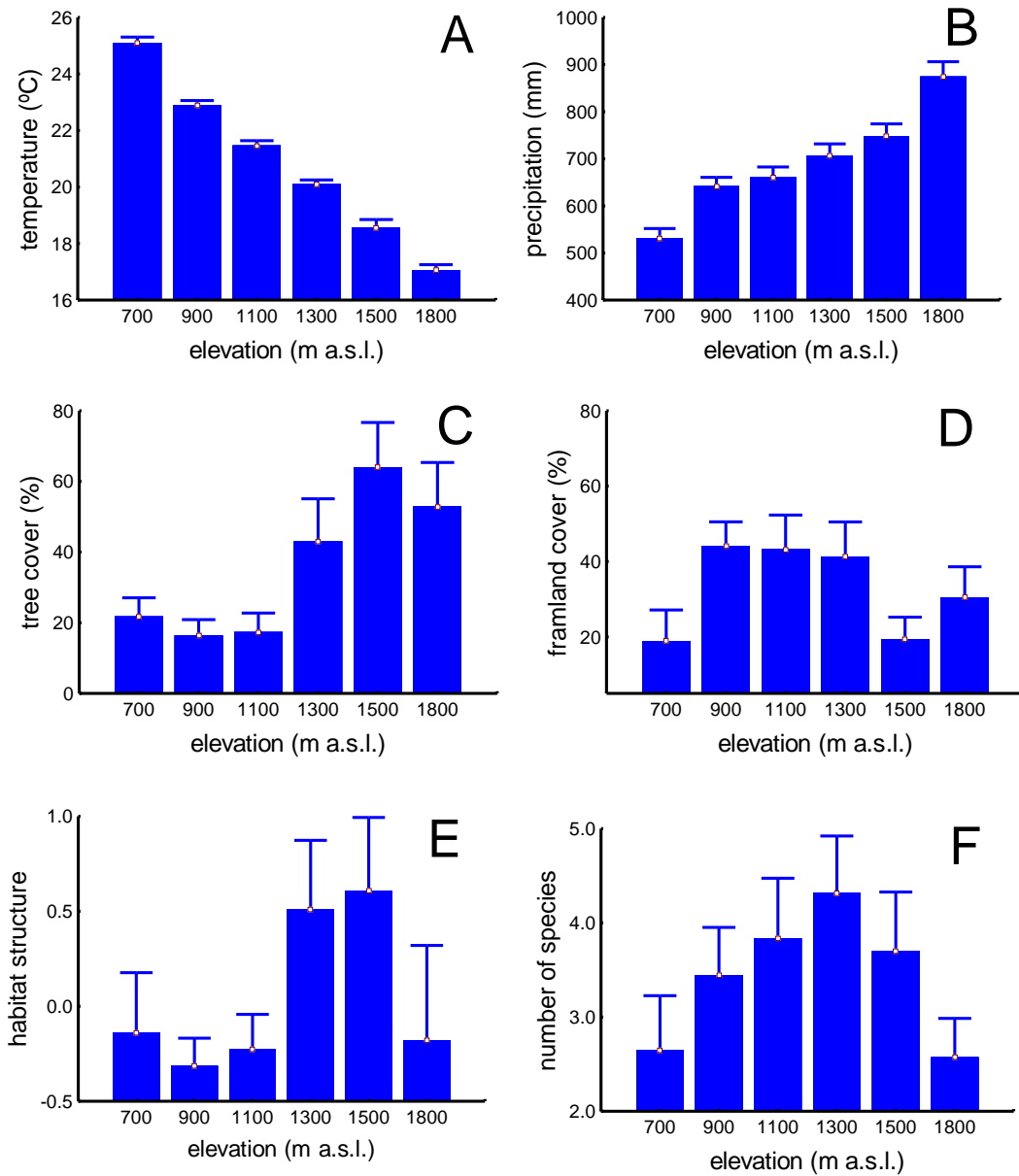


Figure 2. Distribution of temperature (A), precipitation (B), tree cover (C), farmland cover (D), habitat structure (E), and plant richness (F) along the elevation belts of the Guadarrama Mountains. Scores in A show the number of sampling points within belts. Lines show upper part of 95% confidence interval.

Results

We recorded 73 bird species and 11 bat species or different sonotypes (Table 2) within an area that displayed sharp changes in environmental conditions along the elevation gradient (Fig. 2). Precipitation and temperature displayed opposite, monotonic trends with elevation while those variables related to habitat structure and plant diversity displayed the highest scores at mid or elevated mountain levels (Fig. 2). Birds and bats reported different trends in mean species richness along the elevation gradient. Birds displayed the highest mean richness at mid elevations while bats increased monotonically with elevation (Fig. 3). In both cases, the turnover of species along the elevation gradient displayed a nested pattern that differed in some points. Birds displayed the occurrence of more individual species at mid elevations while bats reported more species in lowland areas (Fig 4). In addition, elevation had a stronger effect on bird ($T = 31.33$, $P=0.001$ and $NODF = 64.80$, $P_{r00} = 0.001$; Fig. 4) versus bat distribution ($T = 0.82$, $P=0.005$ and $NODF = 61.25$, $P_{r00} = 0.011$; Fig. 4). Finally, mean species richness was shaped by different environmental drivers in these two groups because bird richness was positively related to fine-grained habitat traits (habitat structure and plant richness) and bat richness was negatively correlated to temperature (Table 3).

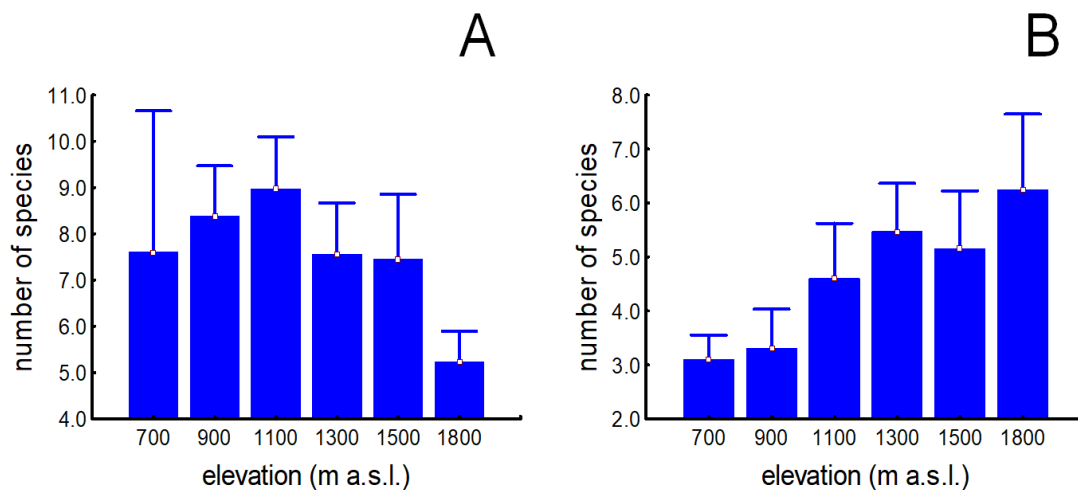


Figure 3. Distribution of mean species densities of birds (A) and bats (B) along the elevation belts of the Guadarrama Mountains. Lines show upper part of 95% confidence interval.

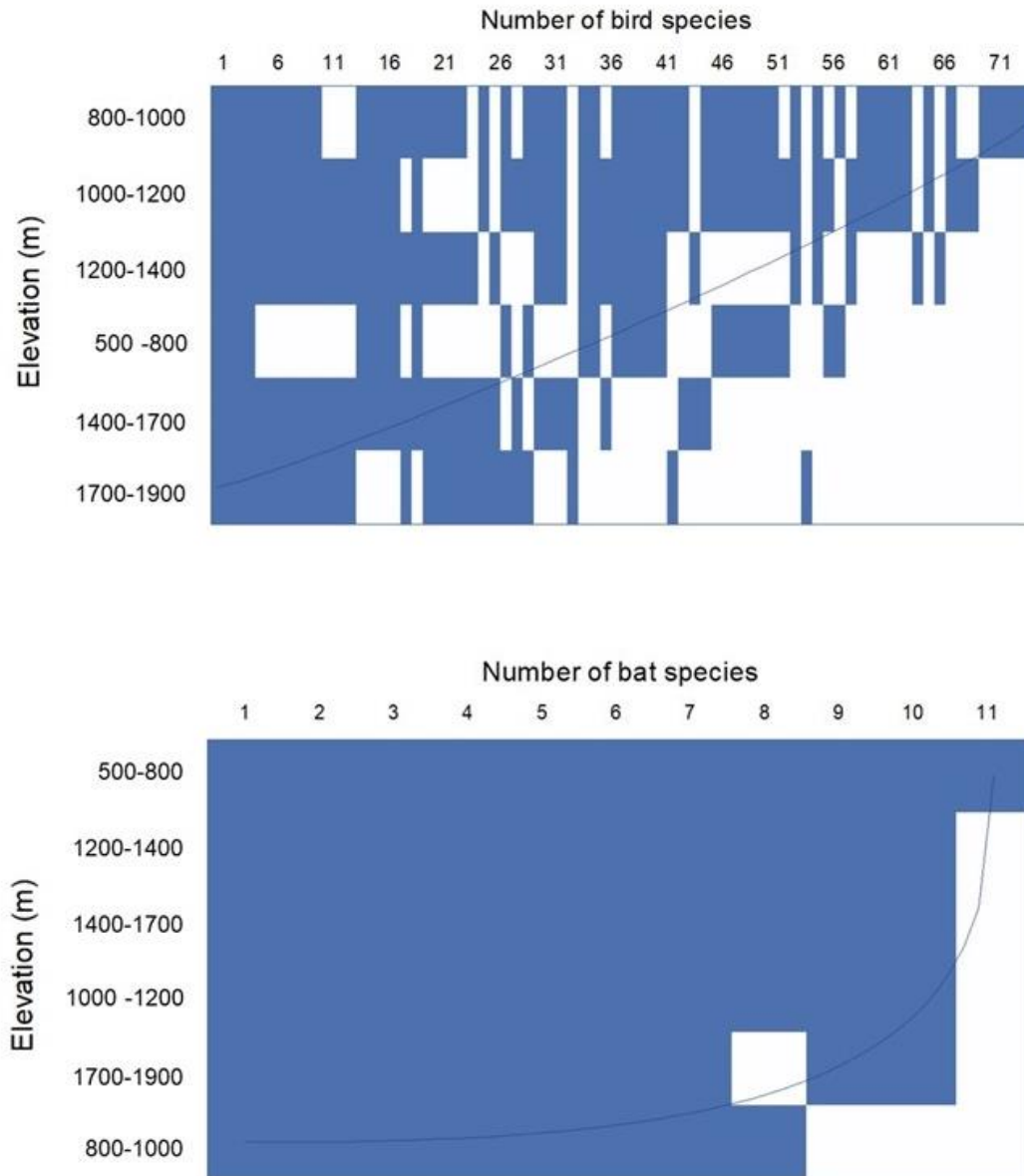


Figure 4. Presence–absence matrices arranged to assess nestedness in bird (above) and bat (below) species distribution along the elevation gradient of the Guadarrama Mountains.

Table 2. List of bird and bat species recorded in the sampling points that have been considered in this study.

Birds
<i>Aegithalos caudatus</i> , <i>Certhia brachydactyla</i> , <i>Columba palumbus</i> , <i>Cyanistes caeruleus</i> , <i>Dendrocopos major</i> , <i>Emberiza cia</i> , <i>Emberiza cirulus</i> , <i>Erithacus rubecula</i> , <i>Ficedula hypoleuca</i> , <i>Fringilla coelebs</i> , <i>Garrulus glandarius</i> , <i>Hippolais polyglotta</i> , <i>Lanius senator</i> , <i>Lophophanes cristatus</i> , <i>Loxia curvirostra</i> , <i>Linaria cannabina</i> , <i>Lullula arborea</i> , <i>Luscinia megarhynchos</i> , <i>Miliaria calandra</i> , <i>Oriolus oriolus</i> , <i>Parus major</i> , <i>Passer domesticus</i> , <i>Periparus ater</i> , <i>Phylloscopus bonelli</i> , <i>Pica pica</i> , <i>Picus sharpey</i> , <i>Prunella modularis</i> , <i>Regulus ignicapillus</i> , <i>Regulus regulus</i> , <i>Serinus citronella</i> , <i>Serinus serinus</i> , <i>Sitta europaea</i> , <i>Streptopelia turtur</i> , <i>Sturnus unicolor</i> , <i>Sylvia atricapilla</i> , <i>Sylvia borin</i> , <i>Sylvia cantillans</i> , <i>Sylvia communis</i> , <i>Sylvia hortensis</i> , <i>Troglodytes troglodytes</i> , <i>Turdus merula</i> , <i>Turdus viscivorus</i> .
Bats
<i>Barbastella barbastellus</i> , <i>Hypsugo savii</i> , <i>Nyctalus/Eptesicus</i> , <i>Myotis sp.</i> , <i>Pipistrellus kuhlii</i> , <i>Pipistrellus pipistrellus</i> , <i>Pipistrellus pygmaeus</i> , <i>Plecotus sp.</i> , <i>Rhinolophus ferrumequinum</i> , <i>Rhinolophus hipposideros</i> , <i>Tadarida teniotis</i> .

Table 3. Results of Generalised Least Squares Mixed models in which the bird and bat species density has been regressed against habitat structure, plant richness, forest and farmland cover, precipitation, and temperature according to different spatial correlation structures. The results show the coefficients ($b \pm se$) and associated t-tests. AICc of different models are also shown. The coefficients of the variables that have a significant effect on bird and bat species richness have been underlined.

Bird species density		Spatial correlation structure			
		Exponential	Spherical	Gaussian	Quadratic
Intercept	$b \pm se$	-5.535±8.523	-1.935±9.111	-5.837±7.899	-5.462±8.358
	t (p)	-0.649(0.517)	-0.212(0.832)	-0.739 (0.461)	-0.646(0.519)
Habitat structure	$b \pm se$	<u>0.710±0.244</u>	<u>0.748±0.241</u>	<u>0.828±0.238</u>	<u>0.769 ± 0.240</u>
	t (p)	<u>2.904(0.004)</u>	<u>3.096 (0.002)</u>	<u>3.502 (<0.001)</u>	<u>3.202(0.001)</u>
Plant richness	$b \pm se$	<u>0.884±0.105</u>	<u>0.892±0.106</u>	<u>0.896±0.103</u>	<u>0.896±0.104</u>
	t (p)	<u>8.374(<0.001)</u>	<u>8.387 (<0.001)</u>	<u>8.696(<0.001)</u>	<u>8.567 (<0.001)</u>
Forest cover	$b \pm se$	-0.014±0.012	-0.015±0.012	-0.013± 0.012	-0.013± 0.012
	t (p)	-1.154 (0.250)	-1.246(0.215)	-1.063(0.289)	-1.136(0.257)
Farmland cover	$b \pm se$	-0.006±0.012	-0.006±0.012	-0.005± 0.011	-0.007±0.011
	t (p)	-0.576 (0.565)	-0.511(0.610)	-0.510(0.611)	-0.560(0.577)
Temperature	$b \pm se$	0.425 ± 0.278	0.306±0.300	0.449±0.255	0.434±0.275
	t (p)	1.526(0.129)	1.022(0.308)	1.760 (0.080)	1.577(0.117)
Precipitation	$b \pm se$	0.002±0.004	0.001±0.004	0.002±0.004	0.002±0.004
	t (p)	0.520(0.604)	0.066(0.947)	0.476 (0.635)	0.407(0.684)
AICc		785.02	786.98	786.03	785.58

Bat species density		Spatial correlation structure			
		Exponential	Spherical	Gaussian	Quadratic
Intercept	b ± se	8.697±5.104	9.013±10.764	8.613±5.063	8.947±5.197
	t (p)	1.724 (0.088)	0.837 (0.404)	1.700 (0.092)	1.721 (0.088)
Habitat structure	b ± se	0.171±0.152	0.139±0.151	0.172±0.152	0.169±0.152
	t (p)	1.118 (0.266)	0.921 (0.359)	1.131 (0.260)	1.112 (0.268)
Plant richness	b ± se	-0.013±0.091	-0.023±0.092	-0.013±0.090	-0.014±0.091
	t (p)	-0.152(0.879)	-0.253(0.800)	-0.144(0.885)	-0.161(0.871)
Forest cover	b ± se	0.012±0.008	0.008±0.009	0.012±0.008	0.012±0.009
	t (p)	1.368 (0.174)	0.958 (0.340)	1.389 (0.168)	1.330 (0.186)
Farmland cover	b ± se	0.006±0.010	0.002±0.010	0.005±0.010	0.005±0.011
	t (p)	0.556 (0.579)	0.275(0.783)	0.543(0.588)	0.527(0.598)
Temperature	b ± se	<u>-0.283± 0.139</u>	<u>-0.250±0.182</u>	<u>-0.278±0.138</u>	<u>-0.285±0.142</u>
	t (p)	<u>2.031(0.045)</u>	<u>1.373(0.173)</u>	<u>2.016(0.046)</u>	<u>2.001(0.004)</u>
Precipitation	b ± se	0.001±0.002	0.000±0.003	0.002±0.003	0.001±0.002
	t (p)	0.645(0.520)	0.234(0.815)	0.688(0.492)	0.595(0.553)
AICc		410.99	411.00	410.81	410.82

Discussion

Bird and bat distribution patterns

Species richness distribution is positively affected by productivity in most environmental settings, with more diverse assemblages in the most productive sectors (Harrison & Grace 2007). In the case of mountain ranges, it has been suggested that species richness decreases monotonically with altitude in humid mountains as productivity is constrained by temperature but not by precipitation. However, species richness shows a unimodal pattern in dry mountains as productivity increases from dry-low to cold-high elevations with the highest scores at mid elevations (Rahbek 2005, McCain 2009). Since the Mediterranean mountains show this last environmental pattern, it could be conjectured that the observed distribution of bird and bat richness adjust to a unimodal pattern with the highest scores at mid elevations. Our results strongly support this pattern in bird richness in the elevation gradient of the Guadarrama Mountains. However, bat richness did not adjust to any of the reported models (monotonic decrease vs. unimodal distribution of species richness, McCain 2009), as it increased monotonically with elevation (Fig. 3).

Bird richness distribution was positively related to increasing habitat complexity and shrub richness (Table 3). Since both variables reach the highest scores at intermediate

elevations (Fig. 2), these relationships explain well the fitting of bird richness to the dry-mountain model (Fig. 3). This interpretation is additionally reinforced by the nested pattern of species distribution along the elevation gradient in which most species occur at mid mountain sectors from where decrease upwards and downwards (Fig. 4). Thus, results in this paper agree with the usually reported positive effect of habitat complexity on bird richness, which has already been reported in the Guadarrama mountains (Diaz 2006, Tellería 2020). The positive relationship between bird and plant richness has been linked to the concomitant diversity of invertebrates on which they rely in spring and a higher assortment of nesting and feeding substrata available to birds (Wiens 1992). Here it is interesting to highlight that, despite the sharp changes along the elevation gradient, neither landscape nor climate traits had a significant effect on bird richness distribution that is usually reported on large scale approaches to the distribution of bird richness (Tellería et al. 2020).

The distribution of bat richness in the Guadarrama mountains displayed a pattern harder to explain. For example, this pattern does not support any significant effect of landscape or fine-grained habitat drivers on bat richness. This is an unexpected result because bats show hunting strategies adapted to different habitat structures (they are classified in open, edge and gleaner species; Schnitzler & Kalko 2001) that could favor the presence of more species in the most diverse habitats (Renner et al. 2018). It has also been suggested that bats avoid the densest vegetation patches that hamper their echolocation calls (Russo et al. 2018). Additionally, it has been reported that bat richness is frequently related to some particular habitat traits within woodlands (Charbonnier et al. 2016, Renner et al. 2018). In fact, these interactions with habitat structure have been specifically tested within woodlands of the Guadarrama mountains (Tena et al. 2020b). However, our results just show a negative relationship with temperature (Table 3). This pattern, which is not easy to interpret according to current models on species richness distribution in mountain ranges (e.g. dry vs. moist mountain models), could be explained by the effect of two alternative processes affecting bat distribution. First, bats are very sensitive to water balance (McCain 2007) so that they could improve body condition moving to cooler areas within the study region. Second, it can be postulated that bats tend to crowd in colder, elevated areas in the search of the most productive feeding fields. This proposal may be supported by the patterns of the Normalized Difference Vegetation Index (NDVI) provided by NASA Earth Observations (NEO) program

(<https://neo.sci.gsfc.nasa.gov/about/>). This index, currently used to estimate primary productivity (Wang et al. 2004, Aubard et al. 2019), shows how the most productive areas in Central Spain tend to accumulate in colder, elevated areas of Central Spain as summer drought increase. Since it is commonly assumed that highly productive sectors could favor the concurrence of many species (Harrison & Grace 2007), it can be conjectured that this could produce the crowding of many bats in these elevated feeding areas.

Bird and bat differences

The simplest conclusion of this study is that bird and bat species richness are not shaped by the same environmental drivers in the Guadarrama Mountains. An obvious explanation of differences is that birds are not bats and vice versa, and that some basic biological differences could produce sharp dissimilarities in the way these groups perceive the environment within the same geographical setting (Lund & Rahbek 2002). From this perspective, we suggest that the reported differences in bird and bat species richness distribution could be related to the way both groups arrange their feeding displacements during the breeding period. The Guadarrama Mountains extend on a small area in which less than 10 km separate the dry piedmont from the most elevated areas (Fig. 1). This means that a flying animal could move within this radius along the elevation gradient in the search of the most suitable food patches. In this context, birds and bats included in this study show very different constraints. Passerines are linked to a small home range around the nest where come and go with invertebrate food throughout the reproductive period making difficult to displace at regional scale looking for food (Odum & Kuenzler 1955). However, bats are able to fly far from their roosting sites during their nightly search of food and go back to breastfeed their young after several hours (Popa-Lisseanu et al. 2009). This would allow many bats to reach each night the highest elevations where meet the most suitable conditions for water balance or feeding. The poorly nested distribution of bat species, where almost all the species are able to occur along the study gradient (Fig. 4) and the high species density in elevated areas seem to support such a free distribution of individual species within the region. However, this study contains a sampling bias when identifying bat species by acoustics (diversity of bat species is lower than in birds) because identification at the species level is not always possible (Russo et al. 2018). On the other hand, it must be taken into account that these results may also vary

over time because the distribution of bats may probably change depending on the productivity of the environment and, consequently, on the food availability (Rydell et al. 1996, Ciechanowski et al. 2007). These must be taken into account for further studies as we agree that these resulting conjectures need to be tested by studying the movements of bats (Kernohan et al. 2001) and that the actual reasons why bats crowd in highlands.

Conclusions

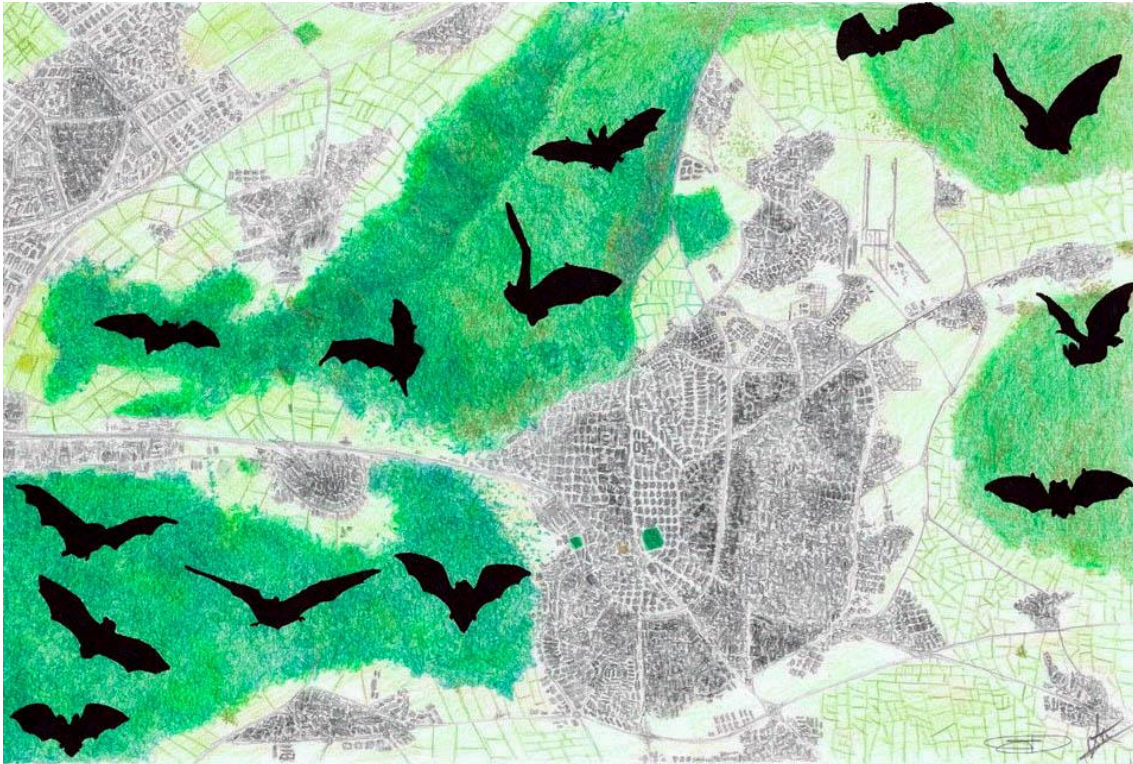
Results in this paper suggest that birds and bats show different patterns of species richness distribution along the elevation gradient of the Guadarrama Mountains during the breeding period. While bird richness was related to local habitat structure (a common pattern in bird assemblages, Wiens 1992), bat richness tracked the regional gradient of temperature, with more species located in the coldest sectors of the mountains. This is an atypical result, as the distribution of bats has been usually related to the internal structure of the occupied habitats (Schnitzler & Kalko 2001, Charbonnier et al. 2016, Renner et al. 2018). An explanation of the observed differences could be related to the contrasting environmental setting of the study mountains where the change of the environmental variables was wider than the displayed in former approaches in which bird and bat distribution was focused on fine-grain differences within forest stands (Renner et al. 2018). However, this particular reaction of bats to climate within the elevation gradient of the Guadarrama Mountains does not exclude at all their ability to track within habitat differences at local scales (Tena et al. 2020a).

Acknowledgements

This paper was supported by Elena Tena's contract from the Council for Culture, Education and Sport in the Autonomous Community of Madrid and European Social Fund. This paper is a contribution to the projects CGL2011-22953/BOS and CGL2017-85637-P of the Spanish Ministry of Economy and Competitiveness. We would like to thank all volunteers who helped us with night surveying for bats, especially to Cristina Gutiérrez del Álamo and Javier Pineda. We are also grateful to Sarah Young for helping in the review of English.

CHAPTER 2

Modelling bat distribution for conservation in a Mediterranean mountain range.



"All models are wrong, but some are useful."

George E. P. Box.

This chapter is based on the manuscript:

Tena, E. & Tellería, J. L. Modelling bat distribution for conservation in a Mediterranean mountain range. *Under revision*.

Modelling bat distribution for conservation in a Mediterranean mountain range

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Abstract

There is a lack of studies dedicated to explore the most important hotspots of richness and rarity for the conservation of bats. Bat activity sectors have been rarely considered in the delimitation of protected areas for bats, which have generally focused to the protection of roosting sites. This has been due to the difficulties of sampling the distribution of these nocturnal animals when moving at night. This methodological constraint has been overcome by the development of bioacoustic sampling, which allows to map the occurrence of active bats over large areas. In this study, we use bat detectors to sample the distribution of bat activity in Central Spain. This region is under the environmental effects of a mountain range (the Guadarrama Mountains) and the urban encroachment of the city of Madrid. In this context, the paper performs a gap analysis to explore whether the most commonly used sectors by active bats are covered by the current network of protected areas. The occurrences provided by the detectors were used to produce species distribution models and the resulting layers were arranged to detect the most suitable sectors for conservation. The results show that the best sectors for bats are located at the piedmont of the mountains and that most of these sectors overlap with the existing network of protected areas. Results also show that the best sectors for bats avoided the most urbanized areas and that, within a similar urban gradient, the protected areas tended to be located in the best sites for conservation. These results suggest that bats benefit today from a network of protected areas initially aimed to protect birds and habitats (Natura 2000). In addition, the paper suggests the potential role of monitoring the activity sectors as a complement to roosting site protection in the conservation of bat assemblages.

Key words: activity sectors, bats (O. Chiroptera), gap analysis, network of protected areas, species distribution models, urban gradient.

Introduction

Bats comprise the second order of mammals in species richness with approximately 1,400 species distributed throughout the planet (Altrigham 2011, Simmons & Cirranello 2020). This taxonomic diversity makes the group an interesting target of conservation, especially because they are increasingly affected by the pervasive effect of habitat loss, pesticides or the alteration of roosting areas (Mickleburgh et al. 2002, Voigt & Kingston 2016). In this context, the location and protection of suitable areas for bats (e.g. both the roosting sites and the foraging sectors) have been considered a suitable approach to their conservation (Russo & Jones 2003, Medellín et al. 2018). The location and protection of bat roosts is a common conservation policy in many countries (EUROBATS 2006) but, unlike other taxonomic groups, easier to detect (e.g. birds, butterflies or plants), there is a lack of cartographic approaches devoted to detect the most important habitats and/or sectors for conservation of bats (Razgour et al. 2016). Since the foraging areas can be located far away from resting sites, it can be assumed that bats will track food resources over large areas (Medellín et al. 2018, Nad'ó et al. 2019) and that this ubiquity will bring the opportunity to map the most used sectors.

The location of activity sectors has been hard to achieve due to the difficulties of detecting active bats at night. But this restriction has been overcome by the improvement of bioacoustic approaches to bat detection (Walters et al. 2012). Bat detectors allow to sample active bats over large areas and to use the resulting occurrences to produce species distribution models (Elith & Leathwick 2009, Razgour et al. 2016). These models provide the occurrence probability of species within the study area, which is reputed as a good indicator of abundance (Tellería et al. 2014, 2016, Weber et al. 2017). In this way, the resulting maps can be used to explore the distribution of the most suitable activity sectors for active bats.

This paper studies bat distribution in Central Spain, an area located within the highly biodiverse Mediterranean region (Myers et al. 2009). The area is crossed by a mountain range (Guadarrama Mountains), which induces an upwards decrease of temperature and increase of precipitation from the surrounding lowlands (Gonzalez-Hidalgo et al. 2016). This climate turnover produces an altitudinal succession of vegetation belts and a concomitant change of animal assemblages (e.g. Ruiz-Labourdette et al. 2012, Flores et

al. 2018). In a context of global change in which the Mediterranean is under the persistent effects of increasing temperature and decreasing precipitation (Giorgi & Lionello 2008), the region is an interesting scenery to assess the potential role of protected areas to conserve these animals in the future. In addition, the region is under the effect of the metropolitan area of Madrid, which has experienced a strong process of urban encroachment (Hewitt & Escobar 2011, Fig. 1). It can be thus conjectured that bat distribution will also be stressed by this process of urban encroachment (Goddard et al. 2010). Therefore, we will focus the study of bat distribution using four complementary approaches: a) we will sample the distribution of bats within the study area to produce species distribution models with Maxent (Phillips & Dudík 2008), b) we will use the occurrence probabilities of the species to detect the best areas for bat conservation (Razgour et al. 2016), c) we will carry out a gap analysis (Scott et al. 1993) to detect if the best areas for bat conservation are included in the regional network of protected areas (Buckman-Sewald et al. 2014, Bosso et al. 2016, Kerbiriou et al. 2018) and finally, d) we will explore if bats avoid the most urbanized sectors (Tena et al. 2020a) and whether the protected areas prevent the potential effects of urban encroachment.

Methods

Study area

The study area is located in Central Spain, in a region of around 10,000 km² divided from NE to SW by the Guadarrama Mountains (Fig. 1). These mountains, which range from 600 to 2400 m a.s.l., are covered by an altitudinal succession of cereal fields, gum rock shrublands (*Cistus ladanifer*) and sclerophyllous Holm oak woodlands (*Quercus ilex*) in the piedmont (under 1000 m) to Scots pine forests (*Pinus sylvestris*) and broom shrublands (*Cytisus oromediterraneus*) in the upper parts of the mountains (above 1400 m). Between 1000 and 1400 m, the vegetation is composed by shrublands dominated by laurel-leaf cistus (*Cistus laurifolius*), Pyrenean oaks (*Quercus pyrenaica*) and ash (*Fraxinus excelsior*) in wet mountain valleys (Tellería 2020). Most of the habitats other than cereal fields are managed as pasturelands for extensive cattle breeding except in the case of pinewoods, which are mainly managed for timber production. Most highlands (over 1700 m a.s.l) of the Guadarrama Mountains were designated a National Park (NP) in 2013 (López & Pardo 2018). The surrounding piedmont has been covered by an extensive network like the buffer areas of the National Park (BNP), natural parks and

reserves and Special Protection Areas for birds, Sites of Community Importance and Special Areas of Conservation resulting from Natura 2000 EU directives (OTHER, Fig. 1). A main part of the regions is densely populated by humans (6.5 million inhabitants, Cincotta et al. 2000) and occupied by a dense network of infrastructures (roads, railways, power lines) and residential areas. As a result, a marked NW-SE gradient is defined between the less urbanized mountain areas and lowland areas intensely occupied by man around the city of Madrid (Fig. 1).

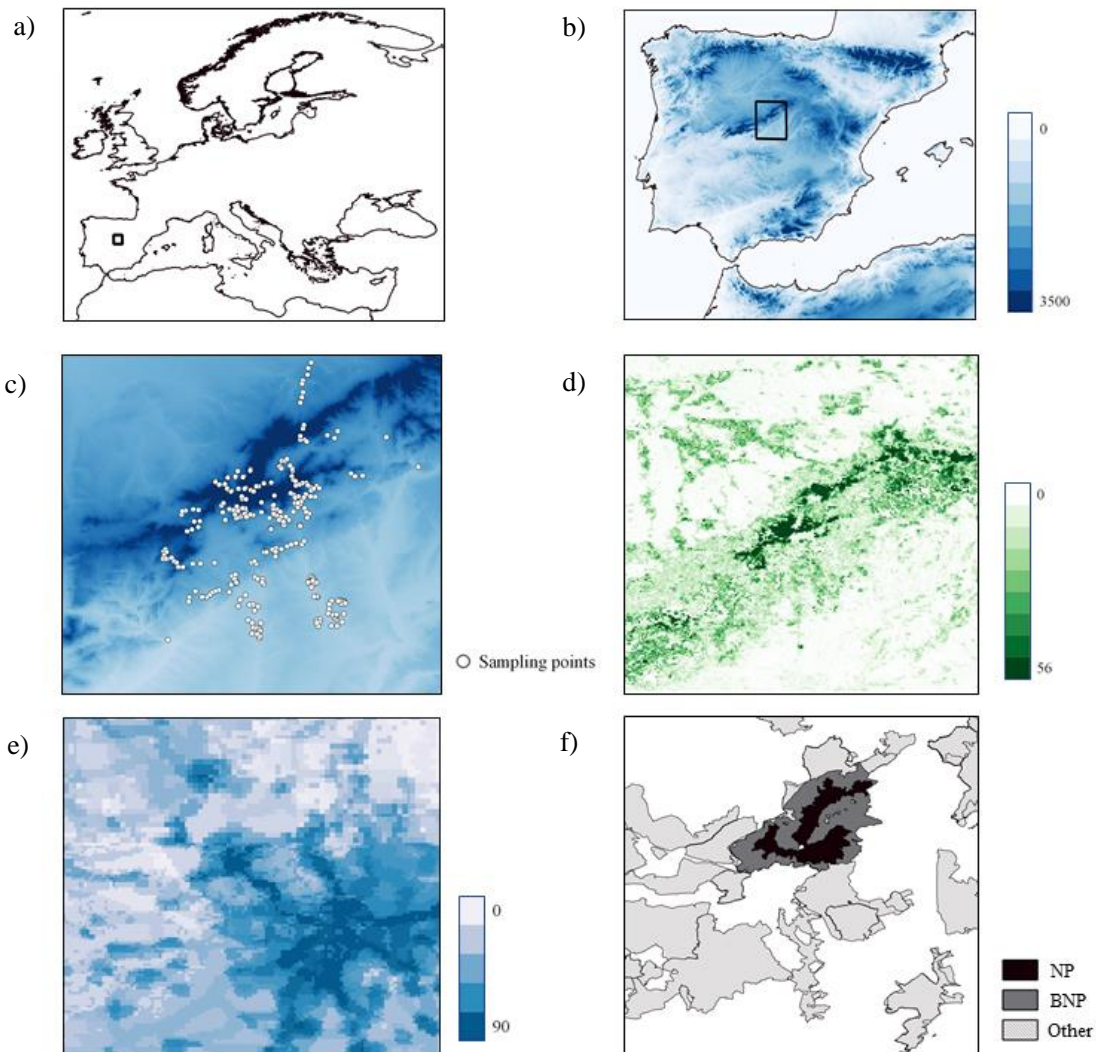


Figure 1. Main traits of the study area: a) map of Europe with the study area marked in a rectangle, b) map of the Iberian Peninsula with an elevation gradient (in hues of blue) and the study area within the rectangle, c) sampling points, d) tree cover, e) human footprint and f) conservation areas inside the study area.

Bat sampling

Bat occurrences were detected by using 274 sampling points distributed within the study gradient during the breeding season (June-August) of the years 2014, 2015 and 2016 (Fig. 1). Bats were recorded by different ultrasound bat detectors (Echo Meter 3, Song Meter 2; Wildlife Acoustics). Bat occurrences resulted from 4 visits (twice in July, and the rest, once per month) for each sampling point carried out within the first 3 hours after the sunset (a period of high bat activity, Barataud 2012). All sequences were recorded as full-spectrum in WAV format and filtered to detect bat calls using the Program Kaleidoscope (Wildlife Acoustics, Inc.). The filter settings were specified to detect any signal between 8 and 120 kHz, from 2 to 500 ms and with a minimum of two calls per sequence. Batch function split each sequence in a maximum duration of 5 seconds. We then analyzed the WAV files by using Bat Sound. The recordings were analyzed using a sampling frequency of 44.1 kHz, with 16 bits/ sample and a 512 pt. Fast Fourier Transform with a Hamming window for analysis. At least, two random echolocation calls were analyzed manually from each sequence to identify the species (Rydell et al. 2017). To do this, we measured the following parameters (Russo & Jones 2002, Barataud 2012): start frequency, end frequency, frequency of maximum energy, duration and inter-pulse interval. It is commonly acknowledged that spectrograms do not give sufficient information to detect individual species (Russo & Jones 2002) so that, in these cases, we ascribed the calls to a group of species (this happens to the genera *Nyctalus*/*Eptesicus* sp., *Myotis* sp. and *Plecotus* sp.). Therefore, we run seven models at the species level and 3 at the genus level. We assumed the presence of one species in a sampling point with just one sequence in any of the visits.

Modeling bat distribution

We recorded climate variables that could affect bat distribution in Chelsa V1.2 for the period 2006-2015 (Karger et al. 2017). Since drought constrains primary productivity (and the concomitant availability of insects) in Mediterranean habitats (Nahal 1981), we selected Mean Temperature of Warmest Quarter (bio 10, TEMP) and Precipitation of Driest Month (PREC, bio14) as two potential drivers of bat distribution. In addition, since bats select three-dimensional landscapes (Dietz & Kiefer 2016), we included bare ground (BARE) and tree (TREE) covers from the Vegetation Continuous Fields MOD44B (as percentages; GlobCover 2.2, Bicherón et al. 2008). Finally, although the elevation is

strongly related to the climate in mountain areas (Pepin & Lundquist 2008), we included this parameter as a complementary indicator of certain meteorological events (as wind, sudden changes in temperature or storms) and as a topographical feature, with a different meaning than climatic variables that can affect bat occurrence. All raster variables were used at a high resolution of 30 arc sec. Cartographic data were managed with QGIS 2.18.11 (QGIS Development Team 2016).

We used Maxent 3.4.1, a machine-learning technique based on the principle of maximum entropy (Phillips et al., 2006) to predict the occurrence probability of species within the study area. We ran Maxent (cloglog output; regularization multiplier $b = 1$; auto-features; convergence threshold = 0.00001, 10000 background points by default) in 10 replicates with 70% of the presences as training data and the rest as test data for internal verification. To explore the importance of each predictor (Table 1), we carried out jack-knife analyses of the regularised gain with training data. The models were evaluated using 10-fold cross-validations measuring the accuracy by means of the area under the receiver operating characteristics curve (AUC, Phillips et al. 2006).

Gap analysis

We averaged the occurrence probabilities of species to map a multi-specific index of habitat suitability for bats (Calabrese et al. 2014). In addition, we calculated an index of rarity ($R = \sum o_i (1/c_i) \{i: c_i \neq 0, 1 \leq i \leq S\}$), where o_i the occurrence probability of the species i , c_i is the number of the 274 sampling points occupied by the species i , and S is the number of bat species within the study area. In this way, the sectors with high occurrence probabilities of rare species will have higher rarity scores (e.g. Williams et al. 1996, Baquero & Tellería 2001). The geographical patterning of the two indices were compared with the distribution of the protected areas reported by the Spanish Government (<https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ENP.aspx>, 2018). The protected areas were classified as National Park (Guadarrama National Park, NP), buffer area of the National Park (BNP), other protected reserved (Other, all of them within the Nature 2000 network) and areas outside the network of protected areas (No protection). To assess the distribution of suitability and rarity indices, we generated 1000 randomly selected points within the study area (985 points were used in the analysis since 15 points with uncompleted data

were discarded). We used analyses of variance (classification factor: protection status) to test for differences in the study indices among protected and unprotected areas. ANOVA analyses were carried out with Rcmdr 3.4.1 (Fox & Bouchet-Valat 2019) and Rcmdr Plug-in NMBU (Liland et al. 2014).

Urban gradient

The potential effect of urbanization on the distribution of suitability and rarity indices were compared with the scores provided by the Human Footprint, an index of population density, human land use and infrastructure (Sanderson et al. 2002). In this way, and by using the 985 random selected points within the study area, we tested whether the study indices were negatively correlated to urban gradients and whether at similarly urbanized areas, the protected areas were located in the most interesting sites (higher suitability and rarity indices) for bat conservation. The statistical analyses (GLM, Poisson distribution and log link) were carried out with Rcmdr 3.4.1 (Fox & Bouchet-Valat 2019) and Rcmdr Plug-in NMBU (Liland et al. 2014).

Results

Modeling bat distribution

We recorded 11 bat species or groups of species (see methods) whose occurrence data were used to produce distribution maps with Maxent (Table 1, Fig. 2). As a rule, all bats reported the highest occurrence probabilities in mid elevations where they decreased according to their particular preferences (see, for instance, *Barbastella barbastella* vs. *Pipistrellus pipistrellus*; Fig. 2). The mean habitat suitability and rarity indices reported a similar pattern with the highest scores in the Guadarrama Mountains and the surrounding piedmont (Fig. 3). Interestingly, both indices were positively correlated (Pearson correlation coefficient, $r = 0.91$, $P < 0.001$, $n: 985$) suggesting that the most suitable sites were also the best ones for the rarest species.

Table 1. Estimates of relative contributions of the environmental variables in models predicting habitat suitability of species. AUC scores show the fitting of models (max values= 1) and the two following values represent the percentage of contribution/ permutation importance of each variable in the model. Percentage of contribution indicates the change in regularized gain by adding the corresponding variable. Permutation importance represents, for each environmental variable in turn, the resulting drop in training AUC when the values of that variable on training presence and background data were randomly permuted, normalized to show percentages. Values are averaged over 10 replicate runs. Symbols in parentheses show the trend of the response curves for the quantitative variables: +, increase; -, decrease; Ω, hump-shaped.

Species	n	ELEV	TEMP	PREC	TREE	BARE	AUC
<i>Barbastella barbastellus</i>	53	35.1/75.6 (+)	1.6/0.0 (Ω)	1.7/2.3 (Ω)	52.1/20.6 (+)	9.6/1.6 (-)	0.916
<i>Hypsugo savii</i>	113	6.5/43.5 (Ω)	25.1/14.6 (+)	8.8/21.5 (+)	56/20.2 (+)	3.6/0.2 (Ω)	0.810
<i>Myotis sp</i>	101	11.7/58.8 (+)	16.1/7.8 (+)	7.2/12.4 (Ω)	47.5/15.9 (+)	17.6/5.1 (Ω)	0.844
<i>Nyctalus/ Eptesicus sp</i>	110	18.8/52.7 (+)	8.0/0.0 (Ω)	7.9/19.5 (Ω)	40.6/10.6 (+)	24.6/17.3 (-)	0.816
<i>Pipistrellus kuhlii</i>	184	12.4/38.9 (+)	22.7/26.1 (+)	18/18.6 (+)	39.1/6.5 (+)	7.8/9.9 (Ω)	0.808
<i>Pipistrellus pipistrellus</i>	274	19.1/53.4 (+)	26.4/27.1 (+)	12.4/11.2 (Ω)	17.9/5.0 (Ω)	26.1/3.3 (+)	0.770
<i>Pipistrellus pygmaeus</i>	197	11.2/46.6 (+)	18.9/25.5 (+)	9.3/6.0 (Ω)	48.8/11 (+)	11.8/10.8 (Ω)	0.826
<i>Plecotus sp</i>	92	18.8/58.7 (+)	7.2/11.5 (+)	10.5/10.8 (Ω)	48.7/9.1 (Ω)	14.7/9.9 (Ω)	0.819
<i>Rhinolophus ferrumequinum</i>	65	0.8/21.6 (Ω)	11.3/0.0 (Ω)	1.6/6.2 (Ω)	49.5/15.1(Ω)	36.8/57.1 (+)	0.833
<i>Rhinolophus hipposideros</i>	10	0.0/0.0 (Ω)	0.0/0.0 (Ω)	17.5/42.7(Ω)	0.0/0.0 (Ω)	82.5/57.3(Ω)	0.623
<i>Tadarida teniotis</i>	104	9.8/62.4 (Ω)	31.9/11.6 (+)	15.2/15.8 (+)	40.7/6.5	2.4/3.6 (Ω)	0.813

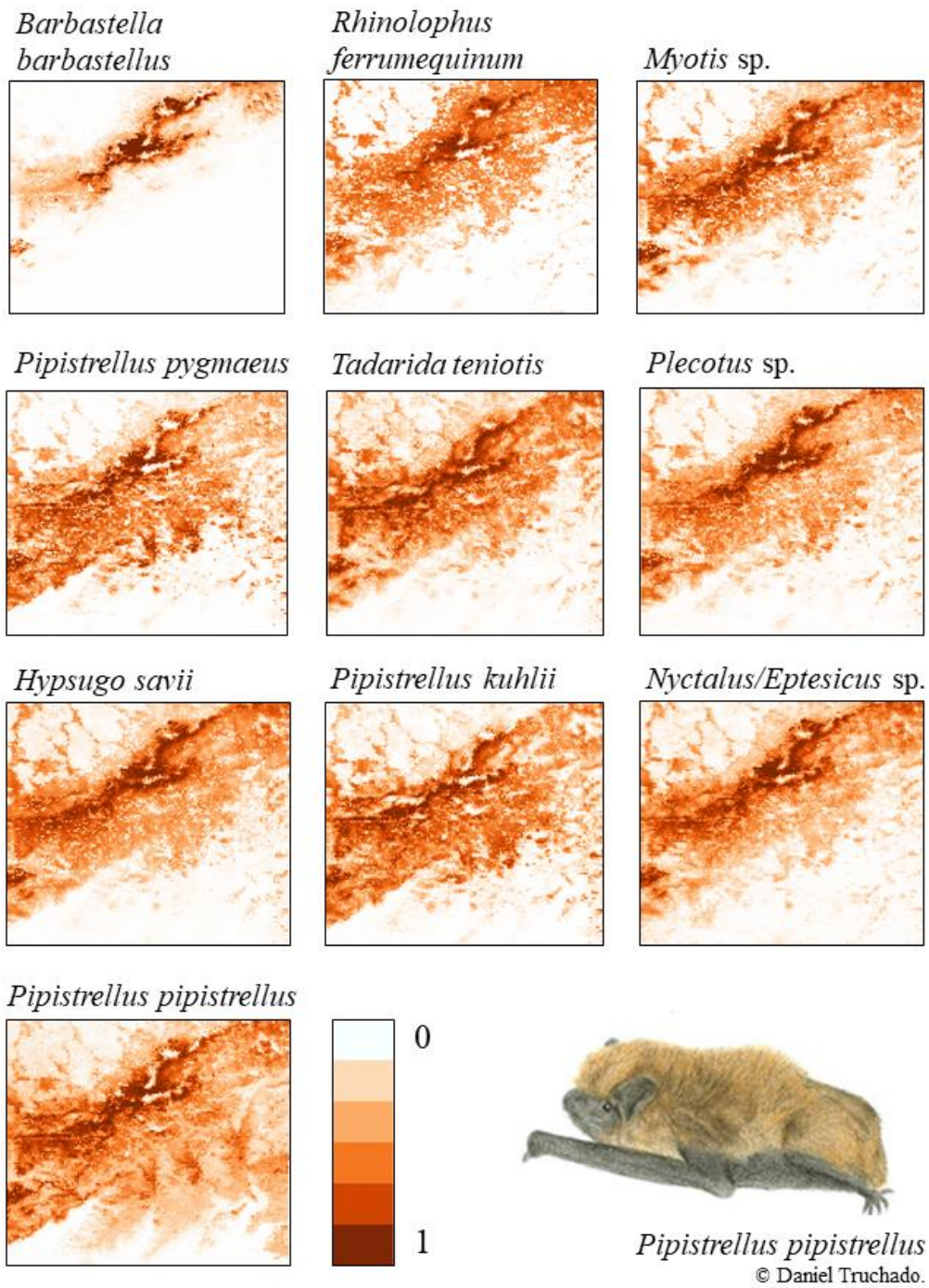


Figure 2. Occurrence probabilities of bat species and groups considered in this study.

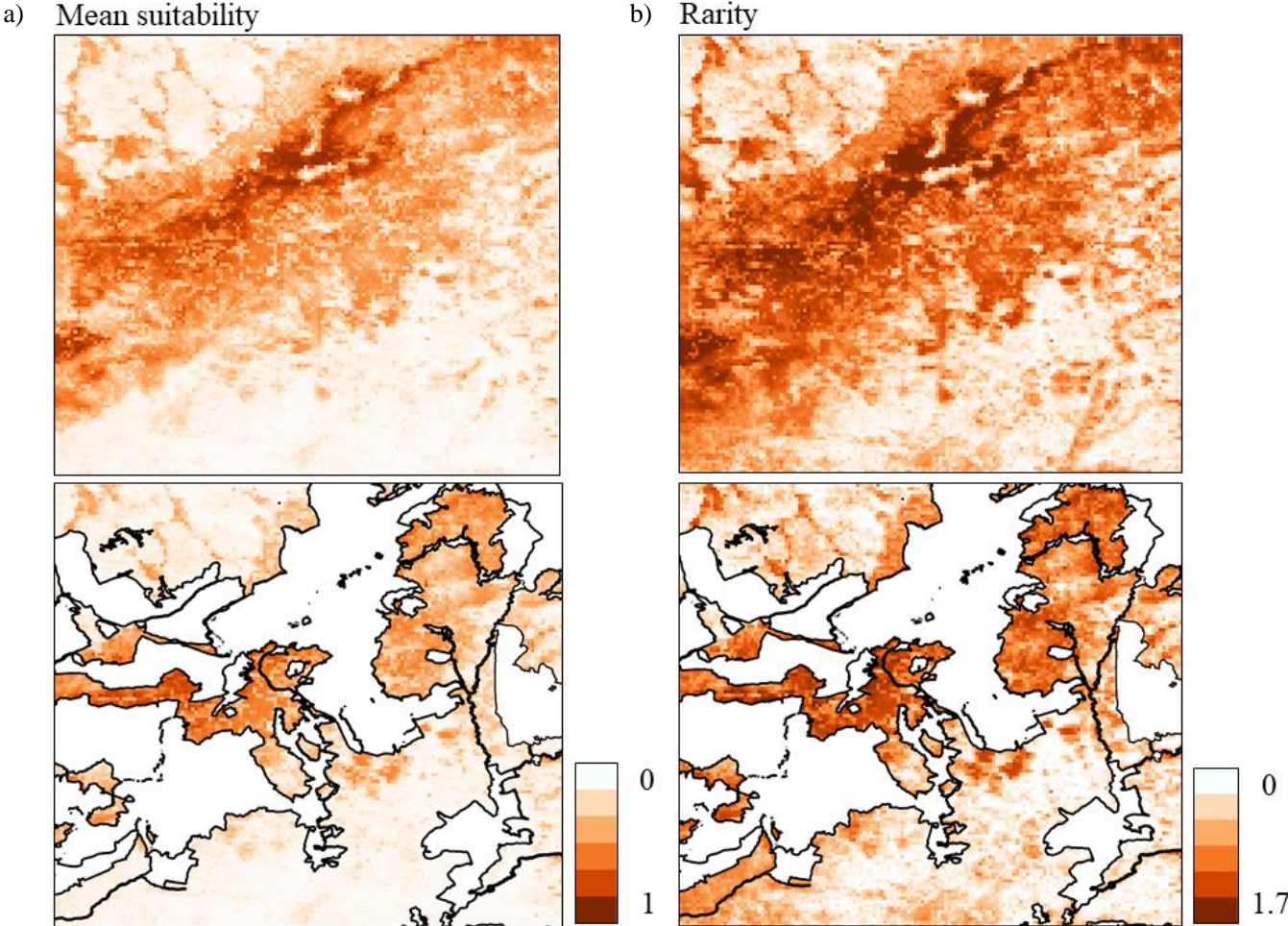


Figure 3. Distribution of (a) mean suitability and (b) rarity indices (above) and overlap by the protected areas in white colour (below).

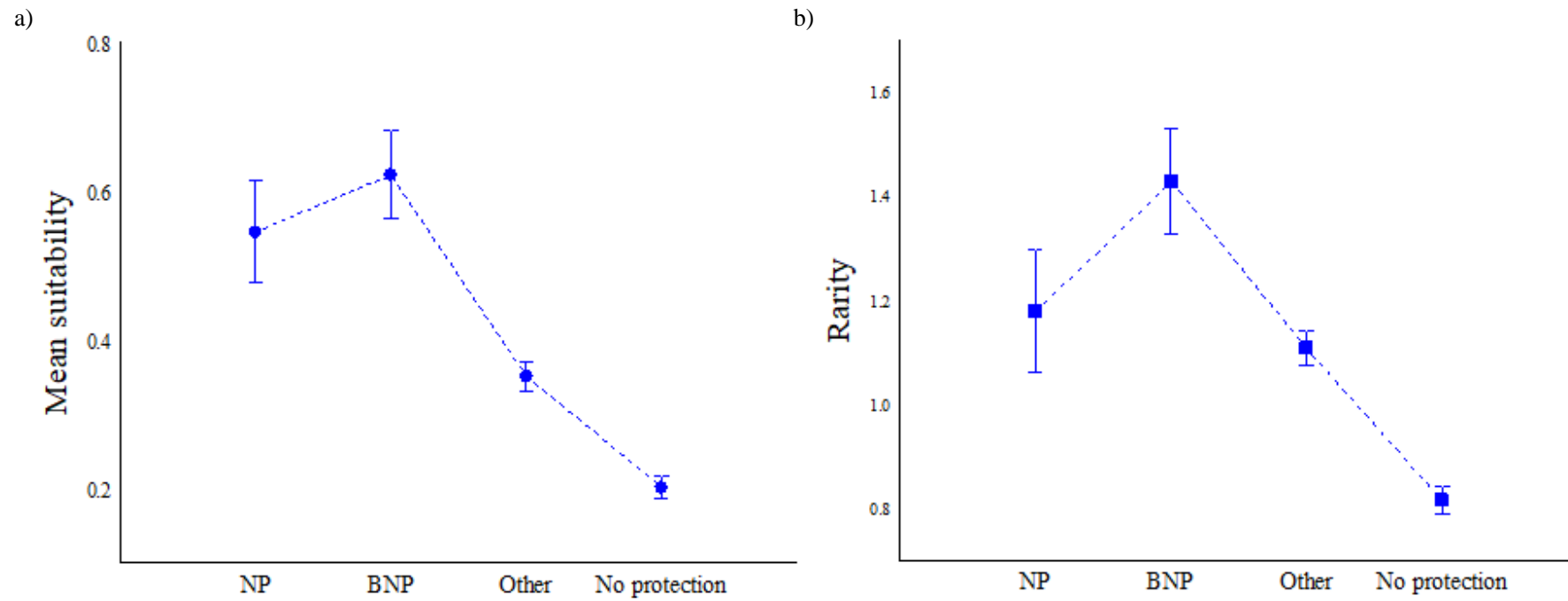


Figure 4. Distribution of (a) mean suitability and (b) rarity indices among protected and non-protected areas (NP, National Park; BNP, Buffer of National Park; Other, other protected areas; No protection, non-protected areas).

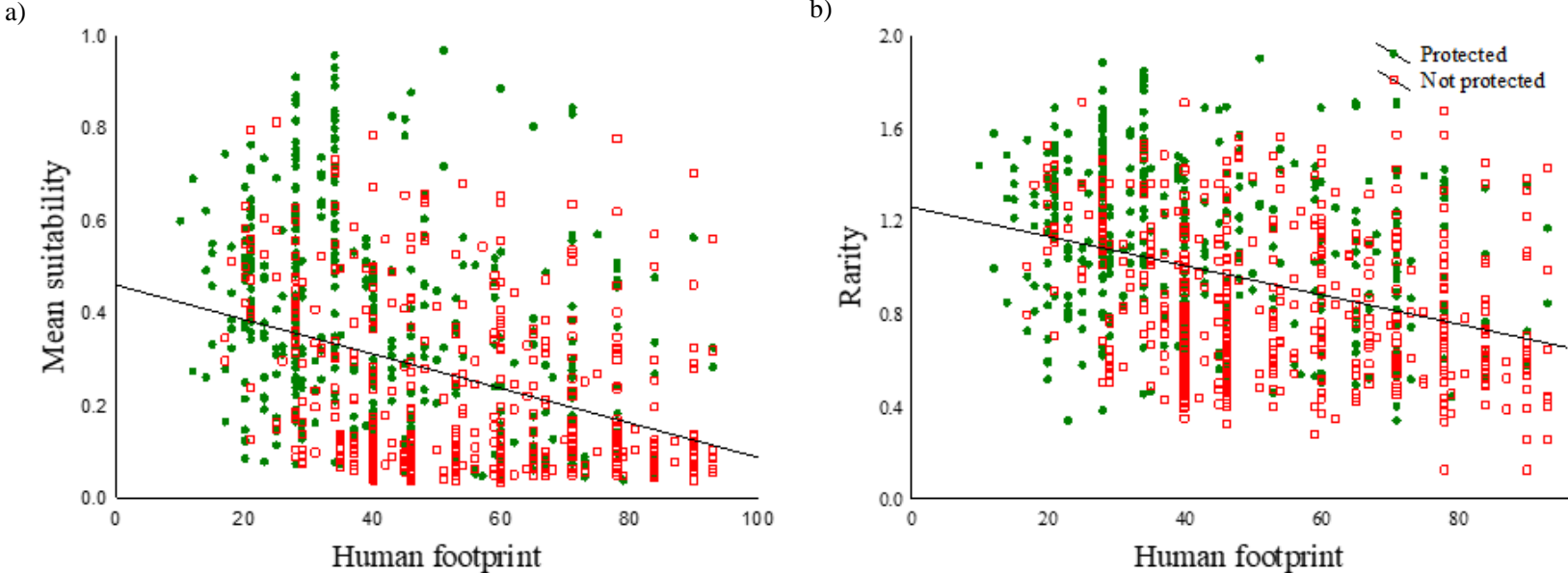


Figure 5. Relationships between human footprint and (a) mean suitability and (b) rarity indices for protected (green circles) and non-protected (red squares) areas.

Gap analysis

The gap analysis reported overlap between the most interesting areas for bats and the network of protected areas (Fig. 3). As a result, the mean scores of the suitability and rarity indices within all the protected areas were significantly higher than the mean scores detected outside the network (suitability index, mean \pm SE, protected: 0.39 ± 0.01 , not protected: 0.20 ± 0.01 , $F_{1,983} = 217.80$, $P < 0.001$; rarity index, protected: 1.14 ± 0.02 , not protected: 0.82 ± 0.02 , $F_{1,983} = 242.44$, $P < 0.001$). There were differences between the Guadarrama National Park (NP) combined with its buffer area (BNP) and the rest (Other) of protected areas (suitability index, NP+BNP: 0.59 ± 0.03 , Other: 0.35 ± 0.01 , $F_{1,430} = 78.14$, $P < 0.001$; rarity index, NP+BNP: 1.32 ± 0.04 , Other: 1.11 ± 0.02 , $F_{1,430} = 24.24$, $P < 0.001$). The highlands protected by the National Park reported similar scores to its buffer area in the suitability index (NP: 0.55 ± 0.04 , BNP: 0.62 ± 0.03 , $F_{1,64} = 1.81$, $P = 0.18$) but reported lower scores in the rarity index (NP: 1.18 ± 0.06 , BNP: 1.43 ± 0.05 , $F_{1,64} = 8.98$, $P = 0.003$). Finally, the National Park also reported higher scores in the mean suitability index than the rest of protected areas (NP: 0.55 ± 0.04 , BNP + Other: 0.38 ± 0.01 , $F_{1,430} = 16.11$, $P < 0.001$) but did not differ in the rarity index NP: 1.18 ± 0.06 , BNP + Other: 1.14 ± 0.02 , $F_{1,430} = 0.39$, $P = 0.530$; Fig. 4).

Urban gradient

Suitability and rarity indices were negatively correlated to the human footprint, supporting a negative effect of infrastructures and urban encroachment on the distribution of the best areas for bats (human footprint vs. suitability index, $r = -0.35$, $P < 0.001$; human footprint vs. rarity index, $r = -0.22$, $P < 0.001$, $n = 985$; Fig. 5). Within this gradient, the protected areas tended to occur in the most suitable sectors for bats (suitability index, human footprint (covariate): $F_{1,981} = 68.47$, $P < 0.001$, protection (factor): $F_{1,981} = 56.04$, $P < 0.001$, human footprint x protection interaction: $F_{1,981} = 8.62$, $P < 0.001$; Fig. 5). A similar trend was detected in the rarity index (human footprint (covariate): $F_{1,981} = 63.57$, $P < 0.001$, protection (factor): $F_{1,981} = 33.47$, $P < 0.001$, human footprint x protection interaction: $F_{1,981} = 0.5975$, $P = 0.440$; Fig. 5).

Discussion

Modeling bat distribution

Despite individual bat species distributing idiosyncratically according to their particular habitat preferences (Dietz & Kiefer 2016), bats seem to report similar trends in European mountain ranges since most of them are particularly frequent at mid-elevations (Jaberg & Guisan 2001, Charbonnier et al. 2016). Results in this study support this view since most bat species show the highest occurrence probabilities at mid elevations of the Guadarrama Mountains, a sector covered by an interspersed distribution of woodlands, scrublands and pasturelands; suitable habitats for a broad range of bat species (Dietz & Kiefer 2016; Fig. 1, 2). The models also suggest that most of species avoid the highest elevations within the mountains, the bare agricultural sectors of the lowlands and the urban sectors distributed around Madrid city (Fig. 1, 2). However, it is interesting to point out that these models also suggest that the reported distribution of bats around the mountains varies per species. For instance, the tree-dwelling Western Barbastelle (*Barbastella barbastellus*) distributes as a mountain species (Russo et al. 2005), with its most suitable sectors in the mature native Scots pinewoods, a northern tree species that in this region reaches its southernmost range edge (Sinclair et al. 1999); the Mediterranean Kuhl's Pipistrelle (*Pipistrellus kuhlii*) shows the most suitable sectors across the Mediterranean dry sclerophyllous woodlands of the piedmont (Sachanowicz et al. 2006) and the potential habitats for the ubiquitous Common Pipistrelle (*Pipistrellus pipistrellus*) expand over most of the region (Davidson-Watts & Jones 2006, Fig. 2).

The distribution pattern of the most suitable sites for bat species in the Guadarrama Mountains is finally replicated in the distribution of mean suitability and rarity indices (Fig. 3). More explicitly, medium elevation ranges in the mountains emerge as the best places for bats according to the study indices. This pattern agrees with the usual distribution of the species richness in dry mountains where productivity, a main driver of species richness (Cusens et al. 2012), increases between dry-low and cold-high elevations (Rahbek 2005, McCain 2009). A similar pattern of increased species richness in medium elevations of the Guadarrama Mountains has already been observed in other taxonomic groups (e.g. ants and birds, Flores et al. 2018) supporting the role of this mountain range as a regional hotspot of biodiversity.

Gap analysis

It is commonly agreed that the network of protected areas is often designed to conserve certain charismatic species or habitats and that it quite frequently ignores the protection of more cryptic or less popular groups (Rodrigues et al. 2004, Chape et al. 2005). This dysfunction has also been reported for different groups of species at the scale of the Iberian Peninsula (Martínez et al. 2006, Araújo et al. 2007, Aragón et al. 2010) and for bats at the scale of the Mediterranean region (Bosso et al. 2016). However, the gap analysis carried out in this study shows that the mean scores of the suitability and rarity indices were higher in the protected areas and that the protected area network in Central Spain overlaps most of the best sectors for bats (Fig. 3). These results support previous approaches in which it has been reported that the network of protected areas in Europe tend to protect the best sectors for some bats species (Kerbiriou et al. 2018). There are, however, some interesting trends at lower scales. For instance, the Guadarrama National Park and its buffer area show higher suitability and rarity indices than the rest of protected areas (Fig. 4). This is a good result in terms of conservation since they are within the highest protection levels of the Spanish legislation (Spanish law; LEY 42/2007, de 13 de diciembre, del Patrimonio Natural y de la Biodiversidad). However, the results also point out some dysfunctions within the protection status and the suitability and rarity indices since the National Park does not protect more suitable sites than its buffer area and shows lower scores in the rarity index (Fig. 4). This can be due to the fact that the National Park was created to preserve the highest mountain elevations (Ley 7/2013, de 25 de junio, de declaración del Parque Nacional de la Sierra de Guadarrama) and these highlands show a low suitability for most bats (Fig. 2). However, mid elevation protected by the buffer area is covered by an interspersed combination of forests, pasturelands, scrublands and small villages where the rarest species in the region thrive (Fernández 2002, Fig. 2).

Urban gradients

Increasing urbanization is usually related to a depletion of biodiversity (Pautasso 2007, Goddard et al. 2010). However, this does not always occur because both biodiversity and human settlements respond positively to increasing levels of primary productivity (Chown et al. 2003). This means that human populated areas occur in sectors of potential high biodiversity while the surrounding wild areas remain as rough unproductive sectors

avoided by human. In this context, it is interesting to note that the best sectors for bats in Central Spain (Fig. 3) are located outside the most urbanized sectors (Fig. 1). This is probably an idiosyncratic trait of the study area where the urban encroachment of Madrid (an administrative city located ad hoc in the geographical centre of Spain) has expanded favoured by a radial road and railway network and not by the effect of climate and agricultural suitability (Dowling 2016). As a result, the far wilderness areas of the Guadarrama Mountains have been hardly affected by urban encroachment. This process is depicted by the negative relationship between conservation interest and urbanization intensity within the study area (Fig. 5). In addition, this trend shows that, regardless the interspersed urbanized vs. bat suitable points, the protected areas tend to be located at the best sectors for bats. This result supports two main ideas. First, that despite the occurrence of bats in urban areas of the study area (Tena et al. 2020a), the group tends to disappear as urban encroachment increases (Avila-Flores & Fenton 2005). Second, it corroborates the view that, at lower spatial scales, the protected areas of Central Spain protect the most adequate activity areas for bats.

Conclusions and conservation prospects

This work shows that the distribution of protected areas in Central Spain overlaps with most of the best sectors for bats as defined by species distribution models. This result is strongly related to some idiosyncratic features of the study area such as the outstanding conservation interest of mean elevations of the Guadarrama mountains and the development of an extensive network of reserves at regional scale. These reserves were originally designed to protect birds (IBAs; Directive 79/409/EEC amended by Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the conservation of wild birds, see Viada 1999) and habitats (Habitat Directives, Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora) and are today included in the Natura 2000 program of the European Union (Evans 2012). After, the reserve network has been reinforced by some national initiatives, as the declaration of the Guadarrama National Park in 2013.

The results of this paper suggest some guidelines for bat conservation in a context of global change. The predictions about climate change in Central Spain suggest a shift upwards of the current vegetation bands (Ruiz-Labourdette et al. 2012), a common

prediction for mountains (La Sorte & Jetz 2010). In fact, this has already been detected in invertebrates of the Guadarrama Mountains during last decades (e.g. butterflies; Wilson et al. 2005, 2007). These trends in the distribution of woodlands and some potential prey species could affect the distribution of their most suitable foraging sectors for bats, which could expand to the highest elevations and could retreat in the piedmont. These trends could also be affected by the ongoing process of forest regeneration and shrub expansion typical of Central Spain and other Mediterranean areas (Kuemmerle et al. 2016, Morales-Molino et al. 2017), which have benefited from the populations of other forest species (e.g. birds, Tellería 2019) but can finally suffocate species richness by the pervasive effect of extreme shrub encroachment and tree densification (Regos et al. 2016, Tena et al. under revision). However, since all these potential changes will occur within a protected area network, it seems important to carry out specific approaches to anticipate and mitigate the potential effects of changes on bat assemblages. Unfortunately, this reserve network has not had effective monitoring of bat populations and their habitats. A group poorly known yet at regional (Paz et al. 2015) and global scale (Mickleburgh et al. 2002) that continue to be relatively invisible to the law makers, conservationists and managers.

Finally, it is interesting to comment the utility and limitations of bioacoustic sampling as a way to generate data to model bat distribution without the use of sometimes skewed information provided by museum and /or bibliographic records (Loiselle et al. 2003, Buckman-Sewald et al. 2014). We consider that the most obvious usefulness of this approach is the quick mapping of bat habitat suitability within the study areas (Rodriguez et al. 2007). And since this information just refers to activity sectors, it seems a promising complementary approach to the location and protection of bat roosts (Medellín et al. 2017). However, more studies are required to advance in the routine application of this methodology for the detection and monitoring of important sectors for bats (Razgour et al. 2011, 2016). For instance, it seems interesting to improve the libraries aimed at determining the bat species that currently still show significant gaps (e.g. *Nyctalus*, *Eptesicus* or *Myotis*; Russo & Jones 2002) and to improve the quality of models by setting sound biological links between the environmental predictors and the targeted bat species and testing the predictive ability of the models (Fois et al. 2018).

Acknowledgements

This paper was supported by Elena Tena's contract from the Council for Culture, Education and Sport in the Autonomous Community of Madrid and European Social Fund. We would like to thank all volunteers who helped us with night surveying for bats, especially to Cristina Gutiérrez del Álamo and Javier Pineda. We are also grateful to Jasper van Heusden for helping in the review of English.

CHAPTER 3

Mind the gap: Effects of canopy clearings on temperate forest bat assemblages.



*¿Eres tú, Guadarrama, viejo amigo,
la sierra gris y blanca,
la sierra de mis tardes madrileñas
que yo veía en el azul pintada?
Por tus barrancos hondos
y por tus cumbres agrias,
mil Guadarramas y mil soles vienen,
cabalgando conmigo, a tus entrañas.*

Antonio Machado.
Camino de Balsaín (Caminos), 1914.

This chapter is based on the manuscript:

Tena, E., Paz, Ó. De, Peña, R. De la, Fandos, G., Redondo, M., & Tellería, J. L. (2020). Mind the gap: Effects of canopy clearings on temperate forest bat assemblages. *Forest Ecology and Management*, 474, 118341.

Mind the gap: Effects of canopy clearings on temperate forest bat assemblages

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Abstract

Gaps in the forest canopy appear to play a major role in local species richness as they increase habitat heterogeneity and border effects. In the case of bats, these small clearings seem to play an important role as foraging and commuting sites. However, further research is required to set the actual role of forest gaps on bat biology in order to consider them as conservation targets in forest management. In this study, we test whether bat species richness and activity are higher in gaps within a large Scot pine (*Pinus sylvestris*) forest than in the adjacent tree covered control sites. We also test these differences in the forest specialists since this group is particularly sensitive to forest management. To investigate this, we used bat detectors in 9 gaps and their adjacent control points during ten nights in July - August 2016 and 2017. The trends resulting from the analysis of 228,108 bat calls support that species richness and activity of bat assemblages were higher in gaps than in the adjacent control points. A similar pattern was detected in the most sensitive tree dwelling bat species. These results stress the importance of gaps as useable areas for the forest bat assemblages and suggest the interest of managing gaps for bat conservation within large areas of continuous tree cover.

Key words: Biodiversity, Chiroptera, forest gaps, forest management, habitat selection, landscape heterogeneity.

Introduction

Forests are among the most diverse biological systems on earth and are also considered important habitats for bats (Lacki et al. 2007). Therefore, it has been set the need to improve management strategies designed to conserve these species in forests, particularly in those exploited for commercial purposes (Tillon et al. 2018). Since bat assemblages are sensible to forest structure and composition, it is commonly agreed that forest management will strongly influence the potential of these habitats to conserve bats (Charbonnier et al. 2016).

Open areas related to the dynamics of forest succession promote habitat heterogeneity and border effects that are usually related to an increase of species richness (Schnitzer & Carson 2001). In this context, tree-less clearings produced by natural or human-induced disturbances (Muscolo et al. 2014) within the matrix of forest canopy (gaps therein) can be very attractive to those bats that exploit the mosaics of open and forest habitat patches (Fukui et al. 2011, Bouvet et al. 2016, Brooks et al. 2017). In fact, some studies have proven greater bat activity in openings and logging decks than in the close canopy of commercial forest (Menzel et al. 2002, Wood et al. 2017). However, the relationships between the bat assemblages and forest structure are very idiosyncratic as they rely on the habitat preferences of the involved species (e.g. tree-dwelling vs. open habitat bats) and the structure of the canopy, including the availability of holes and crevices (Loeb & O'keefe 2006). From this follows that it will be important to assess the actual relationship between gaps and bats before adopting any forest decision-making to protect bats.

In this paper, we compare species richness and activity of bat assemblages between gaps and closed-canopy sites in the Scot pine (*Pinus sylvestris*) forest of Valsaín (Central Spain). This pinewood has been reported as the richest bat hotspot (22 species) of the Iberian Peninsula and therefore, it is an important site for bat conservation in Spain (Paz et al. 2016, 2017). Overall, our hypothesis is that we will detect greater bat species richness and higher bat activity in gaps than in continuous tree canopy stands of the surrounding forest matrix. We also investigate whether the potential increase on species richness and activity is mostly related to the occurrence of bat species typical of open spaces or whether it is also related to an increase of tree dwelling bats. These results can be useful to guide management decisions aimed to conserve this bat hotspot.

Materials and methods

Study area

Valsaín pinewood is located in the northern slope of the Guadarrama Mountains nearby the small village of Valsaín (40.88°N, -4.03°W) and covers around 10,688 hectares distributed between 1100 and 2100 m asl in the northern slope of the Guadarrama Mountains (Fig. 1). The area, under legal protection of the Guadarrama National Park, is mainly covered by Scot pine (*Pinus sylvestris*) intermixed with oak (*Quercus pyrenaica*, *Quercus ilex*) and shrub (*Genista florida*, *Cistus laurifolius*) patches. The forest is covered by a dense pine canopy, managed for wood production where trees are logged selectively. Within the forest there are several small gaps resulting from natural disturbances (fallen trees, wind, snow, lightning, fire, forest pests) or created artificially (by logging, accumulation and loading of tree trunks). Whatever the origin, we randomly selected 9 gaps (Fig. 1) that ranged from 0.13 to 3.07 ha size (mean \pm SD, 0.64 \pm 0.93 ha) and that

had a similar cover of grasses, bushes and forbs (e.g. *Linaria nivea*, *Epilobium lanceolatum*, *Carduus carpetanus* and *Gnaphalium silvaticum*). The study was carried out during two successive years (2016 and 2017) that were differentiated by high (210 mm) and low (110 mm) spring and summer rainfall (January to September) according to the nearby meteorological station of Segovia (<https://www.worldweatheronline.com/>).

Bat sampling

Each studied gap and its adjacent control point were sampled simultaneously with two bat detectors (Song Meter 2 with SMX-U1 ultrasonic microphone, Wildlife Acoustics). The mean (\pm SD) distance between these two bat detectors was 359 ± 70 m (range: 260 - 470 m). To detect bat activity (typically they are more active at sunset), all detectors recorded bat calls throughout the first three hours after sunset during five monthly surveys from July to August. The same sampling points were used in 2016 and 2017 to sample bats within the gaps and the adjacent controls. Bat calls were recorded in WAV format and the noise was filtered using Kaleidoscope (Wildlife Acoustics, Inc.). The filter settings specified a signal of interest between 8 and 120 kHz and 2 to 500 ms and at least 2 calls per sequence. Batch function in Kaleidoscope split each sequence in a maximum duration of 5 seconds. In order to increase the specificity and to reduce false positives, all the files previously filtered with Kaleidoscope were subsequently filtered through the SonoBat Batch Scrubber 5.1 (Méndez-Nogués et al. 2016). The settings included signals from 5- 20 kHz and medium filter (accepts all but poor-quality calls; accepts some noise with tonal content). To identify the individual species, we analysed the WAV files with Bat Sound. The recordings were analysed using a sampling frequency of 44.1 kHz, with 16 bits/ sample and a 512 pt. Power spectrum (Fast Fourier Transform) was analysed with a Hamming window. Finally, echolocation calls were automatically parameterized by

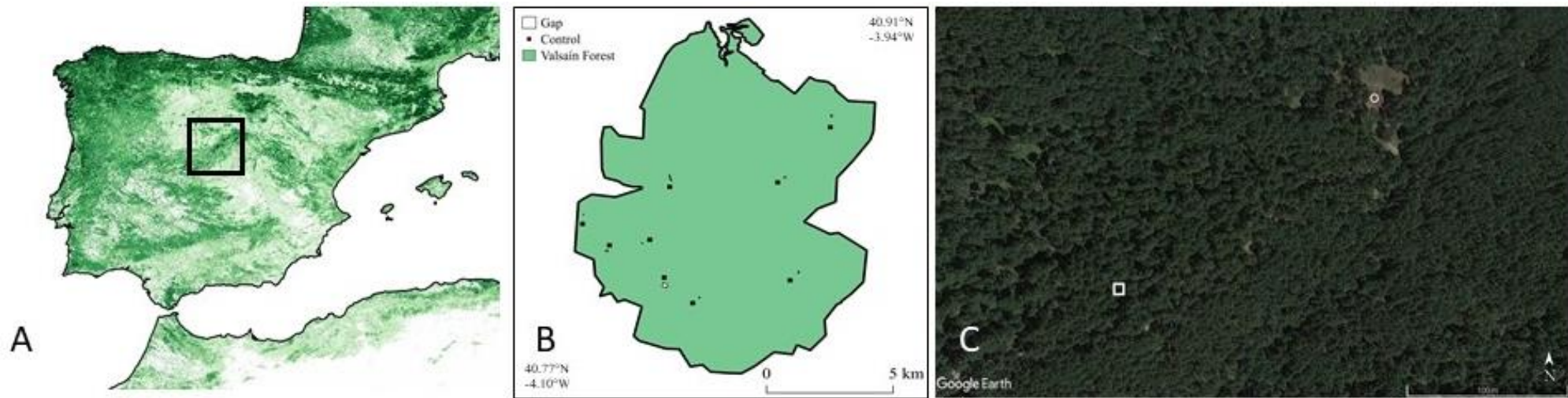


Figure 1. A. Location of the study area. B. Location of the nine study sites of gaps (circles) and each adjacent control forest (squares) in Valsain Forest. C. An example high resolution map of one pair. The gap (circle) and its forest (square) control counterpart.

SonoBat 3.1.2 p and Sonochiro to assist the manual revision for the identification of the species by considering the start and end frequency, frequency of maximum energy, duration and inter-pulse interval (Russo & Jones 2002, Barataud 2015, Rydell et al. 2017). These data were used to assess in each bat detector the cumulative number of species detected during the study period, the total number of calls produced by bat assemblages and the total number of emissions produced by each individual species.

Since it is almost impossible to discriminate some species from their calls (Russo & Jones 2002, Table 1), we carried out a simultaneous sampling with mist nets to identify the species within the study area. As a result, we can assume that the calls of *Plecotus* sp. were of *Plecotus auritus* as this species was the 100% of the captures. However, we were not able to discriminate the *Nyctalus-Eptesicus* and *Myotis* sp. groups as all species were captured several times, especially *Nyctalus* species. Finally, because of the small number of detected *Rhinolophus ferrumequinum* calls, we did not explore the activity trends of this species.

Table 1. Distribution of the mean number of call emissions (\pm SD) by species and results of paired sample t tests to assess inter-year differences in the number of emissions recorded by the eighteen bat detectors. Results of the whole activity of bat assemblages have also been compared. ^Tree-dwelling bat species.

	2016	2017	t	p
	Mean \pm SD	Mean \pm SD		
Species richness	6.48 \pm 1.28	6.28 \pm 1.07	0.673	0.510
Tree dwelling species richness	3.31 \pm 0.81	3.33 \pm 0.49	-0.086	0.932
Bat activity	789.83 \pm 587.88	471.12 \pm 321.06	3.757	<u>0.002</u>
Tree dwelling species activity	134.80 \pm 183.39	94.75 \pm 94.22	1.320	0.204
<i>Barbastella barbastellus</i> [^]	8.42 \pm 8.22	13.50 \pm 27.00	-0.729	0.476
<i>Nyctalus/ Eptesicus</i> [^]	121.02 \pm 183.42	76.68 \pm 87.24	1.532	0.144
<i>Plecotus sp.</i> [^]	5.36 \pm 5.79	4.58 \pm 5.60	0.552	0.588
<i>Myotis sp.</i> [^]	28.13 \pm 22.49	12.51 \pm 9.68	3.193	<u>0.005</u>
<i>Pipistrellus pipistrellus</i>	579.89 \pm 517.27	324.15 \pm 255.39	3.248	<u>0.005</u>
<i>Pipistrellus pygmaeus</i>	26.61 \pm 29.57	6.12 \pm 9.15	3.175	<u>0.006</u>
<i>Pipistrellus kuhlii</i>	10.66 \pm 20.59	9.24 \pm 30.29	0.242	0.812
<i>Hypsugo savii</i>	8.67 \pm 19.53	23.04 \pm 54.59	-1.692	0.109
<i>Rhinolophus ferrumequinum</i>	1.07 \pm 1.99	1.30 \pm 2.55	-0.303	0.766

Data analysis

We analysed the species richness, the tree dwelling species richness (*B. barbastellus*, *Nyctalus/Eptesicus*, *Plecotus* sp. and *Myotis* sp.), the total bat activity, the tree dwelling species activity, and the individual species/ group of species activity recorded by the eighteen bat detectors for gaps and control points between 2016 and 2017. First, we used paired sample t-tests to assess inter-year differences in bat activity between 2016 and 2017. After, we used Generalized Linear Mixed-Effects Models (GLMM, Poisson/Gaussian distribution and log/identity link according to the cases; Bolker et al. 2009) to see if species richness, tree dwelling species richness, bat activity, tree dwelling species activity and the activity of individual species were higher in gaps than in tree covered control points. The analyses were first performed with the 2016 and 2017 data separately to test if the depicted trends repeated between years. In this case, the site was considered as a random factor. In a second round, we studied together the two years to test for differences between gap and tree-covered control sites using sites and years as random factors. In all cases, the resulting models were compared to the null model by Akaike's information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002). GLMM analyses were conducted with 'lme4' (Bates et al. 2014) package in R (R Core Team 2017, version 3.4.1).

Results

We recorded 228,108 bat echolocation calls in the eighteen sampling points (gaps and the adjacent control sites). The results of the paired sample t-tests did show significant inter-year differences in bat activity and in the activity of some individual species (e.g. *Myotis* sp., *P. pipistrellus* and *P. pygmaeus*). In all cases, the results reported more calls during 2016 (Table 1).

Overall, gaps had higher species richness and more bat activity than the control points in 2016 and 2017 (Table 2, Fig. 2). However, this pattern was not statistically significant for species richness in 2017 and tree dwelling species richness during the two years. However, the activity of the tree dwelling species was significantly higher in gaps during the two study years (Table 2, Fig. 2).

For individual species, gaps show significantly higher activity for *B. barbastellus* (2017), *Nyctalus/Eptesicus* (2016 and 2017), *Plecotus* sp. (2017), *P. pygmaeus* (2016 and 2017), *P. kuhlii* (2016 and 2017) and *H. savii* (2016 and 2017). Analysing the data of both years together, they reflected more clearly the patterns outlined above as the bat richness and activity, the activity of tree dwelling bats and the activities of *B. barbastellus*, *Nyctalus/Eptesicus*, *P. pygmaeus*, *P. kuhlii* and *H. savii* were higher in gaps than in the adjacent tree-covered controls.

Table 2. Results of Generalized Linear Mixed-Effects Models that analysed the effect of gaps vs. control points on bat richness and activity as well as the distribution of forest specialists and individual species in Valsain Forest. The results have been analysed for 2016, 2017 and for the two years together. The table shows the effect of gaps (positive in all cases) with the standard error (SE, in parentheses) and P as well as the AICc scores of each model compared to the null model (in parenthesis).

^Tree-dwelling bat species.

	2016			2017			2016- 2017		
	Gap effect (SE)	P	AICc (null)	Gap effect (SE)	P	AICc (null)	Gap effect (SE)	P	AICc (null)
Species richness	0.235 (± 0.090)	<u>0.009</u>	349.59 (354.38)	0.125 (± 0.090)	0.164	323.99 (324.22)	0.181 (± 0.063)	<u>0.004</u>	670.2 (676.34)
Tree dwelling species richness	0.152 (± 0.125)	0.225	282.16 (282.84)	0.090 (± 0.125)	0.470	264.55(266.19)	0.119 (± 0.063)	0.175	544.56 (544.82)
Bat activity	0.220 (± 0.129)	0.090	148.4 (150.00)	0.214 (± 0.125)	<u>0.010</u>	85.74 (86.79)	0.232 (± 0.076)	<u>0.002</u>	234.85 (239.49)
Tree dwelling species activity	0.795 (± 0.136)	<u><0.001</u>	166.04 (189.04)	0.684 (± 0.117)	<u><0.001</u>	137.93 (161.93)	0.737 (± 0.076)	<u><0.001</u>	295.49 (345.38)
<i>Barbastella barbastellus</i> [^]	0.064 (± 0.109)	0.555	125.08 (129.54)	0.274 (± 0.104)	<u>0.008</u>	78 (18.13)	0.168 (± 0.076)	<u>0.030</u>	239.99 (240.76)
<i>Nyctalus/ Eptesicus</i> [^]	0.977 (± 0.140)	<u><0.001</u>	169.08 (202.48)	0.670 (± 0.104)	<u><0.001</u>	150.54 (169.82)	0.820 (± 0.076)	<u><0.001</u>	307.88 (364.36)
<i>Plecotus</i> sp. [^]	0.058 (± 0.097)	0.550	104.99 (109.68)	0.194 (± 0.104)	<u>0.049</u>	104.79 (105.98)	0.132 (± 0.071)	0.062	205.78 (207.94)
<i>Myotis</i> sp. [^]	0.125 (± 0.131)	0.341	150.64 (154.17)	-0.084 (± 0.104)	0.369	99.88 (104.21)	0.039 (± 0.084)	0.646	258.97 (264.02)
<i>Pipistrellus pipistrellus</i>	0.030 (± 0.143)	0.832	166.3 (170.54)	0.046 (± 0.106)	0.664	117.03 (121.73)	0.053 (± 0.087)	0.543	276.35 (281.17)
<i>Pipistrellus pygmaeus</i>	0.386 (± 0.149)	<u>0.010</u>	176.13 (178.43)	0.275 (± 0.106)	<u>0.012</u>	123.99 (125)	0.315 (± 0.093)	<u>0.001</u>	301.17 (307.16)
<i>Pipistrellus kuhlii</i>	0.322 (± 0.149)	<u>0.007</u>	140.68 (143.08)	0.291 (± 0.098)	<u>0.003</u>	112.95 (116.28)	0.322 (± 0.077)	<u><0.001</u>	242.24 (253.52)
<i>Hypsugo savii</i>	0.489 (± 0.099)	<u><0.001</u>	112.49 (128.76)	0.302 (± 0.139)	<u>0.030</u>	162.77 (163.06)	0.389 (± 0.086)	<u><0.001</u>	275.47 (289.63)

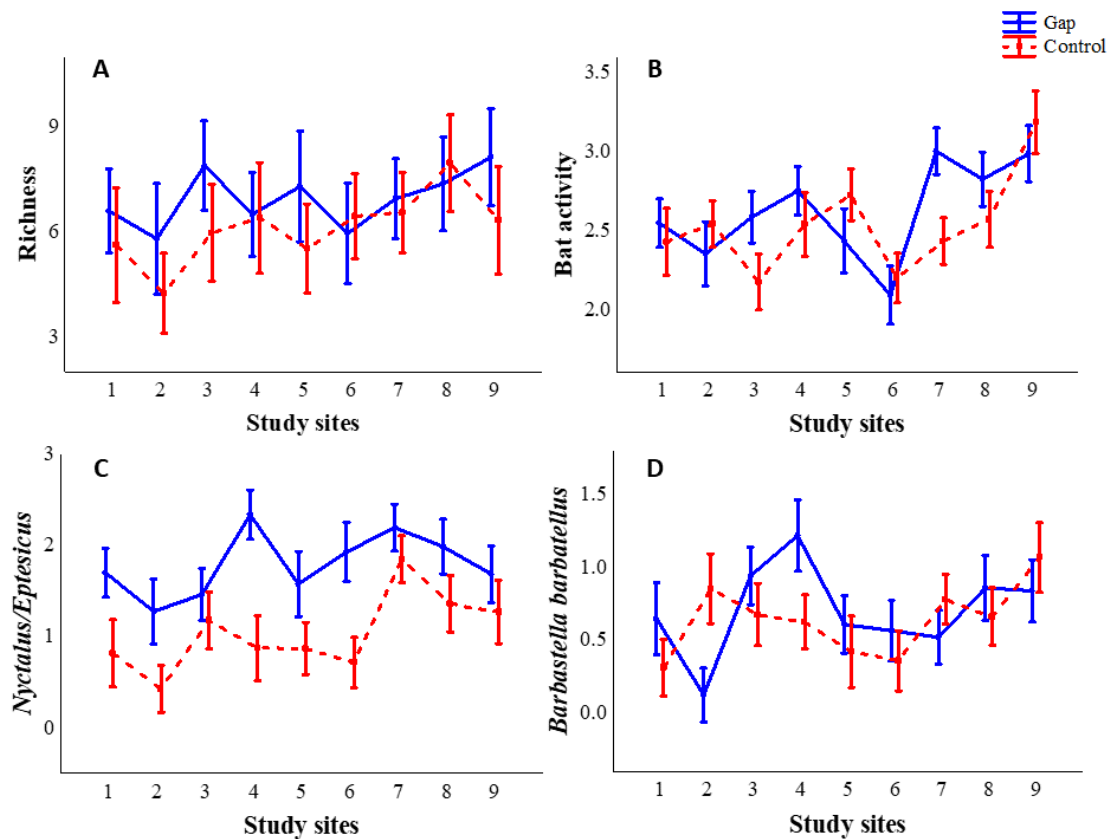


Figure 2. Patterns of bat distribution: comparison between gaps (dark line) and adjacent control forest (dark line) in the nine study sites. The error bars represent the 95 per cent confidence interval. A. Species richness. B. Total activity of bats. C. *Nyctalus/Eptesicus* activity. D. *B. barbatellus* activity.

Discussion

Results of this study show that gaps were used more intensely by bats than adjacent sites covered by trees within the forest matrix, and that they showed similar patterns during the two study years (2016 and 2017) despite inter-year variations in the abundance of bat calls (Table 2, Fig. 2). However, we do not know whether this between-year variation in the number of bat calls reflected an increased use of gaps or, alternatively, reflected a variation in bat abundance. But, considering the potential effect of rainfall on the primary productivity of the Iberian habitats (Alcaraz et al. 2006), it can be conjectured that the observed higher number of calls detected in the rainiest year (2016) could be related to a

regional increase in food (insects) and bat abundance. Unfortunately, our two-year study was not carried out to test these hypotheses as it was specifically designed to validate the inter-annual consistency of the observed patterns in gap use.

The reason why gaps play a vital role on bat distribution within forest can be explained by different processes. For instance, gaps may increase insect availability related to open and border areas and food is a limiting factor for bats (Russo et al. 2004, Zahn et al. 2006). In addition, openings inside the forest canopy favour the occurrence of edge-habitat specialists that may increase bat species richness and abundance (Kusch et al. 2004, Tillon et al. 2016, Brooks et al. 2017). Interestingly, our results suggest that gaps were also selected by forest species so it can be concluded that they positively affected the whole bat assemblage. Thus, it can be assumed that the increase in the complexity of forest structure leads to an increase in diversity and abundance of bats as it has been detected in other animal groups (invertebrates as arthropods; and vertebrates as other mammals, birds, reptiles or amphibians) and plant species (Bazzaz 1975, Tews et al. 2004, Mendes et al. 2017). These traits seem to make gaps and other patchy areas within the forest important foraging habitats for bats and hence important targets for bat conservation (Russo & Jones 2003, Guixé & Camprodon 2018).

Since it is commonly agreed that global deforestation and habitat loss are a major conservation concern (Sala et al. 2000), defending or even promoting gaps within the forest to protect biodiversity could be seen as a counterintuitive conservation guideline. However, it is important to stress that global changes do not only refer to obvious processes of habitat loss and fragmentation, but also refer to subtle within-habitat alterations of habitat structure that may affect biodiversity. For instance, since the mountains are experiencing a process of rural abandonment in many parts of the world, it is expected that increasing forest covers will become a main determinant of changes in

forest biodiversity (e.g. Navarro & Pereira 2015). Interestingly, some palynological sequences of Valsáin pinewoods support a negative effect of tree densification on plant richness during last decades (Morales-Molino et al. 2017) and a similar effect has been reported in bird assemblages (Tellería 2020). In this context, gaps could be viewed as the last clearings within the forest that are used as hunting areas by many bat species. It could be alleged that gap loss or deterioration will only affect those bats typical of open areas arriving from outside the forest, but the gaps used by tree dwelling bats reported in this paper warn us on the negative effect of gap mismanagement on the whole bat assemblage.

Conclusions

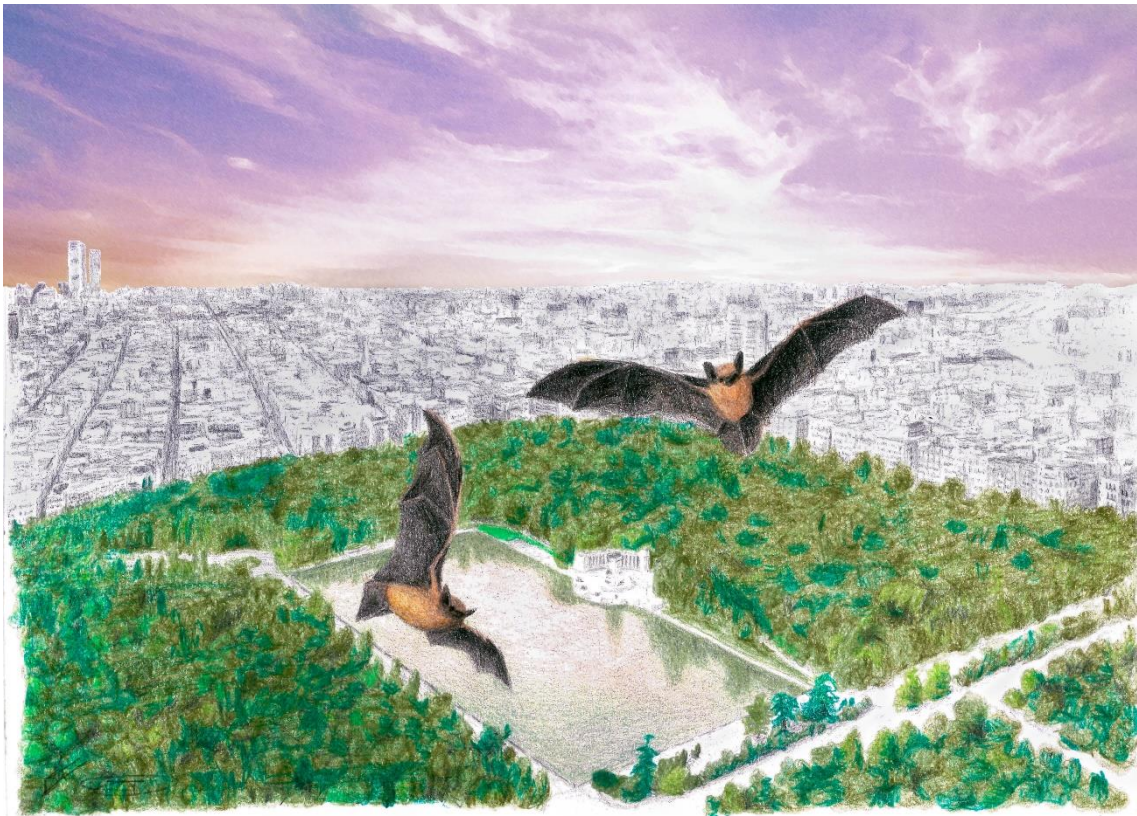
It can be concluded that forest gaps play a vital role in bat conservation since they increase habitat heterogeneity and species richness (Loeb & O’Keefe 2011). However, we consider that further research is required to improve a bat friendly forest management. It might prove interesting to explore, for instance, whether the routinely use of gaps (e.g. log accumulation or machinery movement.) affects their suitability for bats. This will allow some activities to be scheduled to prevent damage to bats. It will also be interesting to investigate the main drivers of gaps used by bats. As it has been suggested in other areas, the use of habitat patches will result from an interaction between some characteristics of gaps (size, shape, vegetation cover, connectivity or prey availability) and species (abundance, habitat selection; Tena et al. 2020a). This assessment will allow us to understand the traits affecting gap use by bats in order to conserve or improve them. In all cases, it can be concluded that any management guideline will require species-centred approaches to the way forest structure affect bats (Betts et al. 2014).

Acknowledgments

This study was supported by Elena Tena's contract from the Council for Culture, Education and Sport in the Autonomous Community of Madrid and European Social Fund. This paper is a contribution to the projects "Trabajos de inventario, distribución e identificación de medidas de conservación de quirópteros en los montes de Valsaín de la provincia de Segovia, en el término municipal del real sitio de san Ildefonso y propiedad del O. A. Parques Nacionales 2016 and 2017". We would like to thank especially to Javier Donés for making it possible. We are also grateful to Jasper van Heusden for helping to review the English and to Octavio Jiménez- Robles for his wise advice. And to the two anonymous reviewers who's comments considerably improved an early version of this manuscript.

CHAPTER 4

Size does matter: Passive sampling in urban parks of a regional bat assemblage.



“Instead of controlling the environment for the benefit of the population, perhaps we should control the population to ensure the survival of our environment.”

David Attenborough.

This chapter is based on the manuscript:

Tena, E., Fandos, G., Paz, Ó. De, Peña, R. De la, & Tellería, J. L. (2020). Size does matter: Passive sampling in urban parks of a regional bat assemblage. *Urban Ecosystems*, 23(2), 227-234.

Size does matter: Passive sampling in urban parks of a regional bat assemblage

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Abstract

We studied the occurrence of bats in urban parks in the city of Madrid (Spain), and the resulting patterns were compared with bat occurrence in the surrounding region. In this way, we addressed if the presence of individual species in the study parks was positively related to their regional occurrence and the way some geographical and environmental traits affected bat richness and composition in urban parks. We analysed urban parks varying in area, structure and distance to the edge of the town. During two years, bats occurring in parks were sampled using ultrasound detectors. A similar sampling method was carried out for four years in the countryside around the city to detect the regional pool of species. The results show that the occurrence of individual species in urban parks was a reduced sample of the regional pool of species and that there was a positive relationship between the occurrence of species in urban parks and the surrounding countryside. This pattern suggests that the more distributed bats at a regional scale were the most frequent ones in parks within the urban matrix. Park area was the main determinant of bat richness. In addition, bat richness distribution reported a nested pattern of species loss as park area decreased. This suggests that bat occurrence in the study parks can be interpreted as the results of a passive sampling of individual species occurring at the regional scale, and that park size was the main determinant of the species occurrence. We conclude that more proactive approaches to bat conservation could be carried out in order to improve the presence of some rare species in urban parks.

Key words: area effect, Chiroptera, habitat fragmentation, habitat selection, nested species distribution, species richness.

Introduction

Urbanization is spreading rapidly at a global scale, a trend that affects biodiversity conservation in many areas. Thus, understanding the effect of urbanization on biodiversity and the way it can be managed is a basic challenge in conservation biology (McKinney 2002). In this context, urban parks are key areas to conserve biodiversity since they are patches of semi-natural habitats where many species thrive within the urban matrix (Baker & Harris 2007). In this respect, and despite bats (Order Chiroptera) being one of the most diverse and distributed mammal orders (Altringham 2011), little attention has been dedicated to explore the way these animals are distributed in urban parks (Gilbert 1989, Jung & Threlfall 2018). The most studied issues have been related to the comparison between rural and urban bat assemblages (Kurta & Teramino 1992, Johnson et al. 2008), the factors influencing bat distribution (Krauel & LeBuhn 2016, Moretto & Francis 2017) or the potential benefits of urbanization for these species (Ancillotto et al. 2016). However, little work has been devoted to assess the main drivers of the structure of bat assemblages occurring in urban parks.

It is commonly agreed that species richness in urban parks is shaped by constraints affecting organisms in fragmented landscapes. These are related to fragmented areas (Avila- Flores & Fenton 2005, Baker & Harris 2007, Garden et al. 2010), distance to the regional pool of species (Krauel & LeBuhn 2016, Jung & Threlfall 2018) or habitat suitability (Schimpp et al. 2018). However, it can be speculated that the relative contribution of these criteria will vary according to the idiosyncratic traits of the species. Bats, for instance, move daily within large home ranges (Nicholls & Racey 2006) so that their occurrence in urban parks will not be regulated by the classical dynamic of colonization vs. extinction typical of terrestrial animal populations distributed within unsuitable habitats (Patterson & Atmar 1986). Alternatively, it can be suggested that bats, wherever the location of their roosting sites, will be able to fly freely among different parks within the urban matrix searching for food. These patterns are congruent with a passive sampling effect, which predicts that the occurrence of individual species in habitat fragments will be a positive function of fragment size and species abundance (Preston 1962, Connor & McCoy 1979, McGuinness 1984). In this context, it can be hypothesized that the occurrence of bats in urban parks will be positively related to the effect of park size (larger parks will sample more species) and the abundance of individual bat species

flying over the study region (e.g. abundant species will occur in more parks than rare ones).

In this paper we look at the use of urban parks by bats in the city of Madrid (Spain, Fig. 1) to address the following issues:

a) First, we test if the occurrence of individual species in the study parks is positively related to their regional occurrence, with the more frequent species occurring in more parks than the rare ones. We assume here that abundance occurrence relationships are commonly positive (Gaston et al. 2010) so that the regional occurrence of the species will be a suitable surrogate of their regional abundance. In addition, we also explore if some species are over or under represented in urban parks in relation to the outlying areas and if these trends can be explained according to their particular biological requirements (e.g. roosting sites, Jung & Threlfall 2018).

b) Second, we explore the factors shaping the species richness of bat assemblages occurring in urban parks. We test the effect on bat richness of some geographical (park area and distance to the edge of the urban matrix) and environmental traits within the parks (e.g. tree cover and floristic diversity, water; Avila- Flores & Fenton 2005). We assume that the largest parks and those parks located near the edge of the town from where many bats may fly within the city will show the highest species richness. These patterns will also be shaped by the positive effect on bat occurrence of tree cover and water availability.

c) Finally, we study if the distribution of bat assemblages shows a nested pattern in urban parks (e.g. Fernandez-Juricic & Jokimäki 2001). This means that bats occurring in parks with low species richness are a subset of those bat assemblages that are progressively richer in species, a pattern that strongly suggests the idiosyncratic reaction of individual species to the features affecting the arrangement of species assemblages (Patterson & Atmar 1986). We also explore if the rank of parks within the nestedness gradient is related to the geographical and environmental variables considered in this study (Ulrich et al. 2009).

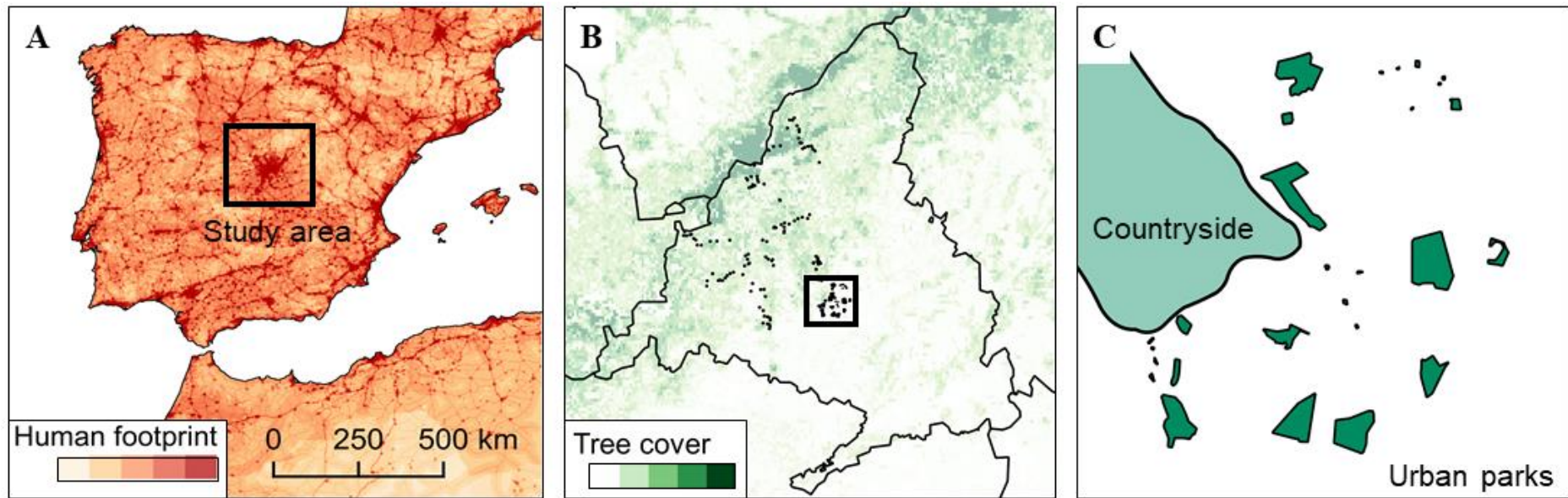


Fig. 1. A. Representation of the study area in the centre of the Iberian Peninsula. Human footprint is shown to represent urbanised areas and highlight the fragmented and altered habitat, and the intensity of the impact of urbanization in the study area. B. Schematic representation of sampling points (shown in black): those in the square represent urban parks; those outside the square represent the sampling points in the countryside. Tree cover is shown to depict the declining abundance of tree-covered areas in the study areas. C. Distribution of the study area within the urban matrix of Madrid. (Q-GIS 2.18.11 and Power Point 2013 were used to create the figure).

Methods

Study area

Madrid and the surrounding urban zones conform a built-up area inhabited by approximately 5 million people. This urban area is located in the piedmont of the Guadarrama mountains, which generates an environment gradient where around 20 bat species occur (Paz et al. 2015). In this context, we explored bat distribution in parks within the urban matrix of the city of Madrid, a large patch (40km² approximately) of buildings and streets within which a small number of parks are scattered. To study bat distribution, we selected 27 parks (Fig. 1) varying in area (0.22-118 ha), distance to the closer edge of the city (0.24-5.6 km) and vegetation structure (Appendix 1). We also considered the presence/absence of water bodies suitable for bat foraging. The area (AREA) and distance to the edge of the city (DISTANCE) was measured using the tool Measure (polygon and line) in Google Earth and vegetation structure was recorded visually in a 25 m radius around the sampling points. These variables included grass, shrub and tree cover (percent of the area covered by < 0.5 m, 0.5- 2 m, > 2 m vegetation layers), number of shrub and tree species, mean tree height and mean trunk thickness (at 1.5 m). With these data, we conducted a principal components analysis in which we retained two component: PC1 (eigenvalue: 2.40, explained variance 30.04%) that we interpreted as a gradient of shrub cover and floristic diversity (FLORISTIC DIVERSITY, factor loadings of grass cover: -0.67, vegetation <0.5 m: -0.56, vegetation 0.5-2 m: 0.70, vegetation >2 m height: -0.17, tree eighth: 0.14, trunk thickness: -0.09, number of shrub species: 0.75 and number of tree species: 0.73) and PC2 (eigenvalue: 2.17, explained variance 27.09%) that we interpreted as a gradient of tree cover (WOOD; factor loadings of grass cover: 0.43, vegetation <0.5 m: -0.03, vegetation 0.5-2 m height: -0.50, vegetation >2 m height: 0.32, tree eighth: 0.92, trunk thickness: 0.86, number of shrub species: -0.19 and number of tree species: 0.08). The factor scores of sampling sites were used to control the effect of vegetation on species richness (Appendix 1).

Bat sampling

We carried out monthly surveys from July to October during 2015 and 2017. Sampling was carried out within the same weather and sound recording conditions (Hayes 2010)

throughout the three hours after sunset to prevent a systematic effect of bat activity (typically they are more active at sunset; Gehrt & Chelsvig 2003, Avila-Flores & Fenton 2005). The order of sampling between sampling points was interleaved between months. Bats were recorded by an Echo Meter 3 (Wildlife Acoustics) bat detector during 10 minutes for every sampling point (Di Salvo et al. 2010, Arias-Aguilar et al. 2015). The sampling points were selected randomly within the polygons of the park areas in QGIS 2.18.11 (<http://www.qgis.org>). The number of sampling points per park ranged from 1 to 8 according to park area, considering the biggest park as the one with 8 due to the difficulties to carry out more sampling stations within the three hours after the sunset (Appendix 1). Species richness (RICHNESS) was assessed by the cumulative number of species detected per park along the study months. occurrence” (Russo & Jones 2003, Jung et al. 2012). The occurrence (OCCURRENCE) was considered as the number of sampling points in which every bat species appeared from the total of sampling points (Russo & Jones 2003, Jung et al. 2012). To obtain the regional structure of bat assemblages around the city, we used the results of 213 randomly selected sampling points carried out in a regional study of bat assemblages around the city of Madrid (Tena et al. under revision). Bats were recorded in a region of 300 km² approximately extended to the piedmont of the Guadarrama mountains from July to October between 2014 and 2017. The sampling points were carried out in the most representative habitats of the region. These habitats are dominated by Holm oak (*Quercus ilex*), Ash (*Fraxinus excelsior*), Pyrenean oak (*Quercus pyrenaica*) and Scot pine (*Pinus sylvestris*) interspersed with scrublands and open spaces. The sampling points were selected randomly in QGIS 2.18.11, 0.24-5.6 km far from villages and small towns. These sites were also surveyed in the same conditions as urban parks, during 10 minutes over the three hours following sunset. Three different bat detectors (Echo Meter 3, Echo Meter Touch Pro 1, Song Meter 2; Wildlife Acoustics) were used to detect bats after a pilot study within urban parks in Madrid reported very similar results (Perea & Tena 2020).

Call analysis

All sequences were recorded as full-spectrum in WAV format. We filtered noise from bat calls using sound analysis software Kaleidoscope (Wildlife Acoustics, Inc.). The filter settings specified a signal of interest between 8 and 120 kHz and 2 to 500 ms and with a

2-minimum number of calls per sequence. We batch split each sequence to a maximum duration of 5 seconds to standardize bat activity for later comparison. Both results were then filtered again by SonoBat Batch Scrubber 5.1 and positive files derived from the two software packages were measured (Méndez-Nogués et al. 2016). We then analysed the WAV files by using BatSound 4 Software. The recordings were analysed using a sampling frequency of 44.1 kHz, with 16 bits/sample and a 512 pt. Fast Fourier Transform with a Hamming window for analysis. At least, two echolocation calls were analysed at random from each sequence. The following parameters were measured manually (Rydell et al. 2017) from each call to identify species (Russo & Jones 2002, Barataud 2012): call structure, start frequency, end frequency, frequency of maximum energy, duration and inter-pulse interval. Some recordings were ignored when the quality of the calls was not clear to avoid misidentifications. Due to the overlap of the values of the acoustic variables of the species of some genera (*Myotis* and *Plecotus*), it has been decided to group the sequences by pairs or groups of species (Vaughan et al. 1997, Russo & Jones 2002). Thus, the species of medium and small size of the genus *Myotis* have been recorded as *Myotis* sp., large *Myotis* such as *M. myotis/blythii* and those of *Plecotus* genera have been recorded as *Plecotus* sp.

Nestedness

Nestedness analysis explores if the loss of species within the presence/absence matrix of study fragments depicts an ordered sequence and provides some metrics to quantify the strength and features of this pattern (Patterson & Atmar 1986). We assessed nestedness among the 27 study parks by using matrix Temperature (T, Ulrich et al. 2009) and Nestedness Overlap and Decreasing Fill (NODF; Rodriguez-Girones & Santamaria 2006, Almeida-Neto et al. 2008). T decreases with nestedness and it is the most commonly used metric for nestedness (Ulrich et al. 2009) and NODF index increases with nestedness (Almeida-Neto et al. 2007). The significance of these indices was estimated by comparison with the results simulated by one hundred randomizations in the original presence/absence matrix. NODF analyses can be used to rank (K) the urban parks and to explore the effect of variables affecting on the nested structure of bat richness (Seoane et al. 2013). Estimates of nestedness were done with the package ‘Vegan’ (Oksanen et al. 2011) in R (R Core Team 2017, version 3.4.1).

Statistical analyses

We tested by simple regressions whether the occurrence of individual species in urban parks was related to their regional occurrence (covariate) and roosting preferences (fissure dwelling bats vs. the rest of bats). Moreover, we used a Wilcoxon Matched Pairs Test to assess whether the occurrence of species in urban parks was higher or lower than in the countryside. In addition, we used general lineal models (GLM) to explore the effect of AREA, DISTANCE, FLORISTIC DIVERSITY and WOOD on the number of bat species (RICHNESS, Poisson distribution and log as function link) and on the nested rank (K, Gaussian distribution and identity link), both in 2015 and 2017. We excluded the presence of water bodies (most of them constrained to the largest parks) after a variance inflation factor (VIF) analysis detected that this explanatory variable was above the recommend threshold of 3 (Zuur et al. 2010). We also used Generalized Linear Mixed-Effects Models (GLMM) with the same variables and YEAR as a random factor to study the conjoint effects of the explanatory variables on RICHNESS and K during the two study years (2015-2017). We conducted a Multi-Model Inference approach to select the best models (we used all top-ranked models summing to 0.95 AICc and that were better than the null model, Anderson & Burnham 2002). In all cases, models were adjusted to normality and heteroscedasticity of the resulting residuals. GLMM analyses and Multi-Model Inference analyses were conducted with ‘lm4’ (Bates et al. 2014) and ‘MuMin’ (Bartoń 2018) R packages, respectively. Analyses were performed in R (R Core Team 2017, version 3.4.1).

Results

Bat assemblage composition

We recorded 11,429 bat echolocation calls in urban parks of Madrid that, after processing, reported seven bat species (*Pipistrellus pipistrellus*, *P. pygmaeus*, *P. kuhlii*, *Tadarida teniotis*, *Eptesicus serotinus*, *Nyctalus leisleri* and *Hypsugo savii*) and some individuals of Genus *Myotis* (other than *M. myotis/blythii*) that we have considered in this paper as one additional species (*Myotis* sp., Table 1). However, several cave and tree-dwelling bats recorded in the region did not occur in urban parks (e.g. *Rhinolophus ferrumequinum*, *R. hipposideros*, *Plecotus* sp., *Barbastella barbastellus*, *N. lasiopterus* and *M. myotis/M.*

blythii). The occurrence of individual species in urban parks was positively related to their occurrence in the region around the city (Simple regression; 2015: $R^2= 0.86$; $P<0.005$, $N= 14$; 2017: $R^2= 0.93$; $P<0.005$, $N=14$; Fig. 2) but was not affected by the selection of roosting sites (2015: $P=0.48$; 2017: $P=0.18$; Fig. 2). This supports the view that the most common species in the countryside were the commonest in urban parks and that the scarce ones were absent from this urban habitat. Finally, the individual species occupying urban parks reported lower occurrence than in similar sample units of the countryside (Wilcoxon Matched Pairs Test for two dependent variables; 2015: $Z = 2.20$, $P=0.03$, $N=8$; 2017: $Z = 2.10$, $P=0.04$, $N=8$). This supports an underuse of urban parks by bats if compared to the countryside.

Table 1. Bat occurrence at urban parks and across the countryside outside the city. The scores show the percentage of sampling sites (n) in which each individual species has been detected. Asterisks refer to multi-specific sets in which individual species differ in roosting sites.

Species	Roosting	Parks-2015 (n=27)	Parks-2017 (n=27)	Regional (n=213)
<i>Pipistrellus pipistrellus</i>	Fissure	1	0.96	1
<i>Pipistrellus pygmaeus</i>	Fissure	0.74	0.85	0.82
<i>Pipistrellus kuhlii</i>	Fissure	0.59	0.70	0.81
<i>Hypsugo savii</i>	Fissure	0.04	0.22	0.39
<i>Tadarida teniotis</i>	Fissure	0.15	0.15	0.28
<i>Eptesicus serotinus</i>	Fissure	0.15	0.11	0.10
<i>Myotis</i> sp*	Fissure/Tree/Cave	0	0.07	0.18
<i>Nyctalus leisleri</i>	Tree	0.04	0.04	0.23
<i>Plecotus</i> sp*	Tree/Cave	0	0	0.30
<i>Myotis myotis/blythii</i>	Cave	0	0	0.16
<i>Barbastella barbastellus</i>	Tree	0	0	0.08
<i>Rhinolophus ferrumequinum</i>	Cave	0	0	0.22
<i>Rhinolophus hipposideros</i>	Cave	0	0	0.06
<i>Nyctalus lasiopterus</i>	Tree	0	0	0.02

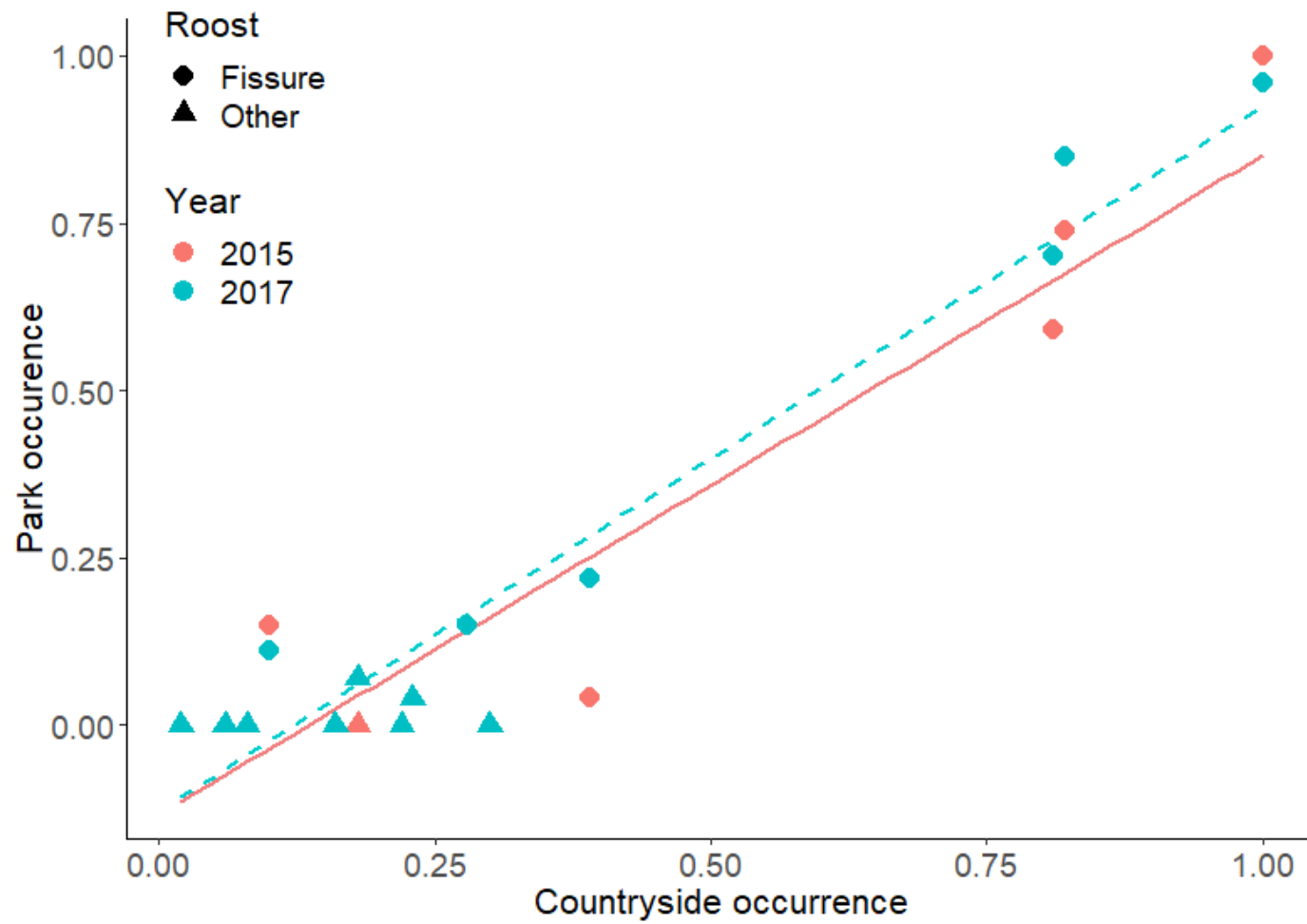


Fig. 2. Relationships between the occurrence of individual species in parks and in the countryside. Trend lines represent the trends in the two study years. The roosting preferences are also shown with different symbols. (R Studio version 3.4.1 was used to create the figure).

Factors affecting species richness and nestedness

According to our Multi-Model Inference approach, AREA was positively correlated to the variation of RICHNESS within the range of the study parks (Table 1). DISTANCE suggested a minor negative effect (the number of species decreases as distance from the parks to the edge of the city increases) and FLORISTIC DIVERSITY and WOOD were the less explanatory variables. These results suggest that bat richness is strongly related to landscape configuration and not to the internal habitat structure of the urban parks.

Species distribution among the urban parks of Madrid presented a significant nested pattern, with the rarest species (e.g. *N. leisleri*) located in the largest park and the most common one (e.g. *P. pipistrellus*) distributed along the whole study gradient. According to nestedness analyses, the bat distribution in parks in 2015 had a significantly ordered loss of species, ($T = 8.26$, $P = 0.001$ and $NODF = 76.91$, $P = 0.001$). In 2017 the distribution had a similar pattern ($T = 9.15$, $P = 0.001$, and $NODF = 65.86$ $P_{r1} = 0.001$). Finally, the two-year distribution matrix also reported a significant nested pattern ($T = 7.12$, $P = 0.001$, and $NODF = 71.12$, $P_{r1} = 0.001$). The nestedness rank (K) of parks was negatively related to AREA in all the models (Table 2). DISTANCE was also positively related to nestedness in some models while FLORISTIC DIVERSITY and WOOD did not correlate with the reported patterns (Table 2).

Table 2. Results of the Multi-Model Inference approach models (top-ranked models summing to 0.95 AICc and better than the null model) to explain which variables determinate the richness and nestedness of bat species in urban parks. All variables have been standardized so that magnitudes of results can be directly comparable. The relative importance of variables is reported by ΣW_i (where n refers to the number of averaged models).

	Richness				Nestedness			
	Estimate (β)	Adjusted SE	p-value	ΣW_i	Estimate (β)	Adjusted SE	p-value	ΣW_i
Average GLM model (2015)	(n=6)				(n=3)			
Intercept	0.87	0.14	< 0.001		0.50	0.03	< 0.001	
Wood	-0.02	0.08	0.79	0.21	0.02	0.04	0.51	0.43
Floristic diversity	0.01	0.06	0.89	0.17	0.00	0.02	0.79	0.15
Distance	-0.15	0.16	0.36	0.61	0.15	0.03	< 0.001	1.00
Area	0.34	0.11	0.001	1.00	-0.21	0.04	< 0.001	1.00
Average GLM model (2017)	(n=7)				(n=5)			
Intercept	1.09	0.12	< 0.001		0.50	0.04	< 0.001	
Wood	-0.00	0.06	0.96	0.20	0.00	0.02	0.98	0.12
Floristic diversity	0.02	0.06	0.80	0.24	0.00	0.02	0.88	0.18
Distance	-0.02	0.07	0.80	0.23	0.01	0.03	0.68	0.28
Area	0.28	0.10	0.005	1.00	-0.19	0.05	< 0.001	1.00
Average GLMM model (2015-2017)	(n=6)				(n=2)			
Intercept	0.99	0.09	< 0.001		0.50	0.07	< 0.001	
Floristic diversity	-0.01	0.05	0.82	0.20	-	-	-	-
Wood	0.01	0.05	0.78	0.22	-	-	-	-
Distance	-0.08	0.10	0.40	0.56	0.09	0.04	0.02	0.91
Area	0.31	0.07	< 0.001	1.00	-0.19	0.03	< 0.001	1.00

Discussion

Bat assemblage composition

It is commonly agreed that bat species are supported by the roosting and foraging opportunities provided by the urban environment (Russo & Ancillotto 2015, Ancillotto et al. 2016, Uhrin et al. 2017). This means that the presence of bats within the urban matrix will be related to some particular ecological requirements of species that will filter their occurrence in urban parks.

According to the reported patterns, it seems that the roosting preferences are correlated with the availability and resources of roost for bats in urban habitats since most bats detected in parks are fissure-dwelling species and neither tree or cave-dwelling bats were detected in the city (except *N. leisleri* or possibly *Myotis* sp. group, Table 1; Jung & Threlfall 2018). This could be related to the lack of suitable caves or abandoned structures, or to the scarcity of suitable crevices in urban trees. However, roosting

preferences are also a main determinant of bat occurrence at regional scale since the most distributed bats are fissure-dwelling species (Table 1). In this context, our analyses have been unable to detect a significant effect of roosting preferences on the distribution of bat species in urban parks after controlling for the effect of their regional occurrence. This means that the regional occurrence of bat species is the only significant correlation of bat presence in urban parks, with the most distributed species being the best represented species in this urban habitat. In addition to this effect, our results show that most of the species in the parks of Madrid show lower occupancies in this habitat than in farmlands and woodlands of the countryside around the city (Table 1, see Paz et al. 2015 for further information on bat fauna in Central Spain). Thus, it can be concluded that a limited set of regional abundant species occur in the urban parks of Madrid and that, when they do, are less frequent than in the countryside surrounding the city (Kurta & Teramino 1992, Avila-Flores & Fenton 2005, Krauel & LeBuhn 2016).

Factors affecting species richness and nestedness

Our results support that the park area was the main determinant of bat species richness. Park area within the urban matrix has already been reported as a main driver of species richness in different taxa, including bat assemblages (Gaisler et al. 1998, Everette et al. 2001, Gehrt & Chelsvig 2003, Avila-Flores & Fenton 2005, Krauel & LeBuhn 2016). This main role of the park area agrees with the early described positive relationships between the number of species and the surveyed area (Preston 1962), an association that has been often referred to as the closest thing to a rule in ecology (Lomolino 1996). These patterns are not similar to the effect of distance to the countryside, wood cover and floristic diversity of the urban parks of Madrid reported a minor effect on bat richness. Despite this, well-vegetated areas have been proven to be the main foraging habitat for insectivorous bats within urban landscapes (Everette et al. 2001, Avila-Flores & Fenton 2005, Parkins & Clark 2015).

In addition, bat richness distribution depicts a nested pattern in which the more abundant species occur in the full range of park sizes while the scarcer ones tend to be increasingly restricted to the largest parks. For instance, the rarest species (*N. leisleri*) has only been detected in the largest park while the most common ones (*P. pipistrellus* and *P. pygmaeus*) were present in almost the full range of park area. As a result, species

assemblages in smaller areas tended to be subsets of the pool of species occurring in larger habitat fragments (Patterson & Atmar 1986).

These patterns are congruent with the passive sampling hypothesis (Connor & McCoy 1979). In this context, processes operating on larger spatial scales (e.g. regional abundance of bats) are likely to be important determinants of species richness within these particular habitat fragments (Gallo et al. 2018). They will decide, for instance, the regional species pool from which local communities can be assembled and will set the individual species distribution and species richness in fragmented habitats (Collins & Glenn 1991, Caley & Schluter 1997).

We agree, however, that there are other subtle factors that can affect the distribution of bats in urban parks which need further research. This is the case of park age, water availability (McCain 2007, in this study highly correlated with large parks), anthropogenic noise, road traffic, light pollution and diversity of prey (Moretto & Francis 2017). For bat surveying, sampling with other methodologies should also be considered to register the complete richness of bat assemblages (Flaquer et al. 2007).

Conclusions

Results in this paper show that park area was the main driver of an ordered occupation of parks by bat species. The study has failed to detect any additional effect of vegetation structure and distribution on bat assemblages but strongly suggests that the urban parks of Madrid are passive receptors of the regional pool of bat species. More explicitly, large parks are just able to sample some individuals of the most abundant bat species at a regional scale. From a conservation perspective, these results suggest that the urban parks of Madrid are not particularly attractive for the regional pool of bat species. To reverse this situation, a proactive approach to bat conservation by improving the attractiveness of these habitats would be required. This may include an increase of park size and roosting sites, diversification of the forest, protection or connection of parks with the existing natural habitat (Moretto & Francis 2017). However, there is still a need for studies of bats in urban parks to improve their conservation and management at a regional scale.

Acknowledgements

This paper was supported by Elena Tena's contract from the Council for Culture, Education and Sport in the Autonomous Community of Madrid and European Social Fund. We would like to thank all volunteers who helped us with night survey bats, especially to Javier Pineda, Cristina Gutiérrez del Álamo, Carmen Soria, Santiago Perea and Carmen Román. We are also grateful to Javier Seoane for helping with the nestedness analysis, to Stewart Finlayson and Tyson Lee Holmes for their support in the review of English and to Octavio Jiménez- Robles for his good advice and wise guidance. And to the two reviewers that considerably improved an early version of this paper.

Appendix 1. Characteristics of the urban parks in Madrid selected for this study. *Straight-line distance to the countryside.

Park name	Area (ha)	Floristic diversity	Wood	Sampling points	Water	Distance* (km)	Total richness
<i>Retiro</i>	118.2	-0.49	0.93	8	1	3.3	7
<i>Parque Oeste</i>	77.9	-0.59	1.54	6	1	0.81	5
<i>Pradolongo</i>	67.51	0.78	-0.12	5	1	3.97	5
<i>Dehesa de la Villa</i>	57.62	2.14	0.92	4	0	2.78	4
<i>Emperatriz de Austria</i>	57.35	0.85	1.45	4	0	4.65	4
<i>Tierno Galván</i>	44.25	1.35	-0.54	3	1	4.86	4
<i>De las Cruces</i>	33.66	1.81	-0.62	2	1	2.58	3
<i>San Isidro</i>	27.87	0.67	0.51	2	1	1.82	3
<i>Cerro Almodóvar</i>	22.94	0.82	-0.91	2	1	1.54	3
<i>Aluche</i>	15.45	0.75	-0.30	1	1	0.96	3
<i>Roma</i>	13.85	0.70	1.09	1	0	5.18	4
<i>Atenas</i>	5.79	-0.38	1.49	1	0	0.53	3
<i>CIU</i>	5.47	-1.61	-0.10	1	1	1.65	4
<i>Berlín</i>	5.04	-0.28	1.17	1	1	5.15	2
<i>Alberto Alcocer</i>	1.54	-0.35	0.38	1	0	5.11	2
<i>Chino</i>	1.04	-0.17	-0.07	1	0	1.18	4
<i>Gasómetro</i>	0.94	-1.00	-0.29	1	0	1.72	3
<i>Sor Angela de la Cruz</i>	0.84	-0.67	-0.55	1	0	4.73	3
<i>Jeringas</i>	0.61	0.82	-0.61	1	0	0.24	3
<i>Peñuelas</i>	0.52	0.03	-0.67	1	0	2.45	3
<i>Infanta de las Mercedes</i>	0.48	0.34	-2.63	1	0	4.31	2
<i>Víctor Andrés Belaunde</i>	0.4	-1.85	-0.45	1	0	5.6	1
<i>Valparaíso</i>	0.33	-0.48	-0.61	1	0	5.45	3
<i>Arcángel</i>	0.26	-1.04	-1.62	1	0	0.46	3
<i>Tirso de Molina</i>	0.23	-1.43	0.90	1	0	1.66	1
<i>Oxford</i>	0.23	-0.34	-0.80	1	0	0.7	4
<i>La Habana</i>	0.22	-0.39	0.53	1	1	4.3	2

GENERAL DISCUSSION

*“The searching human mind is not satisfied merely to discover facts.
We also want to know how things happen and why.”*

Ernst W. Mayr, *What Evolution Is*.

GENERAL DISCUSSION

In this thesis, I carried out an extensive sampling program of bats along an altitudinal gradient and of different fragmented landscapes in the Guadarrama Mountains and the city of Madrid.

Variations along the altitudinal gradient of the study area affected to changes within species richness distribution. Richness is usually correlated with the most productive sectors (Harrison & Grace 2007) and in Mediterranean mountains, the productive sectors are usually located at mid elevations (Rahbek 2005, McCain 2009). Bird richness fitted well to this model, as the mid elevated sectors displayed the more diverse bird assemblages. However, bat richness distribution did not fit to this pattern since it increased monotonically with elevation. Therefore, bird and bat species richness distribution were not shaped by the same environmental drivers in the Guadarrama Mountains. Obviously, birds and bats have biological differences that can explain the differences (Lund & Rahbek 2002). For instance, passerines are linked to their small home ranges around the nest during breeding, while bats can fly long distances from roosts in search for the most attractive foraging areas (Popa-Lisseanu et al. 2009). Therefore, birds are limited at a local scale while bats disperse within different habitats at a regional scale searching for food (Tena et al. 2020a). They showed opposite strategies as dissimilar animal groups which have different requirements.

The high bat species richness detected in high areas of the mountain range was also displayed in the distribution models. It could be explained because bats are very sensitive to water balance (McCain 2007) so that they could move in order to track cooler areas within the elevation gradient and searching the most productive feeding areas, as it was mentioned above. In summer, the most productive areas in Central Spain could tend to occur in colder elevated areas as summer drought increase. Hence, highly productive sectors could favor occurrence of bats species (Harrison & Grace 2007) tracking preys in the most productive areas. From a conservation perspective, mean suitability and rarity indices reported the highest scores in the protected areas, especially at mid and high elevation areas of the Guadarrama Mountains.

The Guadarrama Mountains have a wide network of protected areas designed for biodiversity conservation. However, some less popular or secretive groups (as bats) are

not considered in these conservation approaches (Rodríguez et al. 2004, Chape et al. 2005). The gap analysis carried out in this thesis shows, however, that the mean scores of the suitability and rarity indices were higher in the protected areas than in the rest of the study area. The Guadarrama National Park and its buffer area reported higher suitability and rarity indices than the rest of protected areas. This supports the role of the highest protection levels of the Spanish legislation. However, the buffer area displayed higher rarity index scores than the National Park. This can be explained because this National Park was created to preserve the highest mountain elevations and did not include mid elevations where most species thrive (Fernández 2002).

In addition, the effect of urban encroachment on bat assemblages was also studied in our analyses. Despite the most populated areas are frequently located in sectors of potential high biodiversity (Chown et al. 2003), the human footprint of Madrid and the surrounding urban areas are located mostly in the lowlands areas. Therefore, the human footprint did not overlap with the best sectors for bats and mean suitability and rarity indices sharply decreased in urban areas (Tena et al. 2020a). In conclusion, despite the protected areas not having been delimited to protect bat assemblages (Natura 2000, Evans 2012), most bats are under the coverage of the regional network of reserves and isolated from human impact.

The Guadarrama Mountains are composed of heterogeneous and fragmented landscapes which promote the richness of species. Gaps operate as small patches of herbaceous plants within the large matrix of Scot pine, which end up attracting insects and, consequently, other fauna such as bats. Results in this study show that gaps were used more intensely by bats than the adjacent forest matrix. A similar pattern was detected in the most sensitive tree dwelling bat species. Because all bats in Europe are insectivores, this study suggests that gaps seem to be good foraging areas for them. It has also been seen that gaps generate an edge effect, that delimit a border between the forest and the grassland, an ecotone that bats use as corridors to move and forage between the different landscape patches (Guixé & Camprodon 2018). Obviously, deforestation and habitat loss are a major conservation concern (Sala et al. 2000). However, alterations of current habitat structure may affect biodiversity as well. As rural abandonment is being a process widely spread in the mountains, gaps could represent the last clearings within the forest as corridors and foraging places for the whole bat assemblage. Therefore, gaps and other

patchy areas within the forest represent important habitats for bat activity and hence, important targets for bat conservation (Russo & Jones 2003).

Other fragmented landscapes that have been studied in this thesis are the green areas of the city of Madrid. Urban parks have also shown their importance as small patches within the urban matrix. Most of the bats detected in parks were fissure-dwelling species. This could be explained due to their preferences, as they have both roost and foraging resources available (Ancillotto et al. 2016). Consequently, regional occurrence of bat species is the only significant correlation of bat presence in urban parks, with the most distributed species being the best represented species in this urban habitat (Tena et al. 2020a). It can be concluded that a limited set of abundant species at regional scale occur in the urban parks of Madrid and that, when they do, they are less frequent than in the countryside around the city (Kurta & Teramino 1992, Avila-Flores & Fenton 2005, Krauel & LeBuhn 2016).

Bat species richness in urban parks is mostly determined by park area, which is correlated with water availability. Park area has been already reported in other studies as a main driver for species richness in urban areas, including bat assemblages (Gaisler et al. 1998, Everette et al. 2001, Gehrt & Chelsvig 2003, Avila-Flores & Fenton 2005, Krauel & LeBuhn 2016). It has been confirmed that bat richness distribution was poorly nested in the elevation gradient but nevertheless it was strongly nested in urban parks. This means, that along the mountain gradient, almost all the species are able to occur, while in urban parks just a few species tend to occur from the regional pool. Therefore, species within smaller areas are subsets of the pool of species occurring in the existing natural habitat (Patterson & Atmar 1986). It can be concluded that the effect of the regional occurrence and park size on the distribution of bat species suggest a random sampling by parks of the regional availability of species. This is important to be considered as processes happening at a regional scale might be determinant for species richness in fragmented areas (Gallo et al. 2018).

CONCLUSIONS



“Si tomaste un café, comiste cualquier producto de maíz o estás usando una prenda de algodón, tu vida tiene un vínculo directo con los murciélagos.”

Rodrigo Medellín.

CONCLUSIONS

1. Responses along elevational gradients can be dissimilar for different organism which have different biological requirements. In the case of bird and bat distributions in the Guadarrama Mountains during the breeding period, they show very different constraints in the search for resources. Passerines are linked to a small home range at a local scale while bats can move long distances from the roost to the foraging areas at a regional scale. Therefore, this pattern should be taken into consideration when developing conservation strategies to preserve biodiversity within the same geographical area.
2. The distribution of protected areas in the Guadarrama Mountains overlaps with most of the best sectors for bats defined by species distribution models. Unfortunately, this network of protected areas has not considered bats when it was originally created nor has there been a monitoring of bat assemblages. In the future, global change might cause disturbances occurring within this network, therefore specific approaches must be taken into consideration to anticipate and mitigate the potential effects on bat assemblages.
3. Urbanization is a global threat that should be considered in biodiversity conservation. Potential sectors for high biodiversity usually overlap with the most urbanised ones. Although, in the case of the Guadarrama Mountains, the best sectors for bats are located outside the most urbanized sectors and the protected areas tend to be located at the best sectors for bats. This reinforces the capacity of protected areas of Central Spain to protect the best activity areas for bats.
4. Forest gaps play a vital role in bat conservation since they increase habitat heterogeneity, species richness and activity. Gaps promote ecotones between grassland and forest that can be used by bats as corridors for commuting and foraging, including by tree dwelling bat species. Therefore, any forest and bat friendly management guideline should maintain gaps already created inside a homogenous forest in support of forest species conservation.
5. Urban parks of Madrid are not particularly appealing for the regional pool of bat species as their occurrence is limited by the regional occurrence and with lower occupancies than in the Guadarrama Mountains. To reverse this situation, a proactive

approach to bat conservation would be required by improving the attractiveness of urban biodiversity. This may include an increase of park size and roosting sites, diversification of park vegetation and the protection and connection of urban parks with the existing natural habitat.

- 6.** Bioacoustics increase the possibilities of field work with bats, with new analytical approaches. Although it has limitations, if we take them into consideration, it can be a powerful tool to increase the knowledge on bats and conservation. This thesis can serve as an example.

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APPENDIX

List of other publications and manuscripts coauthored by Elena Tena during the development of the Doctoral Thesis:

Bertran, M., Alsina-Pagès, R. M., & **Tena, E.** (2019). Pipistrellus pipistrellus and Pipistrellus pygmaeus in the Iberian Peninsula: an annotated segmented dataset and a proof of concept of a classifier in a real environment. *Applied Sciences*, 9(17), 3467.

Perea, S., & **Tena, E.** (2020). Different bat detectors and processing software... Same results? *Journal of Bat Research & Conservation*, 13(1), 1-5.

Tellería, J. L., Carbonell, R., Fandos, G., **Tena, E.**, Onrubia, A., Qninba, A., Aguirre, J. I., Hernández- Téllez, I., Martín, C. A & Ramírez, Á. (2020). Distribution of the European turtle dove (*Streptopelia turtur*) at the edge of the South-Western Palaeartic: transboundary differences and conservation prospects. *European Journal of Wildlife Research*, 66(5), 1-9.

Tellería, J. L., Fandos, G., **Tena, E.**, Carbonell, R., Onrubia, A., Qninba, A., & Ramírez, Á. (2019). Constraints on raptor distribution at the southwestern boundary of the Palaeartic: implications for conservation. *Biodiversity and Conservation*, 28(3), 603-619.