Ecología de los Murciélagos Cavernícolas del Este de la Península Ibérica

MARJORIE CAROLINA MACHADO SILVERA

Tesis Doctoral en Biodiversidad

Mayo, 2017

VNIVERSITAT DE VALÈNCIA

Director: Juan Salvador Monrós González

Portada: *Rhinolophus ferrumequinum*

Cova Soterranya-Serra (Valencia-España)

Foto: Miguel Ángel Monsalve

Instituto Cavanilles de Biodiversidad y Biología Evolutiva
Departamento de Microbiología y Ecología

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Tesis titulada " ***Ecología de los Murciélagos Cavernícolas del Este de la Península Ibérica*** **" presentada por MARJORIE CAROLINA MACHADO SILVERA para optar al título de Doctora en Biodiversidad por la Universidad de Valencia.**

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“Cuando alguien busca, suele ocurrir que sus ojos sólo ven aquello que anda buscando, y ya no logra encontrar nada ni se vuelve receptivo a nada porque sólo piensa en lo que busca, porque tiene un objetivo y se halla poseído por él. Buscar significa tener un objetivo, pero encontrar significa ser libre, estar abierto, carecer de objetivos..."

Fragmento de SIDDHARTHA
Hermann Hesse
República de Weimar, 1922

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CONTENIDO GENERAL

CAPÍTULO 1

INTRODUCCIÓN

Sima del Alto de Don Pedro-Macastre

Foto: Marjorie Machado

Los murciélagos son el grupo de mamíferos más diverso luego de los roedores, que presentan una serie de particularidades morfológicas, fisiológicas, ecológicas y conductuales, entre las que destacan el vuelo activo y la orientación mediante la ecolocación (Aguirre *et al*. 2011, Russo 2015, López-Baucells *et al*. 2016). Estas particularidades les han permitido tener una distribución cosmopolita, estando solo ausentes en las regiones polares, así como ventajas en la explotación de amplias áreas de alimentación (Nowak 1991, Nowak 1994). Desempeñan diversos roles ecológicos, como la dispersión de semillas, la polinización y el control de poblaciones, tanto de vertebrados como de invertebrados (Patterson *et al*. 2003). Una alta diversidad de especies de quirópteros basa su alimentación estrictamente en artrópodos, con estrategias especializadas para la detección, captura y manipulación de las presas (Barclay y Brigham 1991, Greenfield y Baker 2003, Simmons 2005).

En la actualidad, sus poblaciones encaran adversidades asociadas con la pérdida y/o fragmentación de hábitats, enfermedades, depredación y cambio climático, entre otros (Arthur *et al*. 2014), lo que hace imprescindible la implementación y prosecución de sistemas de monitoreo, a fin de evaluar sistemáticamente sus estatus poblacionales (Jones *et al*. 2009, Meyer *et al*. 2010).

El monitoreo de poblaciones silvestres es esencial en especies vulnerables o susceptibles a la extinción, principalmente en lugares que están siendo conservados o donde se pretende hacerlo (Battersby 2010). No obstante, los recursos para la conservación son limitados y se requiere de acciones que detecten localidades o especies prioritarias sobre las cuales dirigir esfuerzos. De ahí la necesidad de obtener información de largos periodos de tiempo, para así relacionar eventuales cambios poblacionales con los umbrales mínimos necesarios para la implementación de planes de conservación (Greenwood *et al*. 1995, Collen *et al*. 2007, Battersby 2010). Por su parte, la composición y estructura de los ensambles de especies son parámetros que aportan información valiosa sobre las condiciones locales del refugio o el entorno, puesto que no todas las especies responden igual frente a determinados cambios (Patterson *et al*. 2003).

Incluso desde el punto de vista reproductivo los murciélagos muestran diversas estrategias que les permiten ajustar sus balances energéticos y mantener sus poblaciones (Racey y Entwistle 2000, Jones y MacLarnon 2001).

Los murciélagos han desarrollado esquemas estacionales de reproducción, lo que asegura que tanto las crías al nacer como las madres lactantes, encuentren condiciones favorables para la sobrevivencia (Racey 1982, Altringham 1996). Las especies presentes en ambientes templados presentan mecanismos de sincronización entre la gestación y las condiciones más favorables de disponibilidad de recursos, que promueven mayores oportunidades de sobrevivencia tanto para la cría como para la madre después de un periodo de hibernación. Estos mecanismos son: 1) el retraso de la ovulación y la fertilización, con almacenamiento del esperma en el oviducto de la hembra; 2) el retraso de la implantación del óvulo fecundado y 3) un periodo de latencia después del implante del embrión o diapausa embrionaria (Racey 1982, Altringham 1996, Balmori 1999, Racey y Entwistle 2000, Kunz y Orrell 2004).

Se han documentado diferentes modalidades en los patrones reproductivos para murciélagos (Willig 1995, Estrada y Coates-Estrada 2001), sin embargo, el patrón reproductivo típico en murciélagos de zonas templadas es el monoestro, el cual es un ciclo simple, donde la hembra entra en celo una vez al año ocurriendo un único evento reproductivo (estro-preñez-lactación) (Racey y Entwistle 2000). Este también ha sido reportado para algunas especies de murciélagos de ambientes tropicales pertenecientes a las Familias Emballonuridae, Phyllostomidae y Vespertilionidae (Kunz 1982, Altringham 1996). En el monoestro estacional los individuos se reproducen una vez al año durante el periodo de mayor disponibilidad de alimento. En este patrón generalmente las cópulas se realizan en otoño, el estro se extiende hasta el invierno, la preñez inicia en la primavera y la aparición de juveniles ocurre durante el verano (Balmori 1999).

El hábito alimentario también juega un papel determinante en la energética de estos animales, en este sentido, aquellos murciélagos estrictamente insectívoros son considerados como los euterios con más bajas tasas metabólicas basales (McNab 1986). Una baja tasa metabólica afecta a: (1) la reproducción, tanto a nivel de fecundación y gestación, como en lo que se refiere a lactancia y crecimiento de las crías, (2) la capacidad de respuesta ante depredadores y (3) la termorregulación, es decir, posibilidad de mantener una temperatura corporal constante e independiente del ambiente (McNab 1986).

Una dieta basada exclusivamente en insectos supone la presencia de ciertas adaptaciones que hacen posible la detección, captura, trituración y asimilación de las presas, las cuales pueden variar a nivel intra-especifico en función de los requerimientos energéticos (Belwood y Fenton 1976, Fraser y Fenton 2007, Svanback y Bolnick 2007).

En lo que concierne a alimentación, los murciélagos insectívoros necesitan obtener información precisa de las presas que persiguen; incluyendo presencia, posición, dirección, rapidez y en algunos casos identidad de las mismas. Esta información la obtienen mediante sus llamadas de ecolocación, las cuales varían en estructura, intensidad y frecuencia, dependiendo de la especie (Fenton 1982, Russo y Jones 2003).

La poca discriminación en la obtención del alimento permite que estos murciélagos cambien los componentes de su dieta en función de la disponibilidad de presas (Best *et al*. 1997), lo que sugiere que la gran mayoría de los murciélagos insectívoros pudieran ser básicamente oportunistas, siendo sus dietas en gran medida reflejo directo de variaciones estacionales en la composición y abundancia de insectos (Kunz 1974).

El conocimiento del comportamiento alimentario y la repartición de recursos en especies simpátricas es una pieza clave para entender la diversidad y composición de especies en comunidades locales y su dinámica, aspectos determinantes en la supervivencia de los ensambles (Fenton 1989, Moreno 2006, Andreas *et al*. 2012, Krüger *et al*. 2012), y donde actualmente se necesita más información a nivel poblacional (Sachanowicz *et al*. 2006).

En España se conocen alrededor de 33 especies de murciélagos insectívoros (Wilson y Reeder 2005, Lisón *et al*. 2010), estando buena parte de ellas bajo alguna categoría de amenaza, debido a lo susceptible o poco conocido de sus estados poblacionales. Particularmente, en la Comunidad Valenciana se reconoce la presencia de 21 especies, con información sobre su distribución y algunos aspectos de su historia natural (Jiménez *et al*. 2012).

Considerando el delicado estatus de conservación en que se encuentran la mayoría de las especies de mamíferos en Europa y particularmente en España, resulta necesario usando los datos de censos ya existentes, evaluar en el caso de los murciélagos cómo estas especies encaran el reto energético de la reproducción, aspecto clave en el mantenimiento de las poblaciones silvestres, y que a la vez que permitiría obtener información sobre el uso que le están dando a los refugios maternales durante este período. Estos aspectos son de mucho valor, tanto a la hora de tomar decisiones sobre el manejo de áreas, como para el monitoreo y evaluación de las acciones de conservación que se vienen aplicando para proteger estas especies.

Los murciélagos cavernícolas presentes en la península ibérica estan catalogados por IUCN (2016) desde "Preocupación Menor", como es el caso de *Myotis myotis, M. blythii, M. emarginatus y Rhinolophus ferrumequinum,* hasta "Vulnerables" como *M. capaccinii* y *Rhinolophus mehelyi*, estando consideradas *Miniopterus schreibersii, Rhinoluphus euryale* y *R. hipposideros* como "Casi Amenazadas". Ibáñez *et al*. (2006) encontraron evidencias para separar un linaje del complejo Nattereri distribuido al sureste de la Península Ibérica, al cual le adjudicaron el nombre de *Myotis escalerai*, así quedaría *Myotis nattereri* restringida a Europa central, con un tercer linaje críptico para el noreste de la Península aún no descrito. Es por ello que muchos aspectos de la historia natural de *M. escalerai* permanecen poco conocidos y sigue siendo considerada para diversos fines dentro del complejo Nattereri, con categoría de "Preocupación Menor" (IUCN 2016).

En España estas especies han sido reportadas como en "Peligro de Extinción" (*Myotis capaccinii*), "Vulnerables" (*Miniopterus schreibersii* y *Myotis blythii*) y "No Amenazadas" (*Myotis escalerai*) según Monsalve *et al*. (2003), mientras que González (2006) las considera a todas como "Vulnerables". En la actualidad todos los esfuerzos son necesarios en aras de hacer contribuciones al conocimiento de la historia natural, condición poblacional y requerimientos ambientales de estas especies.

Esta tesis intenta abordar la ecología de estas especies de murciélagos cavernícolas desde cuatro puntos de vista: (1) estatus poblacional, efecto de la protección de refugios y formación de ensambles, (2) patrones de emergencia de los refugios, (3) tasas reproductivas y de productividad y

(4) dieta, ancho y solapamiento de nicho trófico, considerando particularmente a *Myotis myotis* y *M. blythii*, dos especies hermanas simpátricas en los refugios evaluados.

Tendencias poblacionales de los murciélagos cavernícolas al Este de la Península Ibérica y los efectos de la protección de sus refugios. Entre 1950 y 1970, se establecieron acciones a nivel mundial para proteger los refugios de murciélagos. Entre estas acciones estuvo la instalación de rejas en las entradas de las cuevas, lo que tuvo un efecto negativo sobre todo en los períodos de hibernación y reproducción (Tuttle 1977, Ludlow y Gore 2000, Pugh y Altrigham 2005, Berthinussen *et al*. 2014), que consecuentemente llevó a que los refugios fueran a menudo abandonados. Desde entonces, los diseños de rejas han sido modificados y ajustados, especialmente en Europa, ya que especies como *M. schreibersii, R. euryale, R. mehelyi* y *M. myotis/blythii* responden negativamente a dichas instalaciones (Spanjer y Fenton 2005). Los vallados perimetrales alrededor de las cuevas ha mostrado ser la mejor alternativa, aunque menos eficaz en la prevención del acceso humano, y es la opción más recomendada para garantizar que los murciélagos no abandonen los refugios (Mitchell-Jones *et al*. 2007). En este estudio se determinará las tendencias poblacionales analizando los censos disponibles hasta la fecha para las siguientes especies: *Rhinolophus euryale* (Blasius 1853), *R. ferrumequinum* (Schreber 1774), *R. hipposideros* (Bechstein 1800), *R. mehelyi* (Matschie 1901) *Myotis blythii* (Tomes 1857), *M.capaccinii* (Bonaparte 1837), *M. emarginatus* (Geoffroy 1806), *M. escalerai* (Cabrera 1904), *M. myotis* (Borkhausen 1797) y *Miniopterus* *schreibersii* (Kuhl 1819); evaluando el efecto de las acciones de conservación realizadas en los refugios ocupados por estas especies, así como la estructura de los ensambles en el este peninsular.

Fenología de emergencia de murciélagos cavernícolas mediterráneos simpátricos durante su período de cría. El equilibrio entre depredación y disponibilidad de alimentos puede influir en el tiempo de emergencia ideal para cada especie. Los murciélagos que viven en cuevas deben dejar diariamente sus refugios a través de aberturas de tamaño limitado, saliendo individual o grupalmente, lo que puede llevar un tiempo considerable (Davis *et al*. 1962). Dentro del patrón general, el momento exacto de la salida de los refugios puede variar como una respuesta a la presión de selección de la disponibilidad de alimentos, la competencia y la depredación (Erkert 1982, Kunz 1982). En consecuencia, el momento de salida puede no sólo estar vinculado a diferencias en el momento óptimo de aparición, sino también a la competencia intra e inter-especifica. Las variaciones en la demanda de energía entre individuos de la misma especie también pueden ser un factor clave de la variación inter-estacional en el momento de la emergencia diaria. Las hembras lactantes deben surgir antes que las hembras preñadas, ya que sus requerimientos energéticos son mayores (Racey y Speakman 1987, Kurta *et al*. 1989, Duvergé *et al*. 2000; Reichard *et al*. 2009). El objetivo de este capítulo será determinar si existen patrones de emergencia entre *Myotis blythii* (Tomes 1857); *Myotis capaccinii* (Bonaparte 1837); *Myotis escalerai* (Cabrera 1904); *Myotis myotis* (Borkhausen 1797) y *Miniopterus schreibersii* (Kuhl 1817), especies que coexisten en los refugios en el este de la Península Ibérica. Del mismo modo, analizar si dichos patrones varían a nivel inter o intra-específico a lo largo el período de cría.

Fenología reproductiva de los murciélagos cavernícolas en el este de la Península Ibérica y sus implicaciones para la conservación. La teoría de historias de vida predice que en especies con una alta supervivencia de los adultos, la tendencia es a no reproducirse en épocas desfavorables o cuando sus poblaciones atraviesan por declives importantes (Thompson 1987, Hoyle *et al*. 2001, Wilkinson y South 2002). A pesar de ser mamíferos de pequeño tamaño suelen tener solo una o dos crías por evento reproductivo en las zonas templadas, ocurriendo períodos de gestación variables en las zonas tropicales (Happold y Happold 1990). Los quirópteros al ser muy longevos (Gaisler 1989, Barclay y Harder 2003), con eventos reproductivos exitosos y condiciones estables en los refugios podrían garantizar poblaciones estables en el tiempo. En este tercer capítulo se describirá la fenología reproductiva de *Myotis myotis, M. blythii, M. capaccinii, M. escalerai, Miniopterus schreibersii* y *Rhinolophus euryale*, así como se determinará sus tasas reproductivas y de productividad, a la luz de las acciones de conservación que se han venido implementado en sus refugios y áreas de influencia, con miras a mejorar o mantener estrategias para su conservación.

Composición de la dieta y solapamiento de nicho trófico en *Myotis myotis* **y** *Myotis blythii* (Chiroptera: Vespertilionidae) **durante la reproducción al este de la Península Ibérica**. El conocimiento del comportamiento alimentario y la repartición de recursos en especies simpátricas es una pieza clave para entender la diversidad y composición de especies en comunidades locales y su dinámica, aspectos que son determinantes en la supervivencia de los ensambles (Fenton 1989, Moreno 2006, Andreas *et al*. 2012, Krüger *et al*. 2012) y donde se necesita más información actualmente (Sachanowicz *et al*. 2006). *Myotis myotis* (Borkhausen 1797) y *Myotis blythii* (Tomes 1857) son las especies de mayor tamaño dentro del género (Nowak 1991, Nowak 1994), con marcadas similitudes morfológicas, conductuales y acústicas (Arlettaz *et al*. 1991, Russo y Jones 2003, Evin *et al*. 2008). Son insectívoras estrictas, con adaptaciones y estrategias que hacen posible la detección, captura, manipulación y asimilación del mismo espectro de presas de formas muy similares (Belwood y Fenton 1976, Kalko y Schnitzler 1998, Gannon *et al*. 2001, Fenton y Bogdanowicz 2002, Kunz 2004). En el último capítulo determinaremos los componentes de la dieta de *Myotis myotis* y de *Myotis blythii* mediante la evaluación de muestras fecales durante la reproducción, así como la amplitud del nicho trófico y el posible solapamiento del mismo, considerando las marcadas similitudes entre estas especies hermanas.

CAPÍTULO 2

ÁREA DE ESTUDIO Y MÉTODOS

Rhinolophus euryale, Myotis blythii y Myotis myotis, Myotis capaccinii, Myotis emarginatus y *Miniopterus schreibersii* (sentido de las agujas del reloj).
Trampa de arpa. Sima del Alto de Don Pedro-Macastre
Fotos: Marjorie Machado

ESPECIES DE ESTUDIO

Las especies presentes en España se encuentran repartidas en las familias Rhinolophidae, Vespertilionidae y Molossidae, siendo la Familia Vespertilionidae la de mayor diversidad y abundancia (Monsalve *et al*. 2003). La selección de los refugios es un aspecto esencial en este grupo con actividad principalmente nocturna, ya que estos les proporcionan protección ante depredadores, condiciones térmicas estables y la interacción constante entre los miembros de la colonia (Kunz 1982, Kunz y Lomsden 2003). En relación al tipo de refugio que ocupan las especies suelen clasificarse en forestales (huecos de árboles), cavernícolas (cuevas, simas, minas, túneles, entre otros) y fisurícolas (grietas y fisuras) (Simmons y Voss 1998), exhibiendo altos niveles de fidelidad (McCracken y Wilkinson 2000), por lo que la pérdida de los mismos generaría altas tasas de mortalidad y/o reducción del éxito reproductivo de estas especies (Fleming y Eby 2003).

A continuación se describen brevemente las especies cavernícolas consideradas en esta Tesis:

Myotis myotis (Chiroptera: Vespertilionidae)**.** Murciélago ratonero grande. Es la especie de mayor tamaño dentro del género en Europa, tiene un pelaje corto y denso con la base oscura, castaño en el dorso y casi blanco en el vientre (Garrido y Nogueras 2007). Es una especie común en la mayor parte de su distribución, aunque las poblaciones de varias regiones fluctúan en número, forma grandes colonias en cuevas en coexistencia con *M. blythii* (Monsalve *et al.* 2003), especie con la que presenta grandes similitudes eco-morfológicas y acústicas (Evin *et al.* 2008). Es una especie típica mediterránea, presente desde el suroeste de Europa hasta el sur Inglaterra atravesando el centro de Europa y Asia menor (Benda *et al*. 2006, Bachanek y Postawa 2010).

Myotis blythii. (Chiroptera: Vespertilionidae). Murciélago ratonero pequeño. Esta especie se confunde a menudo con *M. myotis* diferenciándose por ser ligeramente más pequeño y menos robusto, con un pelaje más claro, una mancha blanquecina entre las orejas y hocico más agudo (Nogueras y Garrido 2007). Tiene una amplia distribución, que se extiende en el Mediterráneo y sur de Europa central, Israel, Líbano, Turquía, Siria, Irak, Rusia meridional, China, Rajputana, Punjab y Cachemira (DeBlase 1980). Ausente al norte de África (Castella *et al*. 2000) y algunas islas del Mediterráneo (Benda *et al*. 2006), en general es considerada como común (Sharifi *et al*. 2000).

Myotis capaccini. (Chiroptera: Vespertilionidae). Murciélago patudo. Es un murciélago de tamaño mediano, La coloración del pelaje dorsal es gris clara, siendo el pelaje ventral casi blanco. La pata presenta cerdas y es conspicuamente mayor que la mitad de la tibia. La tibia presenta como carácter diagnóstico una densa capa de pelos, que se extiende por las zonas próximas del patagio (Almenar *et al*. 2007a). Es una especie termófila, cuyos refugios suelen estar cerca de ecosistemas acuáticos (ríos, pantanos, zonas húmedas) ya que éste es su hábitat de caza (Fenton y Bogdanowicz 2002). Muestra una distribución mediterránea (Mitchell-Jones *et al.* 1999, Spitzenberger y von Helversen 2001). Al noreste desde Marruecos hasta Túnez, y al sur de Europa desde el este de la Península Ibérica hasta los Balcanes, los Alpes suizos y austríacos, extendiéndose en Asia hasta Oriente próximo (Spitzenberger y von Helversen 2001).

Myotis escalerai. (Chiroptera: Vespertilionidae). Murciélago ratonero gris. Murciélago de tamaño pequeño, con orejas que extendidas sobrepasan el hocico. Presenta una emarginación en la oreja. El calcáneo ocupa la mitad del borde del uropatagio, el resto presenta una conspicua y densa franja de pelos cortos y rígidos, las tibias carecen de pelos. Coloración general grisácea con el vientre más claro que el dorso (Quetglas 2007a). De acuerdo a Ibáñez *et al*. (2006) y Salicini *et al*. (2011), *M. escalerai* corresponde a uno de los cuatro linajes derivados del complejo Nattereri, particularmente este clado ibérico se encuentra al sureste de la península.

Myotis emarginatus. (Chiroptera: Vespertilionidae). Murciélago ratonero pardo. Es de tamaño mediano a pequeño, con orejas de longitud media que extendidas pueden llegar hasta el hocico. Muestra una escotadura en la oreja más marcada que en otras especies. Destaca ausencia de pelos alrededor de los ojos (Quetglas 2012). El pelaje es de coloración marrón-rojizo en el dorso y amarillento en la zona ventral. El plagiopatagio en esta especie se inserta en la base del dedo más externo de la pata (Quetglas 2007b). Se distribuye en el centro y sur de Europa, incluyendo la península ibérica, los Países Bajos, a través de Europa Central, el Mediterráneo Europeo, Crimea, Transcaucasia y Oriente próximo (Horáček *et al*. 2000).

Rhinolophus ferrumequinum. (Chiroptera: Rhinolophidae). Murciélago grande de herradura. Es el representante de mayor tamaño del género en la Península Ibérica. La hoja nasal es ancha, corta y aguzada en el extremo. Muestra un surco vertical central en el labio inferior. Orejas grandes con antitrago ancho y separado del borde externo por una escotadura poco profunda (De Paz 2007). Es un representante del Paleártico sur con una amplia distribución desde Gran Bretaña, Europa occidental, Europa central, norte del Mediterráneo, atravesando la región del Cáucaso, Oriente próximo y Asia central (Benda *et al*. 2006).

Rhinolophus hipposideros. (Chiroptera: Rhinolophidae). Murciélago pequeño de herradura. Es la especie más pequeña de Rhinolophidae en la región Paleártica. Coloración dorsal del pelaje pardo oscuro, con la parte ventral grisácea clara. Orejas y membranas alares siempre más oscuras que el pelo. Principalmente de distribución mediterránea (Horáček *et al*. 2000), desde las Islas Británicas y Europa occidental, sureste de Europa, el Mediterráneo europeo, el Cáucaso, Oriente próximo y Asia Central, llegando hasta la región afro-tropical. Se extiende a lo largo del Valle del Rift desde el Levante, sobre el Sinaí y el oeste de Arabia Saudita a Eritrea, Djibouti, Etiopía y Sudán (Pearch *et al*. 2001).

Rhinolophus mehelyi. (Chiroptera: Rhinolophidae). Murciélago mediano de herradura. Es de tamaño mediano, con la hoja ancha en la base estrechándose bruscamente hacia la porción distal. Muestra un pelaje dorsal de coloración gris parduzco en contraste con el vientre blanco, con un límite bastante marcado. En torno a los ojo el pelaje es muy oscuro (Almenar *et al*. 2007b). Muestra una distribución mediterránea (Horáček *et al*. 2000), presente desde el suroeste de Europa, Mediterráneo europeo, Oriente próximo, hasta Transcaucasia e Irán (Benda *et al*. 2006).

Rhinolophus euryale. (Chiroptera: Rhinolophidae). Murciélago mediterráneo de herradura. Es una especie de tamaño mediano similar a *R. mehelyi* con el que suele confundirse y de quien se distingue por su menor tamaño de antebrazo. La coloración del pelaje dorsal es gris parda más clara en la base, con el vientre blanco, grisáceo o amarillento. Las membranas alares y orejas son pardo grisáceo claro (Goiti y Aihartza 2007). Es una especie de distribución mediterránea (Horáček *et al*. 2000) presente desde el norte de Africa y Europa suroccidental, a través de Europa central, el Mediterráneo europeo, Oriente próximo, Transcaucasia, Irán y el suroeste de Turkmenistán (Benda *et al*. 2006).

Miniopterus schreibersii. (Chiroptera: Vespertilionidae). Murciélago de cueva. Es una especie de tamaño mediano, de rostro muy corto, con orejas pequeñas y triangulares. Pelaje corto y denso, de coloración pardo grisácea en el dorso y más pálido en la zona ventral. Las alas son largas y estrechas, con la segunda falange del tercer dedo tres veces la longitud de la primera (De Lucas 2007). Tiene origen en la región subtropical, de distribución mediterránea (Boye 2004) se encuentra ampliamente distribuida al sur de Europa, África, Oriente próximo, Cáucaso, Asia y Australia (Horáček *et al.* 2000).

ÁREA DE ESTUDIO

Fueron seleccionados cinco refugios de la Comunidad Valenciana, en los cuales se realizaron censos poblacionales y capturas de los individuos tanto para las determinaciones de las categorías reproductivas como para la toma de las muestras fecales, durante los años 2013 y 2014. Estos refugios están registrados en el proyecto LIFE en la Comunidad Valenciana: Cueva del Sardiner (Sagunto), Cueva de la Sima de Don Pedro (Macastre), Cueva de las Maravillas (Llombai), Túnel de Canals (Canals) y Cueva del Puntal de Mateo (Náquera). Para el análisis de las tendencias poblacionales fueron incorporados los censos realizados en los 34 refugios monitoreados de la Comunidad Valenciana entre 1997-2014 (ver Figura 1; Capítulo 3). Catorce de estos refugios permanecen sin protección hasta el momento, los restantes cuentan con vallas perimetrales, que impiden el acceso humano.

PROCEDIMIENTOS GENERALES

TENDENCIAS POBLACIONALES Y PATRONES DE EMERGENCIA

Los censos fueron realizados entre Mayo y Julio, mediante filmaciones y registros acústicos para la identificación y contabilización de los individuos de cada una de las especies consideradas. Dichas filmaciones se iniciaron al atardecer desde el momento en que salía el primer individuo hasta que todos abandonaron el refugio (Rodrigues y Palmeirim, 1994; Russo y Jones, 2002, 2003). Posteriormente, a las filmaciones se les realizó un análisis espectrográfico utilizando el Software GRAM 5.1.7. de R. S. Horne, siguiendo a Russo y Jones (2002) para la comparación de frecuencias. Las tendencias poblacionales se analizaron mediante el programa TRIM 3.54 (trends and indices for monitoring data- Pannekoek y van Strien, 2009). Se realizaron análisis de agrupamiento ('cluster analysis') para evaluar la similitud/disimilitud entre los ensamblajes utilizando medidas de similitud de Bray-Curtis y Jaccard. En cuanto a los datos del tiempo de emergencia se expresaron como el número de murciélagos de cada especie que emergieron del refugio durante intervalos de 2 minutos, hasta completar el tiempo total de filmación (60 minutos). Para poder comparar entre meses y refugios, se transformó el tiempo de emergencia añadiendo el tiempo entre la hora oficial de puesta de sol y el momento de inició del video. Se realizó un análisis GLMM-Poisson considerando el tiempo de emergencia (minutos después de la puesta del sol) como la variable de respuesta, mientras que el mes, las especies y los refugios fueron los factores.

FENOLOGÍAS REPRODUCTIVAS

Durante el período de cría de estas especies cavernícolas (abril-julio) se realizaron capturas (una noche al mes) en los cinco refugios mencionados anteriormente, empleando una trampa de arpa estándar plegable (Tuttle 1974, Tidemann y Woodside 1978). Seguimos los criterios de Anthony (1988) para la asignación de las categorías etarias y de Racey (1988) para determinar la condición reproductiva. Las categorías para hembras adultas fueron: nulípara, preñada, lactante, postlactante y no reproductiva. Para los cálculos de las tasas reproductivas se consideró el número de hembras reproductivas en relación a las hembras adultas totales, mientras que para las tasas de productividad se relacionó la proporción de juveniles con las hembras reproductivas (Barclay 2004). Se determinaron las relaciones de sexo por especie tanto para adultos como para juveniles.

DIETA Y NICHO TRÓFICO

Los componentes de la dieta se determinaron mediante el análisis de muestras fecales, tomadas directamente de cada individuo (Belwood y Fenton 1976, Kunz y Whitaker 1983). Empleando un microscopio estereoscópico Leica EZ4 35x se analizó el contenido de los “droppings” que componen las diferentes muestras fecales (Whitaker, 1988), los fragmentos fueron identificados con la ayuda de claves entomológicas (Borror *et al*. 1981, Shiel *et al*. 1997). Se aplicó un modelo log-lineal para datos categóricos, para determinar la relación entre las variables especie, refugio, mes, sexo y presa (Miñana, 2013). La amplitud de nicho de las especies se determinó mediante los índices de diversidad de Shannon-Wiener, Simpson y Levins, mientras que el solapamiento de nicho se estimó con el índice de Pianka y los coeficientes de competencia de Mac Arthur y Levins.

Todos los análisis estadísticos fueron realizados con SPSS 22.0 y Past 3.03 (Hammer *et al*. 2001). Para todos los casos se consideró un $p<0.05$ como significativo.

CAPÍTULO 3

Population trends of cave-dwelling bats in the Eastern Iberian Peninsula and the effect of protecting their roosts

Colonia de *Rhinolophus ferrumequinum*. Cueva el Campillo.

Foto: Miguel Ángel Monsalve

INTRODUCTION

Bats as a group have high taxonomic and functional diversity. Although European bats are legally protected by national and European decrees (Convention on Migratory Species 1985-2008, Agreement on the Conservation of Populations of European Bats, Habitat Directive-92/43/EEC), some remain vulnerable or at risk of extinction in different parts of their range (IUCN 2014). Bat populations face adversities such as habitat loss and fragmentation, disease, predation and climate change (Arthur *et al*., 2014), which make systematic schemes essential to assess their population status (Jones *et al*. 2009, Meyer *et al*. 2010).

Monitoring wild populations is necessary for protecting vulnerable species or those at risk of extinction (Battersby 2010). However, conservation resources are often limited and research on priority locations or species is needed. The need for long-time population monitoring is critical in order to assess possible population changes and the minimum thresholds required to implement conservation plans (Greenwood *et al*. 1995, Collen *et al*. 2007, Battersby 2010). Monitoring species assemblages will also provide additional information about local conditions in roosts or surrounding areas, as potential species interactions at roost sites (Patterson *et al*. 2003).

Between 1950 and 1970 numerous efforts were undertaken to protect roosts of cave-dwelling bats around the world. Among them, gates placed at cave entrances had a negative effect mostly on hibernation and reproductive periods (Tuttle 1977, Ludlow and Gore 2000, Pugh and Altrigham 2005, Berthinussen *et al*. 2014), which consequently led to these roosts to be abandoned. Since then, gate designs have been amended and adjusted, especially in Europe. For example, species like *M. schreibersii*, *R. euryale*, *R. mehelyi* and *M. myotis/blythii* respond negatively to the presence of gates (Spanjer and Fenton 2005). In these cases perimeter fencing around caves has been proved as a better alternative, which despite being less effective at preventing human access, is the most recommended option to guarantee that bats do not abandon roosts (Mitchell-Jones *et al*. 2007).

The LIFE NAT/E/7337 project is a plan for the conservation of bats in the Valencian Community (autonomous community of Spain-Eastern Iberian Peninsula), funded by the European Community, whose main objectives are to catalog forest and cave-dwelling bats roosts and eliminate potential disturbances of them by fencing the most threatened and monitoring their populations. Monitoring of the roosts with the two most threatened species in the Valencian Community, *R. mehelyi* and *M. capaccinii,* began in 2003, and complied with the obligations set out in the Habitat Directive (92/43/EEC), Law 42/2007 on Natural Heritage and Biodiversity, and in the Valencian Catalogue of Threatened Fauna (Decree 32/2004, Order 6/2013). However, data obtained to date have not been used to assess any population trends of these species.

The objectives of the present work were to determine population trends by analyzing the census data available to date for the following species: *Rhinolophus euryale* (Blasius 1853), *R. ferrumequinum* (Schreber 1774), *R. hipposideros* (Bechstein 1800), *R. mehelyi* (Matschie 1901) *Myotis blythii* (Tomes 1857), *M.capaccinii* (Bonaparte 1837), *M. emarginatus* (Geoffroy 1806), *M. escalerai* (Cabrera 1904), *M. myotis* (Borkhausen 1797) and *Miniopterus schreibersii* (Kuhl 1819); evaluate the effectiveness of conservation activities undertaken to protect roosts occupied by these species; and to determine the structure of community assemblages in several caves in the Valencia of Eastern Spain.

MATERIALS AND METHODS

The monitoring of 34 roosts occurred between May and July 1997 to 2014 in the Eastern Iberian Peninsula (Figure 3. 1). Fourteen of these roosts are unprotected, so far, the remaining, were protected by fences; three (1990-1999), nine (2002-2003) and eight (2013). A network gridded metal fence, 2.5 meters high, with an access gate of the same material was installed in a 20-m radius around the entrance to the roosts. Fourteen of the 22 protected roosts have this type of enclosure, which has proven to be the most effective in restricting human access to the colonies. Two cavities have rigid panels occupying ¾ of the area of the entrance, and ¼ for entrance of bats. Two others have iron bars that occupy the entire entrance, while two roosts have installed gates that block the main entrance, but with special openings (2 x 1 m^2) for free flight. All gates have a lock, the keys to which are kept with the authorities of the Conselleria de Medio Ambiente de la Comunidad Valenciana (Ministry of Environment of the Valencian Community).

Following the same procedure every year, censuses were conducted at the entrances of the roosts using an infrared (IR) video recorder and an ultrasound detector (Rodrigues and Palmeirim 1994, Mitchell-Jones 2007). Roost entrances were lit by a 75w halogen (IR) spotlight (COMPUTAR, angular 42o, 715 nm Filter) or IR lamps (810 nm) with 40 LEDs and a 10^o lighting angle (IRLight model IRLamp3). Filming was carried out using miniDV cameras with a hard disk sensitive to IR light (SONY DCR-TRV33E and SONY HDR-CX560V), while sound recordings were taken using ultrasound detectors with a split frequency system (Petterson D230 and UltraSound Advice U30). Recordings were taken at dusk, when the first bat emerged, and lasted 60 minutes (Rodrigues and Palmeirim 1994, Russo and Jones 2002, 2003).

Myotis myotis and *Myotis blythii* records were pooled for statistical analyses, these species are very similar in morphology and type of flight, which makes their identification by sound tenuous. In each roost, captures of individuals were regularly performed using harp traps; this allowed us to corroborate the species composition of each cave, facilitating the identification of species in audio and video records.

Counts and specific identifications were made by a spectrographic analysis using the SPECTROGRAM 5.1.7. software (R. S. Horne), following Russo and Jones (2002) to compare specific sound frequencies. We also analysed videos frame-by frame to identify species-specific traits such as size and flight style. Thus, each bat was identified both acoustically (spectrogram) and visually (video).

Population trends of the 34 monitored roosts (Figure 3. 1) were analyzed using the TRIM program (TRends and Indices for Monitoring data, version 3.54, Pannekoekand van Strien 2009). Log-linear Poisson regression was used for incomplete censuses of wild populations (Battersby 2010), which classified population trends into six categories: sharp increase (significant increase of >5% per year), moderate increase (significant increase of <5% per year), stable (non-significant increase or decrease of< 5% per year), uncertain (non-significant increase or decrease of >5% per year), moderate decrease (significant decrease of <5% per year) and sharp decrease (significant decrease of > 5% per year).

The category "uncertain" refers to those censuses with wide fluctuations without clear statistical significance, similar to the case of the "stable" category, however in this latter case the fluctuations were less marked. In order to clarify cases with category "uncertain" simple linear regressions were incorporated within species, to determine possible changes in population trends.

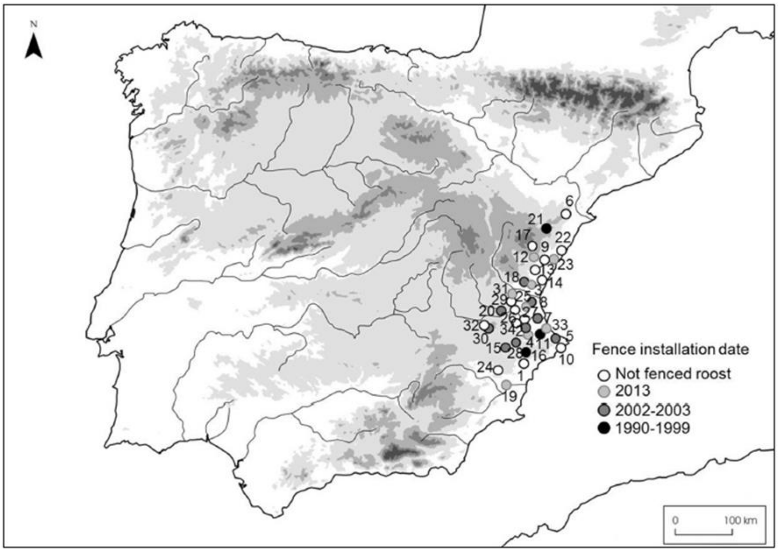


Figure 3. 1. Locations (in parentheses) of the roosts evaluated in the Eastern Iberian Peninsula: 1 = Avenc de Barratxina (Xixona), 2 = Avenc de les Graelles (Tous), 3 = Avenc del Puntal de Mateu (Náquera), 4 = Cova de la Moneda (Cotes), 5 = Cova de la Punta de Benimáquia (Dénia), 6 = Cova de la Puntassa (Pobla de Benifassá), 7 = Cova de les Meravelles (Alzira), 8 = Cova de les Meravelles (Llombai), 9 = Cova de les Meravelles (Castellón de la Plana), 10 = Cova de les Rates (Teulada), 11 = Cova de les Rates Penades (Rótova), 12 = Cova de l’Ocre (Lucena del Cid), 13 = Cova del Onder (Aín), 14 = Cova del Sardiner (Sagunto), 15 = Cova dels Mosseguellos (Vallada), 16 = Cova Juliana (Alcoi), 17 = Cova Oscura (Atzeneta del Maestrat), 18 = Cova Soterranya (Serra), 19 = Cueva del Perro (Cox), 20 = Cueva Hermosa (Cortes de Pallás), 21 = Ermita de la Mare de Deu (Castellfort), 22 = Forat d’en Ferrás (Orpesa del Mar), 23 = Moli de la Font (Castellón de la Plana), 24 = Sima de los Borreguillos (Salinas), 25 = Sima del Águila (Picassent), 26 = Sima del Alto de Don Pedro (Macastre), 27 = Sima del Campillo (Tous), 28 = Túnel de Canals (Canals), 29 = Túnel de Carcalín (Buñol), 30 = Cueva Negra (Ayora), 31 = Cueva del Barranco Hondo (Cheste), 32 = Cueva del Lago (Ayora), 33 = Cova Xurra (Gandía), 34 = Cova de les Dones (Millares). They are indicated by circles times fenced roosts.

Multivariate groupings ("cluster analysis") were conducted to evaluate the similarity/dissimilarity between assemblages in roosts, using Bray-Curtis and Jaccard similarity measures. The effects of fencing around the perimeter of roosts were examined by means of one-way ANOVA. Similarly, the trend of the roosts was evaluated by simple linear regressions, taking into account all the species pooled. The slopes of species' population trends were employed by considering the condition of protection. Statistical analyses were performed with SPSS 17.0 (SPSS 2008) and PAST 3.06 (Hammer *et al*. 2001).

RESULTS

The species with the highest relative abundance in 2014 was *Miniopterus schreibersii* with 62.4%, followed by *Myotis myotis/blythii* (18%) and *M. capaccinii* (6.2%). The abundance of *M. escalerai* decreased compared to 2013 (4.8%), while *Rhinolophus euryale* (5.1%), *R. ferrumequinum* (2.2%), *R. mehelyi* (0.2%) and *R. hipposideros* (0.1%) remained relatively constant (Table 3. 1).

In the last 12 years, *M. schreibersii* was highlighted as the species with the largest population, with around 13000 individuals recorded in 2014, and with stable values for previous years. It was followed by *Myotis myotis/blythii*, which ranged between 3000 and 4000 individuals (Table 3. 1, Appendix 1). The lowest values in the censuses of 2014 were obtained for *R. hipposideros*, with a maximum of 22 individuals, *R. mehelyi* with 34 and *M. emarginatus* with 189; however, the values remained similar to previous years. *Rhinilophus euryale* showed a moderate population decline for the period 1997-2014 and over the last 12 years (2003-2014) (Table 3. 2).

Rhinolophus hipposideros remained stable for the whole period, but underwent a moderate population decline in recent years. *Rhinolophus ferrumequinum* and *R. mehelyi* indicated a stable and uncertain trend, respectively, between 2003-2014. In the overall analysis, the vespertilionids bat species showed an uncertain trend, which changed in recent years to a sharp decline for *M. emarginatus* and a stable trend for *M. myotis/blythii* and *Miniopterus schreibersii* (Table 3. 2).

Linear regressions revealed that species with "uncertain" categories, such as *Myotis capaccinii*, *Myotis emarginatus* and *Myotis escalerai,* showed significant increases, while *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros*, *Miniopterus schreibersii* and *Myotis myotis/blythii*, though not statistically significant, tended toward positive population trends (Figure 3. 2).

Of particular note is *Rhinolophus euryale*, whose population showed negative trends (though nonsignificant), possibly due to marked population declines during the period 2005-2008.

In 2014, *Rhinolophus mehelyi, M. capaccinii, M. myotis/blythii* and *M. schreibersii* had higher relative abundances in the La Cova de les Rates Penades (Rótova) cave with 82.4%, 49.2%, 44.3% and 28.1%, respectively. *Rhinolophus ferrumequinum* was the most abundant species in La Cova de Soterranya (Serra) cave with 63.5%, followed by *R. hipposideros* in La Cueva del Barranco Hondo (Cheste) with 54.5%, *M. emarginatus* in La Cova dels Morsseguellos (Vallada) with 54%, *M. escalerai* in La Cova de Joliana (Alcoy) with 41% and *R. euryale* in La Cova del Onder (Aín) with 38%. The roosts of La Sima del Puntal de Mateo (Náquera) and La Sima del Alto de Don Pedro (Macastre) presented the largest number of species (8 spp), which contrasted with La Cueva del Perro (Cox) as it presented the least richness (1 spp).

Table 3. 1. Censuses and Relative Abundance of the cave-dwelling bats species during periods 1997-2014 in roosts assessed in the east Iberian Peninsula. In each year the higher value corresponds to the census and the lower the relative abundance. There was no census in 2002.

Species	Censuses Relative Abundance (%)																
	1997	1998	1999	2000	2001	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
RE	1179	1742	300	1463	1036	1111	1485	495	534	406	339	709	754	1410	880	698	1082
	5.2	10.4	92.8	83.1	12.6	6.6	8.5	4.2	3.5	2.7	2.5	4.2	3.8	6.2	5	4.5	5.1
RF	500	482	0	3	11	328	289	217	215	115	187	265	659	473	306	418	472
	2.2	2.8	0.00	0.17	0.13	1.9	1.6	1.8	1.4	0.77	1.4	1.6	3.4	2.1	1.7	2.7	2.2
RH	4	9	23	0	1	35	10	8	22	0	0	4	17	28	34	27	22
	0.02	0.05	7.1	0.0	0.01	0.21	0.06	0.07	0.15	0.0	0.0	0.02	0.1	0.1	0.2	0.2	0.1
RM	59	41	0	2	3	8	24	56	46	17	22	23	5	11	71	35	34
	0.2	0.24	0.0	0.11	0.04	0.05	0.14	0.47	0.3	0.11	0.17	0.14	0.0	0.0	0.4	0.2	0.2
MC	1217	560	0	0	536	1170	673	643	1267	1182	917	2000	1568	1777	1232	1488	1302
	5.4	3.3	0.0	0.0	6.5	6.9	3.8	5.4	8.4	7.9	6.8	11.9	8	7.8	7	9.6	6.2
ME	20	0	0	0	0	148	129	0	0	0	0	0	0	277	145	178	189
	0.09	0.0	0.0	0.0	0.0	0.88	0.74	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.8	1.1	0.9
MES	287	280	0	0	0	163	414	0	0	0	0	401	496	1370	756	1509	1020
	1.2	1.6	0.0	0.0	0.0	0.97	2.3	0.0	0.0	0.0	0.0	2.4	2.5	6	4.3	9.7	4.8
MM/MB	3836	1480	0	0	974	4336	3664	1062	3296	2178	2420	1566	2728	3609	2869	2397	3792
	17.12	8.8	0.0	0.0	11.9	25.7	21.0	8.9	21.8	14.6	18.1	9.4	13.9	15.9	16.4	15.5	18
MS	15301	12142	0	291	5624	9518	10753	9336	9721	11010	9435	11771	13396	13803	11240	8749	13138
	68.3	72.5	0.0	16.5	68.7	56.6	61.6	79	64.3	73.8	70.8	70.3	68.3	60.7	64.1	56.4	62.4

Table 3. 2. Population trends of the cave-dwelling bats species during periods 1997-2014 and 2003-2014.

Species	Presence in roosts	**1997-2014**			**2003-2014**		
		Slope	Error	Trend	Slope	Error	Trend
Rhinolophus euryale	25/34	0.9272	0.0288	**Moderate decrease**	0.9622	0.0158	**Moderate decrease**
Rhinolophus ferrumequinum	28/34	0.9852	0.0494	Uncertain	0.9775	0.0116	Stable
Rhinolophus hipposideros	13/34	0.9899	0.0129	Stable	0.9353	0.0217	**Moderate decrease**
Rhinolophus mehelyi	11/34	0.9661	0.0155	**Moderate decrease**	0.995	0.0264	Uncertain
Myotis capaccinii	15/34	1.0065	0.1213	Uncertain	1.0216	0.0212	Uncertain
Myotis emarginatus	6/34	0.9916	0.0432	Uncertain	0.8781	0.0353	**Sharp decrease**
Myotis escalerai	27/34	1.0613	0.0997	Uncertain	0.9969	0.035	Uncertain
Myotis myotis/blythii	25/34	1.0003	0.1385	Uncertain	0.9779	0.0125	Stable
Miniopterus schreibersii	27/34	0.9548	0.0291	Uncertain	0.9717	0.0110	Stable

Regarding the species compositions at each roost, we found that *M. emarginatus* and *R. hipposideros* shared fewer roosts with other species. Meanwhile, *M. myotis/blythii* and *M. schreibersii* shared roosts more frequently (correlation coefficient of 0.95, Figure 3. 3), also coexisting with *R. ferrumequinum* and *R. euryale*.

When assessing species' assemblages during breeding seasons, three roost groups were salient; two were caves that housed the largest number of species, a second group had the most common species (7 spp); a third group comprised the roosts with an average number of species (6 spp) (correlation coefficient of 0.90). In the similarity sequence, another group of caves stood out because it had the largest number of species (8-7 spp) (Fig. 4). Some roosts with a few species (1-3 spp) were separated from the grouping. The grouping of roosts did not apparently relate to the protective fencing since no differences among the various groups was found.

Only three roosts had significant increases pooling all the species. One of them protected during the period 1990-1999 and two in 2002-2003 (Table 3. 4, Figure 3. 5). Two roosts showed significant population declines, one fenced in 2002-2003, and the other with recent protection (2013). The vast majority of fences roosts in 2013 and unprotected roosts seem to show negative, but non-significant trends.

Considering the population census of all species in roosts with different levels of protection, no significant differences were found ($F_{3,\ 32}$=0.415, p=0.744). However, a positive trend was detected in the sample means of population trends of protected roosts, even in those with recently-erected fences (Figure 3. 6).

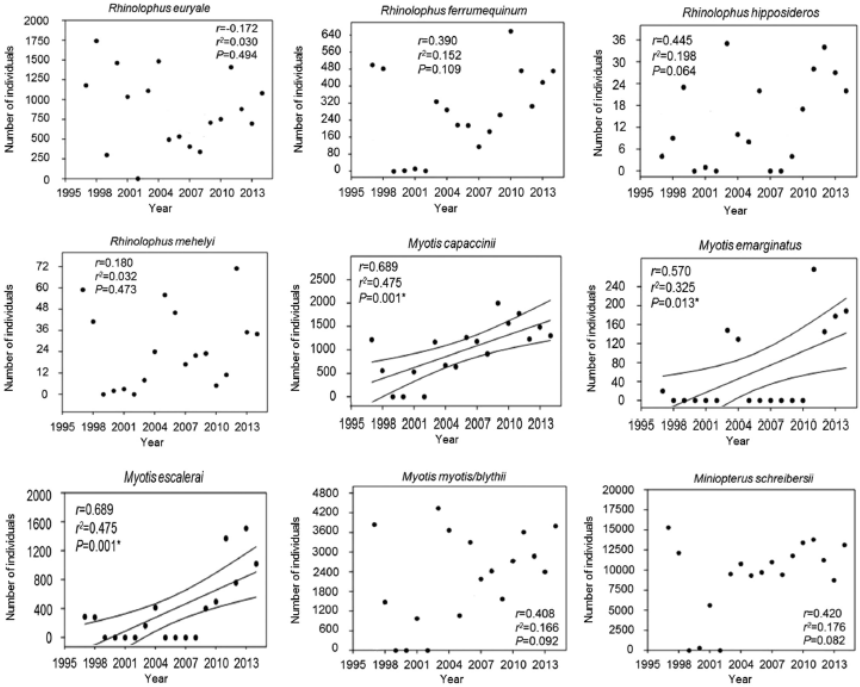


Figure 3. 2. Simple regression of population censuses of the species studied. *Significant values *p*<0.05).

Table 3. 3. Percentage of the occupation of cave-dwelling bats in monitored roosts (roosts that were occupied by each species) in the east Iberian Peninsula and t test of comparison.

	Occupancy rates of roosts		
Species	Protected	Unprotected	Both
Rhinolophus euryale	70	78.6	73.5
Rhinolophus ferrumequinum	75	92.8	82.4
Rhinolophus hipposideros	45	28.6	38.2
Rhinolophus mehelyi	35	28.6	32.6
Myotis capaccinii	40	50	44.1
Myotis emarginatus	25	7.1	17.6
Myotis escalerai	80	78.6	79.4
Myotis myotis/blythii	65	85.7	73.5
Miniopterus schreibersii	75	85.7	79.4
Two-sample paired *t* test			
Mean	56.667	59.522	
Variance	418.75	994.63	
Mean difference	2.8556		
T	-0.2278		
p	0.5605		

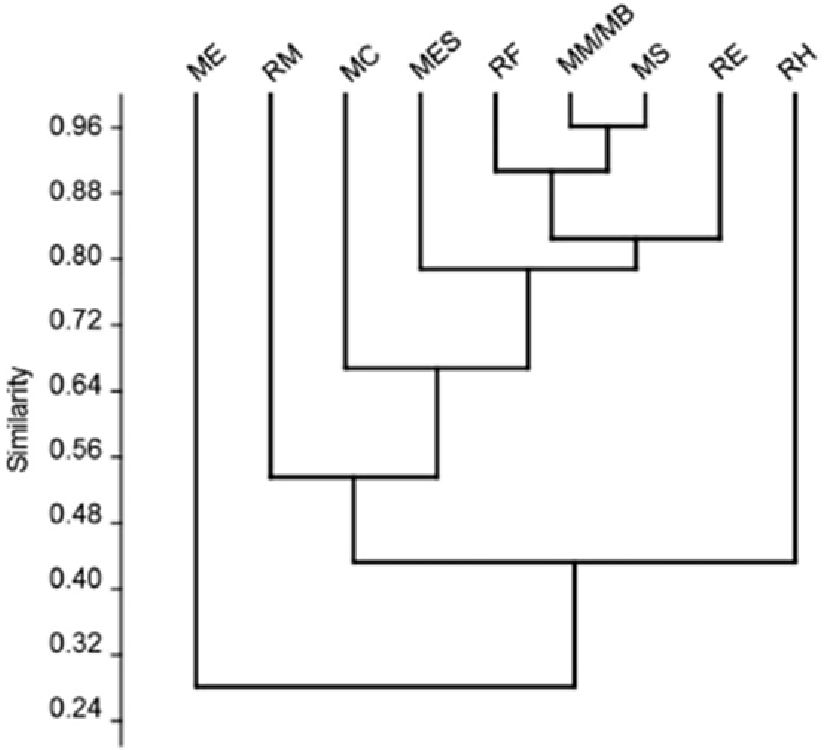


Figure 3. 3. Dendrogram of species grouping according to their presence in the evaluated roosts based on the Bray- Curtis similarity measure. Acronyms: RE: *R. euryale*, RF: *R. ferrumequinum*, RH: *R. hipposideros*, RM: *R. mehelyi*, MC: *M. capaccinii*, ME: *M. emarginatus*, MES: *M. escalerai*, MM/MB: *M. myotis/blythii* and MS: *M. schreibersii*.

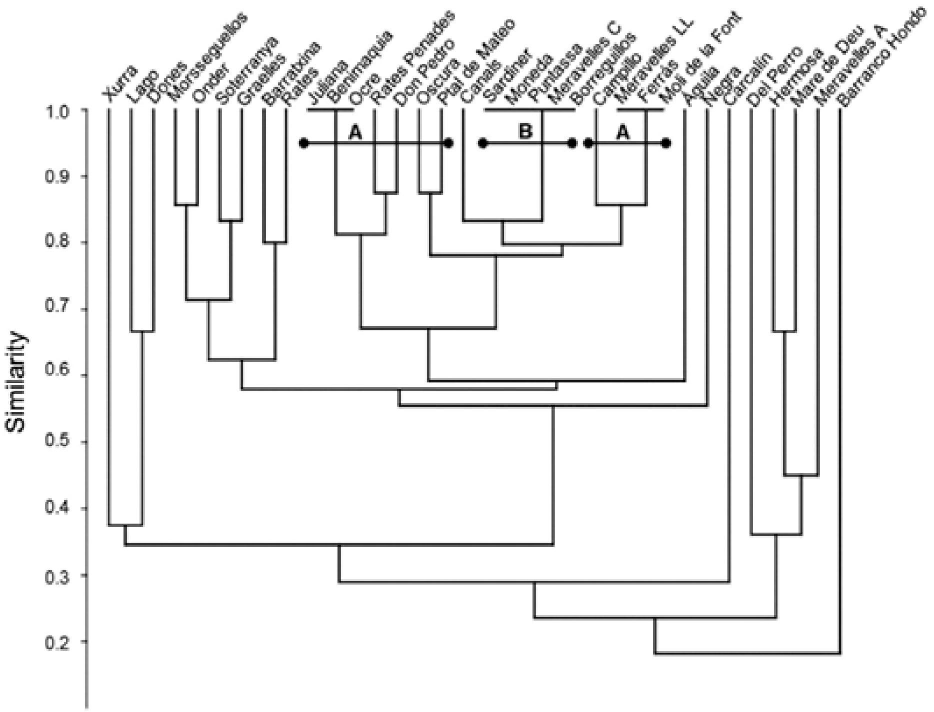


Figure 3. 4. Dendrogram of the grouping of roosts that considers the assemblage of the species housed according to the Jaccard similarity analysis. See Appendix 1 for the full names of the roosts. A=Roosts with largest number of species (7-8 spp) and B= Roosts with an average number of species (6 spp).

Table 4. 4. Simple linear regressions roosts during the evaluation period, considering the total censuses of the populations housed. The time of installation of fences in protected roosts is shown. *Significant values.

N	ROOSTS	Protection	r	r^2	*p*
1	Cova de les Rates Penades (Rótova)	1990-1999	0.489	0.239	0.127
2	Cova Juliana (Alcoi)	1990-1999	0.804	0.646	<0.001*
3	Ermita de la Mare de Deu (Castellfort)	1990-1999	-0.902	0.815	0.097
4	Avenc de les Graelles (Tous)	2002-2003	0.435	0.190	0.209
5	Cova de les Meravelles (Alzira)	2002-2003	-0.519	0.269	0.370
6	Cova de la Punta de Benimáquia (Dénia)	2002-2003	0.007	0.000	0.981
7	Cova de les Meravelles (Llombai)	2002-2003	-0.513	0.263	0.050*
8	Cova dels Morsseguellos (Vallada)	2002-2003	0.850	0.722	0.008*
9	Cova Soterranya (Serra)	2002-2003	0.701	0.491	0.016*
10	Cueva Hermosa (Cortes de Pallás)	2002-2003	-0.239	0.057	0.846
11	Túnel de Canals (Canals)	2002-2003	0.539	0.290	0.087
12	Cueva Negra (Ayora)	2002-2003	0.775	0.601	0.435
13	Cova de la Moneda (Cotes)	2013	-0.009	0.000	0.972
14	Cueva del Perro (Cox)	2013	-0.551	0.303	0.628
15	Avenc del Puntal de Mateu (Náquera)	2013	0.234	0.055	0.464
16	Sima del Aguila (Picassent)	2013	-0.995	0.990	0.064
17	Cueva del Barranco Hondo (Cheste)	2013	-0.628	0.395	0.372
18	Cova Xurra (Gandia)	2013	-0.722	0.522	0.486
19	Cova del Ocre (Lucena del Cid)	2013	-0.810	0.656	0.015*
20	Moli de la Font (Castellón de la Plana)	2013	-0.151	0.023	0.678
21	Forat d'en Ferrás (Oropeza)	Unprotected	0.141	0.020	0.645
22	Cova Oscura (Adzaneta del Maestrat)	Unprotected	0.449	0.202	0.143
23	Cova del Onder (Aín)	Unprotected	-0.258	0.067	0.39
24	Cova del Sardiner (Sagunto)	Unprotected	-0.473	0.224	0.198
25	Avenc de Barratxina (Xixona)	Unprotected	-0.540	0.292	0.460
26	Cova de la Puntassa (Pobla de Benifassà)	Unprotected	-0.648	0.420	0.164
27	Cova de les Rates (Teulada)	Unprotected	-0.688	0.474	0.199
28	Sima de los Borreguillos (Salinas)	Unprotected	-0.193	0.0373	0.569
29	Cova de les Meravelles (Castellón de la Plana)	Unprotected	-0.648	0.420	0.164
30	Sima del Alto de Don Pedro (Macastre)	Unprotected	-0.408	0.167	0.315
31	Sima del Campillo (Tous)	Unprotected	0.048	0.002	0.928
32	Túnel de Carcalín (Buñol)	Unprotected	0.582	0.339	0.604
33	Cueva del Lago (Ayora)	Unprotected	-0.035	0.001	0.978
34	Cova de les Dones (Millares)	Unprotected	-0.019	0.000	0.988

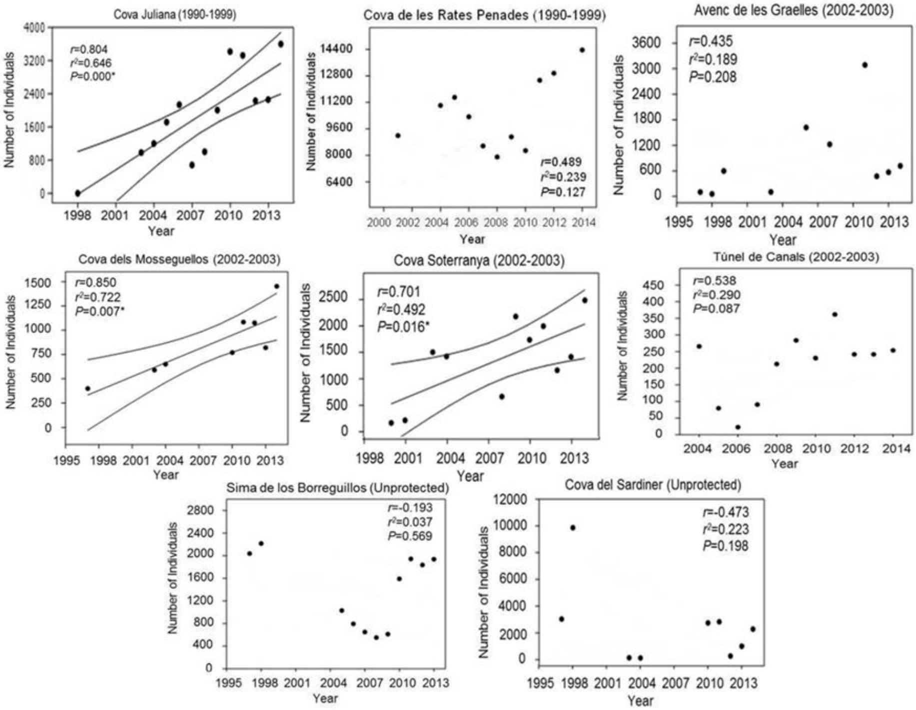


Figure 3. 5. Simple regression of roosts evaluated, considering all the populations hosting. *Significant values ($p<0.05$).

DISCUSSION

M. schreibersii, with almost 300,000 individuals, was the most abundant cave roosting bat surveyed in the East Iberian Peninsula, which coincides with patterns observed throughout Spain (Paz and Alcalde 2000). Notwithstanding, its populations did not increase in the last 12 years, which represents a stable period after the high death rates reported in 2002 in roosts in France, Spain and Portugal (Roué and Némoz 2002). *Myotis myotis/blythii* populations, as well as *M. schreibersii,* remained stable in the roosts studied during the more recent period, and represent 20% of the global Spanish population (Nogueras and Garrido-García 2007), with positive growth trends. We compared the average temperatures in May (time of the census) for the period 1997-2011 of the Valencian Community where roosts are located (where data were available); only a slight increase in 2007 (21°C) was noted, which does not allow us to indicate population declines associated with temperature. We believe that monitoring internal temperatures inside roosts would better reveal potential effects of global climate trends on cave-dwelling bat populations.

Thirteen caves were assessed before this study, and a stable trend for *Myotis capaccinii* was shown (Monsalve *et al.* 2007). Our study categorized this species population trend as “uncertain,” which is likely caused by large population fluctuations over time making it difficult to detect a clear trend. However, these results should be treated with caution, as they may only indicate changes in fluctuations censuses between the years, particularly in the "stable" and "uncertain" category, without significant differences that allowed us to determine whether there was a definite tendency to increase or decrease. Thus the TRIM program assigns these categories ("stable" and "uncertain") 6 of 9 species in the period 2003 to 2014 (Table 3. 3).

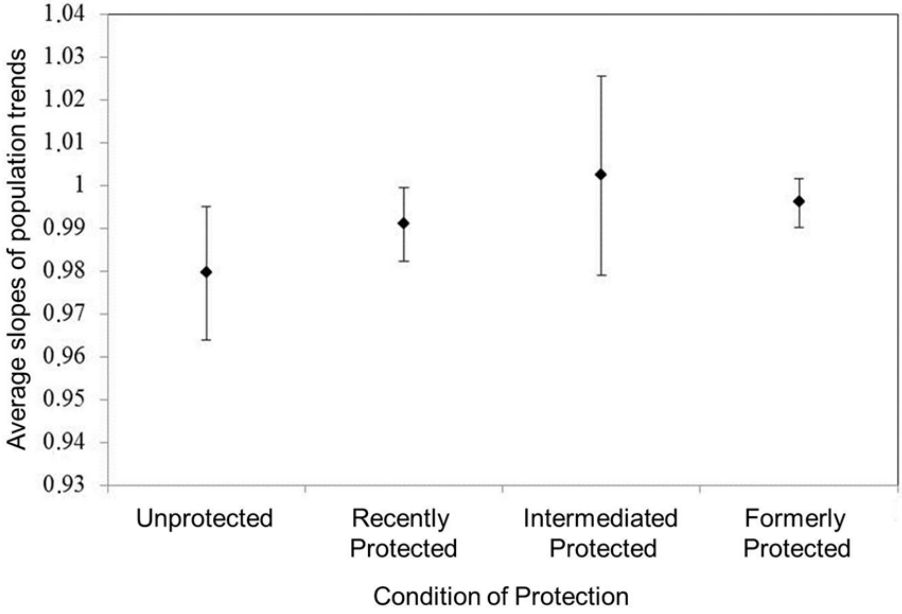


Figure 3. 6. Sample means the slopes population trends of cave-dwelling bats in the roosts with different protection conditions in the Eastern Iberian Peninsula.

Myotis capaccinii was relatively common in our study (present in 44% of the roosts studied) and is not considered a rare species in the Eastern Iberian Peninsula, unlike in other regions of Spain. It is a strictly Mediterranean species with particular requirements, and is usually occupies caves near slow-moving streams and riparian vegetation where it hunts (Almenar *et al*. 2006, Almenar *et al*. 2007, 2009, Biscardi *et al*. 2007). This fits with our finding that La Cova de Les Rates Penades (Rótova) and La Moneda (Cotes), which are caves located near water bodies, were the roosts with highest abundances of this species in our study. *Myotis capaccinii* is the only species of Iberian bat in risk of extinction according to the Spanish National Catalog of Threatened Species (Royal Decree 139/2011). This indicates the need to continue protecting its breeding and hibernation roosts, and also taking actions to conserve the adjacent riparian ecosystems (Daniel *et al*. 2008, Flanders and Jones 2009, Knight and Jones 2009, Papadatou *et al.* 2009, Flaquer *et al*. 2010).

Bat breeding colonies have disappeared in Central-Northern parts of the Iberian Peninsula, and have dropped by 20-30% in Andalusia, Southern Spain, in the last 10 years (Ainhartza *et al*. 2003, Ibáñez *et al.* 2005, Goiti and Aihartza 2007). Although *R. euryale* populations surveyed in this study have strongly fluctuated in the last decade, a possible new population rebound was observed. According to the last census in 2014, *R. mehelyi* and *R. hipposideros* were the species with the lowest abundance (Appendix 2). However, estimates indicate an uncertain trend (not significant or obvious linear trend) in *R. mehelyi* which, along with their sedentary condition, declining populations in France, fragmented geographic distribution and alterations to their foraging habitats and roosts, could exacerbate their vulnerability to extinction (Csősz *et al*. 2015). With regards to the 1020 individuals of *M. escalerai* that were censused in 2014, with an estimate close to 2000, and it is most abundant in the La Cova Juliana cave, where the largest concentration of individuals known in the Valencian Community was found. We wish to stress the importance of the Mare de Deu Shrine (Castellfort), exclusively occupied by *M. escalerai*, where large populations of this species have been previously reported. *Myotis escalerai* is considered frequent elsewhere in Spain, but not abundant (Quetglas 2007). This was corroborated by our finding that this species occupied 79% of censused caves, including unprotected caves, and showed significant population growth. On the other hand, *R. ferrumequinum* was present in 82% of the roosts, occupying a greater proportion of unprotected roosts (92.8%), showing a wide distribution and a stable population during the 2003-2014 period; therefore, we can infer its stable status in recent years. In contrast, *Myotis emarginatus* and *R. hipposideros* offer a less optimistic panorama, showing relative abundances of 0.9% and 0.1%, respectively, and less frequent occupation of the studied roosts (17.6% and 38.2%, respectively). However, when we evaluated *M. emarginatus* and *R. hippossideros* separately, a significant increase was detected, especially in recent years, which might explain the positive population trends. In order to continue controlling these populations, special attention should be paid to the caves harboring their largest populations, e.g. La Cova de los Morsseguellos (Vallada), for *M. emarginatus,* and La Cueva de Barranco Hondo (Cheste), for *R. hipposideros*.

The association of bats in roosts has frequently gone from being considered compulsory to opportunistic, and their choice depends more on the spatial availability than the particular conditions in roosts (Kunz and Lumsden 2003). Nonetheless, some species become strongly dependent on certain roosts because of their vicinity to important foraging areas and or high degrees of philopatry (Kunz 1982, Lewis 1995). The main associations observed in the evaluated roosts lie between *Myotis myotis/blythii*, *Miniopterus schreibersii* and *Rhinolophus ferrumequinum*, these species occupy the most caves, which would explain a strong association among them (Figure 3. 2). This indicates greater flexibility when selecting roosts, unlike *M. capaccinii,* which commonly occupies caves close to water bodies (Almenar *et al*. 2006), or *R. mehelyi* which prefers warm, humid caves (Csősz *et al*. 2015). This has been observed in the grouping of assemblages in the solitary habit occupied by *R. hipposideros*, particularly during breeding seasons (Migens 2007).

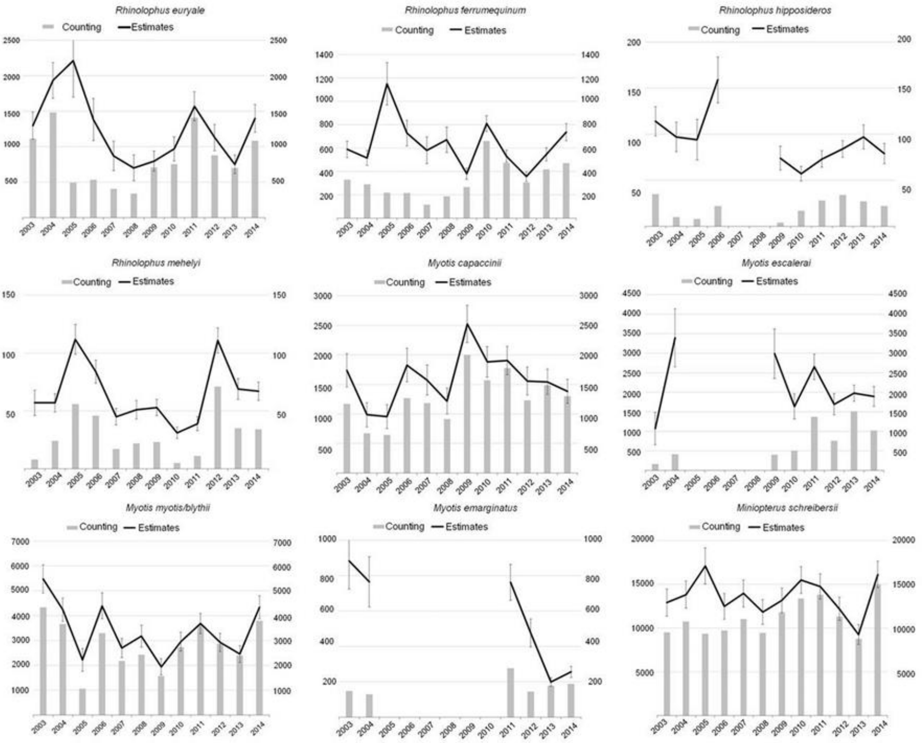
As for the effect of the protective measures taken, La Cova de les Rates Penades (Rótova), and La Cova de Juliana (Alcoi) caves are the most salient. In 2014, the former housed the most abundant populations of *Miniopterus schreibersii, Myotis myotis/blythii, M. capaccini* and *R. mehelyi*, and has been protected by peripheral fencing since 1999. The latter has been protected since 1990, and is occupied by the most numerous *M. escalerai* colony. Even though only significant improvements were found in three protected roosts, the increases in the sample mean seem to point to a positive trend for roosts with fences. This indicates the benefits associated with the physical protection of maternity colonies of these cave-dwelling bats. The low number of roosts with prolonged protection could have prevented us from detecting true population trends. Other associated factors cannot be ruled out. For example, food habitats adjacent to maternal roosts might also influence population estimates (Almenar *et al*. 2006, Biscardi *et al*. 2007). Red Natura 2000 represents the most relevant effort made to conserve species in Europe. Notwithstanding, its effectiveness has been questioned as it does not contemplate the assessment of foraging areas (Maiorano *et al*. 2007, Rainho and Palmeirin 2011), which are critical for some species (Lisón *et al*. 2013, Arthur *et al*. 2014).

Despite the positive growth in several cave-dwelling bat populations, both in protected breeding and hibernation roosts (Figure 3. 4), there is still much debate about the ideal model to limit humans access to roosts (Richter *et al*. 1993; Ludlow and Gore 2000, Pugh and Altringham 2005, Spanjer and Fenton 2005, Slade and Law 2008). However, there is little doubt that these enclosures help increase bat populations (White and Seginak 1987, Tuttle and Taylor 1998, Martin *et al*. 2000, 2003, 2006). As the conservation measures require time to become effective, the long-term population monitoring is necessary if we are to include complementary activities (managing bodies of water, preserving forestry resources, controlling pesticides on crops, etc.) which, collectively, guarantee the continuity of these species and a too useful for studying the population dynamics of cryptic species.

This long-term population trends also allow for a comparison to climate variability over the same period, while not ignoring factors such as food, roosts, reproduction and biogeography (Sherwin *et al*. 2012). Four of the seven risk factors documented for European bat species, occurred in our study: small range, cave/tree roosting, water stressed and aerial hawking. *Miniopterus schreibersii* and *Rhinolophus mehelyi* are considered two of the seven species most at risk from climate change in Europe and North Africa (Sherwin *et al*. 2012).

At biogeographical level, the Mediterranean bats seem to be the least affected by climate change, given that they have already have adapted to warmer conditions. Models predict a gradual expansion of this group to locations further towards central northern Europe in the next 40-45 years (Rebelo *et al*. 2010). *Myotis blythii, Myotis myotis and Rhinolophus euryale* would be most affected by a reduction in the habitat areas they currently occupy. The loss of roosts, the reduction in prey availability and the need for specific feeding habitats could represent a strong threat to the survival of many of these species in the near future (Russo and Jones 2003, Russo *et al*. 2004).

APPENDICES



Appendix 1. Population trends of the cave-dwelling bat species evaluated during 2003-2014. The dotted lines for some species correspond to non censused periods.

Appendix 2. Presence and percentage of the occupation of cave-dwelling bats in monitored roosts. RE: *Rhinolophus euryale*, RF: *R. ferrumequinum*, RH: *R. hipposideros*, RM: *R. mehelyi*, MC: *Myotis capaccinii*, ME: *M. emarginatus*, MES: *M. escalerai*, MM/MB: *M. myotis/blythii* and MS: *Miniopterus schereibersii*.

ROOSTS	**SPECIES**								
	RE	**RF**	**RH**	**RM**	**MC**	**ME**	**MES**	**MM/MB**	**MS**
Protected roosts									
Avenc de les Graelles (Tous)		X				X	X	X	X
Avenc del Puntal de Mateu (Náquera)	X	X		X	X	X	X	X	X
Cova de la Moneda (Cotes)	X	X			X		X	X	X
Cova de les Meravelles (Alzira)			X	X			X		X
Cova de la Punta de Benimáquia (Dènia)	X	X	X	X			X	X	X
Cova de les Meravelles (Llombai)	X	X		X	X		X	X	X
Cova de les Rates Penades (Rótova)	X	X	X	X	X			X	X
Cova dels Morsseguellos (Vallada)	X	X	X			X		X	X
Cova Juliana (Alcoi)	X	X	X	X			X	X	X
Cova Oscura (Adzaneta del Maestrat)	X	X			X	X	X	X	X
Cueva del Perro (Cox)							X		
Forat d'en Ferrás (Oropeza)	X	X		X	X		X	X	X
Cova Soterranya (Serra)	X	X				X	X	X	X
Cueva Hermosa (Cortes de Pallás)		X	X				X		
Ermita de la Mare de Deu (Castellfort)			X				X		
Sima del Aguila (Picassent)	X	X						X	X
Túnel de Canals (Canals)		X			X		X	X	X

Cueva Negra (Ayora)	X	X	X				X		X
Cueva del Barranco Hondo (Cheste)	X		X						
Cova Xurra (Gandia)	X				X		X		
Percentage of Occupation (%)	70	75	45	35	40	25	80	65	75
Unprotected roosts									
Avenc de Barratxina (Xixona)		X	X				X	X	X
Cova de la Puntassa (Pobla de Benifassà)	X	X			X		X	X	X
Cova de les Meravelles (Castellón de la Plana)	X	X			X		X	X	X
Cova de les Rates (Teulada)		X					X	X	X
Cova del Ocre (Lucena del Cid)	X	X	X	X			X	X	X
Cova del Onder (Aín)	X	X	X			X	X	X	X
Cova del Sardiner (Sagunto)	X	X			X		X	X	X
Moli de la Font (Castellón de la Plana)	X	X		X	X		X	X	X
Sima de los Borreguillos (Salinas)	X	X			X		X	X	X
Sima del Alto de Don Pedro (Macastre)	X	X	X	X	X		X	X	X
Sima del Campillo (Tous)	X	X		X	X			X	X
Túnel de Carcalín (Buñol)								X	X
Cueva del Lago (Ayora)	X	X							
Cova de les Dones (Millares)	X	X					X		
Percentage of Occupation (%)	78.6	92.8	28.6	28.6	50	7.1	78.6	85.7	85.7
% of General Occupation	**73.5**	**82.4**	**38.2**	**32.6**	**44.1**	**17.6**	**79.4**	**73.5**	**79.4**

CAPÍTULO 4

Phenology of emergence by mediterranean sympatric cave-dwelling bats during their breeding period

Miniopterus schreibersii

Foto: Steve Bourne

INTRODUCTION

The vast majority of bats are nocturnal animals that spend most of the daytime in roosts that offer stable microclimates, which they tend to leave at dusk and return at around sunrise (Aschoff 1966, Erkert 1978, Erkert 1982, Kunz 1982). However, within this general pattern, the exact timing of departure from roosts can vary as a response to selection pressure from food availability, competition and predation (Erkert 1982, Kunz 1982). Nocturnality seems to be related to an increased predation pressure to bats that fly during the daytime, which could be as much as 10-fold higher (Speakman 1991b, Rydell and Speakman, 1995). An extensive study of bat predation done in the British Isles showed that the main predators for bats are barn owls (*Tyto alba*), tawny owls (*Strix aluco*) and long-eared owls (*Asio otus*). Nonetheless, there are many other occasional daily predators with a high predation incidence, such as peregrine falcons (*Falco peregrinus*), Eurasian sparrowhawks (*Accipiter nisus*), common ravens (*Corvus corax*) or black-headed gulls (*Larus ridibundus*) (Speakman 1991a). All of them are residents in the study area and, therefore, could be candidates for predation (De Juana and Varela 2005). Nocturnality also reduces food competition between bats and diurnal birds as their ecological niches do not overlap (Jones and Rydell 1994). Individuals of many bat species emerge before it gets completely dark to take advantage of flying insect abundance peaks around dusk (Racey and Swift 1985, Rydell *et al.* 1996, Pavey *et al.* 2001). The trade-off between predation and food availability may influence the ideal emergence time for each species. Because cave-dwelling bats must leave their roosts through openings of a limited size, they have to leave individually, or within small groups, which can take a considerable time (Davis *et al.* 1962). Consequently, the time of departure may be not only linked to differences in the optimum time of emergence, but also to inter and intra-specific competition.

Variations in energy demand among individuals of the same species may also be a key factor of inter-seasonal variation in the time of daily emergence. Lactating females should emerge before pregnant females as their energetic requirements are higher (Racey and Speakman 1987, Kurta *et al.* 1989, Duvergé *et al.* 2000, Reichard *et al.* 2009). Moreover, heavily pregnant bats are expected to emerge later as they experience heavier wing loading (ratio between weight and wing surface) than during lactation. Therefore, their agility and manoeuvrability diminish, which entails a higher predation risk (Hughes and Rayne 1993, Metcalfe and Ure 1995, Duvergé *et al.* 2000). Likewise, reproductive females should tend to leave earlier than non-reproducing females or males (Kunz and Anthony 1996, Lee and McCracken 2001). In the months when juveniles are present, both colony size and food demand increase. Thus, bats need to travel longer distances to seek prey because of an increase in the intra-specific competition for food, which could mean leaving earlier and/or returning later (Kunz 1974).

Despite many studies investigating factors that affect emergence times of a single species, only one to our knowlegde have compared the emergence times of different species that share the same roost (Thomas and Jacobs 2013). In that study, researchers found inter-specific differences in the times of emergence between seven species of sympatric insectivorous bats linked to body size, foraging strategy, diet, and factors that are associated with predation risk (Thomas and Jacobs 2013). Those results are in line with other studies that compared emergence times by bats living in different roosts. For example, Jones and Rydell in 1994 investigated different emergence times between 17 bat species and found differences subjected to variation in flight technique and foraging strategy. However, they did not investigate possible intra-specific differences and the effect of the trade-off in the time of emergence. Duvergé and colleagues (2000) found that age, reproductive state and body condition influenced intra-specific differences in evening emergence time of the species *Eptesicus nilssonii*, *Rhinolophus ferrumequinum* and *R. hipposideros*. No study to date has investigated these intra-specific factors in sympatric cave-dwelling bats.

Therefore, our objective was to determine whether emergence patterns existed between the cave-dwelling bat species *Myotis blythii* (Tomes, 1857); *Myotis capaccinii* (Bonaparte, 1837); *Myotis escalerai* (Cabrera, 1904); *Myotis myotis* (Borkhausen, 1797) and *Miniopterus schreibersii* (Kuhl, 1817), which share roosts in the east of the Iberian Peninsula. We also aimed to analyse whether these patterns varied according to inter-specific differences competition for resources at distinct stages of their breeding period.

MATERIAL AND METHODS

Study Site

This study was carried out during the 2013 breeding season in four maternity roosts in the province of Valencia (the Valencian Community), E Spain (Figure 4. 1). All the roosts are natural caves whose main openings are between approximately 1.2 m and 1.75 m high, and from 1 to 2 m wide. The only exception is the Canals tunnel, which is an artificial cavity with an opening of 2.5 m high and 2 m wide, and bats can only leave through a small opening that roughly measures 30 cm x 2 m. This fact was due to an enclosure at the entrance that allows free passage of bats but prevents the visit of humans.

In Sagunto (Figure 4. 1), the cave is a cleft along the lines of a joint. Two rectilinear galleries link two openings with a perpendicular gallery around 20 m deep. The gallery total length is about 50 m and from 5 to 6 m high. The cave in Náquera has several chasms and a gallery with a total length of 165 m and 73 m deep. The tunnel in Canals is an artificial cavity whose original purpose was to establish a rail link but it was not finished. Its length is 500 m and 0 m deep. The aperture in the cave in Macastre leads to a fracture, with a chasm of 2.5 m. This charm leads to two galleries, one with 7 m and another with 10 m, which ends in a narrow well unexplored about 60 m long.

The roost in Sagunto holds important breeding colonies of *Myotis myotis, M. blythii, M. capaccinii, M. escalerai* and *Miniopterus schreibersii*. Three other cave-dwelling species have been observed in the cavity (*Rhinolophus euryale, R. hipposideros* and *R. ferrumequinum*). In Náquera, the roost has a breeding midsize colony of *M. capaccinii* and *M. schreibersii*. There is also a breeding group of *M. myotis* and *M. blythii.* Occasionally, the presence of *R. ferrumequinum* and *R. euryale* have been observed.

Figure 4. 1. Location of the four study roosts in the province of Valencia, the Valencian Community, Spain. Roosts: 'Cova del Sardiner' (Sagunto), 'Sima del Puntal de Mateu' (Náquera), 'Sima del Alto de Don Pedro' (Macastre) and 'Túnel de Canals' (Canals).

Canals hosts important breeding colony of *M. myotis* and *M. blythii*. Recently, a small breeding colony of *M. capaccinii* and *M. escalerai* has become established. The occasional presence of *M. schreibersii* and *Rhinolophus mehelyi* has been detected. Regarding the roost in Macastre, there are six reproductive species (*M. schreibersii*, *M. myotis, M. blythii, M. capaccinii, M. escalerai* and *R. euryale*). Another three species in this cave have been reported in a small numbers (*R. hipposideros, R. ferrumequinum* and *R. mehelyi*). All these data were taken from unpublished reports written by the General Board of Natural Resources and Environmental Quality of the Regional Valencian Government (Generalitat Valenciana), which has carried out a monitoring program of cave dwelling bats since 1997.

Data collection

The study was conducted from April to July 2013. Each of the four roosts were filmed one night during the last week of April, May, June and July, coinciding with new moon nights. Therefore, we were more likely to obtain higher number of individuals emerging from the roosts due to reduced lunar phobia (Morrison 1978, Erkert 1982, Jones and Rydell 1994, Rydell and Speakman 1995, Lang *et al.* 2006) although this has not been observed in the present study species. We never filmed two roosts during the same night. Emergence patterns were filmed after we observed the first individual of any species had left and lasted 60 minutes, when more than the 95% of the individuals that wanted to emerge already did (personal observations from a preliminary study; Thomson *et al.* 2010). Video and audio recordings were done simultaneously with the microphone of the ultrasound detector connected to the camera. Video recordings were done using infrared light either 810 nm (40 LEDs at a lighting angle of 10°, IRLight model IRLamp3), or IR 75W halogen spotlight with a 715nm filter (COMPUTAR, angular 42º) at the entrance of the roosts. The IR lights with the filter allowed us to record the animals without disturbing their activity (Elliott *et al.* 2006, Kunz *et al.* 2009). Recordings were done with IR light-sensitive cameras (SONY DCR-TRV33E), while sound recordings were recorded using an ultrasound detector equipped with a split frequency system (Petterson D230) attached to the camera (Rodrigues and Palmeirim 1994; Mitchell-Jones *et al.* 2007). The ultrasound detector was placed at the entrance of the roosts and was connected to the camera by a long cable. If the cave had secondary openings, those were covered with a fabric, so all individuals had to emerge by the opening that was being filmed. In all cases when present, secondary openings were closely located to the main entrance. Estimations of the colony size in the roosts were made according to the number of bats detected of each species during June. During this month, there was a larger proportion of individuals that left the roosts (personal observations), probably due to the appearence of the first juveniles (Table 4. 3), and before adults had left (Rodrigues and Palmeirim 2008; Kunz *et al.* 2009).

Capturing was carried out with a harp trap (Tidermann and Woodside 1978) to know the reproductive status of the studied species. Captures were done when individuals returned to roosts by placing the trap immediately after finishing recordings and up to approximately two hours afterwards. Thus, we ensure that these captures had any effect on the emergence patterns. Moreover, the decision was made in order to disturb the bats as little as possible since they had already fed and, therefore, suffered less stress. Individuals were marked with an indelible red marker (Sharpie®) on the ear to not measure double captures, and the following details were noted: capturing time, species, age class, gender and reproductive status. We follow the criteria of Anthony (1988) for the allocation of the age class and Racey (1988) to determine the reproductive status, which was meant to be a sample of the population and not a reproductive census. The categories for adult females were: nulliparous, pregnant, lactating, postlactating and non-reproductive. These stages were determined by direct palpation of the abdomen, development of the nipples and milk production (Racey 1988, Heideman 1988, Kunz *et al.* 1996). To reduce errors in pregnancy determination, the stage of pregnancy was allocated exclusively in the mid and final phases of the pregnancy, when the distention of the lower abdomen and palpation of the fetus were clearly evident (Racey 1988). Similarly, the lactation stage was adjudicated only when observed in combination with nipple lengthening, alopecia around the nipple, and the appearance of milk at minimal pressure on the mammary gland (Kunz *et al.* 1983). The appearance of the nipples in the postlactating females was very similar to those of the lactating females, and only distinguished by a slightly darkened and hardened terminal portion in the nipples and lacking milk (Racey 1988). All protocols followed guidelines approved by the American Society of Mammalogists (Gannon and Sikes 2007), and permits to access roosts and to capture bats were approved by the Regional State Environmental Office of the Regional Valencian Government (Generalitat Valenciana) and the Canals Town Council (number: 121/13-FAU13_019).

Species Identification

We used the video together with the audio to count the emergence of each individual and perform their specific identification. Specific identifications were made by a spectrogram analysis using the GRAM 5.1.7. software (R. S. Horne). We followed Russo and Jones (2002) for the specific range calls and species identification. For species in which echolocation call parameters overlap, we also relied upon visual cues like the size of the animal or the flight pattern. When needed, we analysed in slow motion the video (with the corresponding adjustment in the audio frequency), and as many times as required to performance the correct identification. We did not distinguish between large *Myotis* (*M. myotis* and *M. blythii*) given both their morphological and spectrogram similarities, and we considered them to form the same group. As the emergence rate from the Sima del Alto de Don Pedro Cave (in the town of Macastre) was very high, it was not possible to separate *M. capaccinii* and *M. escalerai* in June and July. Therefore, we did not include these data in the analysis.

Data Analysis

The emergence time data was taken after the first individual left its roost, both per month and roost. Data was expressed as number of bats of each species that emerged from the roost during 2-minute intervals. To be able to compare between months and roosts, we transformed the time of emergence by adding the time between the official sunset time to the time the video started (when the first individual left its roost). A GLMM-Poisson was run by taking these variables: emergence time (minutes after sunset) as the response variable, and month, species and roost as factors. The emergence time fitted a Poisson distribution positively skewed. Month was taken to compare between different reproductive stages. Because the reproductive stage was not the same for all the bats in the roosts at the same time, this allowed us to see whether emergence patterns varied during the breeding season. The multiple comparison *post hoc* analysis was made using sequential Sidak method for both analyses. The sequential Sidak method gives slightly smaller adjusted p-values than sequential Bonferroni, but it guarantees the strict control of the familywise error rate when the comparisons are independent. All the statistical analyses were performed with SPSS 22.0. For all the analyses, a *p* value below 0.05 was considered significant.

RESULTS

In the GLMM-Poisson analysis with all the data from the different roosts, we compared only the species *M. schreibersii, M. myotis/blythii, M. capaccinii* and *M. escalerai,* as they were found in most of the studied roosts. Figure 4. 2 shows the peak of emergence (minutes after sunset) within the months of April, May, June and July for the pooled data from all roosts. This analysis showed significant differences in the emergence time between species and months and their interaction, but not between roosts (Table 4. 1). When controlling for the roost factor, we found that overall *M. schreibersii* was the first to emerge after sunset and took a mean time of 34 minutes (*post hoc* Sidak, $p<0.0001$). It was followed by *M. myotis/blythii* and *M. capaccinii* about 9 minutes later (*post hoc* Sidak, $p=0.673$), and then by *M. escalerai* around 5 minutes afterwards (*post hoc* Sidak, $p<0.001$; Table 4. 2). We also found significant differences for the month factor among all the species. Bats emerged as a whole earlier in June in a mean time of 35 minutes after sunset when controlling for the factor roost (*post hoc* Sidak, $p<0.0001$).

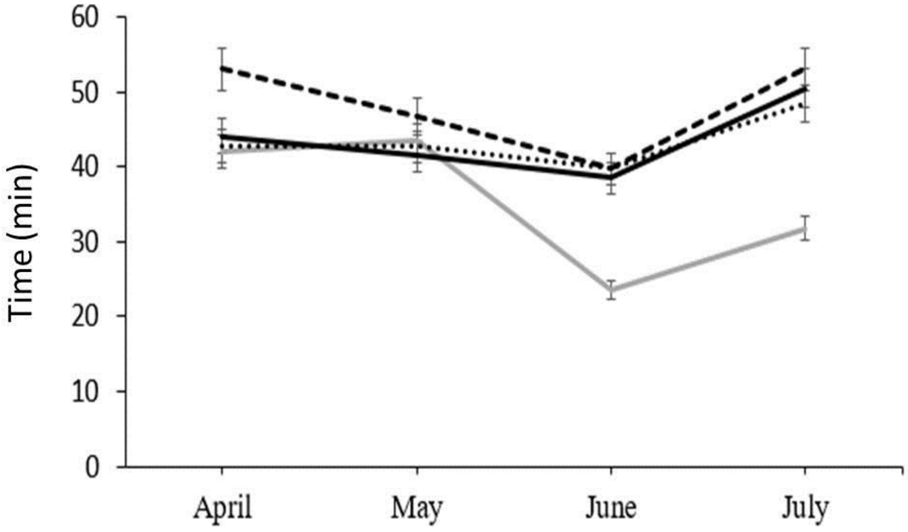


Figure 4. 2. Peak emergence times (minutes after sunset) ± SE for bat species *Miniopterus schreibersii* (grey line), *Myotis myotis/blythii* (black point line), *Myotis capaccinii* (black continuous line) and *Myotis escalerai* (black dashed line) within the months of April, May, June and July controlling for the factor roost.

Table 4. 1. GLMM-Poisson analysis showing the effect of species, month and roost on emergence time considering all the roosts information in the analysis. The statistic for species and month was F and for roost Wald Z. Only the species *Miniopterus schreibersii, Myotis myotis/blythii, Myotis capaccinii* and *Myotis escalerai* were included.

Parameter	*F (*Wald *Z)*	df 1	df 2	*p*
Species	809.273	3	11.348	<0.0001
Month	762.920	3	11.348	<0.0001
Species x Month	525.349	9	11.348	<0.0001
Roost	1.221	3	-	0.222

Table 4. 2. Estimated mean emergence times of bats ± SE in minutes for pooled data and controlling for the roost factor, counted from the official sunset time in each roost. MS= *Miniopterus schreibersii*, MM/MB= *Myotis myotis/blythii*, MC= *Myotis capaccinii*, MES= *Myotis escalerai*.

	April	**May**	**June**	**July**	Average
MS	41.98 ±2.26	43.41 ±2.24	23.60 ±1.22	31.72 ±1.63	34.18 ±1.76
MM/MB	42.75 ±2.23	42.62 ±2.20	39.69 ±2.06	48.46 ±2.51	43.27 ±2.23
MC	44.08 ±2.37	41.42 ±2.15	38.47 ±2.03	50.49 ±2.62	43.39 ±2.24
MES	53.01 ±2.84	46.71 ±2.45	39.73 ±2.10	53.00 ±2.77	47.79 ±2.47
Average	45.25± 2.35	43.49± 2.24	34.59± 1.78	45.03± 2.32	

They left around 8 minutes later in May (*post hoc* Sidak, $p<0.0001$), and about 2 minutes later in July and April, with no significant differences between these latter two months (*post hoc* Sidak, $p=0.547$) (Figure 4. 2; Table 4. 2).

When considering month per month and after controlling for the factor roost, we found that *M. schreibersii* left the roots significantly first in June and July (*post hoc* Sidak, $p<0.0001$). However, in April the emergence time of this species was not significantly different from the *M. myotis/blythii* group or *M. capaccinii* (*post hoc* Sidak, $p>0.05$). In May *M. schreibersii* emerged significantly after *M. capaccinii* and *M. myotis/blythii* (*post hoc* Sidak, $p<0.05$). The *M. myotis/blythii* group emerged significantly in second place in May and July (*post hoc* Sidak, $p<0.05$). In June, there were no significant differences with *M. capaccinii* or *M. escalerai* (*post hoc* Sidak, $p>0.05$). *Myotis capaccinii* emerged significantly first in May (*post hoc* Sidak, $p<0.01$) and in third place in July (*post hoc* Sidak, $p<0.001$). *Myotis escalerai* emerged significantly last in April, May and July (*post hoc* Sidak, $p<0.001$).

When considering species separately and after controlling for the factor roost, we found that all the species emerged earlier in June (*post hoc* Sidak, $p<0.001$). *Miniopterus schreibersii* emerged secondly in July, then in April and finally in May (*post hoc* Sidak, $p<0.05$). In contrast, all the *Myotis* emerged secondly in May (*post hoc* Sidak, $p<0.001$), but in the *M. myotis/blythii* group this month was not significantly different from April (*post hoc* Sidak, $p>0.1$). The genus *Myotis* emerged latterly in July (*post hoc* Sidak, $p<0.001$), but in *M. escalerai* this month was not significantly different from April (*post hoc* Sidak, $p>0.1$).

In reproductive data terms, the pregnant females of all the species were observed mainly in April and May, and lactating females in May and June (Table 4. 3). Only lactating *M. capaccinii* females appeared in July (Table 4. 3).

DISCUSSION

During our study, we registered an event of predation by tawny owl (*Strix aluco*). This species has been observed previously in the vicinity of these roosts, and is a known predator of bats (Speakman 1991a, Lesiński *et al.* 2009, Spitzenberger *et al.* 2014). Hence, predation pressure may to explain the earlier emergence time of *M. schreibersii* and posterior emergence of the large-sized *Myotis* and *M. capaccinii* due to faster, larger sized species are expected to leave earlier (Jones and Rydell 1994, Rydell *et al.* 1996, Thomas and Jacobs 2013). *Miniopterus schreibersii* has a high wing loading, about 10.2 Nm^{-2}, and longer and narrower wings, which means a high aspect ratio of approximately 7.0 ($[\text{wing length from tip to tip}]^2$/wing surface; Norberg and Rayner 1987; Neuweiler, 2000). High wing loading and aspect ratio make them fast animals that hunt in places, but with little manoeuvrability (Norberg and Rayner 1987, Neuweiler 2000).

Because the M. myotis/blythii group are large-sized heavy species, wing loading was 11.2 Nm-2, but their aspect ratio was lower (6.3), which make them fast fliers in clutter-edge habitats (Norberg and Rayner 1987, Neuweiler 2000). M. escalerai had a light wing loading, 6.1 Nm-2, and a low aspect ratio value (6.4), which correlates with slow yet highly manoeuvrable flights in clutter areas (Norberg and Rayner 1987, Neuweiler 2000).

Table 4. 3. Reproductive data of adult females and juveniles of the species *Miniopterus schreibersii, Myotis myotis, Myotis blythii, Myotis capaccinii* and *Myotis escalerai*. NR = Not Reproductive, P = Pregnant, L = Lactation, PL = Post-lactation, J = Juvenile. The percentage of each reproductive status is shown in brackets.

		NR	**P**	**L**	**PL**	**J**
M. schreibersii	April	1 (1)	161 (99)	0	0	0
	May	0	33 (97)	1 (3)	0	0
	June	4 (50)	1 (12)	3 (38)	0	0
	July	5 (4)	0	0	0	130 (96)
M. myotis	April	2 (4)	44 (96)	0	0	0
	May	0	6 (86)	1 (14)	0	0
	June	5 (19)	0	2 (7)	0	20 (74)
	July	0	0	0	0	6 (100)
M. blythii	April	1 (8)	11 (92)	0	0	0
	May	0	5 (100)	0	0	0
	June	0	0	4 (100)	0	0
	July	0	0	0	0	12 (100)
M. capaccinii	April	0	13 (100)	0	0	0
	May	0	7 (70)	3 (30)	0	0
	June	0	0	7 (30)	6 (26)	10 (44)
	July	0	0	1 (5)	8 (38)	12 (57)
M. escalerai	April	0	3 (100)	0	0	0
	May	0	1 (25)	3 (75)	0	0
	June	0	0	2 (18)	0	9 (82)
	July	1 (50)	0	0	0	1 (50)

Myotis capaccinii has a wing loading of 10.5 Nm^{-2}, but there is not data available on the aspect ratio, which might be presumably around 6.4 like the other *Myotis* (Norberg and Rayner 1987). Therefore, *M. schreibersii* fly relatively faster and consequently would be more likely to escape predators. In size terms, the *M. myotis/blythii* group were the largest of all the analysed species (forearm: 56.5-62.3 mm, weight: 21.0-35.0 g and 50.5-62.0 mm, 18.0-29.5 g, respectively; Garrido-García and Nogueras, 2007; Nogueras and Garrido, 2007), followed by *M. schreibersii* (42.9-49.9 mm, 10.1-20.8 g; De Lucas, 2007), *M. capaccinii* (38.2-44.6 mm, 5.5-15.0 g; Monsalve *et al.* 2007), and the smallest species was *M. escalerai* (35.6-41.9 mm, 6.4-8.5 g; Quetglas 2007) which barely differed from *M. capaccinii*. Therefore, size and mainly speed could explain its emerge earlier than all the others due to a lower predation pressure. Those results are in line with Thomas and Jacobs (2013) who tested whether the emergence times amongst seven species of sympatric insectivorous bats were explained by predation risk, and found that larger, faster flying bat species emerged earlier than smaller, slower flying species. However, they found that clutter foragers emerged earlier than clutter-edge and open foragers (Thomas and Jacobs 2013). Contrarily, we found that clutter-edge foragers like the *M. myotis/blythii* group and especially open foragers as *M. schreibersii* tended to emerge earlier than clutter foragers like *M. escalerai* (Norberg and Rayner, 1987; Schoeman and Jacobs, 2008).

The recordings indicated that individuals had a tendency to emerge accompanied by other individuals of either their same species or another species, followed by time lapses during which no bats emerged (personal observations). This fact may relate to a dilution effect for potential predators (Fenton *et al.* 1994, Petrželková and Zukal 2001). Our study indicated that the largest number of individuals of any species left close to dusk and more sparsely at later hours, especially the species that left earlier. This peak could be accounted by the trade-off between leaving early to benefit from better feeding opportunities, and leaving late to avoid greater predator pressure (Racey and Swift 1985, Rydell *et al.* 1996, Pavey *et al.* 2001). The first bat species' emergence time could also be related to colony size because the dilution effect is stronger in colonies with more individuals, which means that individuals could leave earlier (Fenton *et al.* 1994). In all the roosts in which the studied species were present, the largest colony was the *M. schreibersii* one. Therefore, it would be reasonable to expect *M. schreibersii* to leave earlier than the other species, as its colony size was larger. However, this fact could be the result of intra-specific competition. The bigger the colony size is, the larger the number of intra-specific competitors for feeding opportunities, hence increasing the probability of flying longer distances to seek prey (Kunz 1974). More data is needed to back this possibility.

Another predation-related factor that could affect bat emergences is light intensity (Lang *et al.* 2006, Mello *et al.* 2013). Flights inside roosts close to openings can allow bats to evaluate the levels of light outside before emerging and starting to forage (Twente 1955). As we took the data during new moon nights, this behavior may relate to the optimum light intensity to emerge. However, we observed this behavior in the *Myotis* species but not in *M. schreibersii,* so it might simply be a case of flight warm-up (Cowles 1947).

Energy requirements could explain the differences we found between months (Lee and McCracken 2001). In the months when females are lactating, the individuals of these species are expected to emerge sooner than in months when females are pregnant. The reason may be the higher energetic requirements of the lactating females (Racey and Speakman 1987, Kurta *et al.* 1989, Duvergé *et al.* 2000, Henry *et al*. 2002, Reichard *et al.* 2009). For instance, females of *Myotis lucifugus* required an average of 33.7 kJ d^{-1} of assimilated energy in pregnancy compared to 41.3 kJ d^{-1} during lactation (Henry *et al*. 2002). Moreover, pregnant females displaying less agility and diminished manoeuvrability as they are heavier (Hughes and Rayner 1991, Metcalfe and Ure 1995, Duvergé *et al.* 2000). Alternatively, species may leave their roosts earlier during lactation, as the need to return during the night to feed offspring may limit foraging distances (Kurta *et al.* 1989). The home range of Myotis lucifugus dropped by 51% between pregnancy and lactation, resulting in a 35% decrease in flight distances due to the need of feeding their offspring (Kurta *et al.* 1989). Consequently, greater competition, and lower food availability near roosts might contribute to earlier emergence to take advantage of the dusk insect peak. Hence, species may be expected to leave earlier in June, then in May, and finally in April and July (Table 4. 2). Generally, our data indicated that *Myotis* individuals left earlier in June and then in May (Figure 4. 2; Appendix 1), and *M. schreibersii* emerged earlier in June and then in July (Figure 4. 2; Appendix 1). Our results are consistent with energy requirements as a cause of the differences in emergence between months in the genus *Myotis*, as bats always left earlier in the months when more lactating females were present. Although *M. schreibersii* also left earlier in June, the fact that they left sooner in July than in May may imply other variables acting on this species. One possible factor is the presence of juveniles. It is unlikely that juveniles emerge earlier, due to the fact that they are still suckling. This has been confirmed with *Myotis* species (Kunz 1974, Audet 1990, Kunz and Anthony 1996, Duvergé *et al.* 2000). Moreover during the initial flights they can be more vulnerable to predation (Hughes *et al.* 1995). However, other studies reported the earlier juvenile emergence of juveniles (Lee and McCracken 2001, Reichard *et al.* 2009). It is possible that juveniles of this species were more matured and emerged earlier as they were weaned (Reichard *et al.* 2009). Therefore, we should consider juveniles as a possible factor of early *M. schreibersii* emergence in July of the *M. schreibersii* species. Further studies are required to evaluate possible reasons.

Prey selectivity could be another factor that influences intra-specific differences (Bell 1982, Jones and Rydell 1994). Bats that specialize in insects that are active only in complete darkness (moths) would not benefit from emerging sooner as it would be more harmful given the increased predation risk. Conversely, bats that hunt insects that are active at twilight would emerge while they are most active (Bell 1982, Jones and Rydell 1994). We were unable to assess this aspect because the diet of most of the studied species in the Iberian Peninsula remains unknown. Diet could also change spatio-temporally.

In conclusion, there is evidence of different emergence patterns depending on the species and the season. Predation related factors such as wing loading, aspect ratio and size (which affect speed flight and manoeuvrability), could explain differences between species. Colony size could also influence the predation pressure due to a dilution effect.

However, this would affect also intra-specific competition and, therefore, be related to energetic requirements. Females lactating could explain the differences between the emergence time we observed between month due to higher energetic requirements, and the higher predation pressure on pregnant females. Further studies are needed to assess the influence of the diet, average distance to seek prey and the effect of the colony size.

CAPÍTULO 5

Reproductive phenology of cave-dwelling bats in the Eastern Iberian Peninsula and its conservation implications

Myotis capaccinii

Foto: Marjorie Machado

INTRODUCTION

Bats are characterized by several distinctive adaptations, among which stand out their capability of flying, echolocation for orientation and the use of a wide spectrum of trophic resources and strategies for obtaining them (Barclay and Harder 2003). This has allowed them to occupy a large variety of habitats and reach a high taxonomic diversity (Aguirre *et al*. 2011, Russo 2015, López-Baucells *et al*. 2016). Even from the reproductive point of view, bats show various strategies that allow them to adjust their energetic balances and maintain their populations (Racey and Entwistle 2000, Jones and MacLarnon 2001). The theory of life histories predicts that in a type of species with a high survival of adults, the trend is to avoid reproducing in unfavourable periods or when their populations face important declines (Thompson 1987, Hoyle *et al*. 2001, Wilkinson and South 2002). Despite being tiny mammals, bats use to have only one or two pups per reproductive event in temperate areas, occurring variable gestation periods in tropical areas (Happold and Happold 1990). Moreover, they tend to be very long-lived (Gaisler 1989, Barclay and Harder 2003), so that successful reproductive events and stable conditions in roosts could guarantee stable populations through time.

There are global efforts for protecting these species and their environments (Maiorano *et al*. 2007, Battersby 2010, Arthur *et al*. 2014, Berthinussen *et al*. 2014). But there is also a need to evaluate if these efforts really lead to the maintenance or recovering of bat populations or if is necessary to reorient the actions (Lisón *et al*. 2013). Additionally, it is necessary to evaluate nearby habitats and foraging areas, as they are essential requirements for the selection of particular maternal refuges in certain species (Arthur *et al*. 2014).

Ten of the 22 recorded species in the Valencian Community are cave-dwelling bat and all of them are included in some sort of threat category or have insufficient data about their biology and population status (Palomo *et al*. 2007). At the present, *M. capaccinii* is the specie with the highest threat, being considered as "in danger of extinction" in whole Spain by the Spanish Catalogue of Endangered Species (Royal Decree 139/2011 of the Spanish Ministry of Natural, Rural and Marine Environment 2011). The eastern Iberian populations of this species are among the most important, representing about 30% of the known population in whole Western Europe (Hutson *et al*. 2001, Monsalve *et al*. 2007, Monsalve 2012).

The objective of this study was to describe the reproductive phenology of six cave-dwelling bats and to determine their reproductive and productivity rates. Finally, we evaluated the conservation efforts implemented in their refuges and influence areas in order to improve their success.

MATERIALS AND METHODS

Between April and June (reproductive period of the species) of 2013 and 2014 we captured individuals belonging to six species: *Myotis myotis*, *M. blythii*, *M. capaccinii*, *M. escalerai*, *Miniopterus schreibersii*, and *Rhinolophus euryale*. All captures were made in five different refuges once per month. These roosts are registered in the LIFE Project in the Valencian Community: Cueva del Sardiner (Sagunto), Cueva de la Sima de Don Pedro (Macastre), Cueva de las Maravillas (Llombai), Túnel de Canals (Canals) and Cueva Puntal de Mateo (Náquera) (Figure 5. 1). The access to the latter three is restricted by perimeter fencing as they are considered "Special Conservation Areas" (Zonas Especiales de Conservación, ZEC), since 2002, 2003 and 2012, respectively.

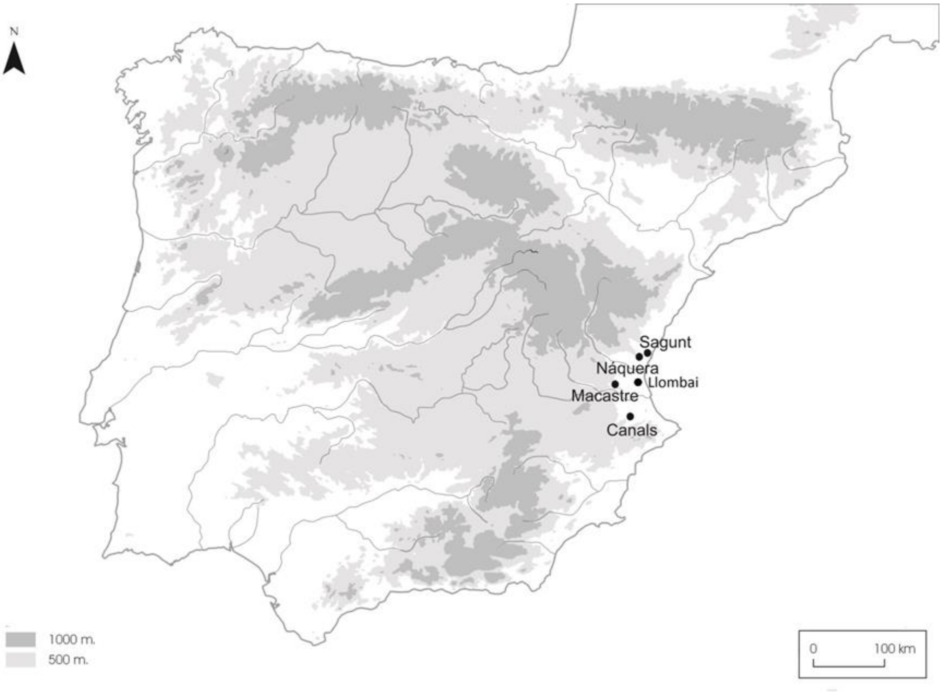


Figure 5. 1. Location of the five study roosts in the province of Valencia, the Valencian Community, Spain. Roosts: 'Cova del Sardiner' (Sagunto), 'Sima del Puntal de Mateu' (Náquera), 'Cova de les Maravelles' (Llombai), 'Sima del Alto de Don Pedro' (Macastre) and 'Túnel de Canals' (Canals).

We captured individuals using a standard folding harp trap with 1.5 m^2 action area (Tuttle 1974, Tidemann and Woodside 1978, Kunz and Kurta 1988, Francis 1989, Álvarez 2004), which is known to cause less stress and to be more efficient than mist nets (Tidemann and Woodside 1978). We decided to install the trap at the entrance of each roosts once the bats had emerged, in order to minimize the stress for individuals. The trap was active between 23:00 and 02:00 hours (when the bats returned to the roost).

We followed Anthony (1988) for the assignation of the age category and Racey (1988) for determining the reproductive condition. We estimated the relative age of each individual by the combined observation of the fusion between epiphysis-diaphysis and metacarpus-falange of the III finger; also using the fur colouring and body mass as identification recourse. The following categories were considered: juveniles (not fused) and adults (fused). For adult females we distinguished the following reproductive stages: nuliparous, pregnant, lactating, post-lactating and not reproductive. These conditions were determined by directly touching the abdomen, the nipple development and milk production (Racey 1988, Heideman 1988, Kunz *et al*. 1996). In order to avoid errors when determining pregnancy we only assigned to this group females with middle and late stage pregnancy (when the distension of the lower abdomen was clearly visible and the fetus clearly touchable) (Racey 1988). Similarly in the case of lactating, we only assigned to this group individuals with the combination of nipple elongation, alopecia around the same and milk emerging with minimal pressure on the mammal gland (Kunz *et al*. 1983). The nipple appearance in post-lactating females was very similar to lactating females, only a bit darker and hardened at the terminal portion and without milk production (Racey 1988). We marked temporarily individuals with a waterproof marker on one ear, in order to avoid an overestimation, given that the individuals tend to enter and emerge of the roosts several times in one night. Finally, we released individuals inside the refuges.

We estimated the capture success (S) (individuals/hour/night), standardizing the total number of individuals captured with the sampling effort (hours/trap/night). To calculate the reproductive rate, we included the proportion of adult reproductive females (pregnant, lactating and post-lactating) (Barclay 2004), and we considered the number of reproductive females in relation to the total of adult females. We defined the productivity rate as the relation between the proportion of juveniles and reproductive females (Barclay 2004). Finally, we determined the sex ratio for each species, including adults and juveniles.

RESULTS

We captured a total of 1224 individuals (724 females and 500 males), with a sampling effort of 96 hours/trap/night and a capture success of 12.75 individuals/hour/night. *Miniopterus schreibersii* was the most represented (53.76%), being the most captured in four of the five refuges. It is followed by *Myotis myotis* (16.42%), *Myotis capaccinii* (11.68%), *Myotis blythii* (8.74%), *Myotis escalerai* (3.84%) and *Rhinolophus euryale* (5.56%). We also captured other species of bats (less representative), as *R. ferrumequinum* (3 ind.)*, R. hipposiderus* (4 ind.) and *M. emarginatus* (1 ind.), which were not considered in the analysis.

The sex ratio (males: females) showed an important presence of males in maternal refuges, even being higher than females in the case of *M. capaccinii* (1:0.96) and *R. euryale* (1:0.92). Whilst in the other species, females were more abundant *M. schreibersii* (0.65:1), *M. escalerai* (0.65:1), *M. myotis* (0.3:1) y *M. blythii* (0.25:1) (Figure 5. 2).

In general, we observed a high proportion of females involved in the reproductive process, being *M. capaccinii* the species with a higher percentage of pregnant, lactating or postlactating, with 98.1%. It was followed by *M. escalerai* (95%), *M. schreibersii* (91.8%), *M. blythii* (90.3%), *M. myotis* (90.1%) y *R. euryale* (89.2%) (Table 5. 1).

Juveniles represented the 35.9% of the population in the case of *M. schreibersii,* 29.8% in *M. escalerai*, 28.4% in *M. myotis*, 27.1% in *M. blythii,* 23.1% in *M. capaccinii* and 20.6% in *R. euryale* (Table 5. 2).

All species presented mid to late stage pregnant females from April (Figure 5. 3). The presence of lactating females in may leads to the supposition that the pups are born during this month. The juveniles were capable of flying beginning in June, with the maximum on July. In the case of *M. schreibersii* and *M. blythii* we observed a delay of the apparition of lactating females beginning in June, with the presence of juveniles in July. This pattern was observed in 2013 and 2014.

The reproductive rates of all species were high, especially in the case of *M. capaccinii* (0.98); the lowest rate corresponded to *R. euryale* (0.89) (Table 3). Nevertheless, productivity rates resulted to be lower in relation to reproductive rates, excepting for *M. schreibersii* (1.0) (Table 5. 3). This suggests that 89 to 98% of females participated in the reproductive event during the study period, with a productivity between 52 and 100%. Regarding the productivity rates, the 100% corresponded with *M. schreibersii*, meaning that a 100% of females contributed independent juveniles. The lower extreme (52%), corresponded with *M. blythii*, meaning that this species only contributed with 52% of the juveniles.

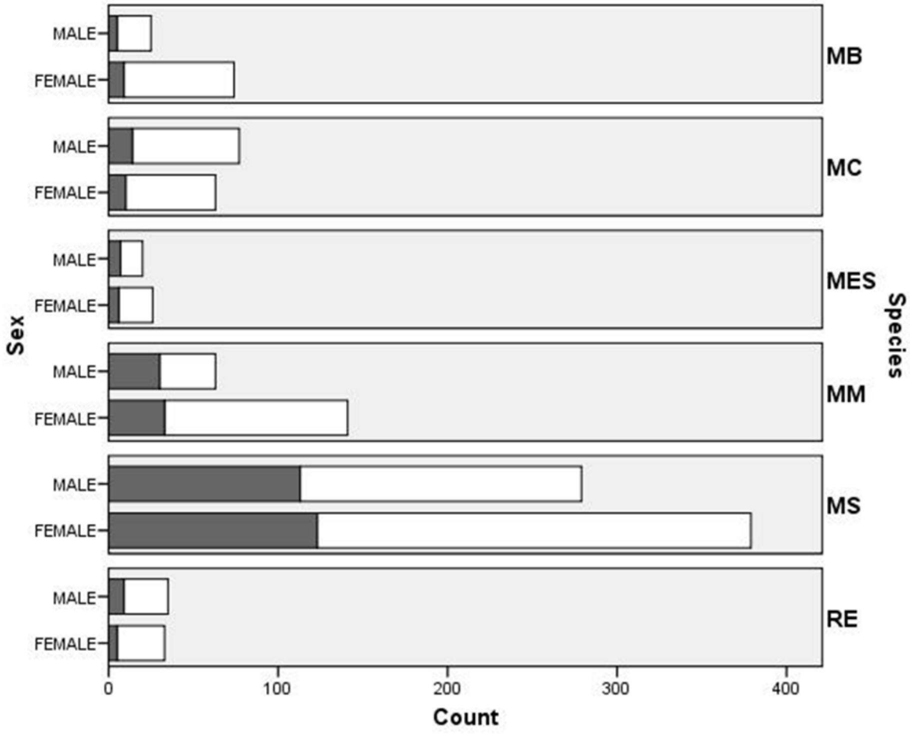


Figure 5. 2. Number of adults (gray bars) and juveniles (white bars) by sex during 2013 and 2014. MS= *Miniopterus schreibersii*, MC= *Myotis capaccinii*, MES= *Myotis escalerai*, MM= *Myotis myotis*, MB= *Myotis blythii* and RE= *Rhinolophus euryale.*

Table 5. 1. Number of adult females of the species of cave bats considered during 2013-2014, according to their reproductive condition. MS=*Miniopterus schreibersii*, MC= *Myotis capaccinii*, MES= *Myotis escalerai*, MM= *Myotis myotis*, MB= *Myotis blythii* and RE= *Rhinolophus euryale*.

	SPECIES						
REPRODUCTIVE CONDITION	**MS**	**MC**	**MES**	**MM**	**MB**	**RE**	**TOTAL**
PREGNATE	229	23	7	79	20	13	371
LACTANT	6	15	9	21	36	12	99
POST-LACTANT	0	15	3	0	0	0	18
NULIPAROUS	14	1	1	8	4	3	31
NO REPRODUCTIVE	7	0	0	3	2	0	12
TOTAL	256	54	20	111	62	28	531

Table 5. 2. Adults and juveniles of cave-dwelling bats during 2013-2014. Adult females are shown in parenthesis. MS=*Miniopterus schreibersii*, MC= *Myotis capaccinii*, MES= *Myotis escalerai*, MM= *Myotis myotis*, MB= *Myotis blythii* and RE= *Rhinolophus euryale*.

ETARY CATEGORIES	**SPECIES**						
	MS	**MC**	**MES**	**MM**	**MB**	**RE**	**TOTAL**
JUVENILES	236	33	14	57	29	14	383
ADULTS	422 (256)	110 (54)	33 (20)	144 (111)	78 (62)	54 (28)	841 (531)
TOTAL	658	143	47	201	107	68	1224

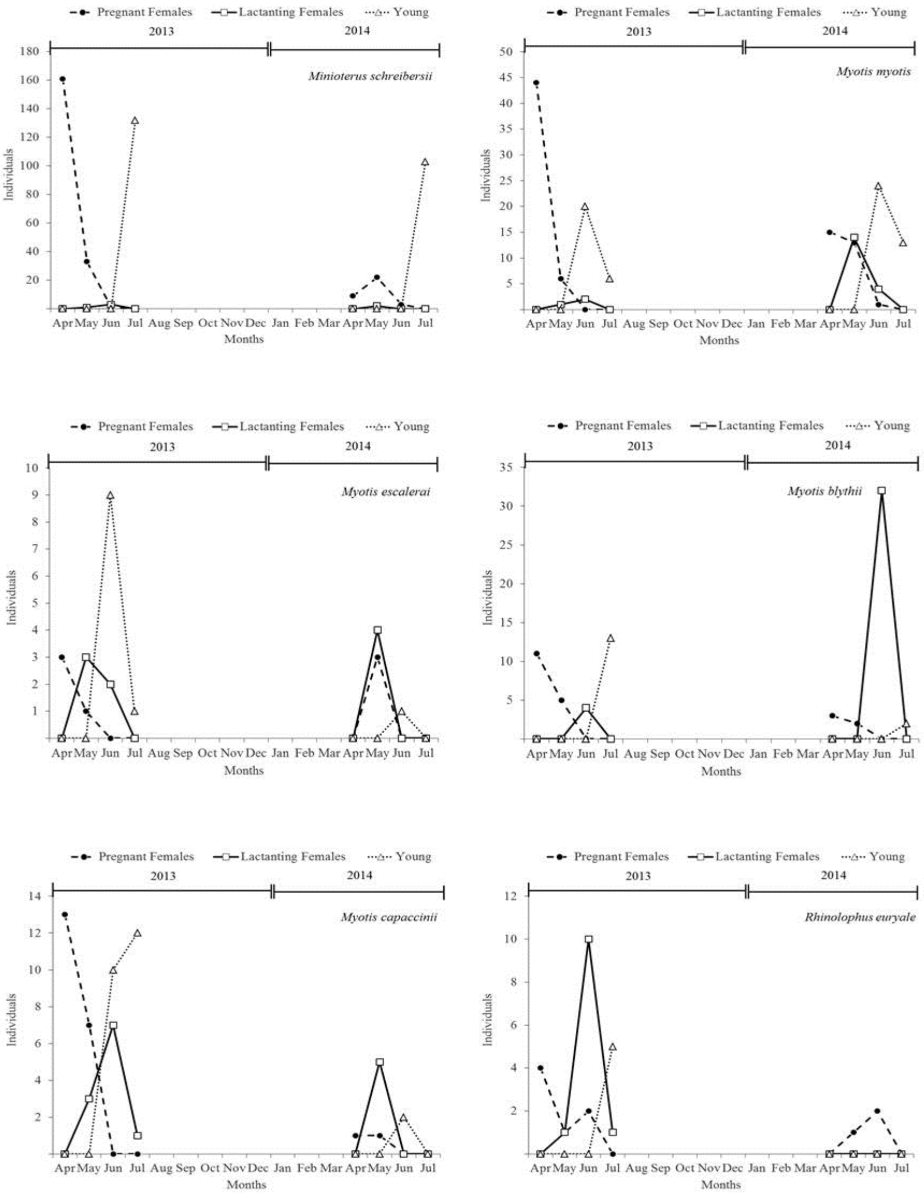


Figure 5. 3. Reproductive fenology of *Miniopterus schreibersii, Myotis capaccinii, Myotis escalerai, Myotis myotis, Myotis blythii* and *Rhinolophus euryale* in the Eastern Iberian Peninsula, in the period 2013 and 2014.

Table 5. 3. Reproductive and productivity rate of cave-dwelling bats in the east of Iberian Peninsula during 2013-2014. MS=*Miniopterus schreibersii*, MC= *Myotis capaccinii*, MES= *Myotis escalerai*, MM= *Myotis myotis*, MB= *Myotis blythii* and RE= *Rhinolophus euryale*.

	SPECIES					
INDEX	MS	MC	MES	MM	MB	RE
Reproductive rate	0.92	0.98	0.95	0.90	0.90	0.89
Productivity rate	1.0	0.62	0.74	0.57	0.52	0.56

DISCUSSION

Miniopterus schreibersii is the most abundant cave-dwelling bat in the eastern Iberian Peninsula, with very stable populations, at least in the last 12 years (Machado *et al*. 2017). Moreover this species has a good prognostic from the reproductive point of view, given that it presents high reproductive and productivity rates. This means that the energetic investment of females during the reproductive period culminates into an important contribution of new individuals to the population. Lower but equally important values of productivity are shown by *M. escalerai* and *M. capaccini.* With high reproductive rates, this species still can contribute between 62 and 74% of offspring. *Myotis myotis, M. blythii* and *R. euryale* showed a more modest juvenile production, (about 50%). This is equally important, especially for the last species, as it has less stable population trends (Machado *et al*. 2017). Periods with adverse climatic conditions, low availability of resources or an energetic maladjustment could lead to spontaneous aborts or that not all females participate in the reproduction (Myers 1977, Racey and Entwistle 2000). There are reports of females that went to colder roosts in order to delay the pregnancy (Balmori 1999). It is also known that young females do not tend to participate in the reproduction, directing energy inputs to growing and energy storage (Kunz and Orrell 2004). These strategies guarantee saving energy, the successful ending of the reproduction or the possibility to participate in the next event in better conditions.

However, in this study we do not have data regarding the survival of young, so that we only refer to the pregnancies that apparently ended successfully and produced independent flying juveniles. The juveniles were capable of flying when about two weeks old (Balmori 1999). The thermal conditions inside the refuges also can affect the fetal development rate, the growing of pups and even the milk production (Tuttle and Stevenson 1982, Zahn 1999, Racey and Entwistle 2000). Moreover, the selection of safe roosts also means saving the energy the females would invest in flying with their However, in this study we do not have data regarding the survival of young. Indeed, flying with However, in this study we do not have data regarding the survival of young is very energy consuming, given that the higher weight increases wing loading and reduces maneuverability, what leads to a decreased hunting efficiency and a higher vulnerability against predators (Hayssen and Kunz 1996, Wilde *et al*. 1999, Kunz and Hood 2000). In this context we have to say that we only recorded females of *Rhinolophus euryale* flying with their However, in this study we do not have data regarding the survival of young. However, the However, in this study we do not have data regarding the survival of young were very young so that we suppose that this only occurs during the first days after birth.

We have to remark the high presence of adult males in maternal roosts from most of the studied species; in some cases being equally or even more abundant than females, for example *R. euryale* or *M. capaccinii*. This could be associated to the temperature increase related to the association of individuals and/or the roosts surveillance. We expected that males increase in numbers towards the end of July, when juveniles fly independently and females get in oestrus again, initiating the next mating period (Rodrigues *et al*. 2003).

We also recorded a higher proportion of juvenile females, especially in *M. schreibersii*, but also in *M. myotis* and *M. blythii*. The previously refereed means an excellent prognostic for future reproductive events and the probability of increasing the populations. In the case of *R. euryale* y *M. escalerai*, the proportions are more balanced, considering that females reach sexual maturity earlier than males (Balmori 1999). On the other side, we recorded a slightly higher dominance of juvenile males in *M. capaccini*. Although, the total amount of juveniles contributed to the population seems to be sufficient to secure the reproductive success in the next years. However, the sex ratio among juveniles could vary between reproductive seasons, being biased towards females in events with early births and favorable environmental conditions (Barclay 2012).

Three of the studied roosts have access restriction with fencing (defined as special conservation areas), given that the perturbation of maternal roosts also represented an important threat for the populations, especially in periods with high vulnerability (Racey and Entwistle 2000). In the case of *M. capaccinii*, we suggest to maintain the protection and the monitoring in maternal roosts and also in hibernation roosts. This also includes actions on the near riparian ecosystems (Almenar *et al*. 2006, Daniel *et al*. 2008, Flanders and Jones 2009, Knight and Jones 2009, Papadatou *et al*. 2009, Flaquer *et al*. 2010).

Finally, we remark the importance and the need for continuing the populational and reproductive monitoring of the studied cave-dwelling bats species. In this context we emphasize the sex ratio, survival rates and growth rates of young. In this way, changes can be detected and timely actions can be taken to maintain the stability of these species as well as the integrity of their habitats.

CAPÍTULO 6

Dietary composition and trophic niche overlap between *Myotis myotis* and *Myotis blythii* (Chiroptera: Vespertilionidae) during reproduction in the East Iberian Peninsula

Myotis myotis. Túnel de Canals

Foto: Isabel Gomís

INTRODUCTION

Various authors have suggested that insectivorous bats are able to capture mostly every insect within their size and hardness spectrum, appropriate for their body mass and biting force, discarding detailed discriminations regarding form and texture (Belwood and Fenton 1976, Fenton and Morris 1976; Anthony and Kunz 1977, Barclay and Brigham 1991, Greenfield and Baker 2003, Ochoa *et al*. 2008). In this manner, the poor discrimination in food obtention would allow these species to vary the components of their diet in relation to prey availability (Best *et al*. 1997, Feldman *et al*. 2000, Rostovskaya *et al*. 2000). This suggests that the great majority of insectivorous bats could basically be opportunistic, being their diets mainly a direct reflection of seasonal and spatial variations in abundance and composition of insects (Kunz 1974, Whitaker *et al*. 1996; Whitaker and Rodríguez-Durán 1999, Kanuch *et al*. 2005, Lasso and Jarrin 2005). The knowledge of feeding habits and the distribution of food resources in sympatric species is a key piece for understanding the diversity, species composition and population dynamics in local communities of bats (Kramer 2001, Moreno 2006, Andreas *et al*. 2012, Krüger *et al*. 2012). These aspects are closely related to survival and there is an actual lack of information at a more local population level (Sachanowicz *et al*. 2006).

Myotis myotis (Borkhausen 1797) and *Myotis blythii* (Tomes 1857) are the largest species within the genus (Nowak 1991). They present remarkable morphological and acoustic similarities (Arlettaz *et al*. 1991, Russo and Jones 2002). They are strictly insectivorous, and developed similar strategies and adaptations that allow them to detect, capture, manipulate and assimilate the same prey spectrum (Belwood and Fenton 1976, Kalko and Schnitzler 1998 Gannon *et al*. 2001, Kunz 2004). The foraging strategy in these species consists in low and rapid flights over the ground or the vegetation (gleaning bats), capturing individually prey objects. Several authors reported that these species may change eventually this behaviour to an aerial hunt active. In *M. myotis* it has been reported that it even descends and captures preys situated directly on the ground (Fenton 1982, Faure and Barclay 1991, Krull *et al*. 1991).

Myotis myotis is the biggest representative of the genus in Europe, in addition to be the species with the highest body mass, it is specialized in capturing big and slowly flying invertebrates (Zahn *et al*. 2006, Boyles *et al*. 2007). In the Iberian Peninsula it appears frequently, given that it occupies reproductive refuges in large subterranean cavities, like tunnels, chasms or caves. These refuges are adjacent to mature open forests or grasslands with trees and areas with none or short grass (Audet 1990, Arlettaz *et al*. 1997, Garrido and Nogueras 2007). *Myotis blythii*, in contrast, is slightly smaller and less frequent than its congener, but it seems to select areas with similar characteristics for prey hunting (Nogueras and Garrido 2007), although the ecology of this species is not well known yet.

In the diet composition of these two species, a variety of insect orders have been described. The most important and frequent groups being Coleoptera (Carabidae), Orthoptera (Tettigonidae, Gryllotalpidae, Gryllidae, Acrididae) Lepidoptera and Diptera (Arlettaz *et al*. 1993, Arlettaz 1996, Arlettaz *et al*. 2001, Zahn *et al*. 2006, Graclik and Wasielewski 2012).

Given the variety of their diets, both temporarily and spatially (Bontadina *et al*. 2008), it is necessary to have information about the trophic spectrum and its variations along the entire distribution range. Thus, our main objective is to determine diet composition of *M. myotis* and *M. blythii* during the reproductive season and also determine the amplitude of the trophic niche and the possible overlap, considering the remarkable similarities between these sister species.

MATERIAL AND METHODS

We determined the diet through the analysis of fecal samples taken directly from each individual (Black 1974, Belwood and Fenton 1976, Anthony and Kunz 1977, Whitaker *et al*. 1977, Kunz and Whitaker 1983). Our study area included three reproductive refuges in the East of the Iberian Peninsula (Figure 1). We captured the individuals using a standard foldable harp trap with 1.5m^2 action area (Tuttle 1974, Tidemann and Woodside 1978, Kunz and Kurta 1988, Francis 1989, Álvarez 2004). We put the trap at the entrance of each refuge once the bats had leaved to feed and captured them when they returned to the refuge. We carried out our sampling during the reproductive season (April, May and June) of 2014. We put each bat into an individual fabric bag for about one hour in order to obtain the fecal sample. Afterwards, before releasing them, we determined the sex, age category (juvenile or adult) and reproductive condition in the case of females (nilipara, pregnant, lactating or post-lactating) (Racey 1982, 1988, Anthony 1988). We put each fecal sample into a hermetic plastic bag and froze it until the posterior analysis in the laboratory.

We analysed the droppings under a stereoscopic microscope Leica EZ4 3.5x (Whitaker 1988). We separated, quantified and identified taxonomically all recognizable arthropod fragments with the help of entomological guides (Borror *et al*. 1981, Collessa and McAlpine 1991, Laurence and Britton 1991, Naumamm 1991, Merritt and Cumming 1996).

We applied a log-lineal model for categoric data in order to determine the

Figure 1. Map of the Iberian Peninsula with the locations of the reproductive refuges used in this study.

relation between the variables of species, refuge, month, sex and prey in a contingency table where all were considered independent (Cords 1986, Christensen 1997). We determined the species' niche amplitude using diversity indexes of Shannon-Wiener, Simpson and Levins. The first one by the equation $H' = -\sum[pi \log pi]$ (Shannon 1948), the Simpson index (1949) was calculated as $D' = 1 - D$ where $D = \sum\left[(pi)^2\right]$ and Levin's amplitude index was calculated as $B = 1/D$ (Krebs 1989). We determined the overlap of trophic niches using the Pianka index $O = {\sum pi\ qi}\Big/{\sqrt{\sum(pi^2)\ \sum(qi^2)}}$ (Pianka 1973) and the competition coefficients of Mac Arthur and Levins, as $M_1 = {\sum(pi)(qi)}\Big/{\sum pi^2}$ and $M_2 = {\sum(pi)(qi)}\Big/{\sum qi^2}$ (Mac Arthur y Levin 1967).

RESULTS

We captured a total of 115 individuals of which 72 contributed fecal samples. We identified 131 arthropods from 10 different orders of the Insecta class and two of the Chilopoda class.

Myotis myotis represented the 59.1% of our captures (38 individuals). Due to the sampling being carried out during the reproductive period the proportion of females (87.8%) highly overcame the males (12.2%). In the diet of this species we identified 8 orders of insects and one individual of the Chilopoda class. Mostly Coleoptera, Diptera and Orthoptera and a minor proportion of Lepidoptera, Hymenoptera, Ephemeroptera, Neuroptera and Dermaptera (Table 1).

In detail, Coleoptera dominates the diet (48.2%), followed by Diptera (28.6%) and Orthoptera (11.6%). The orders Lepidoptera (3.6%), Hymenoptera (3.6%), Ephemeroptera (0.9%), Neuroptera (0.9%) and Dermaptera (0.9%) the same as the Chilopoda class (1.7%) were less represented (Figure 2). Within the Coleoptera order we could identify rests of the Carabidae, Scarabaeidae and Staphylinidae families. Within the Diptera order we could identify the Rhagionidae and Anisopodidae families. Other families we identified were Acrididae (Orthoptera), Chrysopidae (Neuroptera) and Formicidae (Hymenoptera).

We found significant differences in diet composition of *M. myotis* between refuges, the months May and June and also between sexes. Those differences were determined by the orders Coleoptera (Z= 4.577; $p< 0.001$), Diptera (Z= 3.804; $p< 0.001$) and Orthoptera (Z= 2.464; $p= 0.014$).

In the case of *M. blythii* we captured 47 individuals (40.9%), 44% males and 56% females, of which 34 contributed fecal samples. We found 7 orders of the Insect class: Diptera (32%), Coleoptera (28%), Lepidoptera (16%), Hemiptera (8%), Tricoptera (8%), Orthoptera (4%) and Dermaptera (4%). We could further identify the following families: Coccinellidae (Coleoptera), Chrysomelidae (Coleoptera), Muscidae (Diptera), Gryllotalpidae (Orthoptera) and Tingidae (Hemiptera). Equally, we found differences in diet composition of *M. blythii* between refuges, months and sexes. The orders that determined these differences are Coleoptera (Z= 3.311; $p= 0.001$), Diptera (Z= 2.195; $p= 0.028$), Orthoptera (Z= 2.195; $p= 0.028$) and Hemiptera (Z= 2.870; $p= 0.004$).

Both bat species coincide in five insect orders (Coleoptera, Diptera, Orthoptera, Lepidoptera and Dermaptera), being Coleoptera and Diptera

Table 1. Arthropods found in fecal samples of *M. myotis* and *M. blythii* in the Eastern Iberian Peninsula.

Class	Order	Family	*Myotis myotis*	*Myotis blythii*
Insecta	Coleoptera	Carabidae	+	
		Coccinelidae		+
		Crysomelidae		+
		Scarabeidae	+	
		Staphilinidae	+	
		Unidentified	+	+
	Diptera	Anisopodidae	+	
		Muscidae		+
		Rhagionidae	+	
		Unidentified	+	+
	Hemiptera	Tingidae		+
		Unidentified		+
	Neuroptera	Chrysopidae		
		Unidentified	+	
	Tricoptera	Unidentified		+
	Lepidoptera	Unidentified	+	+
	Tricoptera	Unidentified		+
	Hymenoptera	Formicidae	+	
		Unidentified		+
	Orthoptera	Acrididae	+	
		Gryllotalpidae		+
		Unidentified	+	+
	Dermaptera	Unidentified	+	+
	Psocoptera	Unidentified		+
	Ephemeroptera	Unidentified	+	
Chilopoda	Unidentified	Unidentified	+	

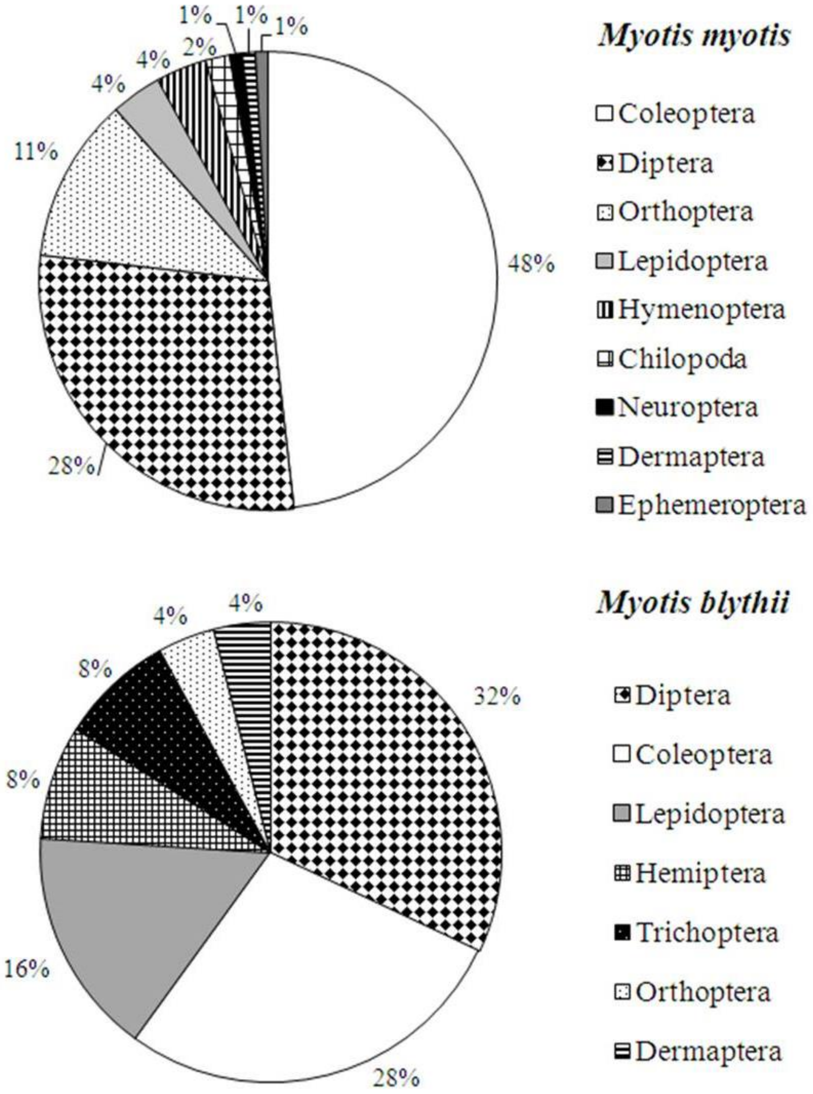


Figure 2. Diet composition (percentage) for each bat species studied.

the most represented with more than 60% in both cases.

We found significant differences in diet composition between both bat species (Z= 2.531; *p*= 0.011). Between sexes we found differences in both species: *M. myotis* (Z= -6.81; *p*< 0.001) and *M. blythii* (Z= -5.701; *p*< 0.001).

Myotis myotis also shows significant differences between pregnant females (Z= 4.907; *p*< 0.001) and lactating females (Z= 3.599; *p*< 0.001). In samples from juvenile and not reproductive females we found only Coleoptera and Diptera, while in pregnant and lactating females we found also other groups like Orthoptera, Neuroptera and even Chilopoda.

Respect *M. blythii*, we also found significant differences between pregnant females (Z= 2.148; *p*= 0.032) and lactating females (Z= 4.733; *p*< 0.001). Post-lactating and not reproductive females seem to feed basically on Coleoptera and Hemiptera, while pregnant and lactating females consumed orders like Diptera, Orthoptera or Lepidoptera.

The indexes of niche amplitude showed that both species are generalists. But *M. blythii* showed a slightly greater niche amplitude than *M. myotis* (Table 2). Additionally we determined an overlap of trophic niches of *O*= 0.816, corresponding to approximately 82% of similarity in consumed resources. The competence coefficients were M_{MM}= 0.719 for *M. myotis* and M_{MB}= 0.926 for *M. blythii*. These coefficients mean that a 72% of the total consumed resources of *M. myotis* coincide with the ones used by *M. blythii*, while the latter one has 92% of its preys in common with *M. myotis*. As we evaluated the same at an intraspecific level we found that *M. myotis* showed an overlap of 80% between sexes while *M. blythii* had an overlap of 77%. We also found a trophic niche overlap value of 96% between pregnant and lactating females in *M. myotis*, while it was only 51% in the case of *M. blythii*.

Table 3. Niche amplitude and overlap indexes of *M. myotis* and *M. blythii.*

Species	Indexes				
	Niche Amplitude			Niche overlap	
	Shannon-Wiener (*H'*)	Simpson (*D'*)	Levin (*B*)	Pianka (*O*)	Mac Arthur and Levins (*M*)
Myotys myotis	0.673	0.688	3.212	0.816	0.719
Myotis blythii	0.728	0.758	4.138		0.926

DISCUSSION

The presence of ground-living beetles (Coleoptera) as a dominant group of insects in the diet of *M. myotis* coincides with results obtained in other studies carried out in other regions of Europe (Bauerová 1978, Arlettaz *et al*. 1993, Beck 1995, Arlettaz 1996). The Carabidae family is not only the most important beetle group in the diet of this species; it is also the most numerous group among all consumed invertebrate taxa (Bauerova 1978, Arlettaz *et al*. 1993, Arlettaz 1996, Arlettaz *et al*. 2001, Pereira *et al*. 2002.). The high abundance of Coleoptera in the species' habitats (Sienkiewicz and Konwerski, 2006) and exploited areas (Arlettaz 1996, Pereira *et al*. 2002.), as the reduced mobility and high energy content of this type of insects, seem to be the most probable reasons why they are so dominant in bat diets (Arlettaz and Perrin 1995).

The low proportions of orders like Dermaptera, Neuropteraor Ephemeroptera could be related to random ingestions, being appealing preys in highly energy demanding periods, like the reproduction (Bauerová 1978, Arlettaz 1996, Arlettaz *et al*. 2001). Something similar could be stated for Orthoptera, Hymenoptera and Lepidoptera (Arlettaz *et al*. 1997, Ma *et al*. 2008). *M. blythii* fed exclusively on the Insecta class, being the predominant orders Diptera and Coleoptera. Arlettaz *et al*. (1997) they stated that this bat species exploits preferably grasslands with low vegetal cover. This would also mean a different feeding strategy, based on insects associated to this type of habitat, as crickets, grasshoppers or bugs, and not on Coleoptera (Arlettaz *et al*. 1993, Arlettaz and Perrin 1995). Our results indicate that, in contrast to *M. myotis*, *M. blythii* did not have a preference for one particular group of insects. The diet was more based on the alternation of various groups so that the decrease or absence of one of them could be compensated with other items (Willig and Moulton 1989, Findley 1993). In this context we would like to remark the low representation of Orthoptera in our study. This group is usually cited as a fundamental part of the diet of *M. blythii* (Arlettaz *et al*. 1993, Arlettaz and Perrin 1995, Arlettaz *et al*. 1997). The appearance of groups like Dermaptera, Orthoptera or Trichoptera could represent opportunistic captures (Heller and Helversen 1989). The diet of *M. blythii* does not seem to be as rich as the one of *M. myotis*, but it showed to be more equitable and regular. This also explains the high niche amplitude values for this species (Arlettaz *et al*. 1993, Arlettaz 1995, Arlettaz and Perrin 1995).

The differences we found between the diets of both bat species could be explained by the importance of each arthropod order in the diet of each bat species. While Coleoptera represents a 48.2% of the diet of *M. myotis*, for *M. blythii* it represents only 28%. In the same manner, Orthoptera appears with 11.6% in the diet of *M. myotis*, but only with 4% in *M. blythii*. The predominance of these groups is also related to foraging strategies used by each bat species. These strategies are based on low flights and rapid descents to capture insects on the ground (*M. myotis*), grass or low shrubs (*M. blythii*) (Audet 1990, Arlettaz 1995, Aguirre *et al*. 2003, Garrido and Noguera 2007). So that *M. myotis* seems to specialize on preys living on hard ground, like beetles, while *M. blythii*, in addition to beetles, captures moths, crickets, bugs and cicadas perched on the low vegetation (Arlettaz *et al*. 1997). However, we can also remark the dominance of Diptera in the diet of *M. blythii*, which suggests the, at least partial, use of active flight capture as a feeding strategy, previously described for the capture of Melolontha (Arlettaz *et al*. 1993, Nogueras and Garrido 2007). The substitution of crickets by other groups like Diptera or Coleoptera on the beginning of the reproductive season (May) could be related to a low availability of this type of prey during this period. This has already been described in populations in Switzerland, being the maximum values in abundance in July (Arlettaz 1995, Arlettaz *et al*. 1997, Arlettaz *et al*. 2001). Precisely in July, in a work in progress parallel to the present study (Machado and Monrós, in evaluation) we registered the appearance of juveniles of *M. blythii*, retarded to juveniles of *M. myotis*, which have their maximum in June. It has been described a retard of the moment when *M. blythii* finishes hibernation, what means an extended torpor and, in consequence, a prolongation of the gestation. This would allow the individuals to synchronize their phenology with their most exploited resource and carry out a more optimal foraging (Arlettaz *et al*. 2001). We evidenced the presence of pregnant females of *M. blythii* from April (in 2013 and also in 2014) as in *M. myotis*, but the juveniles appeared only in July. So that we confirm that the births could depend more on the availability of resources than the weather conditions per se (Arlettaz *et al*. 2001).

It has been described that these bat species can occupy very distinct trophic niches along their geographic distribution (Arlettaz *et al*. 1995, Perrin and Houser 1997). Kurta and Whitaker (1998) affirm that species of the genus *Myotis* base their diet on a large diversity of (mainly soft) insects. So that there may appear seasonal changes in consumption levels and composition of the diets, these could be associated to variations in energy demands, mostly imposed by variations in resource availability, reproductive condition and fur change (Anthony and Kunz 1977, Whitaker and Rodríguez-Durán 1999, Kunz and Orell 2004).

The cause of the observed difference in the diet of females could be associated to higher energy requirements they have to affront during pregnancy and lactation, being the latter one the most demanding event, especially in small mammals (Oftedal 1985, Gittleman and Oftedal 1987, Racey and Entwistle 2000). Energy requirements during lactation increase as the pups grow until they are able to feed independently (Kunz and Orrell, 2004).

Predators tend to specialize when the resources with the highest energy content are common (Begon *et al*. 1986, Stephens and Krebs 1986). In comparison to their main prey types (Coleoptera for *M. myotis* and Diptera for *M. blythii*), alternative preys can increase their densities in certain periods of the year. This happens for example in Hemiptera or Lepidoptera in spring, coinciding the increased consume levels with higher energy demands (due to pregnancy and lactation) and the growth of the population, given the appearance of new individuals. This could explain diet variations in females during the different periods of the reproductive season (Arlettaz *et al*. 1993, Arlettaz and Perrin 1995).

It has been described previously that these bat species exploit different trophic niches, especially when they are in sympatry, only sharing some minor groups of preys, with low representation in their diets (Arlettaz 1999, Arlettaz *et al*. 2001, Patterson et al. 2003). However, energy requirements associated to the different reproductive conditions, and also a high prey availability (Kurta *et al*. 1989), could determine the high value of trophic overlap we detected in our study. It has also been described that opportunistic species can feed on areas further away from refuges in comparison to specialized species, which in general have to defend territories closer to the refuge (Patterson *et al*. 2003).

We also detected high trophic overlap at an intraspecific level. Both bat species show that both sexes share an important part of the trophic resource (80% for *M. myotis* and 77% for *M. blythii*). However, pregnant and lactating females of *M. blythii* showed an overlap of only 51% of the prey spectrum. Unsafe refuges and the high energy cost associated to the flight carrying the pups (Kunz and Hood 2000) could imply that lactating females tend to feed on areas closer to the refuge, exploiting different resources than pregnant females, which can move without major restrictions.

Despite that the diet composition of these bat species has already widely been described, it is clear that, as it happens with other species of the genus (Husar 1976, Andreas *et al*. 2012, Krüger *et al*. 2012), their behaviours and feeding strategies seem to be labile. They are ruled by energy demands and changes in prey availability. This seems to occur in the case of *M. blythii*, which births coincide with availability peaks of their most exploited resource. This raises the need for increasing diet evaluation periods (at least until they leave the maternal refuges) and also the determination of resource availability in these Mediterranean environments. So that we know more precisely the strategies adopted by these two and other species in such crucial periods as it is the reproduction. Because on these strategies depends the coexistence, the reproductive success and the population stability.

CONCLUSIONES

Myotis myotis. Túnel de Canals

Foto: Isabel Gomís

1. *Miniopterus schreibersii* resultó la especie cavernícola más abundante de la porción Este de la Península Ibérica. Al considerar el periodo 1997-2014, sus poblaciones mostraron una condición incierta, al igual que *M. capaccinii, M. emarginatus, M. escalerai*, *M. myotis/blythii* y *R. ferrumequinum*. Por su parte, las poblaciones de *R. mehelyi* y *R. euryale* presentaron un disminución moderada. Un pronóstico más alentador lo tuvo *R. hipposideros* con una tendencia estable.
2. Tomando en cuenta las regresiones de los censos pareciera haber un repunte de las poblaciones de *M. capaccinii*, *M emarginatus* y *M. escalerai*, particularmente en la última década. Del mismo modo, a pesar de las fluctuaciones de *R. euryale* se observó un rebote de la población.
3. *R. ferrumequinum* ocupó el 82% de los refugios, particularmente aquellos no protegidos (92,8%), seguido en importancia de ocupación por *M. myotis/blythii* y *Miniopterus schreibersii.* Por el contrario, la menor presencia fue de *M. emarginatus*, con muy baja ocupación de refugios no vallados.
4. Las principales asociaciones de especies en las colonias maternales fueron las constituidas por *M. myotis/blythii*, *Miniopterus schreibersii* y *R. ferrumequinum*, ocupando la mayoría de las cuevas. Destacan los hábitos más solitarios de *M. emarginatus* y *R. hipposideros*.
5. Se resalta la importancia de los refugios: Cova de Les Rates Penades (Rótova), La Moneda (Cotes) y Mare de Deu (Castellfort), los dos primeros por representar refugios óptimos, dada su cercanía a cuerpos de agua, lo que coincide con las altas abundancias de *Myotis capaccinii.*

6. Los refugios que albergaron el mayor número de especies fueron: Juliana, Benimaquia, Ocre, Rates Penades, Don Pedro, Oscura, Puntal de Mateo, El Campillo, Las Maravillas (Llombai), Ferrás y Moli de la Font.
7. Debido al incremento significativo de individuos a lo largo del periodo censado resaltan particularmente las cuevas: Juliana, dels Morceguellos y Soterranya.
8. No se encontraron diferencias significativas entre los refugios protegidos y no protegidos, no obstante hubo promedios más elevados en las pendientes de incremento poblacional en aquellos refugios con mayor tiempo de protección, lo que supone que el efecto de la protección es un aspecto que podría evidenciarse a largo plazo.
9. *Miniopterus schreibersii* es la primera especie en abandonar diariamente los refugios, seguida de *M. myotis/blythii*, *M. capaccinii* y *M. escalerai*. La velocidad de *M. schreibersii* y el mayor tamaño de *M. myotis/blythii* pudieran permitirle evadir mejor a los potenciales depredadores durante el crepúsculo, de modo que *M. capaccinii* y *M. escalerai* podrían tomar más ventaja de los periodos de mayor oscuridad para abandonar las colonias.
10. En conjunto las salidas se realizaron primero en Junio, luego en Mayo y más tardíamente en Julio y Abril. Las marcadas demandas energéticas propias del incremento poblacional por la presencia de juveniles independientes (Junio) y la lactancia (Mayo) estarían determinando estas diferencias.
11. Se obtuvo una alta representación de machos adultos en los refugios maternales, siendo incluso mayoritaria en el caso de *M. capaccinii* y *R. euryale*.

12. En términos generales, los partos ocurrieron en Mayo con juveniles independientes desde junio con máximos en julio. *Miniopterus schreibersii* y *M. blythii* presentaron desplazamiento en estos eventos, con hembras lactantes en junio y aparición de juveniles en julio.
13. Las tasas reproductivas de todas las especies fueron altas, principalmente las de *M. capaccinii*. No obstante, las tasas de productividad resultaron ligeramente más bajas que las reproductivas a excepción de *M. schreibersii*. Entre un 89 y 98% de las hembras adultas participaron en el evento reproductivo, con una productividad entre 52 y 100%.
14. Coleoptera (Carabidae, Scarabaeidae y Staphylinidae) domina la dieta de *M. myotis*, seguido por Diptera (Rhagionidae y Anisopodidae) y Orthoptera (Acrididae). Mientras que Díptera (Muscidae), Coleóptera (Coccinellidae y Chrysomelidae) y Lepidoptera, suelen ser los mayores representantes de la dieta de *M. blythii*. Se encontraron diferencias significativas entre las dietas de estas especies, basadas principalmente en las proporciones en que estos rubros son explotados.
15. Tanto *M. myotis* como *M. blythii* son especies generalistas con un 82% de solapamiento de nicho trófico. A nivel intra-específico, ambas especies tuvieron un alto porcentaje de solapamiento entre sexos. No obstante, las hembras preñadas y lactantes de *M. blythii* solo compartieron aproximadamente el 50% de las presas, lo que permite inferir cambios en el comportamiento alimentario y/o en la oferta de los recursos que esta especie explota en la época reproductiva.

CONSIDERACIONES FINALES

Sima del Alto de Don Pedro-Macastre

Foto: Marjorie Machado

Al finalizar esta Tesis se desprenden una serie de consideraciones que pudieran implementarse a futuro, lo que permitiría abordar tópicos derivados del desarrollo de este trabajo, con miras a ahondar en aspectos de la historia natural de estas especies cavernícolas, de cara a los retos que demanda hoy día su conservación. Algunas de ellas se mencionan a continuación:

1. Representaría un aporte importante al conocimiento de las condiciones de las colonias maternales el registro climático de los refugios. Lo que supone el monitoreo continuo de la temperatura y la humedad relativa de los espacios efectivamente seleccionados y utilizados por estas especies dentro de los refugios.

2. La implementación del monitoreo reproductivo en algunos refugios, a fin de detectar cambios importantes en la condición reproductiva de las hembras y la aparición de juveniles, lo que constituiría un indicativo directo del estatus energético de la población.

3. Determinar tasas de crecimiento y supervivencia de los juveniles antes que abandonar las colonias maternales, lo que permitiría conocer la condición de los individuos de la población justo antes de la entrada al proceso de hibernación y comparar entre especies.

4. Evaluar los componentes de la dieta de estas especies mediante técnicas moleculares, lo que indicaría con mayor precisión el componente de presas explotadas.

5. Evaluar la disponibilidad de recursos en las áreas aledañas a los refugios permitiría acceder a información como selectividad de presas, que junto al análisis fino de la dieta aportaría información relevante sobre la repartición de recursos en los ensambles y las estrategias detalladas de forraje empleadas por las especies, sobre todo de cara a las repercusiones del cambio climático.

BIBLIOGRAFÍA

Hembra lactante y cría de *Miniopterus schreibersii*

Foto: Marjorie Machado

Aguirre, L., A. Herrel, R. Van Damme y E. Matthysen. 2003. The implications of food hardnees for diet in bats. Functional Ecology 17: 201-212.

Aguirre, L., E. Anderson, G. Brehm, S. Herzog, P. Jørgensen, G. Kattan, M. Maldonado, R. Martínez, J. Mena, J. Pabón, A. Seimon y C. Toledo. 2011. Phenology and interspecific ecological interactions of Andean biota in the face of climate change. Pp. 68–92, en: Climate change and biodiversity in the tropical Andes. (S. K. Herzog, R. Martinez, P. M. Jørgensen y H. Tiessen, eds.) Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), Saõ José dos Campos, São Paulo.

Aihartza, J., I. Garin, U. Goiti, J. Zabala y I. Zubero-Goitia. 2003. Spring habitat selection by the Mediterranean horseshoe bat (*Rhinolophus euryale*) in the Urdaibai Biosphere Reserve (Basque Country). Mammalia 67: 25–32.

Almenar, D., A. Alcocer y M. A. Monsalve. 2007a. *Myotis capaccinii* (Bonaparte 1837). Pp. 194–196, en: Atlas y Libro Rojo de los mamíferos terrestres de España (J. Palomo, J. Gisbert, y J. Blanco, eds). D.G. de la Biodiversidad- SECEM-SECEMU, Madrid, 588 pp.

Almenar, D., A. Alcocer y M. A. Monsalve. 2007b. Murciélago mediano de herradura *Rhinolophus mehelyi* Matschie, 1901. Pp. 148-150, en: Atlas y Libro Rojo de los Mamíferos Terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.

Almenar, D., J. Aihartza, U. Goiti, E. Salsamendi y I. Garin. 2009. Foraging behaviour of the long-fingered bat *Myotis capaccinii*: implications for conservation and management. Endangered Species Research 8: 69–78.

Almenar, D., J. Aihartza, U. Goiti, E. Salsamendi y I. Garín. 2006. Habitat selection and spatial use by the trawling bat *Myotis capaccinii* (Bonaparte 1837). Acta Chiropterologica 8: 157–167.

Altringham, J. 1996. Bats: Biology and Behaviour. Oxford University Press. 262 pp.

Álvarez, J. 2004. From the field: An easily constructed Tuttle trap for bats. Wildlife Society Bulletin 32: 264-266.

Andreas, M., A. Reiter y P. Benda. 2012. Dietary composition, resource partitioning and trophic niche overlap in three forest foliage-gleaning bats in Central Europe. Acta Chiropterologica 14(2): 335-345.

Anthony, E. 1988. Age determination in bats. Pp. 47-58, en: Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington.

Anthony, E. y T. Kunz. 1977. Feeding strategies of the little brown bat *Myotis lucifugus*, in southern New Hampshire. Ecology 58: 775–786.

Arlettaz, R. 1996. Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. Animal Behavior 51: 1–11.

Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology 68(3): 460–471.

Arlettaz, R. y N. Perrin. 1995. The trophic niches of sympatric sibling *Myotis myotis* and *Myotis blythii*: do mouse-eared bats select prey? Symposium of Zoology Society of London 67: 361-376.

Arlettaz, R., M. Ruedi y J. Hauser. 1991. Field morphological identification of *Myotis myotis* and *Myotis blythii* (Chiroptera. Vespertilionidae): a multivariate approach. *Myotis* 29: 7-16.

Arlettaz, R., M. Ruedi y J. Hausser. 1993. Ecologie trophique de deux especes jumelles et sympatriques de chauves-souris: *Myotis myotis* et *Myotis blythii* (Chiroptera : Vespertilionidae). Premiers resultats. Mammalia 57 (4): 519-531.

Arlettaz, R., N. Perrin y J. Hausser. 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology 66:897-911.

Arlettaz, R., P. Christe, A. Lugon, N. Perrin y P. Vogel. 2001. Food availability dictates the timing of parturition in insectivorous mouse-eared bats. Oikos 95: 105–111.

Arthur, L., M. Lemair, L. Dufrêne, I. Le Viol, J. Julien y C. Kerbiriou. 2014. Understanding bat-habitat associations and the effects of monitoring on long-term roost success using a volunteer dataset. Acta Chiropterologica 16:397–411.

Aschoff, J. 1966. Circadian activity pattern with two peaks. Ecology 47: 657-662.

Audet, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). Journal of Mammalogy 71: 420-427.

Balmori, A. 1999. La reproducción en los quirópteros. Galemys 11(2): 17-34.

Barclay, R. 2012. Variable Variation: Annual and Seasonal Changes in Offspring Sex Ratio in a Bat. PLoS ONE 7(5): e36344. doi:10.1371/journal.pone.0036344.

Barclay, R. y L. Harder. 2003. Life histories of bats: Life in the slow lane. Pp. 209-253, en: Bat Ecology (T.H. Kunz y B. Fenton, eds.). The University of Chicago Press, Chicago. Illinois.

Barclay, R. y R. Brigham. 1991. Prey detection, dietary niche breadth and body size in bats: Why are aerial insectivorous bats so small? American Naturalist 137(5): 693-703.

Barclay, R., J. Ulmer, C. MacKenzie, M. Thompson, L. Olson, J. McCool, E. Cropley y G. Poll. 2004. Variation in the reproductive rate of bats. Canadian Journal of Zoology 82: 688–693.

Battersby, J. (comp.). 2010. Guidelines for surveillance and monitoring of European bats. EUROBATS Publication Series No. 5. UNEP/EUROBATS Secretariat, Bonn, 95 pp.

Bauerova, Z. 1978. Contribution to the trophic ecology of *Myotis myotis*. Folia Zoologica 27: 305-316.

Beck, A. 1995. Fecal analyses of European bat species. *Myotis* 32-33:109-119.

Begon, M., J. Harper y C. Townsend. 1986. Ecology: individuals, populations and communities. B lack well Scientific Publications, Oxford.

Bell, G. P. 1982. Behavioral and ecological aspects of gleaning by a desert insectivorous bat *Antrozous pallidus* (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology 10: 217-223.

Belwood, J. y M. Fenton. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 54: 1674–1678.

Benda, P., M. Andreas, D. Kock, R. Lučan, P. Munclinger, P. Nová, J. Obuch, K. Ochman, A. Reiter, M. Uhrin y D. Weinfurtová. 2006. Bats (Mammalia: Chiroptera) of the Eastern Mediterranean. Part 4. Bat fauna of Syria: distribution, systematics, ecology. Acta Societatis Zoologicae Bohemicae 70: 1–329.

Berthinussen, A., O. Richardson y J. Altringham. 2014. Bat conservation: global evidence for the effect of interventions. Synopses of Conservation Evidence Series. Pelagic Publishing. Gwynedd, 120 pp.

Best, T., B. Millan, T. Hass, W. Cvilikas y L. Saidak. 1997. Variation in diet of the gray bat (*Myotis grisescens*). Journal of Mammalogy 78(2): 569-583.

Biscardi, S., D. Russo, V. Casciani, D. Cesarini, M. Mei y L. Boitani. 2007. Foraging requirements of the endangered long-fingered bat: the influence of micro-habitat structure, water quality and prey type. Journal of Zoology (London) 273: 372–381.

Black, H. 1974. A north temperate bat community: structure and prey populations. Journal of Mammalogy 55: 138-157.

Bontadina, F., S. Schmied, A. Beck y R. Arlettaz. 2008. Changes in prey abundance unlikely to explain the demography of a critically endangered Central European bat. Journal of Applied Ecology 45: 641-648.

Borror, D., D. De Long y C. Triplehorn. 1981. An introduction to the study of insects. Saunders college publishing. Philadelphia. 827 pp.

Boyles, G., M. Dunbar, J. Storm y V. Brack. 2007. Energy availability influences microclimate selection of hibernating bats. Journal of Experimental Biology 210: 43443-43450.

Castella, V., M. Ruedi, L. Excoffier, C. Ibáñez, R. Arlettaz y J. Hausser. 2000. Is the Gibraltar Strait a barrier to gene flow for the bat *Myotis myotis* (Chiroptera: Vespertilionidae)?. Molecular Ecology 9: 1761–1772.

Christensen, R. 1997. Log-Linear Models and Logistic Regression. Springer-Verlag Inc. New York, New York, USA.

Collen, B., J. Loh, S. Whitmee, L. Mcrae, R. Amin y J. Baillie. 2007. Monitoring change in vertebrate abundance: the living planet index. Conservation Biology 23: 317–327.

Colless, D. y D. McAlpine. 1991. Diptera. Pp. 717-786, en: Insects of Australia. VOL II. (CSIRO, eds). Melbourne University Press and Cornell University Press. 1137 pp.

Convention on Migratory Species. 1995–2008. Convention on migratory species of wild animals. Appendix II (as amended by the Conference of the Parties in 1985, 1988, 1991, 1994, 1997, 1999, 2002, 2005 and 2008). Available at http://www.cms.int/.

Cords, M. 1986. Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. Journal of Animal Ecology 55: 811-827.

Cowles, R. B. 1947. Vascular changes in the wings of bats. Science 105: 362-363.

Csősz, I., C. Jére, S. Bücs, C. Bartha, L. Barti y F. Szodo -Ray-Parádi. 2015. The presence of Mehely's horseshoe bat *Rhinolophus mehelyi* in South-Western Romania. North-Western Journal of Zoology 11: 152801.

Daniel, S., C. Korine y B. Pinshow. 2008. Central-place foraging in nursing, arthropod-gleaning bats. Canadian Journal of Zoology 86: 623–626.

Davis, R. B., Herreid, C. F. y Short, H. L. 1962. Mexican free-tailed bats in Texas. Ecological Monographs 32: 311-346.

De Blase A. 1980. The bats of Iran: Systematic, distribution, ecology. Fieldiana Zoology 4: 85-101.

De Juana, E. y Varela, J. M. 2005. Aves de España. Seo/BirdLife-Lynx Editions, Barcelona, Spain, 165 pp.

De Lucas, J. 2007. *Miniopterus schreibersii* (Kuhl, 1817). Pp. 262-266, en: Atlas y Libro Rojo de los Mamíferos Terrestres de España (L. J. Palomo, J. Gisbert y J. C. Blanco, eds.). Dirección General para la Biodiversidad-SECEM-SECEMU.

De Paz O. 2002. Murciélago grande de herradura *Rhinolophus ferrumequinum* (Schreber, 1774). Pp. 136-138 en: Atlas y Libro Rojo de los Mamíferos Terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.

De Paz, O. y J. Alcalde. 2000. Catálogo nacional de especies amenazadas: propuestas. Barbastella 1: 17–21.

Duvergé, P. L., Jones, G., Rydell, J. y Ransome, R. D. 2000. Functional significance of emergence timing in bats. Ecography 23: 32-40.

Elliott, W., S. Samoray, S. Gardner y J. Kaufmann. 2006. The MDC method: Counting bats with infrared video. Pp. 147-153, en: Proceeding of the 2005 National Cave and Karst Management Symposium. Albany, NY.

Erkert, H. G. 1978. Sunset-related timing of flight activity in neotropical bats. Oecologia 37: 59-67.

Erkert, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201-242, en: Ecology of bats (T. H. Kunz, ed.). Plenum Publishing Corporation. New York.

Estrada, A. y R. Coates-Estrada. 2001. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. Journal of Tropical Ecology 17:27-646.

Evin, A. M. Baylac, M. Ruedi, M. Mucedda y J. Pons. 2008. Taxonomy, skull diversity and evolution in a species complex of *Myotis* (Chiroptera:

Vespertilionidae): a geometric morphometric appraisal. Biological Journal of the Linnean Society 95: 529–538.

Faure, P. y R. Barclay. 1992. The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. Animal Behaviour 44: 31–39.

Feldman, R., J. Whitaker y Y. Yom-Tov. 2000. Dietary composition and habitat use in a desert insectivorous bat community in Israel. Acta Chiropterologica 2(1): 15-22.

Fenton, B. y W. Bogdanowicz. 2002. Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. Canadian Journal of Zoology 80: 1004–1013.

Fenton, M. 1982. Echolocation, insect hearing, and feeding ecology of insectivorous bats. Pp. 261-285, en: Ecology of bats (T. Kunz, ed.). Plenum Publishing Corporation, New York.

Fenton, M. 1989. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology 68: 411-422.

Fenton, M. B., Rautenbach, I. L., Smith, S. E., Swanepoel, C. M., Grosell, J. y Van Jaarsveld, J. 1994. Raptors and bats: threats and opportunities. Animal Behaviour 48: 9-18.

Fenton, M. y G. Morris. 1976. Opportunistic feeding by desert bats (*Myotis* spp.). Canadian Journal of Zoology 54: 526–530.

Findley, J. 1993. Bats, a community perspective. Cambridge University Press, Cambridge.

Flanders, J. y G. Jones. 2009. Roost use, ranging behavior, and diet of greater horseshoe bats (*Rhinolophus ferrumequinum*) using a transitional roost. Journal of Mammalogy 90: 888–896.

Flaquer, C., X. Puig, E. Fàbregas, D. Guixé, I. Torre, R. Ràfols, F. Páramo, J. Camprodon, J. Cumplido, R. Ruíz-Jarillo, A. Baucells, L. Freixas y A. Arrizabalaga. 2010. Revisión y aportación de datos sobre quirópteros de Catalunya: propuesta de lista roja. Galemys 22 (1): 29-61.

Fleming, T. y P. Eby. 2003. Ecology of bat migration. Pp. 156–208, en: Bat Ecology. (T. Kunz y M. Fenton, eds.). The University of Chicago Press, Chicago.

Francis C. 1989. A comparison of mist nets and two designs of harp traps for capturing bats. Journal of Mammalogy 70: 865-870.

Fraser, E. y M. Fenton. 2007. Age and food hardness affect food handling by insectivorous bats. Canadian Journal of Zoology 85: 985-993.

Furman, A., E. Oraman, Y. Elik, T. Postawa, J. Bachanek y M. Ruedi. 2014. Cytonuclear discordance and the species status of *Myotis myotis* and *Myotis blythii* (Chiroptera). Zoologica Scripta 43: 549-561.

Gaisler, J. 1989. The r-K selection model and life history strategies in bats. Pp. 117–124, en: European bat research (V. Hanák, I. Horáček y J. Gaisler, eds.). Charles University Press, Prague.

Gannon, W., R. Sherwin, T. Decarvalho y M. O'farrel. 2001. Pinnae and echolocation call differences between *Myotis californicus* and M*. ciliolabrum* (Chiroptera: Vespertilionidae). Acta Chiropterologica 3(1): 77-91.

Garrido-García, J. A. y Nogueras, J. 2007. *Myotis myotis* (Borkhausen, 1797). Pp.153-157, en: Atlas y Libro Rojo de los Mamíferos Terrestres de España. (L. J. Palomo, J. Gisbert y J. C. Blanco, eds.). Dirección General para la Biodiversidad-SECEM-SECEMU.

Gittleman, J. L. y O. Oftedal. 1987. Comparative growth and lactation energetics in carnivores. Symposia of the Zoological Society of London 57: 41-77.

Goiti, U. y J. Aihartza. 2007. Murciélago mediando de herradura *Rhinolophus euryale* (Blasius, 1853). Pp. 144–147, en: Atlas y Libro Rojo de los mamíferos terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). D.G. de la Biodiversidad-SECEM-SECEMU, Madrid, 588 pp.

González, F. 2006. Revisión del estado de conservación y protección de los quirópteros en España (Península y Baleares). Ministerio del Medio Ambiente de España. 18 pp.

Graclik, A. y O. Wasielewski. 2012. Diet composition of *Myotis myotis* (Chiroptera, Vespertilionidae) in western Poland: results of fecal analyses. Turkish Journal of Zoology 36(2): 209-213.

Greenfield, M. y M. Baker. 2003. Bat avoidance in non-aerial insects: the silence response of signaling males in an acoustic moth. Ethology 109 (5): 427–442

Greenwood, J., S. Baillie, R. Gregory, W. Peach y R. Fuller. 1995. Some new approaches to conservation monitoring of British breeding birds. Ibis 137: S16–S28.

Hammer, O., D. Harper y P. Ryan. 2001. PAST: Paleontological software package for education and data analysis. Paleontología Electrónica 4(1): 1–9. Disponible en http://folk.uio.no/ohammer/past.

Happold, D., y M. Happold. 1990. Reproductive strategies of bats in Africa. Journal of Zoology (London) 222: 557–583.

Hayssen, V. y T. Kunz. 1996. Allometry of litter mass in bats: comparisons with respect to maternal size, wing morphology, and phylogeny. Journal of Mammalogy 77: 476-490.

Heideman, R. 1988. The timing of reproduction in the fruit bat *Haplonycteris fischeri* (Pteropodidae): geographic variation and delayed development. Geographic variation and delayed development. Journal of Zoology (London) 215: 577-595.

Heller, K. y O. Helversen. 1989. Resource partitioning of sonar frequency bands in rhinolophoid bats. Oecologia 80(2): 178–186.

Henry, M., Thomas, D. W., Vaudry, R. y Carrier, M. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). Journal of Mammalogy 83: 767-774.

Horáček, I., V. Hanák y J. Gaisler 2000. Bats of the Palearctic region: a taxonomic and biogeographic review. Pp.: 11–157, en: Proceedings of the VIIIth European Bat Research Symposium. Vol. I. Approaches to Biogeography and Ecology of Bats (B. Wołoszyn, ed.). Kraków: Chiropterological Information Center, Institute of Systematics and Evolution of Animals PAS, Kraków.

Hoyle, S., A. Pople y G. Toop. 2001. Mark–recapture may reveal more about ecology than about population trends: demography of a threatened ghost bat (*Macroderma gigas*) population. Australian Ecology 26: 80–92.

Hughes, P. M. y Rayner, J. M. 1991. Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. Journal of Experimental Biology 161: 285-298.

Hughes, P. M. y Rayner, J. M. 1993. The flight of pipistrelle bats Pipistrellus pipistrellus during pregnancy and lactation. Journal of Zoology 230: 541-555.

Hughes, P. M., Rayner, J. M. V. y Jones, G. 1995. Ontogeny of 'true' flight and other aspects of growth in the bat *Pipistrellus pipistrellus*. Journal of Zoology 236: 291-318.

Husar, S. 1976. Behavioral character displacement: evidence of food partitioning in insectivorous bats. Journal of Mammalogy 57: 331-338.

Hutson, A., S. Mickleburgh y P. Racey. 2001. Microchiropteran bats: global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group, IUCN Glan, Switzerland y Cambridge. pp. 258.

Ibáñez, C., J. García-Mudarra, M. Ruedi, B. Stadelmann y J. Juste. 2006. The Iberian contribution to cryptic diversity in European bats. Acta Chiropterologica 8: 277–297.

Ibáñez, C., J. Garrido, J. Nogueras, E. Migens y A. Fijo. 2005. Inventario, seguimiento y conservación de refugios de murciélagos cavernícolas en Andalucía: listado de refugios importantes y propuesta de Zonas de Especial Conservación (Z.E.C.) para las poblaciones de murciélagos cavernícolas de Andalucía. Agencia de Medio Ambiente, Junta de Andalucía, 48 pp.

IUCN, 2016. The IUCN Red List of Threatened Species. Version 2016-2. Disponible en http://www.iucnredlist.org. (Acceso: 04 Septiembre 2016).

IUCN. 2014. The IUCN Red List of Threatened Species. Version 2014-3. Disponible en http://www.iucnredlist.org. (Acceso: 17 Marzo 2015).

Jiménez, J., M.A. Monsalve y J.A. Raga (Eds.). 2012. Mamíferos de la Comunitat Valenciana. Colección Biodiversidad, 19. Conselleria d'Infraestructures, Territori i Medi Ambient. Generalitat Valenciana. Valencia.

Jones, G. y Rydell, J. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 346: 445-455.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig y P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered Species Research 8: 93–115.

Jones, K. y A. MacLarnon. 2001. Bat life histories: testing models of mammalian life-history evolution. Evolutionary Ecology Research 3: 465–476.

Kalko, E. y H. Schnitzler. 1998. How echolocating bats approach and acquire food. Bats: phylogeny, morphology, echolocation, and conservation biology. Smithsonian Institution Press, Washinton DC.

Kanuch, P., A. Kristín y J. Kristofík. 2005. Phenology, diet, and ectoparasites of Leisler's bat (*Nyctalus leisleri*) in the Western Carpathians (Slovakia). Acta Chiropterologica 7(2): 249-257.

Knight, T. y G. Jones. 2009. Importance of night roosts for bat conservation: roosting behaviour of the lesser horseshoe bat *Rhinolophus hipposideros*. Endangered Species Research 8: 79–86.

Krebs, C. 1989. Ecological methodology. Harper & Row Publishers, Inc. New York 656 p.

Krüger, F., I. Harms, A. Fichtner, I. Wolz y R. Sommer. 2012. High Trophic Similarity in the sympatric north european trawling bat species *Myotis daubentonii* and *Myotis dasycneme*. Acta Chiropterologica 14(2): 347–356.

Krull, D., A. Schumm, W. Metzner y G. Neuweiler, 1991. Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). Behavioral Ecology and Sociobiology 28: 247–253.

Kunz, T. 2004. Foraging habits of north american insectivorous bats. Pp 13-25, en: Bat Echolocation Research: Tools, Techniques, and Analysis. (Brigham, R., E. Kalko y G. Jones, eds.). Bat Conservation International. Austin, Texas. 167 pp.

Kunz, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology 55: 693-711.

Kunz, T. H. 1982. Roosting ecology of bats. Pp. 1–55, en: Ecology of bats (T. H. Kunz, ed.). Plenum Publishing Corporation, New York, 425 pp.

Kunz, T. H. y Anthony, E. L. P. 1996. Variation in nightly emergence behavior in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Pp. 225-236, en: Contributions in Mammalogy: a memorial volume honoring J. Knox Jones, Jr. Texas Tech University Press.

Kunz, T. H. y L. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89, en: Ecology of bats (T. H. Kunz y M. B. Fenton, eds.). University of Chicago Press, Chicago, 779 pp.

Kunz, T. H., Betke M., Hristov, N. I. y Vonhof, M. J. 2009. Methods for assessing colony size, population size, and relative abundance of bats. Pp. 133-157, en: Ecological and Behavioral methods for the study of bat (T. H. Kunz y S. Parsons, eds.). John Hopkins University Press.

Kunz, T. H., Wemmer, C. y Hayssen, V. 1996. Sex, age, and reproductive condition of mammals. Pp. 279-290, en: Measuring and Monitoring Biological Diversity: Standard Methods for Mammals (D.E. Wilson, F.R.

Cole, J.D. Nichols, R. Rudran y M.S. Foster, eds.). Smithsonian Institution Press, Washington.

Kunz, T. y A. Kurta. 1988. Capture methods and holding devices. Pp. 1-29, en: Ecological and behavioral methods for the study of bats (T. Kunz, ed.). Smithsonian Institution Press, Washington D.C.

Kunz, T. y J. Whittaker. 1983. An evaluation of fecal analysis for determining food habits of insectivorous bats. Canadian Journal of Zoology 61: 1317-1321.

Kunz, T. y K. Orrell. 2004. Energy cost of Reproduction. Encyclopedia of Energy 5: 423–442.

Kunz, T. y W. Hood. 2000. Parental Care and Postnatal Growth in the Chiroptera. Pp. 415-468, en: Reproductive Biology of Bats (E. G. Crichton y P. H. Krutzsch, eds.). Academic Press, Cambridge.

Kunz, T., P. August y C. Burnett. 1983. Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Biotropica 15: 133-138.

Kurta, A. y J. Whitaker Jr. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. American Midland Naturalist 140: 280-286.

Kurta, A., Bell, G. P., Nagy, K. A. y Kunz, T. H. 1989. Energetics of pregnancy and lactation in freeranging little brown bats (*Myotis lucifugus*). Physiological Zoology 62: 804-818.

Lang, A. B., Kalko, E. K., Römer, H., Bockholdt, C. y Dechmann, D. K. 2006. Activity levels of bats and katydids in relation to the lunar cycle. Oecologia 146: 659-666.

Lasso, D. y P. Jarrin. 2005. Diet variability of *Micronycteris megalotis* in pristine and disturbed habitats of Northwestern Ecuador. Acta Chiropterologica 7(1):121-130.

Lawrence, L. y E. Britton. 1991. Coleoptera. Pp. 543-683, en: Insects of Australia. Vol II. (CSIRO, eds). Melbourne University Press and Cornell University Press. 1137 pp.

Lee, Y. F. y Mccracken, G. F. 2001. Timing and variation in the emergence and return of Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. Zoological Studies Taipei 40: 309-316.

Lesiński, G., Ignaczak, M. y Manias, J. 2009. Opportunistic predation on bats by the tawny owl Strix aluco. Animal Biology 59: 283-288.

Lewis, S. 1995. Roost fidelity of bats: a review. Journal of Mammalogy 76: 481–496.

Lisón, F., J. Palazón y J. Calvo. 2013. Effectiveness of the Natura 2000 network for the conservation of cave-dwelling bats in a Mediterranean region. Animal Conservation 16: 1–10.

Lisón, F., N. Yelo, A. Haz y J. Calvo. 2010. Contribución al conocimiento de la distribución de la fauna quiropterológica de la región de Murcia. Galemys 22 (1): 11-28.

López-Baucells, A., R. Rocha, P. Bobrowiec, E. Bernard, J. Palmeirim y C. Meyer. 2016. Field guide to Amazonian Bats. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus. pp.173.

Ludlow, M. y J. Gore. 2000. Effects of a cave gate on emergence patterns of colonial bats. Wildlife Society Bulletin 28: 191–196.

Ma, J., B. Liang, S. Zhang y W. Metzner. 2008. Dietary composition and echolocation call design of three sympatric insectivorous bat species from China. Ecological Research 23: 113-119.

Machado, M., M. Monsalve, A. Castelló, D. Almenar, A. Alcocer y J. Monrós. 2017. Population trends of cave-dwelling bats in the Eastern Iberian Peninsula and the effect of protecting their roosts. Acta Chiropterologica 19(1): 107–118.

Maiorano, L., A. Falcucci, E. Garton y L. Boitani. 2007. Contribution of the Natura 2000 network to biodiversity conservation in Italy. Conservation Biology 21: 1433–1444.

Martin, K., D. Leslie, Jr., M. Payton, W. Puckette y S. Hensley. 2003. Internal cave gating for protection of colonies of the endangered gray bat *Myotis grisesens*. Acta Chiropterologica 5: 143–150.

Martin, K., D. Leslie, Jr., M. Payton, W. Pucketteand y S. Hensley. 2006. Impacts of passage manipulation on cave climate: conservation implications for cave-dwelling bats. Wildlife Society Bulletin 34: 137–143.

Martin, K., W. Puckette, S. Hensley y D. Leslie, Jr. 2000. Internal cave gating as a means of protecting cave-dwelling bat populations in eastern Oklahoma. Proceedings of the Oklahoma Academy of Science 80: 133–137.

McArthur, R. y R. levins. 1967. The limiting similarity, convergence and divergence of coexisting species. The American Naturalist 101: 377-385.

McCracken, G. y G. Wilkinson 2000. Bats mating systems. Pp. 321-362, en: The Reproductive Biology of Bats (E. Crichton y P. Krutzsch, eds.). Academic Press, New York.

McNab, B. 1986. The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 56(1): 1–19.

Mello, M. A., Kalko, E. K. y Silva, W. R. 2013. Effects of moonlight on the capturability of frugivorous phyllostomid bats (Chiroptera: Phyllostomidae) at different time scales. Zoologia (Curitiba) 30: 397-402.

Merritt, R. y K. Cummins. 1996. An introduction to the aquatics insects of North America. Kendall/Hunt Publishing Company. New York. 722 pp.

Metcalfe, N. B. y S. E. Ure. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. Proceedings of the Royal Society of London. Series B: Biological Sciences 261: 395-400.

Meyer, C., L. Aguiar, L. Aguirre, J. Baumgarten, F. Clarke, J. Cosson, S. Estrada, J. Fahr, D. Faria, N. Furey, M. Henry, R. Hodgkison, R. Jenkins, K. Jung, T. Kingston, T. Kunz, M. Macswiney, I. Moya, J. Pons, P. Racey, K. Rex, E. Sampaio, K. Stoner, C. Voigt, D. von Staden, C. Weise y E. Kalko. 2010. Long-term monitoring of tropical bats for anthropogenic impact assessment: gauging the statistical power to detect population change. Biological Conservation 143: 2797–2807.

Migens, E. 2007. *Rhinolophus hipposideros* (Bechstein 1800). Pp. 139–143, en: Atlas y Libro Rojo de los mamíferos terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). D.G. de la Biodiversidad-SECEM-SECEMU, Madrid, 588 pp.

Ministerio de Medio Ambiente, y Medio Rural y Marino, 2011. Royal Decree 139/2011 para el desarrollo del Listado de Especies Silvestres en Régimen de Protección Especial y del Catálogo Español de Especies Amenazadas. Boletín Oficial del Estado. Madrid. pp. 39.

Mitchell-Jones, A., Z. Bihari, M. Masing y L. Rodrigues. 2007. Protecting and managing underground sites for bats. EUROBATS Publication Series No. 2 (English version). UNEP/EUROBATS Secretariat, Bonn, 38 pp.

Monsalve, M. 2012. *Myotis capaccinii*. Pp. 117-119, en: Mamíferos de la Comunitat Valenciana (J. Jiménez, M.A. Monsalve y J.A. Raga, eds.). Colección Biodiversidad, 19. Conselleria d'Infraestructures, Territori i Medi Ambient. Generalitat Valenciana. Valencia.

Monsalve, M., D. Almenar, A. Alcocer y A. Castelló. 2007. Murciélago ratonero patudo *Myotis capaccinii* (Bonaparte 1837). Pp: 194–196, en: Atlas y Libro Rojo de los mamíferos terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). D.G. de la Biodiversidad-SECEM-SECEMU, Madrid, 588 pp.

Monsalve, M., D. Almenar, A. Alcocer y A. Monsoriu. 2003. Los murciélagos de la Comunidad Valenciana. Sociedad Española de Espeleología y Ciencias del Karst. 4: 22-33.

Moreno, C., H. Arita y L. Solis. 2006. Morphological assembly mechanisms in Neotropical bat assemblages and ensembles within a landscape. Oecologia 149: 133-140.

Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Animal Behaviour 26: 852-855.

Myers, P. 1977. Patterns of reproduction of four species of vespertilionid bats in Paraguay. University of California Press. Berkeley. pp. 41.

Naumann, I. 1991. Hymenoptera. Pp. 916-1000, en: Insects of Australia. VOL II. (CSIRO, eds). Melbourne University Press & Cornell University Press. 1137 pp.

Neuweiler, G. 2000. Functional anatomy and locomotion. Pp. 9-42, en: The Biology of Bats. Oxford University Press.

Nogueras, J. y J. Garrido-García. 2007. Murciélago ratonero mediano *Myotis blythii* (Tomes 1857). Pp. 161–162, en: Atlas y Libro Rojo de los mamíferos terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). D.G. de la Biodiversidad-SECEM-SECEMU, Madrid, 588 pp.

Norberg, U. M. y Rayner, J. M. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 316: 335-427.

Nowak, R. 1991. Walker's mammals of the world. Fifth edition. The Johns Hopkins University Press, Baltimore.

Nowak, R. 1994. Walker's bats of the world. The Johns Hopkins University Press, Baltimore.

Ochoa, J., J. Sánchez, F. García y J. Clavijo. 2008. An undescribed behavior of the Isabelle’s ghost bat (*Diclidurus isabellus*), with distributional notes in Venezuela. Memoria de la Fundación La Salle de Ciencias Naturales 170: 145-151.

Oftedal, O. 1985. Pregnancy and lactation. Pp 215-238, en: The bioenergetics of wild herbivorous (R. J. Hudson y R. G. White, eds). CRC Press, Boca Raton, Florida.

Palomo, L., J. Gisbert y C. Blanco. 2007. Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid. pp. 588.

Pannekoek, J. y A. Van Strien. 2009. TRIM 3 manual (trends and indices for monitoring data). Project no. 100384. Statistics Netherlands, Voorburg, 58 pp.

Papadatou, E., R. Butlin, R. Pradel y J. Altringham. 2009. Sex-specific roost movements and population dynamics of the vulnerable long-fingered bat, *Myotis capaccinii*. Biological Conservation 142: 280–289.

Patterson, B. M, Willig y R. Stevens. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pp. 536–579, en: Bat Ecology (T. H. Kunz y M. B. Fenton, eds.). University of Chicago Press, Chicago, 784 pp.

Pavey, C. R., Grunwald, J. E. y Neuweiler, G. 2001. Foraging habitat and echolocation behaviour of Schneider's leafnosed bat, *Hipposideros speoris*, in a vegetation mosaic in Sri Lanka. Behavioral Ecology and Sociobiology 50: 209-218.

Pearch M., P. Bates y C. Magin. 2001. A review of the small mammal fauna of Djibouti and the results of a recent survey. Mammalia 65: 387–409.

Pereira, M., H. Rebelo, A. Rainho y J. Palmeirim. 2002. Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region. Acta Chiropterologica 4: 183-193.

Petrželková, K. y Zukal, J. 2001. Emergence behaviour of the serotine bat (*Eptesicus serotinus*) under predation risk. Netherlands Journal of Zoology 51: 395-414.

Pianka, E. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53-74.

Pugh, M. y J. Altringham. 2005. The effects of gates on cave entry by swarming bats. Acta Chiropterologica 7: 293–299.

Quetglas, J. 2007a. *Myotis escalerai* (Cabrera 1904). Pp. 186–188, en: Atlas y Libro Rojo de los mamíferos terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). D.G. de la Biodiversidad-SECEM-SECEMU, Madrid, 588 pp.

Quetglas, J. 2007b. Murciélago ratonero pardo *Myotis emarginatus* (Geoffroy, 1806). Pp. 166-168, en: Atlas y Libro Rojo de los Mamíferos

Terrestres de España (J. Palomo, J. Gisbert y J. Blanco, eds.). Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.

Quetglas, J. 2012. *Myotis escalerai*. Pp: 117-119, en: Mamíferos de la Comunitat Valenciana (J. Jiménez, M.A. Monsalve y J. Raga, eds.). Colección Biodiversidad, 19. Conselleria d'Infraestructures, Territori i Medi Ambient. Generalitat Valenciana. Valencia.

Racey, P. 1982. Ecology of bat reproduction. Pp. 57-104, en: Ecology bats. (T. Kunz, ed.). Plenum Press, New York and London. 425 pp.

Racey, P. 1988. Reproductive assessment in bats. Pp. 31-45, en: Ecological and behavioral methods for the study of bats. (T. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

Racey, P. A. y Speakman, J. R. 1987. The energy costs of pregnancy and lactation in heterothermic bats. Symposia of the zoological society of London. Published for the Zoological Society by Academic Press 57: 107-125.

Racey, P. A. y Swift, S. M. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. The Journal of Animal Ecology 54: 205-215.

Racey, P. y A. Entwistle. 2000. Life-history and reproductive strategies of bats. Pp. 363-414, en: Reproductive Biology of Bats (E. G., Crichton y P. H. Krutzsch, eds.). Academic Press, San Diego, California.

Rainho, A. y J. Palmeirim. 2011. The importance of distance to resources in the spatial modeling of bat foraging habitat. PLoS ONE 6: e19227.

Rebelo, H., P. Tarroso y G. Jones. 2010. Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16: 561–576.

Reichard, J. D., Gonzalez, L. E., Casey, C. M., Allen, L. C., Hristov, N. I. y Kunz, T. H. 2009. Evening emergence behavior and seasonal dynamics in large colonies of Brazilian free-tailed bats. Journal of Mammalogy 90: 1478-1486.

Richter, A., S. Humphrey, J. Cope y V. Brack, Jr. 1993. Modified cave entrances: thermal effect on body mass and resulting decline of endangered Indiana bats (*Myotis sodalis*). Conservation Biology 7: 407–415.

Rodrigues, L. y J. M. Palmeirim. 2008. Migratory behaviour of the Schreiber's bat: when, where and why do cave bats migrate in a Mediterranean region? Journal of Zoology 274: 116-125.

Rodrigues, L. y J. Palmeirim. 1994. An infrared video system to count and identify emerging bats. Bat Reasearch News 35: 77–79.

Rodrigues, L., A. Zahn, A. Rainho y J. Palmeirim. 2003. Contrasting the roosting behavior and phenology of an insectivorous bats (*Myotis myotis*) in its southern and northern distribution ranges. Mammalia 67(3): 321-335.

Rostovskaya, M., D. Zhukova, , A. Illarionova, , S. Ustyugova, A. Borissenco y A. Sviridov. 2000. Insect prey of the long-eared bat *Plecotus auritus* (Chiroptera: Vespertilionidae) in central Russia. Russian Entomological Journal 9 (2): 185-189.

Roué, S. y M. Némoz. 2002. Mortalité exceptionnelle du Minioptère de Schreibers en France lors de l'année 2002. Bilan national. Société Française pour l'Etude et la Protection des Mammifères, Paris, 28 pp.

Russo, D. 2015. Bats as bioindicators: an introduction. Mammalian Biology 80: 157-158.

Russo, D. y G. Jones. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of their echolocation calls. Journal of Zoology (London) 258: 91–103.

Russo, D. y G. Jones. 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. Ecography 26: 197–209.

Russo, D., L. Cistrone, G. Jones y S. Mazzolenis. 2004. Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. Biological Conservation 117: 73–81.

Rydell, J. y Speakman, J. R. 1995. Evolution of nocturnality in bats: potential competitors and predators during their early history. Biological Journal of the Linnean Society 54: 183-191.

Rydell, J., Entwistle, A. y Racey, P. A. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76: 243-252.

Sachanowicz, K., M. Ciechanowski y K. Piska. 2006. Distribution patterns, species richness and status of bats in Poland. Vespertilio 9-10: 151-173.

Salicini, I., C. Ibáñez y J. Juste. 2011. Multilocus phylogeny and species delimitation within the Natterer's bat species complex in the Western Palearctic. Molecular Phylogenetic Evolution 61(3):888-898.

Shannon, C. 1948. A mathematical theory of communication. Bell Systems technical Journal 27: 379-423.

Sharifi, M., Z. Hemmati y P. Rahimi. 2000. Distribution and conservation status of bats in Iran. *Myotis* 38: 61-68.

Sherwin, H., W. Montgomery y M. Lundy. 2013. The impact and implications of climate change for bats. Mammal Review 43(3): 171–182.

Shiel, C., C. McAney, C. Sullivan y J. Fairley. 1997. Identification of arthropod fragments in bat droppings. Occasional Publication. The Mammal Society London 17: 1–56.

Sienkiewicz, P. y S. Konwerski, 2006. Carabidae (Coleoptera: Carabidae) of central Wielkopolska. Wiadomości Entomologiczne 25: 87-95.

Simmons, N. 2005. Order Chiroptera. Pp. 312–529, en: Mammal species of the World: a taxonomic and geographic reference (Wilson, D. y D. Reeder, eds.). 3ra edición. Johns Hopkins University Press, Baltimore.

Simpson, E. 1949. Measurement of diversity. Nature 163: 688.

Slade, C. y B. Law. 2008. An experimental test of gating derelict mines to conserve bat roost habitat in southeastern Australia. Acta Chiropterologica 10: 367–376.

Spanjer, G. y M. B. Fenton. 2005. Behavioral responses of bats to gates at caves and mines. Wildlife Society Bulletin 33: 1101–1112.

Speakman, J. R. 1991a. The impact of predation by birds on bat populations in the British Isles. Mammal Review 21: 123-142.

Speakman, J. R. 1991b. Why do insectivorous bats in Britain not fly in daylight more frequently? Functional Ecology 5: 518-524.

Speakman, J. R., Hays, G. C. y Webb, P. I. 1994. Is hyperthermia a constraint on the diurnal activity of bats?. Journal of Theoretical Biology 171: 325-341.

Spitzenberger, F., Engelberger, S. y Kugelschafter, K. 2014. Real time observations of *Strix aluco* preying upon a maternity colony of *Myotis emarginatus*. Vespertilio 17: 185–196.

SPSS. 2008. SPSS Statistics for Windows. Version 17.0. SPSS Inc., Chicago.

Stephens, D. y J. Krebs. 1986. Foraging Theory. Princeton University Press Princeton, New Jersey.

Svanback, R. y D. Bolnick. 2007. Intraspecific competition drive increased resource use diversity within a natural population. Proceedings of the Royal Society of London B Biological Sciences 274: 839-844.

Thomas, A. J. y Jacobs, D. S. 2013. Factors influencing the emergence times of sympatric insectivorous bat species. Acta Chiropterologica 15: 121-132.

Thompson, M. 1987. Longevity and survival of female pipistrelle bats (*Pipistrelus pipistrellus*) on the Vale of York, England. Journal of Zoology 211:209-214.

Thomson, T. J., Scott, J. A. y Castleberry, S. B. 2010. Evaluation of methods for monitoring long-term population trends in cave-roosting bats. Proceedings of the annual conference/Southeastern Association of Fish and Wildlife Agencies 64: 75-80.

Tidermann, C. y Woodside, D. 1978. A collapsible bat-trap and a comparison of results obtained with the trap and with mist-nest. Australian Wildlife Research 5: 355-362.

Tuttle, M. 1974. An improved trap for bats. Journal of Mammalogy 55 (2): 475-477.

Tuttle, M. D. 1977. Gating as a means of protecting cave-dwelling bats. Pp. 77–82, en: National Cave Management Symposium Proceedings (T. Aley y D. Rhodes, eds.). Speleobook, Albuquerque, 106 pp.

Tuttle, M. y D. Stevenson. 1982. Growth and survival of bats. Pp. 105-150, en: Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York.

Tuttle, M. y D. Taylor. 1998. Bats and mines. Resource Publication No. 3. Bat Conservation International, Austin, Texas, 52 pp.

Twente, J. W. 1955. Some aspects of habitat selection and other behavior of cavern-dwelling bats. Ecology 36: 706-732.

Whitaker, J. 1988. Food habits analysis of insectivorous bats. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, DC.

Whitaker, J. y A. Rodríguez-Durán. 1999. Seasonal variation in the diet of mexican free-tailed bats, *Tadarida brasilensis antillularum* (Miller) from a colony of Puerto Rico. Caribbean Journal of Science 35:23–28.

Whitaker, J., C. Maser, y L. Keller. 1977. Food habits of bats western Oregon Northwest. Northwest Science 55: 281–292.

Whitaker, J., C. Neefus y T. Kunz. 1996. Dietary variation in the mexican free-tailed bat (*Tadarida brasiliensis mexicana*). Journal of Mammalogy 77 (3): 716-724.

White, D. y J. Seginak. 1987. Cave gate designs for use in protecting endangered bats. Wildlife Society Bulletin 15: 445–449.

Wilde, C., C. Knight y P. Racey. 1999. Influence of torpor on milk protein composition and secretion in bats. Journal of Experimental Zoology 284: 35-41.

Wilkinson, G. y J. South. 2002. Life history, ecology and longevity in bats. Aging Cell 1:124–131.

Willig, M. 1995. Reproductive activity of female bats from Northeastern Brazil. Bat Research News 26:17-20.

Willig, M. y M. Moulton. 1989. The role of stochastic and deterministic processes in structuring neotropical bat communities. Journal of Mammalogy 70 (2): 323-329.

Wilson, D. y D. Reeder. 2005. Mammals Species of The World: A taxonomic and geographic reference. 3ra Edición. The Hopkins University Press. Baltimore.

Zahn, A. 1999. Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. Journal of Zoology (London) 247: 275-280.

Zahn, A., A. Rottenwallner y R. Güttinger. 2006. Population density of the greater mouse-eared bat (*Myotis myotis*), local diet composition and availability of foraging habitats. Journal of Zoology 269: 486–493.