Alimentación y color del plumaje en el carbonero común *Parus major*

¿Son las aves lo que comen?

Emilio Pagani-Nuñez

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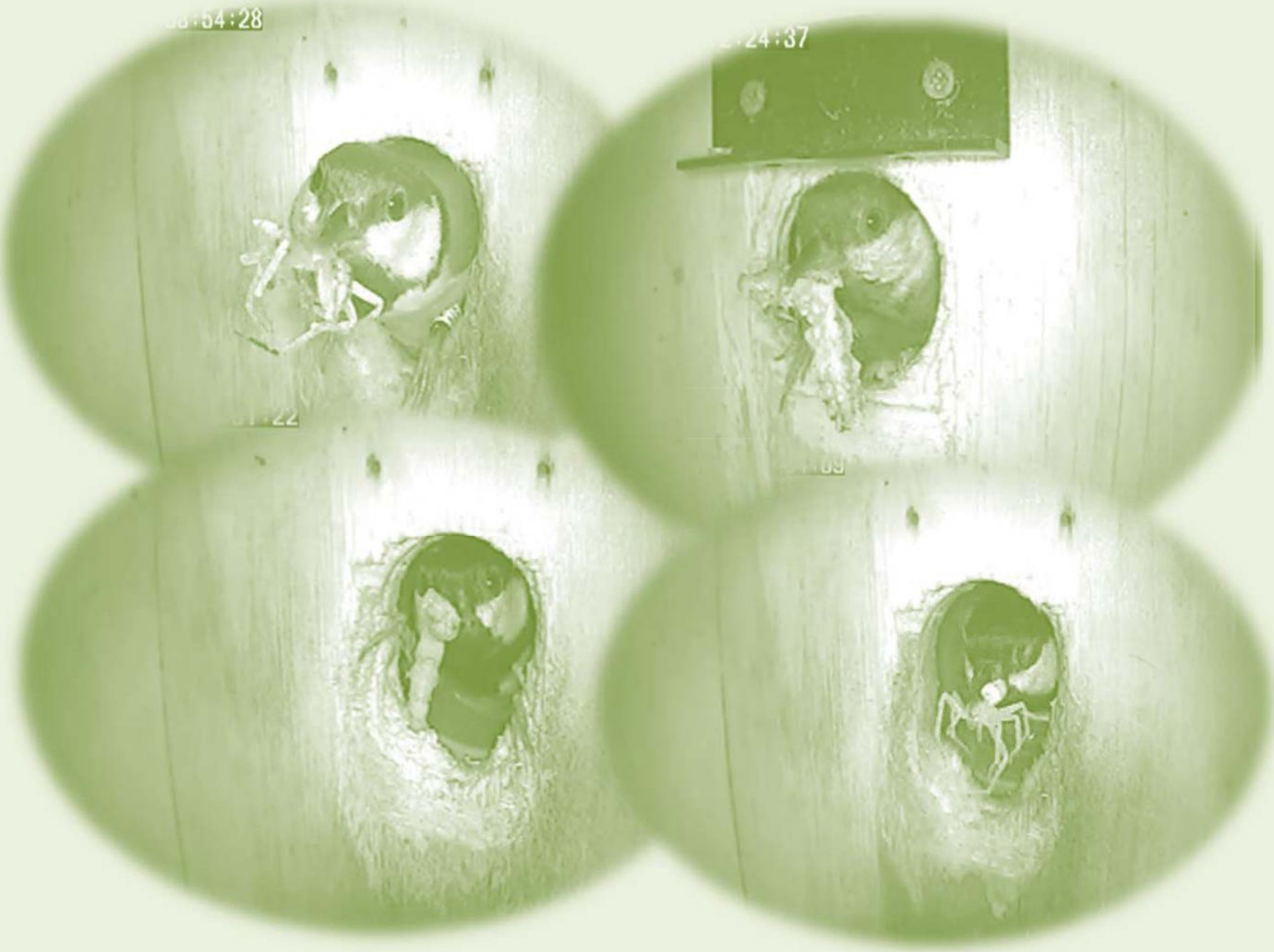

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Línea de investigación: Ecología Evolutiva y del Comportamiento
Tutoría: Departamento de Biología Animal – Universidad de Barcelona
Centro: Museo de Ciencias Naturales de Barcelona

Tesis Doctoral
Barcelona, Julio de 2014

Memoria presentada por el Licenciado en Ciencias Ambientales Emilio Pagani Núñez para optar al grado de Doctor por la Universidad de Barcelona a través del Museo de Ciencias Naturales de Barcelona

Juan Carlos Senar Jorda
Jefe de Investigación
Unidad Asociada CSIC de Ecología Evolutiva y de la ConductaMuseo de Ciencias Naturales de Barcelona

Carolina Sanpera Trigueros
Profesora asociada
Departamento de Biología Animal
Universidad de Barcelona

Dedicado a la memoria de Javier Núñez Yáñez: abuelo, camarada, amigo.

Agradecimientos

En la vida de una persona se presentan pocas oportunidades que realmente determinen el curso de la misma. Sin duda, mi estancia en Barcelona ha sido una de ellas. En la sociedad actual, y en comparación con décadas pasadas, las personas jóvenes disponemos de alguna oportunidad para nuestro desarrollo personal, y cuando estas oportunidades se presentan hay que aprovecharlas. Parafraseando a Lenin, soñar es muy importante siempre y cuando no nos limitemos a eso, y hagamos todo lo que esté en nuestra mano para convertir esos sueños en realidad.

Todo empezó hace poco más de treinta años, que ya son años. Desde pequeño me inculcaron un sentido del deber, de la disciplina y del esfuerzo, que no he sabido recuperar en su plenitud hasta una edad ya tardía. Recuerdo gratamente el interés enciclopédico de mi abuelo Javier por todas las cosas, su meticulosidad. Durante mi infancia, entrar en su “guarida”, como llamaba jocosamente a su estudio, colmaba mis sentidos. Siempre había un fondo de tenebrosa música barroca, cierta penumbra, y las paredes estaban cubiertas de estanterías atiborradas de libros, de cuadros y carteles llenos de medallas y rostros de gente desconocida para mí por aquel entonces. Mi abuela Ana, siempre silenciosa, nos solía traer un té bien caliente. Con los años aprendería que aquellos rostros eran los de García Lorca, Picasso, el Che, Mao o Lenin. Pasé muchas tardes estudiando matemáticas y otras ciencias allí, bajo su tutela. ¡Siempre estarás presente en mi corazón, camarada! Varios años después de su muerte sigo hablando con él, recordando su sabiduría cuando las dificultades ensombrecen mi ánimo. Gracias por todo, gracias por ser y gracias por estar.

Pero fue Maritín, una prima de mi madre, quien me formó como naturalista en mi más remota infancia. Tristemente fallecida de una terrible enfermedad pulmonar, fue una de las personas que introdujo en mí esa curiosidad insaciable por conocer y comprender la vida que nos rodea. Cuando visitaba nuestra casa estaba deseando que fuéramos a la playa para darme largos paseos con ella siguiendo la orilla. En esas caminatas íbamos recogiendo todo resto de vida marina que encontrábamos a nuestro paso. Como suele ser habitual en estos casos, acabé llenando la casa de mi madre de botes con bichos muertos bañados en alcohol.

Y claro, a todo esto hay que añadir la influencia de Arancha, mi madre. Su desarrollado sentido de la disciplina, del respeto por lo demás y por uno mismo, han sido, son y serán las líneas que dirigen mi vida. Le tengo que agradecer muchas cosas, entre ellas que me regalara unos prismáticos y una guía de aves cuando tenía doce años, o que me acompañara o simplemente me llevara en coche al campo tan a menudo cuando era niño. Siempre ha sido un apoyo, una referencia, y un ejemplo a seguir. Seguramente es la persona más trabajadora que he visto y veré. Mi padre, Rafael, y mi hermano, Sergio, a los que también agradeceré eternamente su amor y comprensión, pueden dar fe de ello.

Es preciso resaltar el papel que, más recientemente, tuvieron mis maestros José Antonio y Javier, anilladores de la Sociedad Española de Ornitología en Málaga, en la recuperación de mi amor por la naturaleza. Más bien, en convertir ese amor en pasión y obsesión. La primera vez que vi un pajarillo en mano, ya con veintitantos años, produjo tal impacto en mí que cambió para siempre mi existencia. De ellos he de destacar, no sólo sus conocimientos enciclopédicos, sino un comportamiento y una actitud ejemplares. Grandes naturalistas y mejores personas.

Y que decir de mi amada Melissa, mujer hermosa, luchadora y valiente. Un torbellino de fuerza, energía y ganas de cambiar el mundo. Un aluvión de sentimientos, cuando sólo quedaba tristeza, apatía y desesperanza en mi alma. Mil gracias por devolverme al sendero de la rectitud y del amor, ojalá el despiadado azar nos sea favorable en nuestro largo camino.

Finalmente, he de agradecer a Juan Carlos Senar la oportunidad de venir a Barcelona para trabajar en su equipo. También he de agradecer a todo el personal del Museo de Ciencias Naturales de Barcelona, empezando por mis compañeros Sergio, Alba y Sepand, que hayan estado ahí aunque sólo fuera para hablar un momento de nuestros problemas comunes. Espero que el futuro sea benévolo con nosotros, que estamos empezando una carrera investigadora en un contexto muy desfavorable. También merecen una mención especial todos los amigos, en Nerja, en Granada, en Barcelona, que tantas me veces me quisieron y me odiaron, me apoyaron, me aconsejaron, me ayudaron o que simplemente estuvieron ahí cuando los necesitaba, aunque al final la vida y el tiempo nos hayan separado.

Contenido:

Esta tesis está basada en los siguientes artículos:

1. **Pagani–Núñez, E.**, Ruiz, Í., Quesada, J., Negro, J. J. & Senar, J. C. 2011. The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. ***Animal Biodiversity and Conservation***, 34(2), 355-361.
2. Hernández-Gómez, S., **Pagani-Núñez, E.**, Ruiz, I. & Senar, J. C. 2014. Nestling diet matches prey abundance in Mediterranean Blue Tits *Cyanistes caeruleus*. ***Animal Biodiversity and Conservation***. En prensa.
3. **Pagani-Núñez, E.** & Senar, J. C. 2013. One hour of sampling is enough: Great Tit *Parus major* parents feed their nestlings consistently across time. ***Acta Ornithologica***, 48(2), 194-200.
4. **Pagani-Núñez, E.**, Hernández-Gómez, S., Riyahi, S. & Senar, J. C. 2014. Year-round preference of spiders for Mediterranean great tits *Parus major*. ***Ardeola***. En prensa.
5. **Pagani-Núñez, E.**, Valls, M. & Senar, J. C. 2014. Individual diet specialization in a generalist population: the case of breeding Great tits *Parus major* in the Mediterranean area. Submitted.
6. **Pagani-Núñez, E.** & Senar, J. C. 2014. Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. ***Acta Oecologica***, 55, 23-28.
7. **Pagani-Núñez, E.**, Uribe, F., Hernández-Gómez, S., Muñoz, G. & Senar, J.C. 2014. Habitat structure and prey composition generate contrasting effects on carotenoid-based colouration of Great tit *Parus major* nestlings. ***Biological Journal of the Linnean Society***. En prensa.

Resumen

Los animales despliegan diferentes estrategias de forrajeo a la hora de buscar alimento para su descendencia, mostrando gran variabilidad entre especies, poblaciones e individuos. Este patrón es especialmente acusado en los bosques mediterráneos debido a su elevada biodiversidad. Tres factores son cruciales a la hora de caracterizar estas estrategias: el tipo de presas que seleccionan preferentemente, el grado de consistencia del comportamiento en el corto plazo y a lo largo del ciclo anual, y la estructura trófica de la población en la que se inserta este comportamiento. En relación con esto, una cuestión de gran interés es determinar cómo se relacionan estas preferencias tróficas con el grado de ornamentación mostrado por lo individuos. Según la “hipótesis de los buenos padres”, las hembras se deben fijar en los ornamentos masculinos como indicativos de sus habilidades como progenitores. En consecuencia, sería esperable que individuos más ornamentados muestren estrategias de forrajeo más eficientes. Esto es especialmente cierto en el caso de coloraciones basadas en carotenos, los cuales sólo se pueden obtener a través de la comida. Nuestro objetivo fue caracterizar las estrategias de forrajeo que mostraban los progenitores en nuestra población de estudio, y cómo éstas interaccionaban con los ornamentos basados en carotenos de padres y descendientes. Nuestra especie de estudio modelo fueron los carboneros comunes *Parus major* mediterráneos. En primer lugar, encontramos que aunque la oruga fue su presa principal, en nuestra zona se usan grandes cantidades de arañas como alimento. Existe también una gran variabilidad entre individuos (rango de uso de arañas por pareja 0-50%). Demostramos que los carboneros comunes son muy consistentes en sus estrategias de forrajeo en el corto plazo, y que preferían estas arañas no sólo en la época reproductora, sino a lo largo de todo el ciclo anual. Es destacable que aunque la población se podría caracterizar como generalista trófica, los individuos mostraron la tendencia a especializarse. Aquellas parejas más especialistas seleccionaron menos orugas y sacaron adelante más pollos. Al analizar la relación entre dieta y coloración del plumaje, encontramos que los padres más ornamentados (mayor tono en el amarillo del pecho) dieron más arañas a sus pollos, que mostraron mejor condición física. Además, aquellos pollos que

recibieron más arañas mostraron colores más brillantes. Podemos concluir que en el contexto mediterráneo y en lo que se refiere a la dieta de las aves, la inversión parental es una cuestión de calidad y las arañas tienen una gran importancia como presa alternativa.

Introducción general

"Dime a dónde te diriges, y te diré el mejor camino a seguir"
Alicia en el país de las maravillas
Lewis Carroll

- Definiendo el contexto: el comportamiento de forrajeo de las aves en el área mediterránea

El área mediterránea ha sido caracterizada tradicionalmente como una región geográfica diversa, heterogénea y, en consecuencia, extremadamente rica en especies de artrópodos y frutos (Blondel et al. 2010). Este patrón tiene consecuencias fundamentales para el comportamiento de forrajeo de las aves. Las orugas aquí son mucho más escasas que en latitudes más norteñas del continente europeo, por lo que éstas suelen ser sustituidas por otros tipos de presas (Blondel et al. 1991; Bańbura et al. 1994). En el caso particular de los ambientes mediterráneos, un tipo determinado de presa es frecuentemente seleccionada entre todo el abanico de artrópodos disponibles: las arañas. Se ha demostrado que las arañas son ricas en distintos aminoácidos y otros compuestos, como la taurina, lo que podría explicar en parte por qué es una presa tan atractiva para las aves (Ramsay & Houston 2003; Magrath et al. 2004; Arnold et al. 2007; Wiesenborn 2012). En todo caso, la selección de distintos tipos de presas no sólo es explicable a partir de su composición nutricional en un sentido estricto. Tres elementos adicionales pueden influir esta dinámica: la estructura trófica de las poblaciones (Alatalo 1982; Atienzar et al. 2013), la abundancia relativa de presas (Naef-Daenzer et al. 2000), así como los mecanismos de transmisión de diferentes técnicas de caza (Slagsvold & Wiebe 2011).

- Estructura trófica de las poblaciones en el área Mediterránea

Las estrategias de forrajeo seguidas por las aves reproductoras se pueden caracterizar en un sentido amplio como generalistas o especialistas (Stephens et al. 2007; Newsome et al. 2009). Sin embargo, dentro de cada especie, distintas poblaciones, y los individuos dentro de cada población, pueden diferir considerablemente en sus estrategias (Bolnick et al. 2011). Esto puede ser debido, no sólo a que seleccionen distintos tipos de presas, sino también a que pueden mostrar diferentes grados de generalismo o especialismo trófico (Woo et al. 2008; Newsome et al. 2009; Vander Zanden et al. 2010). En los últimos años, diversos trabajos han prestado especial atención a lo que se ha denominado “la ecología de los individuos” (Bolnick et al. 2003), resaltando que se debe prestar especial atención a la variabilidad entre individuos dentro de una población. Es decir, aunque una especie dada sea considerada generalista desde el punto de vista de la ecología trófica, se debe precisar además si esto es debido a que todos los individuos de una población determinada se comportan como generalistas, o si, en cambio, desarrollan diferentes grados de especialización en distintos tipos de presas que conforman esa estructura generalista a nivel poblacional (Bolnick et al. 2002; Bolnick et al. 2003). Dada la gran diversidad de fuentes de comida, el impacto que la ingesta de distintos tipos de nutrientes tiene sobre las historias vitales de los organismos (ver por ejemplo Catoni et al. (2008)), así como la gran variabilidad del comportamiento entre individuos, propia de los ambientes mediterráneos, consideramos de vital interés examinar en detalle esta cuestión en este contexto determinado.

- ¿Expresa el color del plumaje la habilidad de forrajeo del portador?

Un tema central en el estudio de la señalización animal es poder establecer los mecanismos que aseguran la honestidad de las señales (Grafen 1990; Maynard Smith & Harper 2003). Diversos trabajos sugieren que la coloración del plumaje señaliza las distintas cualidades del individuo y, muy a menudo, estas cualidades se relacionan con la habilidad de los individuos para conseguir recursos (Hill & McGraw 2006). Por ejemplo, dado que los pigmentos carotenoides son necesariamente adquiridos a través de la comida, tradicionalmente se ha sugerido que la honestidad de las señales basadas en carotenos podría recaer en la dificultad de conseguir estos componentes: sólo los individuos capaces de obtener estos carotenos pueden mostrarlos (Endler 1980; Hill 1990; Hill 2006). A pesar de la aparente lógica detrás de este razonamiento, la relación entre dieta y color del plumaje es muy controvertida (Hill 1994; Hudon 1994; Thompson et al. 1997; Hill 2002). Muchos trabajos que defienden esta hipótesis son estudios centrados en la administración de carotenos a aves en condiciones de cautividad (Hill 1992; Hadfield & Owens 2006; Aguilera & Amat 2007; Karu et al. 2007). Sin embargo, esta evidencia no es universal. Además, estos trabajos han sido muy criticados porque las aves en cautividad normalmente tienen peor condición física, lo que puede enmascarar cualquier relación encontrada (Hudon 1994; Zahn & Rothstein 2001). Estudios basados en la administración de carotenos en condiciones naturales encontraron cambios en el color del plumaje (Tschirren et al. 2003; Biard et al. 2006), pero fueron llevados a cabo con pollos, no con adultos. Asimismo, el hecho de que la administración de pigmentos afecte el color del plumaje no significa de manera unívoca que hay una relación directa entre dieta y color. Por lo tanto, una cuestión pendiente es demostrar de manera consistente que el consumo de distintos tipos de presas va asociado a diferentes grados de ornamentación.

Los hábitats naturales pueden diferir en la disponibilidad de comida rica en carotenos (por ejemplo, bosques caducifolios vs bosques perennes, o entre parches de diferente tamaño), y de manera coincidente, el color del plumaje de las aves que viven en estas diferentes áreas puede ser distinto (Slagsvold & Lifjeld 1985; Hill 1993; Ferns & Hinsley 2008). Sin embargo, esta aproximación es bastante indirecta. Como han afirmado Zahn & Rothstein (2001), cualquier test de la hipótesis de la limitación de los carotenos debería mostrar en la naturaleza que el rango de ocurrencia natural de las distintas dietas influye en el color del plumaje.

Actualmente, las evidencias relacionando dieta y color del plumaje en condiciones naturales son bastante escasas. El único trabajo que evalúa directamente la perspectiva de los carotenos como factor limitante del color del plumaje fue obtenida comparando el contenido estomacal de machos con muda activa de pinzones mexicanos *Carpodacus mexicanus* con el color de sus plumas en crecimiento. Se encontró que los machos más rojizos tenían más pigmentos carotenoides en su estómago (Hill et al. 2002). Linville & Breitwisch (1997) relacionaron una caída generalizada de la disponibilidad de frutos para machos de cardenal rojo *Cardinalis cardinalis* durante la época de muda, con un descenso generalizado en el color rojo basado en carotenos de su plumaje. En el mismo sentido, los carboneros comunes *Parus major* en áreas contaminadas, donde hay menos orugas ricas en carotenos disponibles, muestran un color del plumaje menos brillante (Eeva et al. 1998; Horak et al. 2000; Dauwe & Eens 2008).

Existen por tanto una serie de cuestiones de especial interés para la ecología animal que no han sido investigadas en profundidad, y que se refieren principalmente a las interacciones entre el grado de ornamentación de los individuos y la elección de dieta. Este aspecto puede manifestarse de diversas formas, ya sea como la selección de determinados tipos de presa en función del grado de ornamentación de los individuos, o como la presencia de distintas estrategias de forrajeo (por ejemplo, durante el proceso de cría) asociadas a distintos niveles de señalización (Senar & Escobar 2002; Casagrande et al. 2006; García-Navas et al. 2012). Un mayor o menor grado de ornamentación puede llevar a la adopción de estrategias más o menos dependientes de dietas ricas en distintos tipos de componentes, que pueden beneficiar o perjudicar la señalización por sí misma.

- El Carbonero común: una especie modelo

El carbonero común *Parus major* es una especie que se ajusta al patrón descrito, y es un modelo excelente para estudiar el tema considerado (Figura A). Por una parte, muestra un elevado grado de ornamentación (Figuerola & Senar 2000), ya sea en cuanto a colores basados en carotenos (amarillo del pecho), a melaninas (parche negro de la cabeza y corbata), colores estructurales (mancha blanca de la mejilla) y al ultravioleta (en zonas amarillas y negras). Se ha descrito, además, la existencia de un complejo de señalización múltiple, así como la influencia de factores diferentes para cada uno de los aspectos del color (Senar et al. 2003; Quesada & Senar 2007; Senar et al. 2008). Por la otra, aunque considerada especialista en larvas de lepidóptero (Naef-Daenzer, Naef-Daenzer & Nager 2000), es una especie versátil capaz de explotar múltiples tipos de presas (ver por ejemplo: Royama (1970), Barba & Gil-Delgado (1990), Atienzar et al. (2013)), así como de innovar para explotar nuevos nichos cuando las circunstancias lo requieren (Fisher & Hinde 1949; Caris 1958; Estok et al. 2010). La especie es fácilmente capturada en trampas embudo (Senar et al. 1997) y cría en cajas nido, lo que facilita su monitoreo.

Figura A. Macho (arriba) y hembra (abajo) de carbonero común *Parus major*

- Objetivos

Nuestro primer objetivo fue determinar las preferencias de dieta en carboneros (artículo **1**) y herrerillos comunes *Cyanistes caeruleus* (artículo **2**) en nuestra área de estudio, así como los patrones generales de abundancia de los distintos tipos de presas.

Hay otro aspecto de importancia central para garantizar que la información adquirida es relevante y estable: el grado de consistencia del comportamiento de los individuos. Es decir, si sus estrategias de forrajeo, y en particular las presas que seleccionan preferentemente, se mantienen en el corto plazo (Van Baalen et al. 2001; Barba et al. 2009; García-Navas, Ferrer & Sanz 2012), a lo largo del ciclo anual (ver por ejemplo Illera & Atienza (1995)), y bajo diferentes condiciones ambientales (bajo condiciones climáticas adversas: Radford *et al.* (2001), o bajo diferentes niveles de esfuerzo: García-Navas & Sanz (2010)). Usando como modelo el carbonero común, nos centramos en determinar hasta qué punto estas preferencias eran consistentes en el corto plazo (artículo **3**) y a lo largo de todo el ciclo anual (artículo **4**), tanto en condiciones controladas (en cautividad) como en condiciones naturales.

El tercer objetivo fue analizar la estructura trófica de nuestra población de carboneros comunes, con el fin de conocer el grado de especialismo trófico individual que se produce en un contexto poblacional generalista (artículo **5**).

El objetivo final consistió en establecer si el grado de ornamentación de los adultos reproductores de carbonero común se correlacionaba con la composición de presas que llevaban a sus pollos (artículo **6**) y, adicionalmente, examinar el efecto que tenía el esfuerzo parental y el suministro de distintos tipos de presas, sobre el color de los pollos (artículo **7**).

- Material y Métodos

- Área de estudio

Los trabajos desarrollados en condiciones naturales se llevaron a cabo en la estación de campo de Can Catà (Cerdanyola del Vallès, Sierra de Collserola, en las afueras de la ciudad de Barcelona; ver Figura B). Nuestra zona de estudio se puede caracterizar como un bosque mixto mediterráneo, el cual presenta un elevado grado de heterogeneidad ambiental, tanto en lo relativo a las especies de árboles que lo componen como a la altitud sobre el nivel del mar (ver artículo **1**). En este bosque se pueden encontrar especies esclerófilas como el pino carrasco *Pinus halepensis* o la encina *Quercus ilex*, así como especies caducifolias como el roble *Quercus cerroides*. Debe tenerse en cuenta que el factor que determina la estructura del hábitat en los distintos territorios (nidos) no es tanto la composición de especies como el grado de desarrollo y madurez de los árboles, además de la altitud sobre el nivel del mar (ver artículo **7**).

Figura B. Can Catà, fondo de valle

- Procedimientos de campo

Realizamos un seguimiento sistemático de nuestra población de estudio a lo largo de todo el periodo biológico. Las capturas se realizaron mediante el empleo de trampas especiales de embudo (Senar et al. 1997) en invierno y verano, y en los nidos en la época reproductora. Cada individuo (adulto) fue anillado con banda metálica numerada y con anilla de PVC de lectura a distancia.

Realizamos medidas biométricas estándar en todos los individuos capturados (longitud de tarso y de ala, además del peso y la puntuación de músculo y grasa). Para medir el color del plumaje se tomaran los valores de luminosidad (lightness), intensidad (chroma) y tono (hue) de las plumas amarillas del pecho con un colorímetro portátil (Figuerola et al. (1999); Quesada & Senar (2006); ver también artículos **6** y **7**). El tamaño de la mancha negra del pecho se midió a través de fotografías digitales siguiendo el procedimiento establecido en Figuerola & Senar (2000). De cada individuo se recolectaron plumas del pecho y dos rectrices de la cola, utilizadas para análisis de isótopos estables y de barras de crecimiento, y muestras de sangre para posteriores análisis genéticos. Los datos se tomaron de 2010 a 2013.

- Seguimiento de la temporada de cría

A lo largo de tres primaveras (2011-2012-2013) se procedió al seguimiento de la reproducción de las distintas parejas de nuestra población de estudio, anotando fecha de puesta y eclosión, tamaño de puesta, éxito reproductor y otros parámetros de interés. Concluida la primera fase reproductiva, se procedió al marcado y toma de muestras de pollos y padres en los nidos, siguiendo el protocolo establecido en Quesada & Senar (2007).

- Estudio de la alimentación proporcionada a los pollos

Llevamos a cabo grabaciones del trabajo de cebado de los pollos realizado por los padres (todos los años) empleando cámaras integradas en el nido, provistas de sensor de movimiento y luz infrarroja (Figura C). La grabación se realizó a lo largo de 24 o 48 horas, en función del diseño experimental (artículos **5**, **6** y **7**). El análisis posterior de las cintas en el laboratorio permitió identificar las presas aportadas por cada progenitor (Figura D). Los adultos fueron identificados en las grabaciones, al entrar al nido, por la anilla de PVC de lectura a distancia.

Figura C. Cámara integrada en el nido

Figura D. Ejemplos de orugas y arañas aportadas por los padres a sus pollos.

- Experimentos en cautividad

Con el fin de determinar si carboneros comunes prefieren arañas u orugas como alimento, en el invierno de 2012-2013 realizamos una batería de experimentos de elección de presa en cautividad (Rechten (1983); Emmans (1991); ver artículo **4**). Se utilizaron jaulas individuales de 1x1x1 metros. Las presas más habituales, orugas y arañas, fueron ofrecidas de forma confrontada en una serie de experimentos secuenciales (Freidin et al. 2009). Las aves se mantuvieron el mínimo tiempo posible en cautividad, con comida y agua *ad libitum*, además de una pequeña caja nido que actuaba de refugio para minimizar el estrés, siendo posteriormente liberadas en el mismo lugar en que fueron capturadas.

- Determinación del grado de especialización individual de la dieta

Para determinar el grado de especialismo o generalismo trófico de las distintas parejas se empleó una aproximación estadística estándar en ecología trófica conocida como índice de similitud proporcional (proportional similarity index, Psi; Bolnick et al. (2003)). Esta metodología permite confrontar las preferencias tróficas de cada pareja con respecto a la media poblacional. De este modo, es posible encuadrar adecuadamente el comportamiento de cada pareja en un contexto poblacional (ver artículo **5**).

Resultados y discusión

El objetivo principal de esta Tesis era establecer hasta qué punto existe una relación entre el color del plumaje del carbonero común y su dieta, bajo la hipótesis general de si las aves son o no lo que comen. Es decir, si existen un conjunto de adaptaciones funcionales a distintos tipos de dieta o estrategias de forrajeo que son señalizadas a través de sus ornamentos (Hill 1994; Hill 2006). Entrados en el tema de la dieta, un objetivo adicional era discernir el sistema trófico desarrollado en nuestra población mediterránea de carbonero común (Bolnick et al. 2003), centrándonos especialmente en el aprovechamiento de distintos tipos de presas (Bańbura et al. 1994), la eficiencia de las distintas estrategias de forrajeo seguidas (Blondel et al. 1991; Tremblay et al. 2003; Tinker et al. 2009) y su estabilidad en el tiempo (Van Baalen et al. 2001; Krivan & Cressman 2009). Dado que las arañas aparecen como alternativa más interesante a las orugas, quedaría por determinar el grado de generalización en el empleo de esta presa, así como los mecanismos que explican este cambio en nuestra población.

- Preferencias de dieta en carboneros y herrerillos comunes reproductores en un bosque mediterráneo

En primer lugar, era preciso determinar cuáles son las presas más comunes en la dieta de los pollos de carbonero y herrerillo común en ambientes mediterráneos (en línea con Blondel et al. (1991) y Bańbura et al. (1994); ver artículos **1** y **2**). En artículo **1** demostramos que las presas principales de nuestra especie de estudio en la zona mediterránea son las orugas y las arañas. La alta frecuencia de aparición de las arañas (20-80% según las parejas) en distintos años y zonas del bosque, así como independientemente del grado de desarrollo de los pollos, destaca como una característica de nuestras latitudes (ver figura 1).

Figura 1. Publicada en el artículo 1.

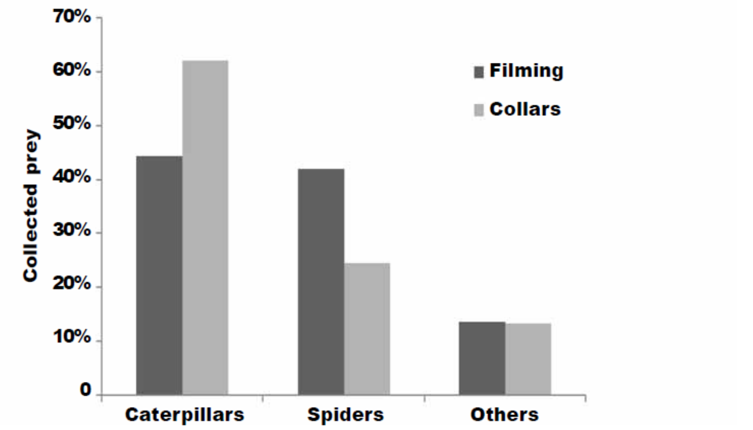


Fig. 1. Percentage of prey collected by Great Tit parents, according to the recording method: video (2001) or neck collars (2004).

Fig. 1. Porcentaje de presas recolectadas por los padres de Carbonero Común, de acuerdo con el método de grabación: vídeo (2001) o collares (2004).

Para comprobar el grado de importancia que tienen las arañas para la dieta de las aves en ambientes mediterráneos desde un punto de vista más general, analizamos cuáles eran las presas más comunes llevadas por padres de herrerillo común, una especie cercana al carbonero común, a sus pollos (artículo **2**). Este estudio se realizó en la misma área de estudio que aquellos centrados en los carboneros comunes. Primero muestreamos artrópodos presentes en hojas de las distintas especies de árboles (Naef-Daenzer, Naef-Daenzer & Nager 2000). Encontramos que las arañas eran más abundantes que las orugas. De manera coincidente, los padres explotaron las arañas como recurso trófico de manera constante a lo largo de toda la temporada de cría, mientras que las orugas, menos abundantes, fueron progresivamente sustituidas por otros tipos de presas.

- Consistencia de las preferencias tróficas en el corto plazo y lo largo del ciclo anual

Numerosos trabajos han estudiado la dieta de las aves cuando ceban a sus pollos (Stephens, Brown & Ydenberg 2007). Sin embargo, en muy pocas ocasiones se ha analizado el grado de consistencia del comportamiento de los individuos a lo largo del tiempo (García-Navas, Ferrer & Sanz 2012). En el artículo **3** encontramos que los individuos de nuestra población presentaron un elevado grado de consistencia en diferentes aspectos de su comportamiento a lo largo del tiempo. Respecto a la tasa de cebas individual se observó una elevada correlación entre las tasas medias y los distintos valores de tasa obtenidos a lo largo de las distintas horas del día. Además, la composición de presas fue muy estable a lo largo del periodo de estudio. Esto permite afirmar que una hora de grabación puede ser suficiente para caracterizar la inversión parental de una pareja (ver figura 2).

Figura 2. Publicada en el artículo 3.

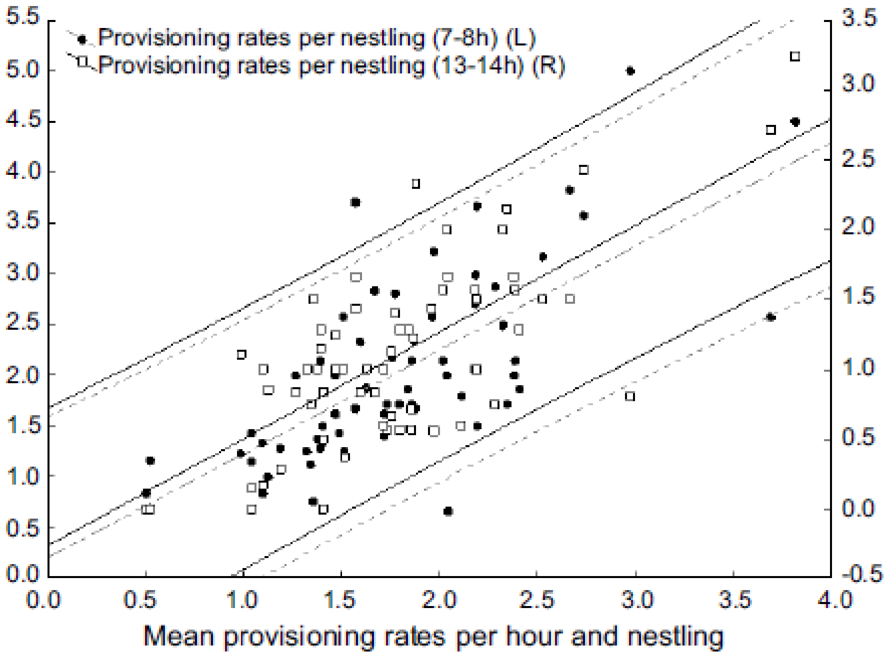


Fig. 5. Graph showing the level of correlation between hourly provisioning rates per nestling from the periods 7–8 h and 13–14 h, which showed the best and the worst fitting with mean values, with mean provisioning rates per nestling across the whole study period. Spotted lines represent confidence intervals.

Adicionalmente, evaluamos en condiciones de cautividad (Emmans 1991) el grado de apetencia que mostraron los individuos por las dos presas principales registradas en condiciones naturales: orugas y arañas (artículo **4**). Lo hicimos fuera del periodo reproductor, e independientemente de la disponibilidad. El estudio analiza dos poblaciones de carbonero común, una forestal (estación de campo de Can Catà) y una urbana (próxima a la ciudad de Barcelona). Los resultados demuestran que la mayoría de los individuos prefirieron una araña cuando fue confrontada con una larva de lepidóptero, aunque machos y hembras mostraron tendencias diferentes dependientes de la edad (del Val et al. 2010). Esto puede estar motivado por el mayor grado de consistencia detectado en aves adultas cuando repetimos el test. En todo caso, nuestros datos confirman que los carboneros comunes mediterráneos prefieren las arañas no sólo durante la primavera sino a lo largo de todo el ciclo anual.

- **Especialización individual de la dieta en un contexto generalista**

Para la mayoría de las especies de vertebrados no está claro si las diferentes especies deben ser consideradas generalistas o especialistas tróficos en el momento de la cría (Stephens, Brown & Ydenberg 2007; Newsome et al. 2009). Para determinar el comportamiento de alimentación de los padres en una población dada, es necesario estudiar dos aspectos: el grado de consistencia de comportamiento en diferentes condiciones en el corto plazo, y el nivel de especialización de la dieta mostrado por diferentes parejas reproductoras con respecto a la media de la población (Woo et al. 2008; Vander Zanden et al. 2010). Investigamos ambos aspectos en el artículo **5**. De un lado, la consistencia del comportamiento mediante un experimento de modificación del tamaño de la puesta (García-Navas & Sanz 2010). Del otro, el grado de especialismo trófico a través del índice de similitud proporcional (Bolnick et al. 2003), partiendo de la base de que el carbonero común es una especie generalista. Los padres mostraron una gran consistencia en el corto plazo. Ajustaron la tasa de trabajo al número exacto de pollos presentes en el nido (ver figura 3), pero no fueron capaces de modificar las proporciones o el tamaño de la presas. Por tanto, podemos caracterizar sus estrategias de forrajeo como altamente consistentes. Registramos, además, una gran variabilidad en los tipos de presas seleccionadas por los padres entre los distintos territorios. Es decir, mostraron un bajo nivel de solapamiento trófico. Curiosamente, las parejas reproductoras más especializados sacaron adelante nidadas más grandes (ver figura 4) y llevaron menos orugas a sus pollos.

Nuestros resultados sugieren que, aunque el carbonero común puede ser considerado un generalista a nivel de especie o población, muchos individuos reproductores dentro de nuestra población de estudio se comportaron como especialistas. Esta alta plasticidad dentro y entre poblaciones puede ser una de las razones de su gran éxito y amplia distribución.

Figura 3. Publicada en el artículo 5.

Cambios en la tasa de cebas por nido en condiciones naturales y después de la modificación experimental del tamaño de puesta en los nidos de 19 parejas de carbonero común. Los círculos rellenos corresponden a puestas reducidas, los círculos vacíos a puestas aumentadas.

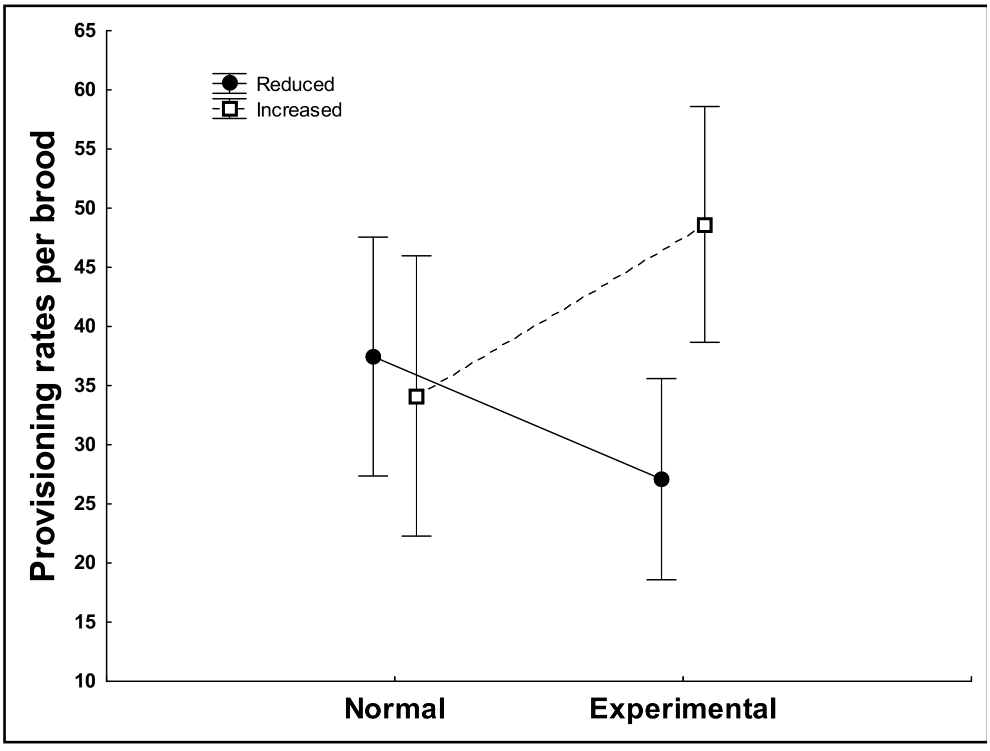
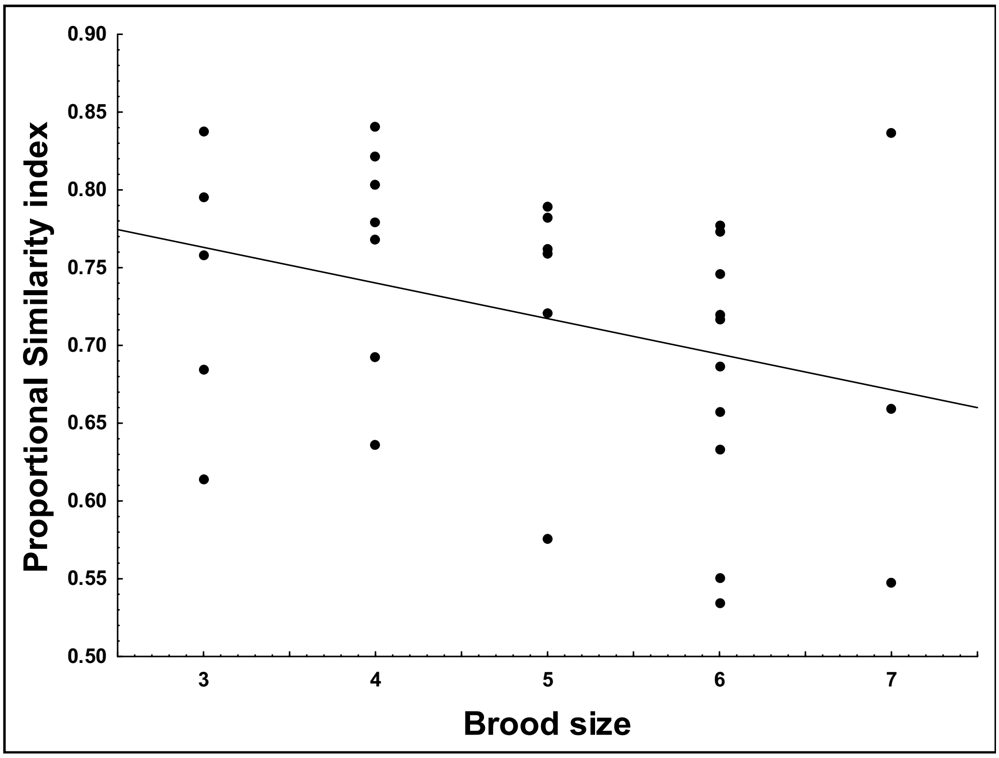


Figura 4. Publicada en el artículo 5.

Relaciones entre las puntuaciones del índice de similitud proporcional (eje Y) y el tamaño de puesta natural (eje X) en el momento del registro de la dieta en 31 parejas de carbonero común.



- Interacciones entre dieta y ornamentos

Centramos los artículos **6** y **7** en el análisis de las interacciones entre el comportamiento de forrajeo de los padres, sus ornamentos y su éxito reproductivo. Dado que las coloraciones basadas en carotenos son consideradas una señal honesta de calidad (Endler 1980; Hill 1990; Hill 2006), predecimos que los machos más ornamentados deberían proporcionar más presas de calidad en la dieta de sus pollos (García-Navas, Ferrer & Sanz 2012). Los resultados del artículo **6** mostraron que los machos más ornamentados (con valores de tono más elevados) llevaron más arañas y menos orugas a sus pollos (figura 5). Además, los pollos que recibieron un porcentaje mayor de arañas, mostraron mejor condición física (figura 6). Por lo tanto, encontramos apoyo para la “hipótesis de los buenos padres”, que afirma que las hembras deben fijarse en los ornamentos externos porque son una señal de la calidad del trabajo de los padres (Hoelzer 1989; Price et al. 1993; Andersson 1994; Wolf et al. 1997). Encontramos también apoyo adicional para la idea de que, al menos en el área mediterránea, las orugas no son la única fuente importante de comida, y que las arañas juegan también un importante papel.

Figura 5. Publicada en el artículo 6.

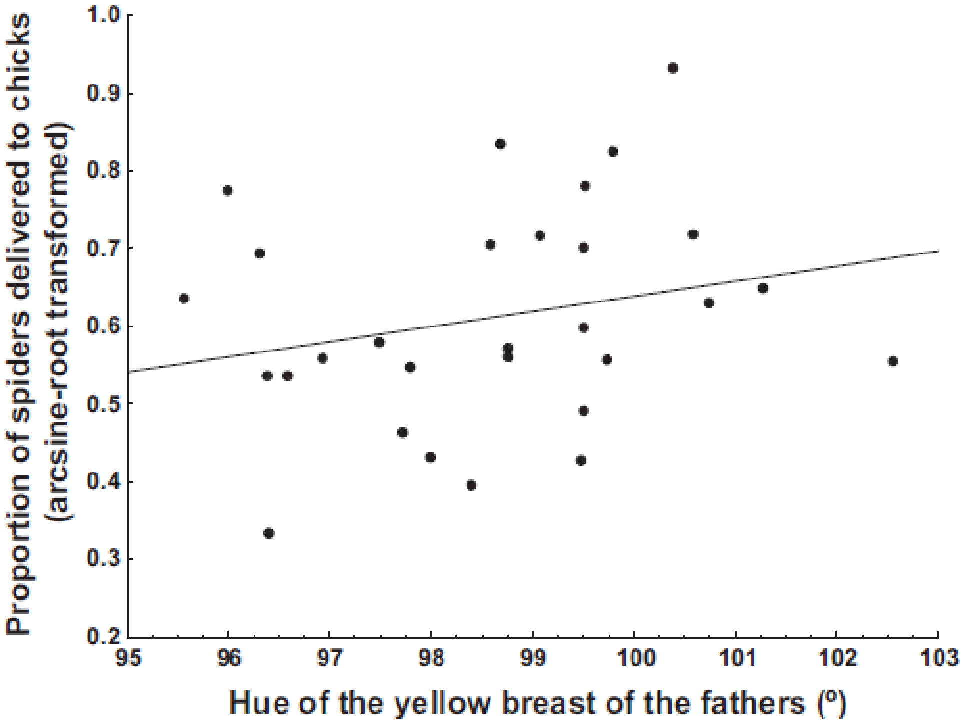


Fig. 1. Relationship between the proportions of spiders (arcsine-root transformed and standardized by the variables showing significant interactions in the model included in Table 3) delivered to their chicks and the hue of the yellow carotenoid-based breast (degrees) of great tit fathers. $R = 0.48$, $P = 0.04$, $N = 29$.

Figura 6. Publicada en el artículo 6.

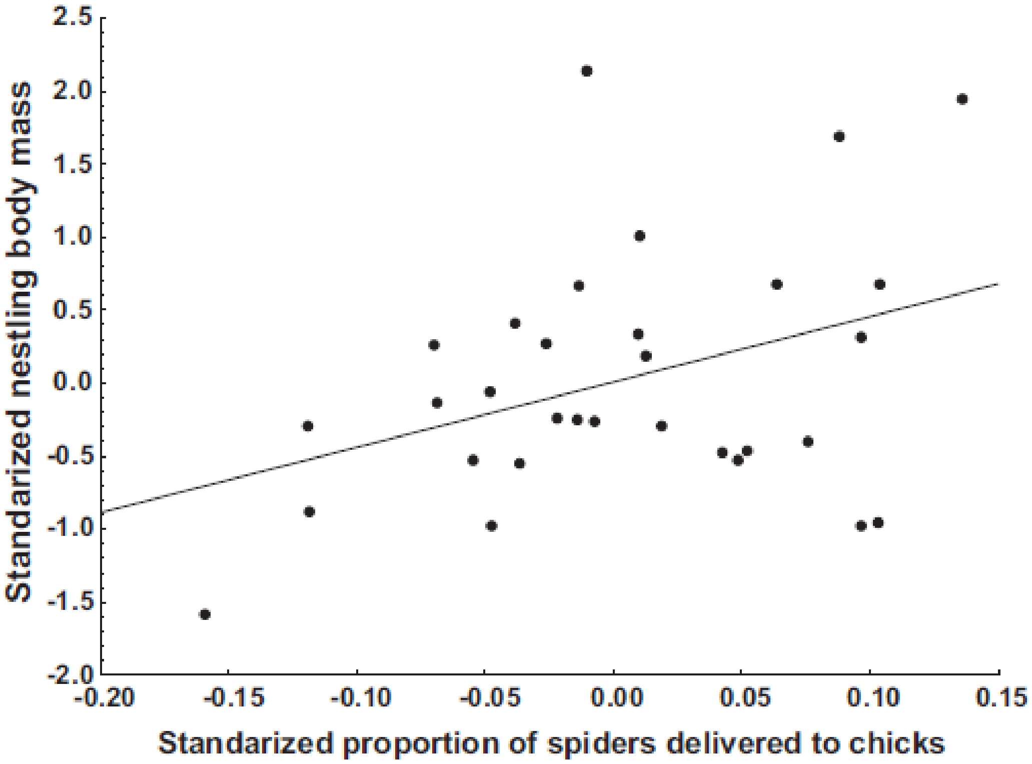


Fig. 4. Relationships between nestling body condition (mass residuals standardized by tarsus length) and the proportions of spiders (arcsin-root transformed and standardized by proportion of oaks surrounding the nest, date and rain, see Table 3) delivered to chicks by fathers. $R = 0.38$, $P = 0.04$, $N = 31$.

En el mismo sentido, e independientemente de su significado funcional (Tschirren et al. 2005; Galván et al. 2008), la coloración basada en carotenos del plumaje de los pollos se ha ligado a la calidad de la dieta (Tschirren, Fitze & Richner 2003; Eeva et al. 2009; Isaksson 2009) y a la estructura del hábitat (Slagsvold & Lifjeld 1985; Arriero & Fargallo 2006; Galvan et al. 2009; Simon & Sheldon 2012). Sin embargo, a la hora de evaluar el color del plumaje de los pollos, consideramos limitada la asimilación directa que a menudo se hace entre dieta y calidad del hábitat, porque no tiene en cuenta la influencia de la inversión parental (Bolnick et al. 2003). En el artículo **7** evaluamos la estructura del hábitat y la composición de presas de la dieta de los pollos para analizar su efecto relativo sobre el color del plumaje basado en carotenos (luminosidad, intensidad y tono) en pollos de carbonero común. Encontramos una baja correlación entre la coloración basada en carotenos de los pollos y la de sus padres. El color de los pollos, en especial la luminosidad y la intensidad, aumentaron con la ingestión de arañas (ver figura 7). La fecha se correlacionó positivamente con la luminosidad y la intensidad, y se correlacionó negativamente con el tono. Por último, la madurez de los árboles de roble y encina que rodeaban las cajas nido se correlacionó negativamente con la luminosidad, y el tamaño de todas las especies de árboles que rodeaban las cajas nido se correlacionó positivamente con la tonalidad del plumaje de los pollos. Nuestros hallazgos apoyan la idea de que la estructura del hábitat y la composición de la dieta pueden producir efectos divergentes sobre la pigmentación del plumaje, y que las proporciones de presas y las variables relacionadas con la inversión parental deben evaluarse al analizar la coloración basada en carotenos de los pollos.

Figura 7. Publicada en el artículo 7.

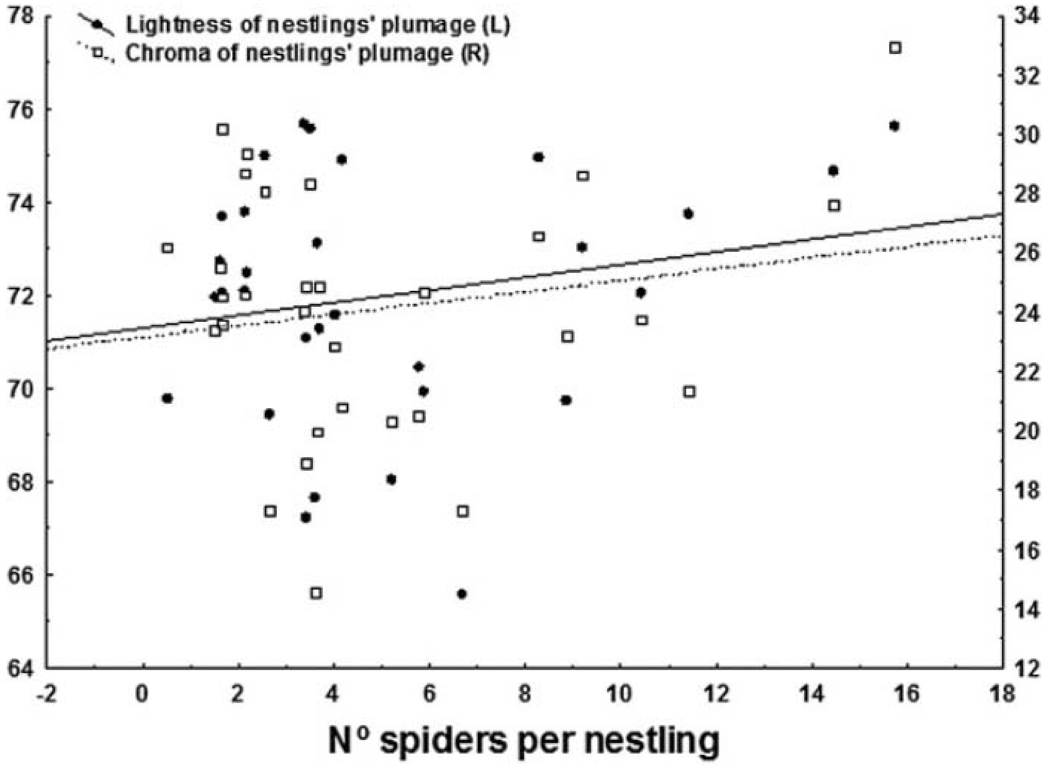


Figure 2. Scatterplot showing the relationships between the number of spiders per nestling delivered by parents, and lightness and chroma of carotenoid-based plumage of great tit *Parus major* nestlings.

Conclusiones

En esta tesis hemos descrito el sistema trófico del carbonero común en un contexto mediterráneo, y en relación con los diferentes niveles de ornamentación mostrado por los individuos. Generalmente, se asume que las coloraciones basadas en carotenos dependen en gran medida de la habilidad de forrajeo del portador porque los carotenos sólo se pueden adquirir a través de la dieta (Endler 1980; Hill 1990; Hill 2006). De acuerdo con esto, se ha sugerido que, a la hora de elegir pareja, estos colores pueden funcionar como señales honestas (ornamentos) de la calidad (es decir, de la habilidad de forrajeo) del portador. A esta teoría se la conoce como la "hipótesis de los buenos padres" (Hoelzer 1989; Price, Schluter & Heckman 1993; Andersson 1994; Wolf, Moore & Brodie 1997), y los resultados desarrollados en la presente tesis la apoyan. En el artículo **6** mostramos que los padres más ornamentados (con valores más altos de tono en el color amarillo del plumaje del pecho) de nuestra población de estudio dieron más arañas a sus pollos. Este tipo de presa es fundamental en nuestra área de estudio (artículos **1** y **2)**. Además, los pollos que recibieron un mayor número de arañas en su dieta mostraron un color más brillante (artículo **7**) y una mejor condición física (artículo **6**). Es decir, no sólo hemos encontrado que los individuos más ornamentados cebaron a sus pollos con proporciones mayores de un tipo de presa singular y, probablemente, más difícil de cazar que las orugas, sino que además comprobamos que este tipo de presa tuvo un efecto muy positivo sobre la condición física y la coloración de los pollos. Sin embargo, ¿por qué se da este patrón con las arañas y no con las orugas, la que es considerada presa principal del carbonero común? En la literatura podemos encontrar dos argumentos principales que pueden ayudar a explicar este cambio. De un lado, la que era previamente considerada como presa principal debe encontrarse en niveles más bajos de lo habitual (Krivan & Cressman 2009; Tinker, Mangel & Estes 2009), como ocurre con las orugas en ambientes mediterráneos. Como contrapartida, debe darse una elevada densidad de la presa alternativa, en este caso las arañas, patrón esperable en nuestra zona dada la elevada ocurrencia de arañas en la dieta (ver también Finch et al. (2008)). Sin embargo, para que se produzca este cambio en la presa preferida de manera eficaz debe darse además un efecto positivo sobre el éxito reproductivo que garantice la continuidad de esta estrategia (Arnold et al. 2007; Krivan 2010). Todo parece indicar que nuestra población de estudio cumple ambas condiciones.

Adicionalmente, para enmarcar correctamente las estrategias de forrajeo de los carboneros en un contexto poblacional, y teniendo presentes las características especiales de los ambientes mediterráneos, hemos determinado el grado de consistencia del comportamiento y de sus preferencias tróficas en el corto plazo y a lo largo del ciclo anual. Como mostramos en los artículos **3** y **5**, los individuos mostraron una elevada consistencia del comportamiento en el corto plazo, tanto en el grado de esfuerzo como en las preferencias tróficas mostradas. Además, en el artículo **4** se puede comprobar que los individuos mostraron preferencia por las arañas de manera coherente a lo largo de todo el ciclo anual. En el área mediterránea, donde las orugas son más escasas que en latitudes norteñas (Blondel et al. 1991; Bańbura et al. 1994), insectívoros generalistas como el carbonero común han de desarrollar aptitudes para explotar recursos tróficos alternativos. Las poblaciones de esta especie (y de herrerillo común) que se encuentran en su margen de distribución norte han sido consideradas tradicionalmente como sub-óptimas por las dificultades que muestran los adultos reproductores para encontrar una cantidad suficiente de orugas con que criar a sus pollos (Rytkonen & Krams 2003). Sin embargo, en esta tesis mostramos que en determinadas circunstancias los individuos son capaces de desarrollar innovaciones del comportamiento exitosas que les permiten marcar la diferencia con el resto de la población (ver artículo **6**). Además, en el artículo **5** mostramos que, en nuestra población, los individuos más especializados en cuanto a la dieta con respecto a la media poblacional sacaron adelante más pollos. Hay que destacar también que estos especialistas tróficos fueron los que menos confiaron en las orugas como presa principal. Esto es, en una especie generalista como el carbonero común, los individuos más especialistas seleccionaron presas alternativas a la que es considerada su presa preferida, las orugas. La elevada diversidad trófica característica del Mediterráneo entronca así con la gran diversidad de estrategias de forrajeo desplegadas por individuos reproductores al alimentar a su descendencia.

Partiendo de esta base, quedan múltiples aspectos de interés por precisar. En primer lugar, sería interesante mostrar el grado de consistencia individual de la estrategias de forrajeo en diferentes años con distintas condiciones ambientales. Esto es, el nivel de repetitividad individual del comportamiento de forrajeo en nuestra población. Pero, además, puede ser altamente relevante determinar el grado de generalismo o especialismo trófico a nivel poblacional, en años con diferentes condiciones ambientales, para ver en qué sentido varía el grado de especialismo trófico mostrado por los individuos. De este modo, será posible continuar investigando qué patrones ecológicos rigen la increíble variabilidad y diversidad propia del Mediterráneo.

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Parc de la Ciutadella
Passeig Picasso s/n
08003 Barcelona
T (+34) 93 256 22 00
www.museuciencies.cat

Informe dels Factors de Impacte de la Tesi Doctoral de Emilio Pagani

1. **Pagani–Núñez, E.**, Ruiz, Í., Quesada, J., Negro, J. J. & Senar, J. C. 2011. The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. ***Animal Biodiversity and Conservation***, 34(2), 355-361.

IF: 0.20.

2. Hernández-Gómez, S., **Pagani-Núñez, E.**, Ruiz, I. & Senar, J. C. 2014. Nestling diet matches prey abundance in Mediterranean Blue Tits *Cyanistes caeruleus*. ***Animal Biodiversity and Conservation***. Submitted.

En revisió. IF: 0.20.

3. **Pagani-Núñez, E.** & Senar, J. C. 2013. One hour of sampling is enough: Great Tit *Parus major* parents feed their nestlings consistently across time. ***Acta Ornithologica***, 48(2), 194-200.

IF: 1.68.

4. **Pagani-Núñez, E.**, Hernández-Gómez, S., Riyahi, S. & Senar, J. C. 2014. Year-round preference of spiders by Mediterranean great tits *Parus major*. ***Ardeola***. En prensa.

Acceptat per a la seva publicació. Data estimada: Desembre de 2014. IF: 0.82.

5. **Pagani-Núñez, E.**, Valls, M. & Senar, J. C. 2014. Individual diet specialization in a generalist population: the case of breeding Great tits *Parus major* in the Mediterranean area. ***Oecologia***. Submitted.

En revisió. IF: 3.01.

6. **Pagani-Núñez, E.** & Senar, J. C. 2014. Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. ***Acta Oecologica***, 55, 23-28.

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7. **Pagani-Núñez, E.**, Uribe, F., Hernández-Gómez, S., Muñoz, G. & Senar, J.C. 2014. Habitat structure and prey composition generate contrasting effects on carotenoid-based colouration of Great tit *Parus major* nestlings. ***Biological Journal of the Linnean Society***. En prensa.

Acceptat per la seva publicació. Data estimada: Setembre de 2014. IF: 2.41.

museu de ciències naturals de Barcelona

Dr. Joan Carles Senar
Cap de Recerca
Unitat Associada CSIC
d'Ecologia Evolutiva i de la Conducta
Investigador Principal Projecte i Director Tesi
8 juliol 2014

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Per la present, i com a Director de la Tesi Doctoral de Emilio PAGANI NÚÑEZ, declaro que cap dels treballs presentats en la seva tesi doctoral ha estat utilitzat, implícitament o explícitament per a l'elaboració de la tesi doctoral de cap dels coautors. Així mateix declaro que la participació del doctorand en cada un dels articles en que ha hagut coautors ha estat la següent:

Pagani–Núñez, E., Ruiz, Í., Quesada, J., Negro, J. J. & Senar, J. C. 2011. The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. ***Animal Biodiversity and Conservation***, 34(2), 355-361.

Les dades van estar recollides pels altres coautors, però Pagani va analitzar tots els resultats i va escriure el corresponent treball.

Hernández-Gómez, S., **Pagani-Núñez, E.**, Ruiz, I. & Senar, J. C. 2014. Spiders as a more predictable food resource than caterpillars in the diet of Mediterranean Blue tits *Cyanistes caeruleus*. ***Animal Biodiversity and Conservation***. Submitted.

Pagani va tenir una part molt activa en la concepció de la idea, va participar en la recollida de dades al camp, va visualitzar una part de les gravacions, i va participar activament en el anàlisis dels resultats i en la redacció del treball.

Pagani-Núñez, E., Hernández-Gómez, S., Riyahi, S. & Senar, J. C. 2014. Year-round preference of spiders by Mediterranean great tits *Parus major*. ***Ardeola***. En prensa.

Pagani va participar molt activament en la concepció de la idea, va realitzar bona part dels experiments i recollida de les dades. Va realitzar els anàlisis dels resultats i va realitzar bona part de la redacció del treball.

Pagani-Núñez, E., Valls, M. & Senar, J. C. 2014. Individual diet specialization in a generalist population: the case of breeding Great tits *Parus major* in the Mediterranean area. Submitted.

La concepció de la idea va ser principalment de Pagani, va recollir les dades de reproducció i va realitzar les filmacions de les caixes niu per l'estudi de la dieta. Va visualitzar una part de les filmacions. Va participar activament en els anàlisis dels resultats i va redactar el treball.

Pagani-Núñez, E., Uribe, F., Hernández-Gómez, S., Muñoz, G. & Senar, J.C. 2014. Habitat structure and prey composition generate contrasting effects on carotenoid-based colouration of Great tit *Parus major* nestlings. ***Biological Journal of the Linnean Society***. En prensa.

La concepció de la idea va ser principalment de Pagani. Va recollir les dades de reproducció i va realitzar les filmacions de les caixes niu per l'estudi de la dieta conjuntament amb alguns altres coautors. Va participar en la recollida de dades de vegetació. Va visualitzar les filmacions. Va participar activament en els anàlisis dels resultats i va redactar el treball.

nat museu de ciències naturals de Barcelona

Dr. Joan Carles Senar
Cap de Recerca
Unitat Associada CSIC
d'Ecologia Evolutiva i de la Conducta
Investigador Principal Projecte
25 juny 2014

Publicaciones

Capítulo 1

Pagani–Núñez, E., Ruiz, Í., Quesada, J., Negro, J. J. & Senar, J. C. 2011. The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. ***Animal Biodiversity and Conservation***, 34(2), 355-361.

The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders

E. Pagani–Núñez, Í. Ruiz, J. Quesada,
J. J. Negro & J. C. Senar

Pagani–Núñez, E., Ruiz, Í, Quesada, J., Negro, J. J. & Senar, J. C., 2011. The diet of Great Tit *Parus major* nestlings in a Mediterranean Iberian forest: the important role of spiders. *Animal Biodiversity and Conservation*, 34.2: 355–361.

Abstract
The diet of Great Tit Parus major *nestlings in a Mediterranean Iberian forest: the important role of spiders*.— The diet of the Great Tit *Parus major* when rearing chicks has been described in many studies. However, data from the Mediterranean area is scarce. Here we describe the diet of nestlings in a population of Great Tits in a Mediterranean forest in Barcelona (north–east Spain) during two breeding seasons using two methods: neck–collars and video recording. The main prey were caterpillars (44% from neck–collar data and 62% from video–recorded data), but in our latitudes spiders also seemed to be an important food resource (24% from neck–collar data and 42% from video–recorded data). We did not find any significant differences in the quantity of spiders collected by parents in relation to stage of chick development, main vegetation surrounding nest boxes, size of the brood, or year. Our results stress the importance of spiders as a food source in Mediterranean habitats.

Key words: Great Tits, Nestlings, Diet, Spiders.

Resumen
Dieta de los pollos de Carbonero Común Parus major *en un bosque Ibérico Mediterraneo: la importáncia de las arañas*.— La dieta del Carbonero Común *Parus major* cuando alimenta a los pollos ha sido descrita en muchos artículos. Sin embargo, la información sobre el área mediterránea es bastante escasa. Aquí describimos la dieta de los pollos en una población de Carbonero Común en un bosque Mediterráneo de Barcelona (nordeste de España) en dos temporadas de cría a través de dos métodos (collares y grabaciones de video). Las principales presas cebadas fueron las orugas (44% a partir de datos de collares y 62% a partir de datos de grabaciones), pero en nuestras latitudes las arañas parecen ser un importante recurso (24% [datos collares] y 42% [datos de grabaciones]). No encontramos diferencias significativas en la cantidad de arañas recolectadas por los padres en relación con el estado de desarrollo de los pollos, vegetación alrededor de las cajas nido, tamaño de puesta y año. Nuestros resultados subrayan la importancia de las arañas como recurso trófico en ambientes mediterráneos.

Palabras clave: Carbonero Común, Pollos, Dieta, Arañas.

(Received: 10 XI 11; Final acceptance: 28 XII 11)

Emilio Pagani–Núñez, Íker Ruiz, Javier Quesada & Juan Carlos Senar, Evolutionary Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, Espanya (Spain).– Juan José Negro, Estación Biológica de Doñana (CSIC), Avda. Americo Vespucio s/n., 41092 Sevilla, España (Spain).

ISSN: 1578–665X

Introduction

The Great Tit *Parus major* has often been used as a model species in studies of feeding behaviour and diet (Royama, 1970; Wansink & Tinbergen,1994; Biard et al., 2006; Senar et al., 2010). Although some variation appears between areas and periods, the species has been reported to focus highly on caterpillars when rearing chicks (Gibb & Betts, 1963; Balen, 1973; Gosler, 1993; Wilkin et al., 2009). Nevertheless, the species has also been recorded to provide other animal content such as butterflies, Phasmidae or Orthoptera. Interestingly, high proportions of spiders have been reported early in the chicks' diet, with a peak around 5–6 days of age (see Ramsay & Houston [2003] for references). These results are independent of date and habitat, which stresses that Tits specifically select spiders in their diet during that period. This preference for arachnids has also been recorded for other similar species such as Blue Tits *Cyanistes caeruleus* (Banbura et al., 1999; Arnold et al., 2007; Arnold et al., 2011; Garcia–Navas & Sanz, 2011), Pied Flycatchers *Ficedula hipoleuca* (Sanz, 1998) and Red–Breasted Flycatchers *Ficedula parva* (Mitrus et al., 2010).

Earlier work found that the proportion of spiders increased markedly in Mediterranean habitats, with this food resource being used right throughout the breeding period. Blondel et al. (1991) reported that although the percentage of spiders in Blue Tit diets was about 16% in the mainland, it rose to 26% in the islands. Naef–Daenzer et al. (2000) found that the percentage of spiders in very earlier stages of Great Tit chick development could rise to 75%, although it rapidly decreased again to 5%.

The aim of this work was to analyse in detail the relative contribution of spiders to the diet of Great Tit nestlings in a typical Mediterranean forest. We analysed the diet in relation to spider availability and Great Tit breeding phenology. Specifically, we aimed 1) to assess whether Great Tits actively selected prey to feed their brood; 2) to determine if there were any differences in the quantity of spiders provided to nestlings by parents in relation to the age of the nestlings, brood size and forest structure; and 3) to determine if there were any differences in the quantity of spiders provided to nestlings according to the sex of the parents.

Material and methods

Great Tits were studied over two breeding seasons in 2001 and 2004, in a mixed forest dominated by oaks and pines in the field station of Can Catà, within the Park of Collserola (Cerdanyola, Barcelona, NE of the Iberian Peninsula, latitude 45º 27' N, length 2º 8' E).

Nest boxes were distributed throughout the whole area (80 ha). They were located on the trunks of oaks, at an approximate height of 1.30 m. Birds entered the nest boxes through a cylindrical tube of 10 cm in length and 5 cm in diameter designed to protect the box from predators.

The study area was highly varied. Altitude ranged from 80 to 225 m a.s.l. At the bottom of the valley vegetation coverage was dominated by Holm Oaks (*Quercus ilex*) and Oaks (*Quercus cerrioides*) and had a highly developed Mediterranean understory. On the slopes the Aleppo Pine (*Pinus halepensis*) was the predominant tree species.

We considered the nest boxes in accordance with the main vegetation surrounding them. We considered two zones, the valley, where *Quercus* trees represented > 70% of the arboreal vegetation, and the slopes, where pines showed higher presence the higher the altitude and *Quercus* trees represented < 70% of the arboreal vegetation.

Recording diet: filming

The diet provided by Great Tit parents to their chicks was studied in spring 2001 by filming the parents' entries and exits from the nest box. Filming was undertaken using a domestic video camera that was camouflaged by means of a net of cryptic colours and vegetation at five meters'distance from the box. The tapes had an hour of duration. Three days before filming we placed a tripod on the ground in the exact position where we later filmed to get the birds used to the setting. The height of the camera with the tripod did not surpass 50 cm above ground level. Wire netting was placed over the entrance of the nest–box to make it more difficult for the birds to enter the box. This delayed their entry, allowing a clear view of each prey item (Currie et al., 1996; Atienzar et al., 2009).

The nest boxes were checked twice each week to gather breeding data, including laying date, clutch size, hatching date, numbers of nestlings and fledglings. We eliminated tapes that recorded fewer than five visits by the male, since we considered they could be biased in some way. This left us with a sample size of 25 nest boxes.

Tape recordings allowed us to determine the sex of the parents and the exact time of each feeding. The method provides a photographic record of the prey items for later identification and is not biased by the size of the prey. Prey are sometimes difficult to identify, however (Barba & Monrós, 1999).

Neck collars

Diet was analysed in spring 2004 using neck collars (Barba & Gil–Delgado, 1990). Neck collars allow simultaneous gathering of samples from several nests. Collars were made from a wire cable, and the loop was carefully laid around the neck of the chick, allowing it to breathe unhindered, but unable to swallow food (Poulsen & Aebischer, 1995).

Collars remained fitted for two hours. We sampled a total of 37 nest boxes. The food was carefully extracted from the mouth and oesophagus of the chick, and the neck collar was removed. The food was suitably stored in individual vials and the number on the box and date were noted. The mass of each sample was later measured in the lab. We recorded the diet of chicks using this method when they were

Table 1. Arthropod abundance in leaves of trees in the study area. We surveyed fifteen trees of each the tree main species (Holm Oaks, *Quercus ilex*; Oaks, *Quercus cerrioides*; and Aleppo Pine, *Pinus halepensis*) on the slopes and at the bottom of the valley. Census made during springs in 2002 and in 2003.

Table 1. Abundancia de artrópodos en las hojas de los árboles de la zona de estudio. Se testaron quince árboles de cada una de las tres espécies principales (encinas, Quercus ilex; *robles,* Quercus cerrioides *y pino carrasco,* Pinus halepensis*) en las laderas y los fondos del valle. El censo se realizó durante las primaveras de 2002 y 2003.*

Prey	N	N / tree	St. Dev	% N	V (mm^3)	% Mass
Lepidoptera larvae	156	0.06	0.29	6.35	600	42.90
Symphita larvae	89	0.03	0.31	3.62	450	18.36
Lepidoptera adults	168	0.07	0.84	6.84	150	11.55
Orthoptera	71	0.03	0.2	2.89	300	9.76
Coleoptera	448	0.18	0.55	18.23	20	4.11
Arachnida	397	0.16	0.53	16.16	20	3.64
Chrysalis	10	0	0.07	0.41	750	3.44
Tipulae	53	0.02	0.17	2.16	120	2.92
Homoptera	119	0.05	0.28	4.84	20	1.09
Phasmida	3	0	0.03	0.12	600	0.83
Neuroptera	25	0.01	0.1	1.02	50	0.57
Formicidae	481	0.19	1.42	19.58	2	0.44
Mantidae	1	0	0.02	0.04		
Heteroptera	1	0	0.02	0.04		
Myriapoda	1	0	0.02	0.04		
Gasteropoda	1	0	0.02	0.04		

both five and twelve days old, to analyse changes in the feeding behaviour in relation to the age of the nestlings. Using this method it is not possible to determine which of the parents deliver every item (Barba & Monrós, 1999).

We used both video filming and neck collar data to characterize the nestling diet and to determine which variables could affect the quantity of spiders provided to nestlings by Great Tit parents.

Phenology of prey

During the breeding seasons of the years 2002 and 2003 we made a census of arthropods present in the leaves of the three main tree species at Can Catà: Holm Oaks (*Quercus ilex*), Oaks (*Quercus cerrioides*), and Aleppo Pine (*Pinus halepensis*). We randomly selected fifteen trees of each species for each year, ten located on the slopes and five at the bottom of the valley; this allowed us to take altitudinal variations into account. Census lasted four minutes per tree. We recorded all insects seen on external branches and leaves (Carrascal et al., 1998). Arthropod volume was estimated and classified into one of eight sizes (2, 20, 120, 150, 300, 450, 600 and 750 mm^3). The mass equivalence was obtained by multiplying volume by abundance. This allowed us to evaluate the abundance of the different groups of arthropods present in the forest and to assess whether there was any active selection of prey by the parents.

Results

Arthropod census on trees

Census of arthropods on tree leaves showed that the groups most frequently recorded were Formicidae (20%), Coleoptera (18%), and Arachnidae (16%). Lepidoptera represented 13% of the records (larvae 6%, adults 7%). When we considered the volume (mm^3) as a proxy for the biomass of the prey delivered, however, their relative importance changed: Lepidoptera became the main prey available (larvae 43%, adults 12%), followed by Symphyta (larvae 18%, adults were not found) and Orthoptera (10%); many other taxa were recorded but their frequencies were very low (table 1).

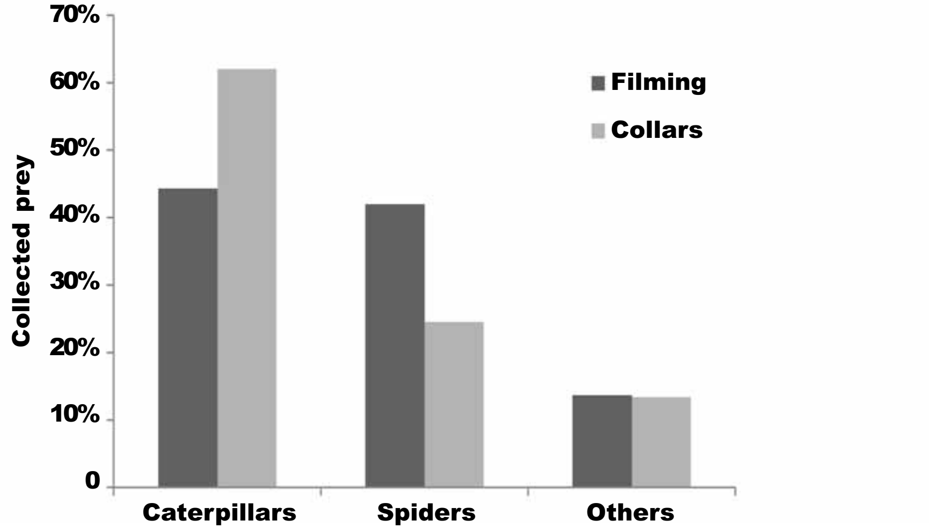

Fig. 1. Percentage of prey collected by Great Tit parents, according to the recording method: video (2001) or neck collars (2004).

Fig. 1. Porcentaje de presas recolectadas por los padres de Carbonero Común, de acuerdo con el método de grabación: vídeo (2001) o collares (2004).

Prey brought by parents to nestlings

Great Tits brought a variety of insects to the nest: caterpillars (both Lepidoptera and Symphyta), spiders (including also eggs), butterflies, Phasmidae, Orthoptera and formless remains. Caterpillars included Symphyta such as *Diprion* sp.; Noctuidae such as *Orthosia* sp., *Catocala* sp. and *Spodoptera* sp.; Geometridae such as *Lycia* sp. and *Idaea* sp.; hairy caterpillars such as *Lymantria* sp. and *Orgyia* sp. Spiders included mainly *Zoropsis* sp., *Olios* sp., *Gibbaranea* sp., *Scotophaeus* sp., *Chiracantium* sp., *Philodromus* sp., *Synema* sp. and *Thomisius* sp. We grouped prey in three groups: caterpillars, spiders and 'others'.

Data obtained from filming nests showed that caterpillars were the main prey provided to nestlings (44%), followed by spiders (42%) (fig. 1). Frequencies did not correspond to availability, since caterpillars and spiders were consumed more than expected when compared to other insects (χ^2 = 360.55; df = 2; P < 0.005). When we compared consumption to availability only for caterpillars and spiders we found that caterpillars were consumed more than expected (χ^2 = 13.73; df = 1; $P \leq$ 0.005).

Data obtained from neck collars showed caterpillars and butterflies were the main (62%) groups of prey brought by the parents to the nestlings. In the second place we found spiders (24%). The remaining arthropods were present at very low frequencies (fig. 1). Again, frequencies did not correspond to availability, since caterpillars and spiders were also more frequently consumed than expected (χ^2 = 375.55; df = 2;

Table 2. MANOVA of quantity of spiders provided by parents to their nestlings according to their age (5 and 12 days old). We included also as factors the size of the brood and the percentage of *Quercus* surrounding (25 m) nest boxes (measured in a qualitative scale: > 70% and < 70% of *Quercus*).

Tabla 2. MANOVA de la cantidad de arañas proporcionada por los padres a sus crías en función de su edad (5 y 12 días). Se incluyeron también como factores el tamaño de puesta y el porcentaje de Quercus *cercanos a las cajas nido (25 m) (medido en una escala cualitativa: > 70% y < 70% de* Quercus*).*

	$F_{1,16}$	P
% *Quercus*	0.3	0.57
Brood size	0.5	0.48
Age of the nestlings	3.0	0.10
% *Quercus* x brood size	0.4	0.52
Age nestlings x % *Quercus*	1.0	0.33
Age nestlings x brood size	1.8	0.20
Age nestlings x brood size x x % *Quercus*	0.4	0.51

$P < 0.005$). When we considered only caterpillars and spiders, we found that caterpillars were ingested more often than expected according to availability ($\chi^2 = 63.64$; df = 1; $P < 0.005$).

Collar data showed that the quantity of spiders provided to nestlings by Great Tit parents did not vary with the age of the nestlings, brood size or forest structure, measured as a percentage of *Quercus* around the nest (table 2).

Video data showed that females provided young with more spiders than males (fig. 2), and that males provided more caterpillars than females (tables 3, 4). However, in absolute terms, males provided more prey items than females, including spiders (table 3). Repeated measures ANOVA within each pair stressed that the males collected more caterpillars whereas females tended to deliver more spiders (table 4). When comparing abundance and selection of caterpillars and spiders in function of sex, we found that males seemed to actively select caterpillars ($\chi^2 = 15.18$; df = 1; $P < 0.005$), but females did not ($\chi^2 = 0.08$; df = 1; $P = 0.77$).

Analyses of pooled data from both recording methods showed no relationship between the quantity of spiders fed by the parents and the factors 'method/year', 'size of brood' or 'habitat structure' measured as percentage of *Quercus* around the nest (table 5).

Table 3. Percentage and absolute values of different preys collected by Great Tit males (n = 25) and females (n = 22) during the 2001 breeding season (filming data).

Tabla 3. Porcentaje y valores absolutos de las distintas presas recolectadas por machos (n = 25) y hembras (n = 22) de Carbonero Común durante la temporada de cría 2001 (grabaciones de video).

		Percentage	N
Males			
	Caterpillars	48.96%	94
	Spiders	40.63%	78
	Others	10.42%	20
	Sum	100%	192
Females			
	Caterpillars	35,56%	32
	Spiders	55.56%	50
	Others	8.89%	8
	Sum	100%	90

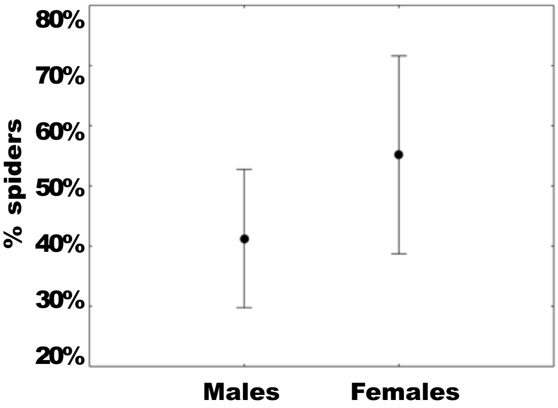

Fig. 2. Mean percentage and 95% confidence intervals of spiders fed to young by males and females during the 2001 breeding season, according to video data (see table 4).

Fig. 2. Porcentaje medio e intérvalos de confianza del 95% de las arañas que alimentan a los jóvenes recolectadas por los machos y hembras durante la temporada de cría de 2001, según grabaciones de vídeo (ver tabla 4).

Discussion

Caterpillars are generally the main food resource used by Tits to feed their chicks (Sillanpaa et al., 2008; Wilkin et al., 2009). Nevertheless, several studies have pointed out the important role of spiders as a key resource during the early stages of chick development (Ramsay & Houston, 2003), when spiders may

Table 4. RM ANOVA comparing males and females within each nest–box in relation to the number of caterpillars and spiders collected. Data recorded during the 2001 breeding season (filming data).

Tabla 4. RM ANOVA comparando machos y hembras dentro de cada caja nido en relación con el número de orugas y arañas recolectados. Datos registrados durante la temporada de cría 2001 (grabaciones de vídeo).

	$F_{1,17}$	P
Caterpillars	11.1	< 0.001
Spiders	3.5	0.08

Table 5. ANOVA on the variation in the abundance of spiders collected by Great Tit parents in relation to the recording method (collars and filming data), percentage of *Quercus* surrounding nest boxes (categorical variable with two classes: > 70% and < 70% of *Quercus*) and size of the brood.

Tabla 5. ANOVA de la variación en la abundancia de las arañas recolectadas por los padres de Carbonero Común en relación con el método de grabación (collares y grabaciones de video), porcentaje de Quercus *que rodean los nidos (variable categórica con dos clases: > 70% y < 70% de* Quercus*) y tamaño de puesta.*

	$F_{1,57}$	P
Method	9.0	0.20
Brood size	3.1	0.33
% *Quercus*	09	0.52
Method x brood size	3.4	0.32
Method x % *Quercus*	1.5	0.43
Brood size x % *Quercus*	0.6	0.59
Method x nº brood x x % *Quercus*	0.2	0.69

constitute 25% of the nestlings' diet (Tinbergen, 1960; Royama, 1970; Balen, 1973; Cowie & Hinsley, 1988, Woodburn, 1997). Our data stress that the overall contribution of spiders to the diet of the nestling Tits is even higher in the Mediterranean ecosystems, where figures can rise to 25 or even 40%, independently of the age of the chicks (see also Blondel et al., 1991; Naef–Daenzer, 2000). It could be argued that the higher use of spiders as a food source in this area is a collateral result of the generalized lack of food and the harder conditions of the Mediterranean forests (Royama, 1970; Blondel et al., 1991). However, the high proportion of spiders fed to the nestlings in our study area, independently of location and habitat structure, suggests that spiders may also be selected as a main food source. Additionally, if we consider the volume of prey rather than frequency, the availability of caterpillar increases greatly, implying that spiders are a more favoured food resource. Further, more detailed data on the size of the prey brought to nestlings is needed, however, to confirm this consideration.

Variations found over the two years of the study may be due to yearly variations or, more probably, to differences in the recording method used. Small spiders may easily be ingested by chicks when collars are used, and videotaping is probably a less biased recording method (Barba & Monrós, 1999).

Another important pattern found was that males and females provided different quantities of spiders to their nestlings, with females capturing a higher percentage of spiders. Sexual differences in the use of spiders has not been previously documented in Great Tits (Atienzar et al., 2009; Garcia–Navas & Sanz, 2010; Mitrus et al., 2010), although the pattern is consistent with results found by Grieco (2001), who stated that female Blue Tits were more flexible in relation to their feeding behaviour, while males maintained a constant proportion of food components between years. Differences between sexes may be determined by sex–differential strategies in feeding, or even, foraging behaviour (Tschirren et al., 2005).

Nevertheless, we should point out that even though females provided a higher proportion of spiders than males, figures reversed when we analysed absolute values, so that males provided in general higher quantities of food, including spiders. Our results contrast with Wright & Cuthill (1990) and Mitrus et al. (2010) who reported higher feeding rates for females. This means that males are responsible for an important part of chick provisioning and development in our population.

Future studies should assess whether the active selection of spiders in the Mediterranean is constant through the different stages within the life–history of the species (*e.g.,* when moulting or breeding) or with the age of the birds. Finally, given the nutritional value of spiders due to their high content in taurine (Ramsay & Houston, 2003), it would be interesting to determine the extent to which their preferential selection in the Mediterranean area can have physiological consequences for the Great Tits.

Acknowledgements

The present study was funded by CGL2009–10652 research project to JCS and JJN, and by FPI grants BES2010–040359 to EPN, from the Ministry of Science and Innovation, Spanish Research Council. Birds were handled with the permission of the Catalan Ringing Office (ICO) and the Departament de Medi Ambient, Generalitat de Catalunya. We thank the owners of Can Catà for kindly allowing us to use their facilities. We also thank J. A. Barrientos for his help with the identification of Arthropods.

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Capítulo 2

Hernández-Gómez, S., **Pagani-Núñez, E.**, Ruiz, I. & Senar, J. C. 2014. Nestling diet matches prey abundance in Mediterranean Blue Tits *Cyanistes caeruleus*. ***Animal Biodiversity and Conservation***. En prensa.

Nestling diet matches prey abundance in Mediterranean Blue Tits *Cyanistes caeruleus*

Sergio Hernández-Gómez*, Emilio Pagani-Núñez, Íker Ruiz and Juan Carlos Senar

Evolutionary Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, España (Spain)

* Corresponding author: hernandez_gomez_sergio@hotmail.com

Abstract

Prey selection made by parents when rearing their offspring is highly variable among individuals, populations and habitats. Additionally, prey abundance may vary in the short and the long term in a given area. Due to the impact of food abundance on breeding fitness, the combined analysis of prey abundance and parental foraging behaviour when rearing their offspring is of remarkable interest. In this paper we analysed parental foraging behaviour of Blue Tits *Cyanistes caeruleus* breeding in a Mediterranean mixed forest together with arthropod abundance. Arthropod survey showed that spiders were more abundant than caterpillars and that, in general terms, arthropod abundance was higher were Oaks predominated. There was also a peak of arthropod abundance in May. In keeping with this, Blue Tit parents fed their offspring a low proportion of caterpillars, which correlated positively with the proportion of *Quercus spp* surrounding nest-boxes and negatively with date. The proportion of spiders delivered by parents was high and almost constant in all nests across the whole breeding season. Moreover, feeding rates correlated positively with the proportion of spiders and negatively with the proportion of caterpillars in nestling diet. Spiders were an abundant trophic resource consistently exploited by breeding Blue Tits, while caterpillars limited parental rates of work, strongly varying among territories and along with date in nestling diet. We may conclude that caterpillars are not everything in relation to nestling diet in the Mediterranean area.

Key-words: caterpillars, deciduous forests, habitat heterogeneity, nestling diet, sclerophyllous forests, spiders**.**

Introduction

Animals confront spatial and temporal variations in food abundance, key factors in determining their foraging behaviour. Among insectivorous birds, caterpillars have been described as the best food source for growing nestlings because *Lepidoptera* larvae require shorter handling times, are easier to ingest (Banbura *et al.,* 1999), and contain more water than other prey types (Edney, 1977). However, although caterpillars are considered a highly profitable prey, they also are a seasonal food resource, and its abundance considerably varies among years, across seasons and between habitats (Arnold *et al.,* 2010; Banbura *et al.,* 1999; Tremblay *et al.,* 2005; Tremblay *et al.,* 2003). These ecological constraints to find caterpillars are especially strong in the Mediterranean area, which would affect their breeding performance through nestling growth, development and survival (Naef-Daenzer & Keller, 1999; Perrins, 1991). As a consequence, a higher occurrence of alternative prey items, such as spiders (Banbura *et al.,* 1994; Blondel *et al.,* 1991; Pagani-Nuñez *et al.,* 2011), has been reported. When caterpillars and spiders are scarce, some individuals also provide their offspring less suitable prey items such as fruits, moths and butterflies (*Lepidoptera* adults), stick-insects from genus *Phasmidae* or grasshoppers from genus *Orthoptera* (Banbura *et al.,* 1994).

One of the main sources of variation for breeding traits, and more specifically for nestling diet, it is habitat heterogeneity (Blondel *et al.,* 1993). Mediterranean forests may be composed by a mixture of evergreen and deciduous tree species. Conversely to deciduous trees, which renew their whole foliage each year, evergreen trees only renew a fraction of their foliage yearly. This pattern has significant consequences for phytophagous insects, such as caterpillars, because they cannot eat leaves of more than a year old (Crawley, 1983). For this reason, arthropod productivity it is lower, especially in the case of caterpillars, in sclerophyllous than in deciduous forests (Feeny, 1970; Varley, 1967). We could consider therefore Mediterranean sclerophyllous habitats of poorer quality than deciduous ones, especially from the perspective of caterpillar availability (Banbura *et al.,* 1994; Blondel *et al.,* 1991; Slagsvold & Lifjeld, 1985). However, Blue Tit parents adjust their feeding behaviour on the basis of caterpillar density, giving the same quantity of caterpillars in both, poor and rich, habitats (Tremblay *et al.,* (2005) ; but see Isaksson & Andersson, (2007)). Consequently, in Mediterranean sclerophyllous habitats, where caterpillar productivity is lower than in deciduous ones, Blue Tits would increase their foraging area decreasing their feeding rates (Tremblay *et al.,* 2005). Previous research found that the intake of spiders in nestling diet increased markedly in some areas to compensate the lack of caterpillars, but it was attributed to marginal or island habitats (Blondel *et al.,* 1991). Recent research, however, highlighted the importance of spiders for nestling development (Arnold *et al.,* 2007; García-Navas *et al.,* 2013; Pagani-Núñez & Senar, 2014; Ramsay & Houston, 2003), which would account for its profitability as suitable alternative prey to caterpillars, especially in the hard conditions of the Mediterranean area (Blondel *et al.,* 2010).

The analysis of the diet of wild passerines is of remarkable interest (Cholewa & Wesolowski, 2011), and approaches combining arthropod censuses and direct observations of nestling diet are especially intriguing (Naef-Daenzer *et al.,* 2000). In this work our aim was to contrast prey abundance with the diet of Blue

Tit nestlings in a predominantly evergreen Mediterranean forest. Here, caterpillars, the preferred prey for Blue Tits, are scarce and parents have to find suitable alternative food, such as spiders and other prey items. We predicted that spiders should be a more abundant and predictable trophic resource than caterpillars. Thus, Blue Tit parents should consistently exploit spiders across the whole breeding season, while they should only exploit caterpillars when they reach enough abundance.

Material and methods

Fourteen pairs of Blue tit were studied in 2012, in Can Catà field station (Cerdanyola del Vallès, Barcelona), a predominantly sclerophyllous Mediterranean mixed forest in NE Spain (see Pagani-Nuñez *et al.*, (2011) for a detailed description of the area).

Phenology of prey

We monitored arthropod availability across the breading season. For this purpose, a weekly census of arthropods present in the leaves was made in our study area from March to June in 2002 and 2003. For these censuses we considered two tree classes: Holm Oaks *Quercus ilex* and Oaks *Quercus cerrioides* in one hand, and Pines *Pinus halepensis* in the other. These are the most common tree species in our study area (Pagani-Nuñez *et al.,* 2011), and we have previously used the proportion of *Oaks spp* as a proxy of habitat quality (Pagani-Núñez & Senar, 2014). Fifteen trees of each species were randomly selected each year. Censuses lasted four minutes per tree. We recorded all caterpillars and spiders seen on external branches and leaves, following Carrascal *et al.,* (1998).

We performed a multivariate analysis of variance using caterpillar and spider density per tree as dependent variable, and date (fortnights from 1st of March), tree class (Oaks or Pines) and arthropod class (spiders or caterpillars), and their interactions, as categorical factors.

Diet recording

We monitored nest-boxes to determine nest building state, laying date, hatching date and brood size. Parental feeding behaviour was filmed between 9-14 days after hatching. Cameras were installed and activated the midday before recordings to minimize possible adverse effects produced by the installation of the device (see Pagani-Núñez & Senar (2014) for a general description of filming procedures). Parents rapidly restarted their usual behaviour. However, to be sure that no bias was present, we only used the recordings obtained during the first four hours after sunrise from the second day for our analysis. This is the time period in which parents of a closely related species, the Great Tit *Parus major*, worked at higher rates in our area (Pagani-Núñez & Senar, 2013). All females were caught at the nest box and marked with a white PVC ring during the incubation period (in the 10th day) to determine the sex of the parents in the recordings. Prey type (caterpillar, spiders, fruits and others) was recorded for each feeding action. We computed the number of feeding actions, the percentage of different prey items fed by each individual at each nest box, date, and brood size.

We used a multiple linear regression approach to investigate which factors determined parental provisioning behaviour and nestling diet. All the percentages were square-root transformed to approximate normal distributions. The first model included feeding rates as dependent variable. As independent variables we used the date of recording (to control for phenology), proportion of *Quercus spp* trees within 25 m surrounding nest-boxes (to control for habitat quality, see Pagani-Núñez & Senar (2014)), mean daily temperature and brood size. We did the same using caterpillar, spider and “other” proportions as dependent variables, and we added feeding rates to the model previously described.

Results

Patterns of arthropod abundance

Arthropod survey showed that Oaks had higher arthropod abundance than Pines, and that, in general terms, spiders were more abundant than caterpillars (Table 1: arthropod class). Both arthropod classes showed a similar pattern of variation with date, with a peak of abundance in May (Table 1). Finally, all the interactions among these three factors (date, tree and arthropod class) were non-significant (Table 1).

Patterns of parental provisioning behaviour

Males worked at higher rates than females ($t = 3.33$, $p < 0. 01$). We did not find any correlation between feeding rates and the proportion of *Quercus spp* surrounding nest-boxes, date of recording, temperature or brood size (all $p > 0.4$). Blue tit parents brought a wide variety of insects to their nestlings: caterpillars, spiders (including also eggs), moths, stick-insects, grasshoppers and formless remains, in addition to fruits. Caterpillars were the main prey provided to nestlings (mean ± SE = 0.36 ± 0.04%), followed by spiders (mean ±

SE = 0.26 ± 0.03%). “Other” prey items constituted a high proportion of the food delivered to nestlings (mean ± SE = 0.38 ± 0.03%), with fruits being the main type with a 14% and the rest all below 10%. The proportion of caterpillars correlated positively with the proportion of *Quercus spp* surrounding nest-boxes and correlated negatively with date and feeding rates (Table 2 & Fig. 1). Conversely, the proportion of spiders correlated positively with feeding rates and did not show any interaction with the proportion of *Quercus spp* (Table 2). Females delivered a higher proportion of spiders than males (Table 2). In the case of the proportion of “other” prey items, we found the opposite pattern to the proportion of caterpillars: a negative correlation with the proportion of *Quercus spp* and a positive correlation with date (Table 2 & Fig. 1). We did not find any interaction with temperature or brood size in any of these cases.

Discussion

We found that, in a Mediterranean mixed forest, spiders were more abundant than caterpillars. Habitat quality also had a relevant effect on arthropod abundance, because there were more arthropods were Oaks predominated (in opposition to Pines). The effect of date was similar and relevant for both arthropod classes: we recorded a peak of abundance in May. Accordingly, Mediterranean Blue tit parents provided to their nestlings fewer caterpillars than usually recorded in the literature (Blondel *et al.,* 1991; Cowie & Hinsley, 1988; Garcia-Navas & Sanz, 2011; Gibb & Betts, 1963), a great and constant proportion of spiders, and an increasing with date proportion of other prey items. Feeding rates correlated positively with the proportion of spiders and negatively with the proportion of caterpillars, which is coherent with their abundance patterns. Both sexes delivered to their nestlings approximately the same proportion of caterpillars and others, although females relied more often in spiders than males. It is generally assumed that Blue tits are caterpillar specialists (Owen, 1977; Rabenold, 1978; Royama, 1970). Actually, caterpillar scarcity and its correspondent diet diversification typical of Mediterranean Blue tit populations have been described as a suboptimal situation (Banbura *et al.,* 1994; Blondel *et al.,* 1991; Dias & Blondel, 1996a; Dias & Blondel, 1996b). The diet of Blue tit nestlings usually follows the same pattern: predominance of caterpillars, a few spiders and a limited quantity of other prey types, being very similar in different parts of Europe (Blondel *et al.,* 1991; Cowie & Hinsley, 1988; Garcia-Navas & Sanz, 2011; Gibb & Betts, 1963). However, Mediterranean Blue tit parents had to rely more often than expected in alternative and profitable prey types, such as spiders, to compensate for the lack of caterpillars. Previous studies showed that *Lepidoptera* larvae, especially *Noctuids* and *Geometrids*, are usually prolific in deciduous oak woodlands and constitute the main food for nestlings (Balen, 1973; Betts, 1955; García-Navas *et al.,* 2012; Gibb, 1960; Hartley, 1953; Minot, 1981; Royama, 1970; Török, 1986). In contrast, and in accordance with our results, evergreen Mediterranean forests are characterized by a great arthropod diversity, although at lower densities (Blondel *et al.,* 2010). Thus, variability in prey abundance between the different tree classes and across the breeding season should be the main cause of the high level of diet heterogeneity recorded.

Generally, Great and Blue Tits adjust their foraging behaviour on the basis of caterpillar density (Dias & Blondel, 1996a; Naef-Daenzer *et al.,* 2000). Regardless of the quantity of caterpillars available in the habitat they feed similar proportions of this kind of prey (Tremblay *et al.,* 2005). However, in a Mediterranean mixed forest, the proportion of caterpillars correlated negatively with feeding rates, while the proportion of spiders correlated positively. This contrasting pattern indicates that relying in caterpillars as the main food source could be counterproductive. Conversely, given their higher abundance, spiders did not limit the rates at which parents worked. The proportion of caterpillars provided to nestlings was also strongly biased by several environmental factors: it was higher in areas where Oaks predominate (places where we recorded a higher density of arthropods), and it decreased across the breeding season (see also Wilkin, (2009)). Caterpillars were progressively substituted by other prey types, such as fruits, butterflies or stick-insects. Similarly, in forest patches dominated by Oaks we recorded an increase in the proportion of “other” prey items to compensate the lack of caterpillars. On the other hand, Blue Tit parents delivered a constant proportion of spiders regardless of habitat quality and date. Our data suggests therefore that in Mediterranean mixed forests spiders are a more profitable trophic resource than caterpillars. Interestingly, several studies have already highlighted the relevance of spiders for nestling diet (García-Navas *et al.,* 2013; Magrath *et al.,* 2004; Pagani-Núñez & Senar, 2014; Wiesenborn, 2012), especially during early stages of chick development (Arnold *et al.,* 2007; Ramsay & Houston, 2003).

When considering other studies on the diet of Blue Tit nestlings (Blondel *et al.,* 1991; Cowie & Hinsley, 1988; Garcia-Navas & Sanz, 2011; Gibb & Betts, 1963), we found that the highest proportions of caterpillars and the lowest proportions of spiders in nestling diet were always related to deciduous forests, regardless of the geographic area (Mediterranean [Montes de Toledo] or Temperate

Europe [Ventoux]; Fig. 2). In addition, this preference for caterpillars was persistent regardless of habitat quality (from a garden [Cardiff] to a sclerophyllous forest [Thetford Chase]; Fig. 2). Conversely, we found relatively low proportions of caterpillars and high proportions of spiders in Mediterranean populations inhabiting predominantly sclerophyllous habitats (Corsica and our population; Fig. 2).

A high occurrence of spiders in nestling diet had previously been attributed to island or marginal habitats (Blondel *et al.,* 1991). Nevertheless, when comparing between different studies of Blue Tit nestling diet carried out in other areas of Europe with our results, we found a relationship between Mediterranean sclerophyllous vegetation and these unusual prey compositions. We suggest therefore that caterpillars are not everything in relation to the diet of Blue Tit nestlings, and that spiders are a relevant food resource in sclerophyllous forests of the Mediterranean area. The assessment of the diet of Blue Tit nestlings and of similar species inhabiting the Mediterranean area (Atienzar *et al.,* 2013) and to perform comparisons with other areas of Europe (Cholewa & Wesolowski, 2011) should be of special interest. This research would help to achieve a deeper understanding of the reasons underlying the great variability in prey types delivered by parents to their offspring, by similar species, in our area.

Acknowledgements

We thank to the Gil family, owners of Can Catà, for kindly allowing us to use their facilities. We also thank J. A. Barrientos for his help with the identification of arthropods, and Carolyn Newey for editing a version of the English. The present study was funded by CGL2012-38262 research project to JCS, by FPI grant BES2010–040359 to EPN, from the Ministry of Science and Innovation, Spanish Research Council and FPI grant FPI2000-0014 to IR, from CIRIT, Generalitat de Catalunya. Birds were handled with the permission of the Catalan Ringing Office (ICO) and the Departament de Medi Ambient, Generalitat de Catalunya.

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Table 1 Multivariate ANOVA analysis of variance of spider and caterpillar density per tree in a Mediterranean mixed forest. We included date (fortnights from 1st of March), tree class (Oaks or Pines), arthropod class (spiders or caterpillars) and their interactions as factors.

	d.f.	*F*	*P*
Date	9, 6150	64.21	< 0.01
Tree class	1, 6150	6.05	0.01
Arthropod class	1, 6150	5.42	0.02
Date x Tree class	9, 6150	0.62	0.77
Date x Arthropod class	9, 6150	1.12	0.34
Tree class x Arthropod class	1, 6150	0.19	0.66
Date x Tree class x Arthropod class	9, 6150	1.13	0.34

Table 2 Multiple linear regressions relating the proportion of caterpillars, spiders and “others” delivered by parents to their nestlings with the proportion of Oak trees surrounding nest-boxes within 25 m, date of recordings, mean daily temperature, brood size (as environmental factors), feeding rates (as variables that characterize parental foraging behaviour) and sex (male or female). We only show significant interactions.

Proportion of caterpillars			
	t	*ß*	*P*
% *Quercus spp*	2.33	0.38	0.03
Date	-3.33	-0.65	<0.01
Feeding rates	-2.29	-0.39	0.03
Proportion of spiders			
	t	*ß*	*P*
Feeding rates	2.12	0.48	0.05
Sex	-2.52	-0.56	0.02
Proportion of “others”			
	t	*ß*	*P*
% *Quercus spp*	-3.91	-0.54	<0.01
Date	3.42	0.57	<0.01

Figure legends

Fig 1 Proportions of different prey items (caterpillar, spider and other prey items) delivered by Blue Tit *Cyanistes caeruleus* parents to their offspring in each nest-box. Nest-boxes were chronologically ordered.

Fig 2 Proportions of the most important prey types (caterpillars and spiders) for Blue Tit *Cyanistes caeruleus* nestling diet in different locations across Western Europe. We also characterized habitat quality.

Fig. 1

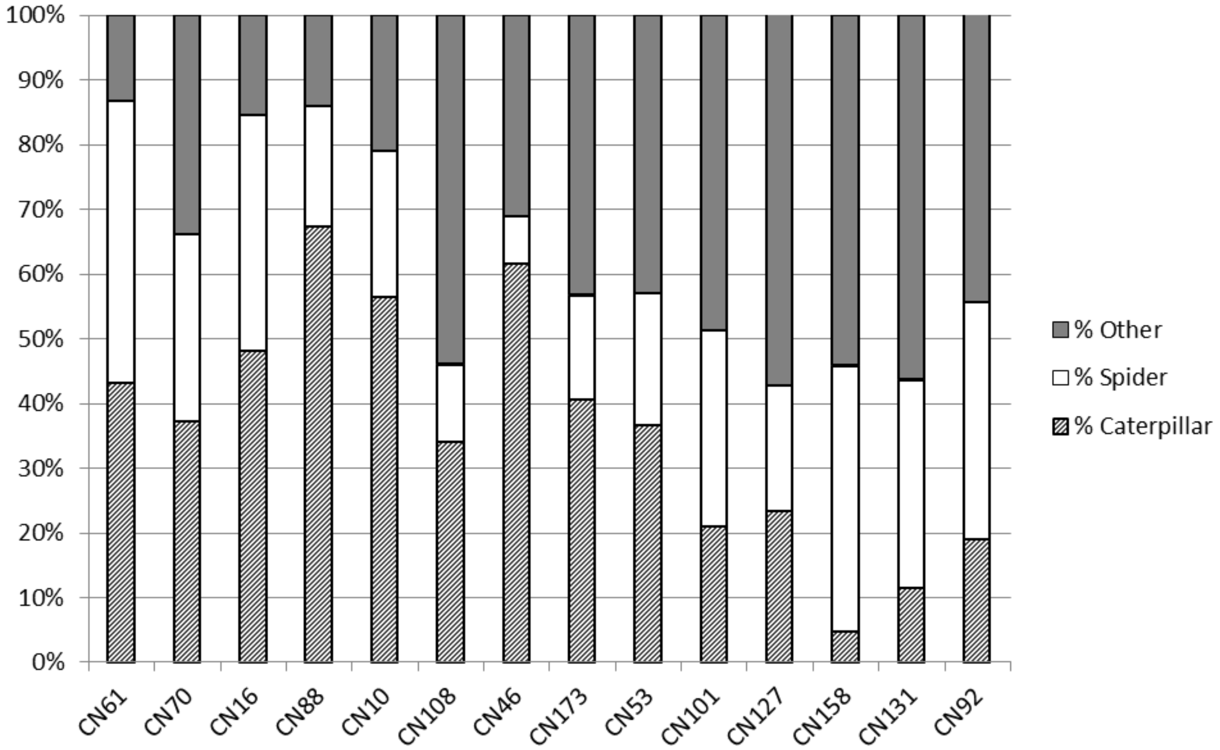
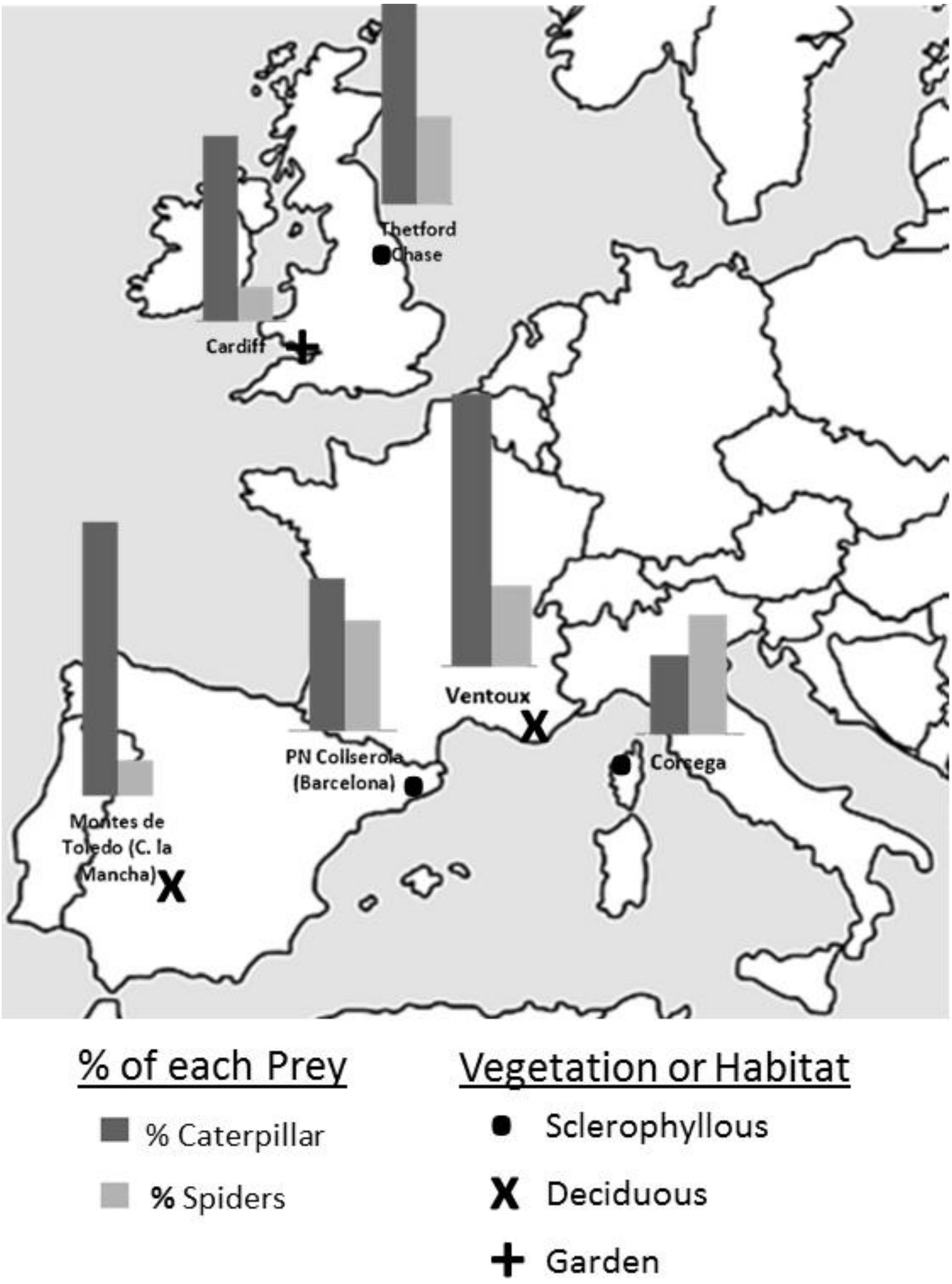

100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
CN61
CN70
CN16
CN88
CN10
CN108
CN46
CN173
CN53
CN101
CN127
CN158
CN131
CN92
% Other
% Spider
% Caterpillar

Fig. 2


Thetford Chase
Cardiff
Ventoux
PN Collserola (Barcelona)
Corsega
Montes de Toledo (C. la Mancha)
% of each Prey
% Caterpillar
% Spiders
Vegetation or Habitat
● Sclerophyllous
X Deciduous
+ Garden

Capítulo 3

Pagani-Núñez, E. & Senar, J. C. 2013. One hour of sampling is enough: Great Tit *Parus major* parents feed their nestlings consistently across time. ***Acta Ornithologica***, 48(2), 194-200.

ACTA ORNITHOLOGICA
Vol. 48 (2013) No. 2

One hour of sampling is enough: Great Tit *Parus major* parents feed their nestlings consistently across time

Emilio PAGANI-NÚÑEZ & Juan Carlos SENAR

Evolutionary Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, SPAIN, e-mail: emipanu@gmail.com

Pagani-Núñez E., Senar J. C. 2013. One hour of sampling is enough: Great Tit *Parus major* parents feed their nestlings consistently across time. Acta Ornithol. 48: 194–200. DOI 10.3161/000164513X678847

Abstract. Parental investment is a key topic in avian ecology, and many authors have focused on nestling-feeding behaviour to analyse this issue. Surprisingly, most studies have based their results on feeding patterns recorded over periods of only one or two hours, possibly leading to over generalizations regarding temporal-dependent behavioural patterns. Irrespective of nestling age or brood size, if we use observations from such short periods as conclusive evidence we must assume that parents behave consistently across time and that the window of time selected is representative of parental effort. To test this assumption, we analysed the time consistency of nestling provisioning rates and prey composition of 32 breeding pairs of Mediterranean Great Tits *Parus major*, from dawn to midday (7 hours recording). Regardless of a parallel decrease in the intensity of work for both sexes, we found that hourly provisioning rates per nestling correlated strongly with the mean number of feedings per nestling and per hour recorded over the whole 7 hours of recording. Weather conditions and nestling age had no effect on hourly provisioning rates per nestling, although parents with older nestlings worked relatively less hard. We also observed that the peak of morning activity was higher in nests with small clutches. Prey proportions showed a high degree of temporal repeatability, but nestling diet composition should be studied with caution. Although prey composition was stable over time, we recorded a strong decrease in the number of prey items delivered by parents throughout the day, along with an increase in prey size. We thus recommend using a wider time window to obtain reliable results when studying prey composition. In any case, considering our results, one hour of recording may be sufficient to describe nestling-feeding behaviour of Great Tit parents.

Key words: caterpillars, feeding behaviour, food, Mediterranean Great Tits, nestling diet, provisioning rate, time consistency

Received — Apr. 2013, accepted — Dec. 2013

INTRODUCTION

The analysis of parental investment has contributed significantly to the elaboration of sexual selection and life history theory models (Roff 1992, Stearns 1992, Andersson 1994). Many field studies in avian ecology have focused on provisioning rates and prey choice made by parents when taking care of their offspring. However, we found that the selection of different windows of time to attain this issue is rather arbitrary. Many of these studies have been based on a single sampling hour or even less (Conrad & Robertson 1993, Nour et al. 1998, Hinde 2006, Wilkin et al. 2009, Mitrus et al. 2010). In some cases this window of time is extended to at the most two or three hours (Smith et al. 1988, Barba & Gil-Delgado 1990, García-Navas & Sanz 2011). Surprisingly, this narrow window of time is considered as sufficient to depict ecological consequences of parental behaviour. A priori analyses of time consistency of parental foraging behaviour are infrequent and described contrasting patterns. While some studies found no variation (Goodbred & Homes 1996, Barba et al. 2009), other studies found a constant decrease from early morning (Low et al. 2008, García-Navas & Sanz 2012), a peak at dusk (Olsson et al. 2000) and a peak at dawn and at dusk (Knapton 1984). Even fewer works have focused on variation in prey selection throughout the day. These papers have reported a decrease in prey diversity with time of day, a higher proportion of spiders than expected over the first hours in the morning (Cowie & Hinsley 1988), and a decrease with time in the proportion of caterpillars (Bańbura et al. 1994). Based on reports that have studied several variables that can affect provisioning rates on a temporal scale, we can summarize that weather conditions, brood size and nestling age are the most important factors related to parental feeding behaviour (Knapton 1984). Regarding weather, it is widely known that rain and heat constrain foraging performance of wild birds (Nager & Wiersma 1996, Radford et al. 2001). In relation to brood size, an increase in the number of nestlings parallels a constant decrease in the number of feedings per nestling (Royama 1966, Nur 1984). And in respect to provisioning rates, prey proportions and prey quality are dependent on nestling age. A trade-off is normally seen between the number of feedings and prey size, which may reverse as nestlings develop (Royama 1966, Grundel 1987). Sampling always at the same hour and at the same stage of nestling development, controlling for brood size, and using feeding rates per nestling instead of, or combined with, feeding rates per brood, are prerequisites for data reliability (Mazgajski 2007).

This variability suggests that analysis is needed to determine whether a single sampling hour is sufficient time to depict the foraging patterns of a pair. And more specifically, we need to determine whether provisioning rates displayed by parents at different hours correlate with mean values within a day. Given that it is difficult to control for all the extrinsic factors that determine feeding behaviour, we need to assess the degree of individual consistency across time. Data on these specific issues are scarce in the case of passerines. The only study we found was that of García-Navas & Sanz (2012), who reported a high level of correlation in provisioning rates of Blue Tits *Cyanistes caeruleus* throughout the day, and hence concluded that one hour of recordings was sufficient to analyse parental behaviour. This pattern, however, likely changes according to species and habitat, although in populations where provisioning rates do not vary much over the day, one random hour could be adequate to characterize parental effort. The Mediterranean area, for instance, has traditionally been associated with particular patterns in relation to prey composition and nestling-provisioning rates (Blondel et al. 2010). Birds in this region rely more on alternative prey, such as spiders, than on caterpillars (Blondel et al. 1991, Pagani-Núñez & Senar 2014), and this could increase variability in parental effort, both between and within individuals (Bańbura et al. 1994).

The aim of this paper was to study time consistency and correlation of parental feeding behaviour to determine whether one hour of recording is sufficient to describe nestling provisioning and prey composition in Great Tits *Parus major*. We focused on the analysis of nestling provisioning rates and prey composition of Great Tit pairs inhabiting a Mediterranean area.

METHODS

A total of 182 nest boxes were checked twice a week to determine nest building state, laying date, hatching date, and brood size during the 2011 breeding season at Can Catà field station, in a predominantly evergreen Mediterranean mixed forest of 80 ha of area (45°27′N, 2°8′E; Barcelona, northeast Spain; see Pagani-Núñez et al. (2011) for details of the area). Once we determined the hatching date, nests were visited only when strictly necessary to film and to take samples from nestlings. Nest-boxes were cleaned before the breeding season, so an anomalous increase of provisioning rates due to parasite load was not expected. We recorded a mean number of 6.6 nestlings per nest (ranging from three to nine). We also recorded periods of rain on days when feeding rates were recorded.

We used Micro-D cameras with an infrared view and motion sensor to analyse parental feeding behaviour. These cameras were installed inside the nest boxes when nestlings were 10–16 days old (Naef-Daenzer & Keller 1999). We camouflaged the external device of the camera the day before recordings to minimize possible effects on parental behaviour. We only analysed first broods from 28th April to 23rd May. Film recordings were taken for seven hours, starting after sunrise on the second day. To homogenise the sample we used full clock hours, excluding the lapse between dawn and 7 a.m. As most studies facing parental feeding behaviour have been carried out during the morning, our study period comprised between 7 a.m. and 2 p.m. We determined the sex of the parent based on colour differences between sexes. We recorded prey type and exact time of each feeding. Prey items were divided into three categories: caterpillars, spiders, and others. We determined prey size accordingly to a semi-quantitative scale; small, medium and large (Barba et al. 1996). To analyse the data (N = 32 pairs), we computed the number of feeding actions and each kind of prey fed by the parents to their offspring for each hour of recording, and we also computed the mean values obtained throughout the whole morning.

We analysed intra-individual variation in hourly patterns of provisioning rates per nestling by performing a repeated measures ANOVA (RMANOVA). Provisioning rate was the dependent variable, time — a within-subject factor, and sex — a between-subject factor. The same approach was used to analyse mean prey size and the percentage of spiders and caterpillars provided by parents to chicks, as dependent variables. We then performed a RMANOVA using provisioning rates as dependent variable, time as a within-subject factor, sex and the presence of rain as between-subject independent factors, and nestling age and brood size (number of nestlings during recordings) as covariates. We tested for significant interactions between time and between-subject factors using post-hoc planned comparisons. We also analysed the correlation between hourly and mean provisioning rates per nestling between 7 a.m. and 2 p.m., which tests whether short-term samples are representative of what occurs over a longer time. We included sex as 0–1 dummy variable. Percentages were square-root-transformed to approximate normality. Means ± standard error are reported. We used Statistica 6.0 to carry out the analyses (StatSoft 2001), and all assumptions of the tests were fulfilled.

RESULTS

Nestling-provisioning rates per nestling decreased throughout the study period (Table 1, Fig. 1; n = 32) and differed significantly between sexes (Table 1), with males showing higher rates than females (Fig. 1). However, the intersexual difference in relation to time was additive, namely, sexual differences did not change across time (i.e. no interaction; Table 1, Fig. 1). Males and females of each pair did not display concordant levels of parental care, since nestling-provisioning rates per hour and nestling within the pairs were not correlated. When considering only provisioning rates per hour, however, the correlation was significant (provisioning rates per hour: r = 0.40, p = 0.02; provisioning rates per hour and nestling: r = 0.28, p = 0.12; n = 64). In parallel with the decrease in hourly provisioning rates, we recorded an increase in mean prey size for both sexes (Table 1, Fig. 2; n = 32). Neither the proportion of caterpillars or spiders provided to chicks differed significantly during the study period or between the sexes (Table 1; n = 32).

Table 1. Hourly provisioning rates per nestling across seven hours of recordings from 7 a.m. to 2 p.m. Differences between hourly values were tested with RMANOVA with time as a within-subject factor and sex as a between-subject factor. We used the same approach for mean prey size and the proportion of caterpillars and spiders. n = 32.

Variables	F	d.f.	p
Provisioning rates			
Sex	6.748	1, 62	0.01
Hourly values	21.92	6, 372	< 0.01
Hourly values × Sex	0.60	6, 372	0.73
Prey size			
Sex	0.54	1, 62	0.47
Hourly values	2.91	6, 372	0.01
Hourly values × Sex	1.49	6, 372	0.18
% Caterpillars			
Sex	1.22	1, 62	0.27
Hourly values	1.02	6, 372	0.41
Hourly values × Sex	0.69	6, 372	0.66
% Spiders			
Sex	1.09	1, 62	0.30
Hourly values	1.20	6, 372	0.30
Hourly values × Sex	1.31	6, 372	0.25

Although brood size had no effect on mean provisioning rates per nestling, the peak of morning activity was higher in nests with small clutches (Table 2, Fig. 3; n = 32). Conversely, nestling age had no effect on hourly provisioning rates, while mean provisioning rates per nestling decreased slightly from day ten to day twelve, and then levelled off (Table 2; Fig. 4). Neither mean provisioning rates nor their hourly values differed

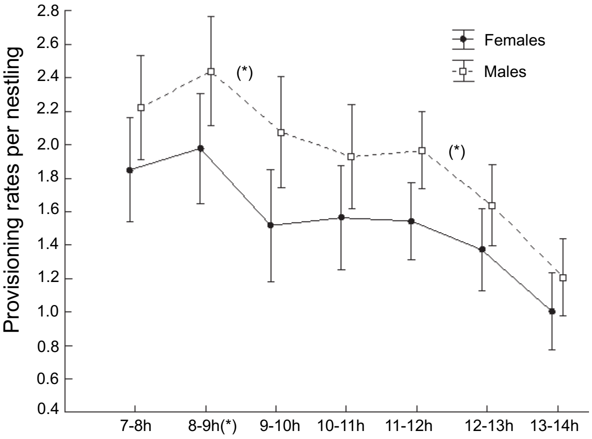


Fig. 1. Hourly provisioning rates per nestling of Mediterranean Great Tit parents across the morning. Inside the graph, the symbol (*) indicates that there are significant differences in provisioning rates between these hourly periods. Hourly periods flagged with (*) indicate that sex-related differences were significant ($p < 0.05$). Means and S.D. are provided.

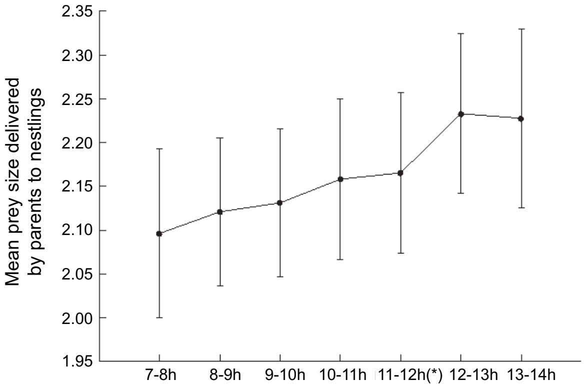


Fig. 2. Hourly values of mean prey size delivered to their nestling by Mediterranean Great Tit parents across the morning. Units in Y-axis correspond to mean values per nest determined from a semi-quantitative scale for prey size: 1-small, 2-medium and 3-large. Hourly periods flagged with (*) indicate significant differences (p<0.05). Means and S.D. are provided.

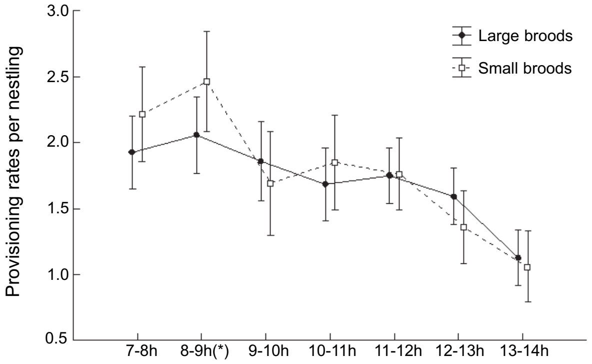


Fig. 3. Hourly provisioning rates per nestling of Mediterranean Great Tit parents across the morning in function of brood size. Nests were divided in small broods (3–6 nestlings) and large broods (7–9 nestlings). Hourly periods flagged with (*) indicate significant differenced ($p < 0.05$). Means and S.D. are provided.

significantly in relation to the presence or absence of rain (Table 2). No differences were found between males and females in function of any of these factors (Table 2).

Hourly nestling-provisioning rates correlated highly with mean provisioning rates across the study period, and no sex effect was detected (Table 3, Fig. 5; n = 64).

DISCUSSION

Analysis of nestling-feeding strategies in birds has demonstrated that their behaviour is strongly affected by intrinsic factors such as brood size (Nour et al. 1998), ecological constraints such as habitat quality (Tremblay et al. 2005), and latitudinal variation in day length (Sanz et al. 2000). At the individual level and within the same breeding attempt, variability in the degree of temporal consistency of parental foraging behaviour among populations is high. Some authors found high temporal consistency in provisioning rates over the course of the day in other Mediterranean areas (Barba et al. 2009, García-Navas & Sanz 2012), but low temporal consistency has also been recorded (Blondel et al. 1991, Bańbura et al. 1994). Parents made a strong effort at early morning, probably to cover the high energetic demand of nestlings after a long night (Royama 1966). Nevertheless, this peak of morning activity was dependent on brood size, suggesting that parents of large broods were not able to find sufficient quality food (Smith et al. 1988). Thus, the

Table 2. Hourly provisioning rates per nestling across seven hours of recordings from 7 a.m. to 2 p.m. We used RMANOVA with time as within-subject factor, sex and the presence of rain as between-subject independent factors, and nestling age and brood size (number of nestlings during recordings) as covariates. We tested for all interactions. N = 32

Variables	F	d.f.	p
Brood size	2.95	1, 58	0.09
Nestling age	10.61	1, 58	< 0.01
Sex	6.61	1, 58	0.01
Rain	< 0.01	1, 58	0.94
Sex × Rain	0.08	1, 58	0.77
Hourly values	3.97	6, 348	< 0.01
Hourly values × Brood size	2.12	6, 348	0.05
Hourly values × Nestling age	1.74	6, 348	0.11
Hourly values × Sex	0.64	6, 348	0.70
Hourly values × Rain	0.32	6, 348	0.92
Hourly values × Sex × Rain	0.44	6, 348	0.85

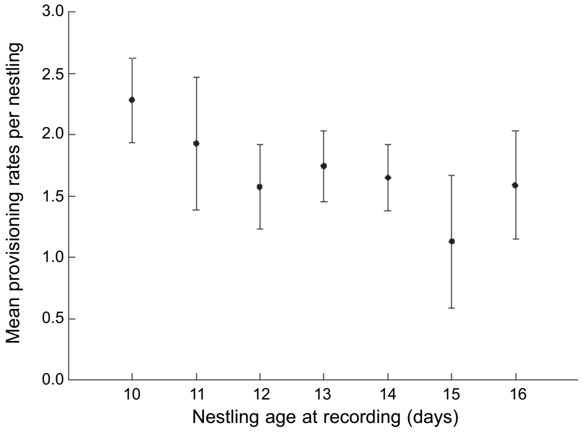


Fig. 4. Mean hourly provisioning rates per nestling displayed by Mediterranean Great Tit parents in function of nestling age (from day ten to sixteen). Means and S.D. are provided.

Table 3. Levels of correlation between hourly and mean values of provisioning rates per nestling of each individual across the morning (from 7 a.m. to 2 p.m.). To assess sexual differences in the level of correlation we introduced sex factor as dummy variable. n = 64 (32 males and 32 females).

Variable	Partial correlation	p
Sex	-0.02	0.88
7–8h	0.94	< 0.001
8–9h	0.90	< 0.001
9–10h	0.90	< 0.001
10–11h	0.88	< 0.001
11–12h	0.80	< 0.001
12–13h	0.87	< 0.001
13–14h	0.77	< 0.001

widespread decrease in nestling-provisioning rates that we found over the study period, plus the fact that we did not find a significant temporal variation in prey composition delivered to the nest, suggests that individuals progressively move further afield to find acceptable prey (Tremblay et al. 2005). This pattern would be more marked in our population since Mediterranean Great Tits deliver a wider range of prey than other relatively close populations (Barba et al. 2009, Pagani-Núñez et al. 2011). Moreover, and as expected (Grieco 2001, 2002), we recorded an increase in prey size and a decrease in provisioning rates across time. Therefore, our findings suggest a trade-off between the selection of quality food and adequate fulfilment of the nestlings' energy needs. This idea is also supported by the fact that mean feeding rates per nestling decreased with nestling age but did not affect daily provisioning patterns (Conrad & Robertson 1993). We can not rule out other possibilities. The absence of morning peak activity in large broods would be an indirect effect of reduced energetic nestling demands (Royama 1966, Nur 1984). Other factors, such as physiological adjustment to the high heat levels in the Mediterranean area (Nager & Wiersma 1996), could also account for the pattern we found of reduction in nestling-provisioning rates throughout the time.

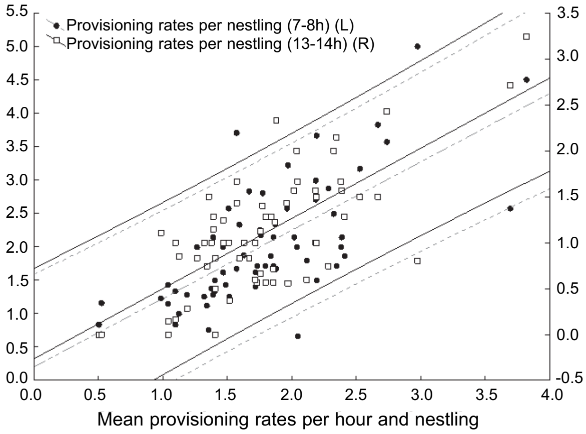


Fig. 5. Graph showing the level of correlation between hourly provisioning rates per nestling from the periods 7–8 h and 13–14 h, which showed the best and the worst fitting with mean values, with mean provisioning rates per nestling across the whole study period. Spotted lines represent confidence intervals.

However, and in spite of temporal variations in provisioning rates, a key aspect from a methodological point of view is whether hourly nestling-provisioning rates throughout the day correlate with mean provisioning rates, because this could guide protocols for future data recordings. Previous work on Blue Tits showed that hourly nestling-provisioning rates were highly correlated within individuals with mean values obtained throughout the day (García-Navas & Sanz 2012). Data from our Great Tits showed a similar pattern. The fact that they inhabit an area with high heterogeneity in prey abundance could potentially relax correlations (Pagani-Núñez et al. 2011, Pagani-Núñez & Senar 2014). In addition, they did not display concordant levels of effort within the pairs. Our results hence, support the view that very few recording hours, or even just one hour, is sufficient to describe the parental effort of a pair within a given population. We additionally provide a novel result in showing that, regardless of the great variability recorded, prey proportions were constant all through the study period (see also Cowie & Hinsley (1988) or Grundel (1990)). Nevertheless, we recommend caution when analysing nestling-feeding patterns based on just one hour of recordings. Given the potential variation in provisioning rates during the day, we suggest that all studies should be performed at the same time of day to allow researchers to make comparisons within a study (Nour et al. 1998). If we are going to analyse nestling diet, it should be kept in mind that the marked decrease in provisioning rates throughout the day could increase measurement error and produce statistical inaccuracies. Consequently, if we are going to study prey composition, we recommend using a wider window of time. In our case, this would comprise the first hours after dawn, given that provisioning rates were higher.

To conclude, we report a high level of correlation between hourly and mean values of nestling-feeding behaviour throughout the study period. Although we did not consider the whole day, the high level of correlation we found supports the reliability of our finding. Despite great variability in relation to Great Tit foraging behaviour and the large quantity of environmental and intrinsic factors governing this trait, we recorded an adequate level of temporal consistency. We suggest that this is a common pattern in Great Tits, especially where diet is less diverse and environmental and/or behavioural heterogeneity is low (Naef-Daenzer et al. 2000, Barba et al. 2009, Wilkin et al. 2009). Hence, when analysing parental effort, one hour of recording may be sufficient. Aspects such as when prey proportions are considered, however, should be interpreted with caution.

ACKNOWLEDGEMENTS

We want to thank the students who helped carry out fieldwork and watch the recordings. We also thank to Lluïsa Arroyo for her help in the lab and Carolyn Newey for her assistance in editing a version of the manuscript. The present study was funded by CGL2009-10652 research project to J.C.S. and by the FPI grant BES2010-040359 to E.P.N., from the Ministry of Science and Innovation, Spanish Research Council. Birds were handled with the permission of the Departament de Medi Ambient, Generalitat de Catalunya. Rings were provided by the Catalan Ringing Office (ICO).

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STRESZCZENIE

[Jednogodzinna obserwacja wystarcza do wiarygodnego pomiaru częstości karmienia piskląt u bogatki]

Inwestycje rodzicielskie są jednym z najczęściej badanych zagadnień w ekologii ptaków, a jednym ze sposobów ich określania jest pomiar częstości karmienia piskląt przez ptaki dorosłe. Większość prac bazuje na liczeniach karmień trwających jedną lub dwie godziny, zakładając, że liczenia w tak krótkim czasie są reprezentatywne dla całego okresu karmienia piskląt (niezależnie od wielu innych zmiennych, takich jak wiek piskląt, czy wielkość lęgu).

Aby sprawdzić te założenia badano częstość karmienia piskląt przez dorosłe bogatki, a także określano rodzaj i wielkość przynoszonego przez nie pokarmu. Badania prowadzono w północno-wschodniej Hiszpanii, w populacji zasiedlającej skrzynki lęgowe rozwieszone w lesie z dominującą roślinnością śródziemnomorską. Zainstalowane wewnątrz skrzynek lęgowych kamery rejestrowały karmienia od wschodu słońca do godziny 14 (7 godzin obserwacji), w okresie, gdy pisklęta miały 10–16 dni. Na podstawie nagrań określano liczbę karmień (w przeliczeniu na jedno pisklę) w kolejnych godzinach, płeć karmiących ptaków, rodzaj zdobyczy (kategorie: gąsienice, pająki, inne) oraz jej wielkość (kategorie: mała, średnia duża). W analizach uwzględniono również warunki pogodowe (opady deszczu). Badaniami objęto 32 pary ptaków.

Stwierdzono, że liczba karmień spadała w kolejnych godzinach, a także, że samce częściej niż samice przynosiły pokarm do gniazda (Tab. 1, Fig. 1). Wraz ze spadkiem liczby karmień wzrastała średnia wielkość przynoszonej zdobyczy (Fig. 2), a proporcja gąsienic i pająków nie różniła się zarówno pomiędzy poszczególnymi godzinami karmień, jak i samcami i samicami (Tab. 1). Wielkość lęgu nie wpływała na średnią częstość karmienia, ale w godzinach porannych pary o mniejszych lęgach (mniej niż sześć piskląt) częściej karmiły pisklęta niż pary z większymi lęgami (Fig. 3). Średnia liczba karmień spadała wraz z wiekiem piskląt (Fig. 4, Tab. 2). Liczba karmień w kolejnych godzinach była silnie skorelowana ze średnią liczbą karmień w całym okresie obserwacji (Tab. 3, Fig. 5). Wyniki te wskazują, że nawet jednogodzinne obserwacje karmienia piskląt wiarygodnie odzwierciedlają poziom wysiłku rodzicielskiego danej pary.

Capítulo 4

Pagani-Núñez, E., Hernández-Gómez, S., Riyahi, S. & Senar, J. C. 2014. Year-round preference of spiders for Mediterranean great tits *Parus major*. ***Ardeola***. En prensa.

YEAR-ROUND PREFERENCE FOR SPIDERS BY MEDITERRANEAN GREAT TITS *PARUS MAJOR*

LOS CARBONEROS COMUNES *PARUS MAJOR* PREFIEREN ARAÑAS DURANTE TODO EL AÑO EN AMBIENTES MEDITERRÁNEOS

Emilio PAGANI-NÚÑEZ[1 *], Sergio HERNÁNDEZ-GÓMEZ [1], Sepand RIYAHI[1] and Juan-Carlos SENAR[1]

Short title: PREY CHOICE IN GREAT TITS

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[1] Evolutionary Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain.

[*] Corresponding author: emipanu@gmail.com

SUMMARY.— A key topic in foraging ecology is whether a particular prey type is consumed because it is more abundant or easier to catch, or because there is a specific preference for it. The great tit *Parus major* is an ideal species for studying this topic. Although it is traditionally regarded as a caterpillar specialist, in certain periods, e.g. during the breeding season, or areas, such as the Mediterranean forests, the great tit seems to show a preference for spiders. We conducted food choice experiments with captive birds to ascertain which of these two main prey types (caterpillars v. spiders) was preferred outside the breeding season when there was an opportunity to prey on both food types. In conclusion, we found that, regardless of any variation in the supply-demand ratio and the amount of food available, Mediterranean great tits showed a preference for spiders.

Key words: arachnids, captivity, caterpillars, Mediterranean area, prey choice.

RESUMEN.—Un tema clave en ecología del forrajeo es si una presa particular es consumida porque es más abundante o fácil de cazar o porque hay una preferencia específica por ese tipo de presa. El carbonero común *Parus major* es una especie ideal para estudiar este tema. Aunque tradicionalmente considerado como especialistas en orugas, en ciertos periodos, por ejemplo durante la temporada de cría, o áreas, como los bosques Mediterráneos, el carbonero común parece mostrar preferencia por las arañas. Llevamos a cabo un experimento de elección de presa con aves en cautividad para averiguar cuál de esas dos presas principales (orugas o arañas) era preferida fuera de la temporada de cría cuando se les daba la oportunidad de cazar ambos tipos a la vez. En conclusión, encontramos que, independientemente de cualquier variación en la tasa de oferta y demanda o de la cantidad de comida disponible, los carboneros comunes mediterráneos mostraron preferencia por las arañas.

Palabras clave: arácnidos, área mediterránea, cautividad, orugas, presas.

INTRODUCTION

Animal foraging behaviour became a popular focus of research several decades ago (Charnov, 1976). The objective at that time was to formulate a coherent theory to explain mechanisms that drive prey selection and hunting behaviour displayed by birds (Krebs *et al*., 1977). The most important outcome of this period was the optimal foraging theory (OFT), which described prey selection as the tendency to maximise net energy intake per unit time (Pyke *et al*., 1977; Krebs *et al*., 1978). Further research, however, stressed that this choice is context-dependent and that it may vary among individuals and species (Stephens and Krebs, 1986; Davies *et al*., 2012). In the case of birds, an early study on pigeons *Columba livia* showed a high occurrence of "non-optimal" preferences (Lea, 1979). Experiments with great tits (Rechten *et al*., 1983) and pigeons (Belke and Kwan, 2000) showed that prey selection was strongly affected by the physical condition of the individuals. Another study, with common starlings *Sturnus vulgaris*, showed these birds took risk-dependent foraging decisions (Bateson, 2002). It was also reported that prey profitability could change with the consumption of successive items across a foraging bout (Hirvonen and Ranta, 1996). This high occurrence of partial preferences (Partridge, 1976; Krebs *et al*., 1977) contradicts OFT assumptions and has led to the classification of foraging strategies as either specialist or adaptive generalist (Fryxell and Lundberg, 1994). This topic has commonly been reviewed from theoretical approaches (Iwasa *et al*., 1981; Fryxell and Lundberg, 1994; Křivan, 1996; Van Baalen *et al*., 2001; Abrams, 2010; Okuyama, 2011), although it has seldom involved field-based experimental studies using passerines as model species (but see Bateson *et al*., (2002)). The only equivalent may be found in the ambit of foraging ecology of waders (Zwarts and Blomert, 1992; Zharikov and Skilleter, 2004;

Van Gils *et al*., 2005), but refined assessments of foraging strategies in relation to prey quality are uncommon among studies focusing on passerines. Moreover, most of these classic experimental works focused on quantity rather than on quality or type of prey items (Krebs *et al*., 1977; Krebs *et al*., 1978; Rechten *et al*., 1983), and results may differ in systems with a higher degree of trophic complexity.

The great tit *Parus major* has long been a model species in foraging ecology studies. Although great tits are considered caterpillar specialists (Royama, 1970; Naef-Daenzer *et al*., 2000; Sillanpää *et al*., 2009), they very often rely on other prey items when and where caterpillars are scarce (Barba and Gil-Delgado, 1990; Blondel *et al*., 2010). A particularly outstanding alternative prey for great tits in the Mediterranean area is spiders which, in spring and for some individuals, can account for more than half the food provided to chicks (Pagani-Núñez *et al*., 2011). A relevant question from the standpoint of foraging theory is whether spiders are just an alternative prey, probably taken because of low general caterpillar availability, or whether they are preferentially selected as highly suitable prey (Pagani-Núñez and Senar, 2014). This latter view stems from several physiological works that show the high benefits of a diet in which spiders form a substantial part (Ramsay and Houston, 2003; Magrath *et al*., 2004; Arnold *et al*., 2007; Wiesenborn, 2012; García-Navas *et al*., 2013; Pagani-Núñez and Senar, 2014). This is supported by research showing that when birds require a high quality diet, such as in the key early stages of development or when the chick sex ratio is biased towards males, individuals shift their diet to spiders (Ramsay and Houston, 2003; Magrath *et al*., 2004). In spite of the fact that great tits preferably select spiders when rearing their offspring, little is known about their dietary preferences outside the breeding season. In this regard, if spiders may be considered a high quality prey for nestlings, it is worth assessing whether adult individuals also exploit this source of food at other stages of their life-histories and to what extent they prefer it.

The only way to test this idea unequivocally is through food choice experiments under controlled conditions (Emmans, 1991). Here, we carried out an experiment to test which of the two most relevant prey types for breeding great tits, caterpillars or spiders, was preferred outside the breeding season. We predicted that if spiders are really a high quality food resource for great tits, these birds should prefer spiders as a first dietary choice.

MATERIAL AND METHODS

The study was carried out during winter 2012–2013 with a sample of sixty-one great tit individuals captured with funnel traps (Senar *et al.*, 1997) in the Barcelona area (NE Spain). Twenty-nine individuals were captured at the Can Cata field station, a predominantly evergreen mixed forest close to Barcelona city (see Pagani-Núñez *et al.*, (2011)), and thirty-two were captured in two urban parks within the city of Barcelona (Björklund *et al.*, 2010). Birds were ringed to allow individual identification. We recorded body mass (g) at both capture and release. Great tits were aged and sexed according to differences in feather abrasion and coloration (Svensson, 1992). Individuals were brought to captivity at the Natural History Museum of Barcelona, at the Ciutadella Park, within two hours of capture. Birds were housed in single cages (1 m × 1 m × 1.5 m) with water and food (mealworms *Tenebrio molitor* and peanuts) provided *ad libitum*. They were also provided with a nest-box for refuge and roosting. We conducted an unrelated set of tests during the second day. Food choice experiments were carried out on the morning of the third day, using the same feeders that individuals used during the earlier tests. Birds were released where captured after three days.

We carried out a trial of two tests, using a consistent combination of simultaneous and sequential choice (see Freidin *et al*. (2009) for a detailed discussion of the methodology). Before the experiments, we removed all mealworms, although we left water and peanuts. In a first experiment, individuals had to choose between a common Mediterranean lycosid spider *Zoropsis* sp. (for a description of the species see Griswold and Ubick, (2001)) and a moth larva (waxworm *Galleria mellonella*). The two potential prey items were each caged in a transparent plastic box (2 cm × 2 cm × 1 cm), and located within two adjacent feeders. This time, we did not allow birds to eat the prey because we always used the same spider. The experimental feeders were removed as soon as the birds first pecked one of the boxes. In a second test, we offered the birds a waxworm alongside two other less profitable prey: a mealworm, to control for prey habituation, and a superworm *Zophobas morio*, a large dark giant mealworm, to control for prey conspicuousness. The three prey items were placed uncaged and together in the same feeder. Although Great Tits are widely known to display a strong appetite for waxworms (Cole and Quinn, 2012), we also performed this second test to check for this preference. This time, the birds were allowed to eat the selected item. Potential prey were left for ten minutes. If birds did not pay attention to the experiment within this time, we removed the prey and waited for fifteen minutes before repeating the test. If an individual did not participate in one of the experiments after this second attempt, we excluded it from the experiment. We performed all the experiments within one hour, at most. All the individuals were already familiar with waxworms because they ate at least one such item on the second day. We cannot guarantee that all individuals had previously had encountered the *Zoropsis* spider, although we know that this prey item is commonly fed to nestlings by parents when rearing their offspring and it is possible that they have eaten it themselves (Pagani-Núñez *et al.*, 2011; Pagani-Núñez and Senar, 2014). We understand that the waxworm is not exactly like caterpillars consumed by birds in their natural environment. However, given the difficulty of obtaining and raising native caterpillars, especially in winter, we used the most suitable alternative. A spider was taken from the wild and kept in optimal captivity conditions. Mealworms and waxworms were purchased from a commercial company. For more information about the characteristics of 'worm' species used in this experiment see Finke (2002).

Data analyses were carried out using a log-linear analysis of frequency tables (test of marginal and partial associations). Factors used were age (young or adult), sex (male or female), habitat (urban or forest) and prey choice. We also conducted a MANOVA to assess the effect of body mass on prey selection, with weight scores as the dependent variable, and age, sex, habitat and prey choice as factors.

RESULTS

As a first choice, most individuals (>70%) selected a spider instead of a caterpillar (table 1, fig. 1). There was a significant three-way interaction (table 1), indicating that prey choice could vary according to sex, but this choice could be modulated by age. Hence we found that whereas all juvenile females selected a spider, more than half the juvenile males selected a caterpillar (fig. 2). This tendency changed with age, with most adult males selecting a spider, and with an increase in the occurrence of caterpillar selection by adult females (fig. 2). No effect of habitat of origin was found over prey choice (table 1).

In the second test, most individuals selected a caterpillar instead of mealworms (fig. 3) and no other factor had a significant effect on prey choice (table 2).

No effect of body mass on prey choice was recorded (table 3). The highest weight scores were recorded in males and urban great tits.

DISCUSSION

A precise analysis of predator-prey interactions has traditionally been considered of major importance for ecologists. Undoubtedly, the understanding of mechanisms predicting predators' prey choice is of great interest to unscramble animal foraging behaviour (Charnov, 1976; Pyke *et al.*, 1977; Abrams, 2000; Chase and Leibold, 2003; Arditi and Ginzburg, 2012). In this work, we tried to compensate for the lack of experimental studies from this point of view, evaluating the appetite of Mediterranean great tits in captive conditions for their most common prey types, namely, caterpillars and spiders (Pagani-Núñez *et al.*, 2011; Pagani-Núñez and Senar, 2014). For the first time, and using a direct approach, we have shown that great tits also have a preference for spiders outside the breeding season.

Traditionally, it has been thought that caterpillars are the main food preference of both breeding and non-breeding great tits (Gosler, 1993). Nevertheless, where this most suitable food type is unavailable, a higher occurrence of profitable alternative prey types, such as spiders, is expected (Murdoch, 1969; Royama, 1970; Krebs *et al.*, 1977; Křivan, 1996). Although the use of spiders as a food source has generally been considered a "partial preference", we found strong indications that they are considered a highly preferred prey type, since our Mediterranean great tits showed a higher specific appetite for spiders than for caterpillars, irrespective of environmental factors that strongly affect their behaviour in natural conditions. We cannot attribute this choice to the higher conspicuousness of spiders: of dark coloration and with long legs, compared to caterpillars, because individuals in our second experiment preferentially selected a caterpillar when confronted with larger and darker prey items (i.e. superworms). We also note that prey choice was independent of the physical condition and habitat of origin of individuals. Indeed, the preference for arachnids should be reinforced by a positive feedback for spiders for their consumer (Arnold *et al*., 2007; Křivan, 2010). Hence, the general preference by great tits of caterpillars as a main food source (Gosler, 1993) is probably more dictated by the greater abundance of caterpillars and the likehood that they may be easier to catch than spiders than to a stronger specific appetite for caterpillars over spiders. In the Mediterranean region, however, where caterpillars are less abundant (Blondel *et al*., 1991; Bańbura *et al*., 1994; Blondel *et al*., 2010), and therefore less profitable (Dias and Blondel, 1996), consumption of spiders is likely to increase (Pagani-Núñez *et al*., 2011; Pagani-Núñez and Senar, 2014).

It is interesting that our finding is consistent with several theoretical approaches that have assessed the evolution of foraging strategies followed at the population level in a scenario where the density of the principal prey drops below a certain threshold (Křivan and Sikder, 1999; Van Baalen *et al*., 2001; Křivan and Cressman, 2009; Tinker *et al*., 2009). In one of these studies, Tinker *et al*., (2009) evaluated the development of behaviour-mediated foraging specialisations. They stressed the great importance of two aspects: the acquirement of new hunting skills by the individuals and the possibility of matrilineal social learning of these abilities. These requirements were considered critical to producing a model analogous to our experimental finding, and we consider that they were met by our study population. Since caterpillars and spiders differ in many respects, they should be hunted using different learned skills (Avery and Krebs, 1984; Slagsvold and Wiebe, 2011; Amo *et al*., 2013). In line with this, we have recorded a strong pattern of change in great tit prey preferences that suggest a main role of foraging ability, which probably increases with age (Del Val *et al*. 2010). Alternatively, it is possible that a process of differential selection at the population level could shape the birds' trophic preferences as they age. Moreover, females from our study population strongly rely on spiders when rearing their offspring (Pagani-Núñez *et al*., 2011). The consistent preference for spiders by females, especially juvenile females, indicates that both sexes differentially perceive prey quality in general terms. Further research may assess whether this pattern is innate to birds or whether it is socially transmitted. In the present case, we have revealed a situation in which great tits, considered caterpillar specialists, develop a high specific appetite for spiders (Pagani-Núñez *et al*., 2014). This finding, however, is unsurprising, since great tits are highly versatile predators, able to adapt their foraging behaviour to several prey types and environmental conditions (Fisher and Hinde, 1949; Caris, 1958; Estók *et al*., 2010).

To conclude, further research should be done to determine the mechanisms driving this switch of preferred prey and of foraging strategies developed by Mediterranean great tits, compared with those from northern European populations. The assessment of densities of the most preferred prey for great tits should help to understand the underlying reasons for these preferences. It is interesting that we have shown that great tit parents are highly consistent in the short term (Pagani-Núñez and Senar, 2013), so that it would be worth ascertaining how these preferences evolve across the annual cycle (e.g. using stable isotopes of blood or nails). Given that previous studies stressed the high dependence of great tits on caterpillars (Naef-Daenzer *et al*., 2000; Tremblay *et al*., 2003), it is necessary to explore whether in our population those pairs feeding more spiders to their nestlings have higher breeding success. Future studies of captive birds from elsewhere in our region would help to narrow the geographical scope of our finding. Furthermore, a sustained analysis of this issue over time will discern whether this is a stable pattern or whether it evolves in a dynamic equilibrium (Van Baalen *et al*., 2001; Křivan and Cressman, 2009; Abrams, 2010). Finally, it would be of great interest to analyse how the variety of foraging strategies and prey preferences recorded in captivity are expressed in natural conditions accordingly to the variation in the availability of both kinds of prey items.

ACKNOWLEDGEMENTS.—We want to thank Carolyn Newey for editing the English and Lluïsa Arroyo for her help in the lab. The present study was funded by research project CGL2012-38262 to J.C.S. and by the FPI grant BES2010-040359 to E.P.N., from the Ministry of Science and Innovation, Spanish Research Council. Birds were handled and kept in captivity with the permission of the Environment Department of the Generalitat de Catalunya. Rings were provided by the Catalan Ringing Office (ICO).

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Received: 2 December 2013

Accepted: 24 March 2014

Editor: José A. Masero

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TABLE 1

Results of a log-linear analysis of frequency tables testing for partial associations between factors ‘sex’ (male or female), ‘age’ (young or adult) and ‘habitat’ (urban or forest) and results of an experiment on choice of either a spider (*Zoropsis* sp.) or a caterpillar (waxworm *Galleria mellonella*). N = 61.

*[Resultados del análisis logarítmico-lineal de tablas de frecuencias en el cual testamos si existen asociaciones parciales entre los factores sexo (macho o hembra), edad (joven o adulto), hábitat (urbano o forestal) y los resultados del primer experimento (elección de una araña (*Zoropsis *sp.) o una oruga (polilla de la miel (*Galleria mellonella*)). N=61.]*

	χ^2	*P*
Sex	0.36	0.55
Age	4.23	0.04
Habitat	0.13	0.72
Food Choice	9.27	< 0.001
Sex × Age	0.69	0.40
Sex × Habitat	0.26	0.61
Sex × Food Choice	0.44	0.51
Age × Habitat	2.81	0.09
Age × Food Choice	0.07	0.80
Habitat × Food Choice	0.77	0.38
Sex × Age × Habitat	0.27	0.60
Sex × Age × Food Choice	9.54	< 0.001
Sex × Habitat × Food Choice	0.18	0.67

Age × Habitat × Food Choice	0.85	0.36

TABLE 2

Results of a log-linear analysis of frequency tables testing for partial associations between factors ‘sex’ (male or female), ‘age’ (young or adult) and ‘habitat’ (urban or forest) and results of an experiment on choice of a waxworm (*Galleria mellonella*), a mealworm (*Tenebrio molitor*) or a supermealworm (*Zophobas morio*). N = 61.

*[Resultados del análisis logarítmico-lineal de tablas de frecuencias en el cual testamos si existen asociaciones parciales entre los factores sexo (macho o hembra), edad (joven o adulto), hábitat (urbano o forestal) y los resultados del segundo experimento (elección de una polilla de la miel (*Galleria mellonella*), un gusano de la harina (*Tenebrio molitor*) o un gusano rey (*Zophobas morio*)). N = 61.]*

	χ^2	*P*
Sex	0.34	0.56
Age	4.00	0.05
Habitat	0.12	0.73
Food Choice	22.41	< 0.001
Sex × Age	0.61	0.44
Sex × Habitat	0.21	0.65
Sex × Food Choice	0.48	0.79
Age x Habitat	2.94	0.09
Age × Food Choice	1.98	0.37
Habitat × Food Choice	0.69	0.71
Sex × Age × Habitat	0.03	0.87
Sex × Age × Food Choice	1.84	0.40

Sex × Habitat × Food Choice	1.16	0.56
Age × Habitat × Food Choice	1.99	0.37

TABLE 3

Results of MANOVA analysis on variation in body mass (g) at release, according to factors ‘sex’, ‘age’ (young *vs.* adult) and ‘habitat’ (urban *vs.* forest) and prey choice in the first experiment (spider *vs.* caterpillar).

[Resultados del análisis MANOVA sobre la variación en masa corporal (g) en el momento de la liberación, de acuerdo con los factores sexo (macho o hembra), edad (joven o adulto), hábitat (urbano o forestal) y los resultados del primer experimento (araña u oruga).]

	$F_{1, 56}$	P
Sex	4.70	0.03
Age	0.02	0.88
Habitat	4.23	0.04
Prey choice	0.00	0.96

FIGURE LEGENDS

FIG. 1—Results of the first food choice experiment. Individuals had to choose between a lycosid spider (*Zoropsis sp.*) or a caterpillar (waxworm (*Galleria mellonella*)). N = 61. *[Histograma que muestra los resultados del primer experimento de elección de presa. Los individuos tenían que elegir entre una araña licósida (*Zoropsis *sp.) o una oruga* (*polilla de la miel (*Galleria mellonella)). *N = 61.]*

FIG. 2—Results of the first experiment as a function of age and sex of individuals. A) young males (N = 10), B) adult males (N = 23), C) young females (N = 12) and D) adult females (N = 16).

[Histogramas que muestran los resultados del primer experimento en función de la edad y el sexo de los individuos. A) machos jóvenes (N = 10), B) machos adultos (N = 23), C) hembras jóvenes (N = 12) y D) hembras adultas (N = 16).]

FIG. 3—Results of the second experiment in which individuals had to choose between a caterpillar (*w*axworm (*Galleria mellonella*)), a mealworm (*Tenebrio molitor*) or a superworm (*Zophobas morio*). N = 61.

*[Histograma que muestra los resultados del segundo experimento en el que los individuos tenían que elegir entre una oruga (polilla de la miel (*Galleria mellonella*)), un gusano de la harina (*Tenebrio molitor*) o un gusano rey (*Zophobas morio*). N = 61.]*

Fig. 1

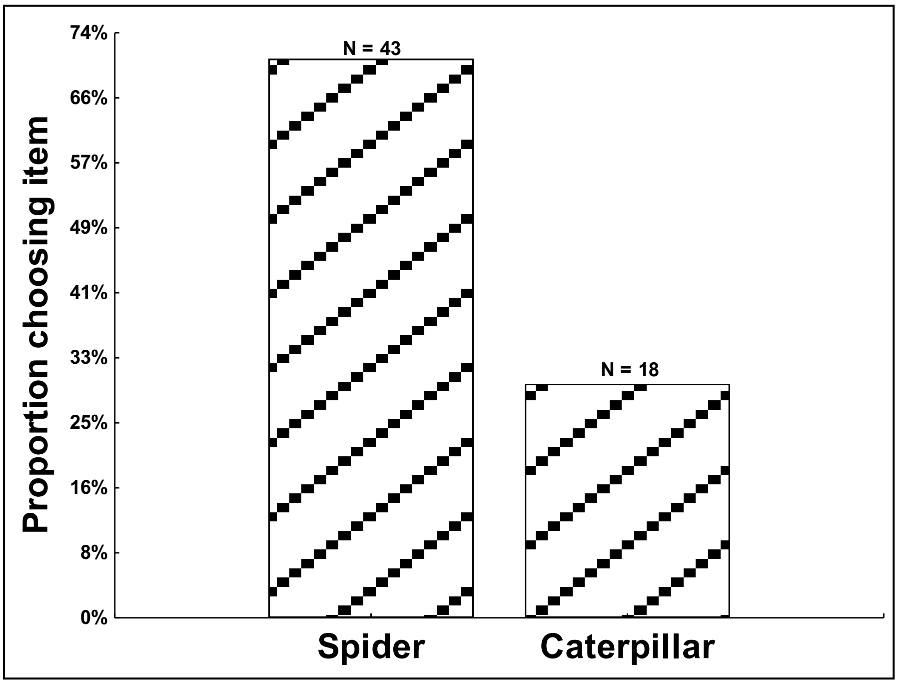

74%
66%
57%
49%
41%
33%
25%
16%
8%
0%
Proportion choosing item
N = 43
N = 18
Spider
Caterpillar

Fig. 2

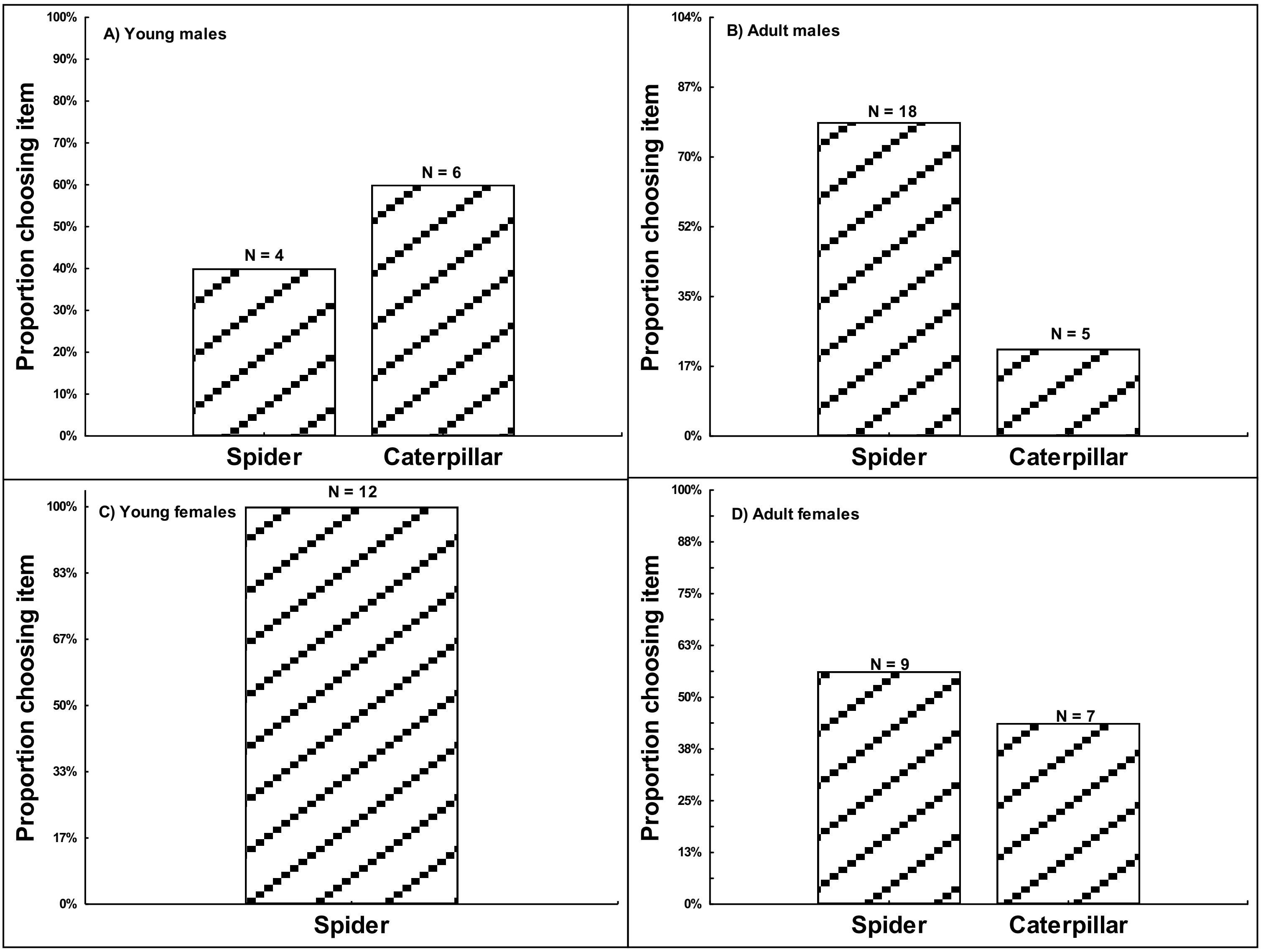
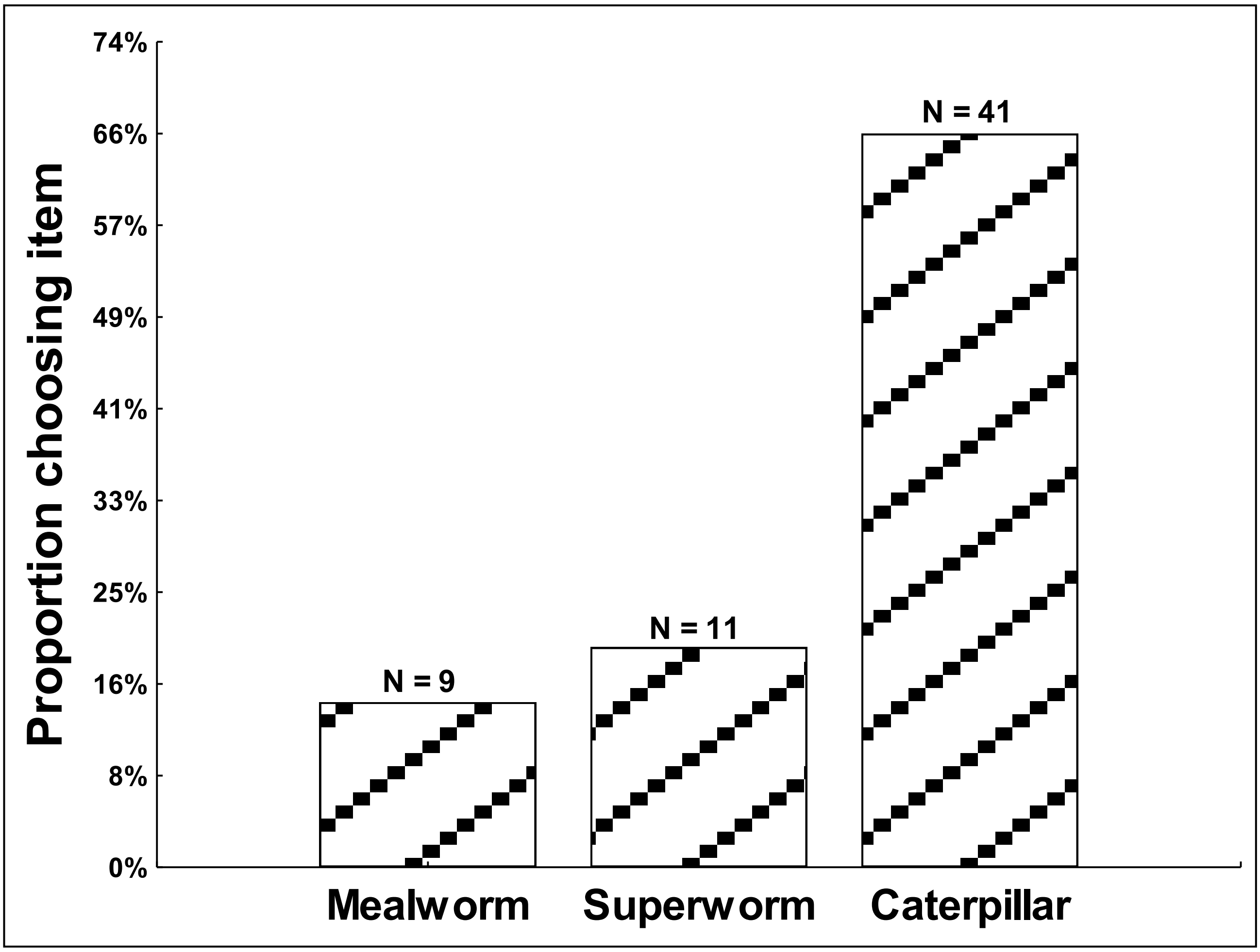

A) Young males
Proportion choosing item
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
N = 4
N = 6
Spider
Caterpillar
B) Adult males
Proportion choosing item
104%
87%
70%
52%
35%
17%
0%
N = 18
N = 5
Spider
Caterpillar
C) Young females
Proportion choosing item
100%
83%
67%
50%
33%
17%
0%
N = 12
Spider
D) Adult females
Proportion choosing item
100%
88%
75%
63%
50%
38%
25%
13%
0%
N = 9
N = 7
Spider
Caterpillar

Fig. 3


Proportion choosing item
74%
66%
57%
49%
41%
33%
25%
16%
8%
0%
N = 9
N = 11
N = 41
Mealworm
Superworm
Caterpillar

Capítulo 5

Pagani-Núñez, E., Valls, M. & Senar, J. C. 2014. Individual diet specialization in a generalist population: the case of breeding Great tits *Parus major* in the Mediterranean area. Submitted.

Individual diet specialization in a generalist population: the case of breeding great tits *Parus major* in the Mediterranean area

E. Pagani-Núñez*, M. Valls & J. C. Senar

Evolutionary Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, Spain

* Corresponding author: emipanu@gmail.com

Abstract

For the majority of vertebrates, it remains unclear whether different species should be considered trophic generalists or specialists. To determine parental foraging behaviour within a population, it is necessary to study two aspects: the degree of behavioural consistency under different conditions in the short term, and the level of diet specialization showed by different breeding pairs with respect to the population mean. We investigated both aspects in a generalist species, a breeding population of Mediterranean great tits *Parus major.* Our aim was to determine whether they were specialists or generalists at the individual level. We experimentally manipulated brood size, and we also analysed niche overlap of pairs using the proportional similarity index and the mean pairwise overlap. We found that parents showed great short-term consistency. They precisely adjusted the number of provisioning trips to the number of nestlings, but they were unable to modify prey proportions or prey size after brood size was changed. We can therefore characterize their foraging strategies as highly consistent. Parents also showed great variability in prey choice between territories, that is, they displayed a low niche overlap. Interestingly, the most specialized breeding pairs showed a tendency to have larger broods and delivered fewer caterpillars to their nestlings. Our results suggest that although the great tit may be considered a generalist at the species or population level, many breeding individuals within our study population behaved as specialists. This high inter- and intra-population plasticity could account for their great success and wide distribution.

Keywords: foraging behaviour, niche overlap, niche partitioning, prey choice, provisioning rates.

Introduction

Studying the foraging behaviour of breeding animals provides key knowledge on the breeding ecology of species (Stephens et al. 2007). At the species level, parents may display a great variety of foraging strategies when rearing their offspring that result in divergent patterns in relation to energy investment and prey choice (Drent and Daan 1980). In the case of passerine birds, great heterogeneity has been recorded in relation to the time consistency of provisioning rates. Some studies have found that provisioning rates were constant (Barba et al. 2009) or decreased over time (García-Navas and Sanz 2012). Other studies, however, have found that provisioning rates showed a peak after dawn (Pagani-Núñez and Senar 2013), at dusk (Olsson et al. 2000) or at dawn and dusk (Knapton 1984). These patterns were usually attributed to prey availability or dynamics (see also Royama (1966), Nur (1984), Grundel (1987), Conrad and Robertson (1993), or Goodbred and Holmes (1996)).

A consistent approach to precisely assess parental investment may be based on brood size manipulation experiments. Many studies have focused on parental responses to changes in brood size (and/or begging intensity) and their consequences for nestlings’ body condition. Most such works relied on provisioning rates to evaluate parental effort (Smith et al. 1988, Saino et al. 1997, Verhulst and Tinbergen 1997, Kölliker et al. 2000, Tinbergen and Verhulst 2000, Nilsson 2002, Ardia 2007) and did not consider prey choice made by parents. Studies considering prey quality reported almost constant provisioning-rates per nestling and prey size irrespective of brood size manipulation (Neuenschwander et al. 2003), a trade-off between provisioning-rates per brood and prey size (Stoehr et al. 2001, García-Navas and Sanz 2010), or changes in the quality of the food delivered to nestlings by fathers but not by mothers (Siikamäki et al. (1998), but see also Wright and Cuthill (1990)). This high variability in parental responses within and among populations and species suggests that there are multiple ecological contexts in which different strategies may be regarded as the most optimal.

Breeding passerines use a great variety of prey as food sources (e.g. Barba and Gil-Delgado (1990), Grundel (1990), Blondel et al. (1991), Bańbura et al. (1994), Gilroy et al. (2009), Maziarz and Wesołowski (2010)). However, in most cases, it remains unclear whether parents may be considered as generalists, or whether different pairs specialize in different prey types within this great range of variation (Estes et al. 2003, Bolnick et al. 2003, Woo et al. 2008, Newsome et al. 2009). In the Mediterranean area, bird populations rely more often on alternative prey than populations of the same species inhabiting northern latitudes, because prey diversity is higher in the Mediterranean but densities are lower (Bańbura et al. 1994, Blondel et al. 2010). In the case of the great tit *Parus major,* we recently reported the great consistency of parental effort and prey choice across time in a population inhabiting a Mediterranean mixed forest (Pagani-Núñez and Senar 2013) and consuming a great variety of prey (Pagani-Núñez et al. 2011, Pagani-Núñez and Senar 2014). Thus, to precisely assess the plasticity of parental foraging behaviour both in relation to their absolute effort (provisioning rates per brood and per nestling) and their capacity to find quality food (prey proportions and mean prey size), we performed a experiment modifying brood size. We also investigated individual diet specialization within our generalist population by means of the proportional similarity index and the mean pairwise overlap (see Bolnick et al. (2002) and (2003)).

In this study, our main objective was to assess provisioning rate and food choice consistency in a brood size manipulation experiment with great tits. We hypothesized that, regardless of prey availability, parents with a generalist feeding strategy should respond to brood size manipulation by adapting prey proportions to an increase or a decrease in their rates of work. In reduced broods we could expect an increase in provisioning rates and/or in the delivery of high quality prey such as caterpillars and spiders, while in increased broods we could expect a contrary response. Conversely, if parents could be considered specialists they should not respond to our experimental manipulation in relation to prey quality. Additionally, we estimated individual diet specialization with respect to the population mean diet to correctly contextualize their behaviour.

Material and methods

- Fieldwork and diet recording

During the spring of 2012, we monitored 182 nest-boxes at Can Catà field station (45°27’N, 2°8’E; Catalonia, northeast Spain), a predominantly evergreen mixed forest. Nest boxes were checked twice weekly to determine laying and hatching dates and brood size. This forest surrounding the nest-boxes has a strong and concordant gradient of variation in relation to predominant tree types (the proportion of oaks (*Quercus spp.*) ranges 5-95%) and height above sea level (from 82 to 219 m.a.s.l.; see also Pagani-Núñez *et al.* (2011) and (2014a)). The main tree species are pine (*Pinus halepensis*), holm oak (*Quercus ilex*) and oak (*Quercus cerrioides*). Nestling diet was recorded by means of Micro-D cameras attached to the covers of the nest-boxes and focused on the entrance (see Pagani-Núñez and Senar (2014) for more details on camera properties and filming procedures). We filmed 48 hours in each nest when nestling age was 10-14 days (Pagani-Núñez and Senar 2013). Cameras were installed and camouflaged the day before recordings to minimize the impact of installing the device. Recordings were made over five hours each day, from 7 a.m. to 12 a.m.. We used full clock hours to standardize for inter-individual differences in the time at which recording began. The sex of parents was easily identified from recordings. In addition, most individuals had been previously marked with numbered PVC rings. We determined prey type and size for each feeding action of each parent within this window of time. Prey were classified as caterpillars, spiders, or “others”. Prey size was determined according to a semi-quantitative scale with three values: 1 = small, 2 = medium or 3 = large (Barba et al. 1996). In this work we refer to brood size as the number of nestlings in a nest at the moment of recording.

- Brood size manipulation experiment

We performed a brood size manipulation experiment in 19 nests when nestlings were 10-14 days old. Our sample consisted of 38 parents and 98 nestlings (a mean of 5.2 nestlings per nest), 20 of which were moved between nests to experimentally modify brood size. We used pairs of nests with the closest hatching dates (up to two days) and the closest brood size. We randomly selected and moved two nestlings from one nest to the other for 24 h, so we obtained a simultaneous experimental increase and decrease of brood size in two complementary nests (“reduced” = -2 or “increased” = +2). The experiment was restricted to two nestlings to keep brood size within the natural range of variation for this species (Orell et al. 1996). If nests did not have the same brood size we reduced the larger nest and increased the smaller nest of the experimental pair. Moreover, we performed the experiment alternatively on the first or the second day. Thus, we controlled each pair by its own “normal” feeding behaviour. After the recording, we placed both nestlings back in their nests. Provisioning rates per hour and provisioning rates per nestling, prey proportions and mean prey size were determined for each individual. Prey proportions were approximated to normality by means of the arcsine-square-root function.

To analyse parental responses to our experiment we used a repeated measures analysis of variance approach. The provisioning rate per brood was the dependent variable, the experimental group (experiment: “reduced” or “increased”) was the within-subject factor, and sex (male or female) was the between-subject factor. We did the same successively using provisioning rates per nestling, the proportion of caterpillars, spiders and “others”, and prey size as dependent variables.

- Diet overlap and trophic specialization

To adequately frame parental behaviour in a population context we assessed between-pair trophic specialization in relation to population niche breadth by means of the proportional similarity index (PSi) and the mean pairwise overlap. Both parameters were obtained through IndSpec (Bolnick et al. 2002). These indexes provide information on the use of trophic resources by individuals properly framed in the context of a concrete population. These scores range from 0 to 1, where the maximum value represents the individuals' diet being proportional to population mean values, while lower scores represent the individuals specializing with respect to the population mean. To perform this analysis we used nestlings' diet proportions from control days (five hour of recordings from 7 a.m., see Pagani-Núñez and Senar (2013)), which represented normal conditions for parents. We used mean values for each pair instead of individual data because our aim was to assess diet overlap between territories (that is, pairs or nests). In addition, we standardized prey proportions by mean prey size of each kind of prey in each nest (following Barba et al. (1996) as previously described): we multiplied mean prey size by the number of prey items and calculated new percentages on this basis. We divided prey in fourteen classes: caterpillars (*Lepidoptera larvae*), spiders (*Araneae*), spider eggs, fruits, grasshoppers (*Orthoptera*), stick-insects (*Fasmidae*), moths and butterflies (*Lepidoptera* adults), chrysalis (*Lepidoptera pupae*), mosquitoes (*Diptera*), bees and flying ants (*Hymenoptera*), "other" *larvae*, beetles (*Coleoptera*), unidentified arthropods, and formless remains. Sample size for these analyses involved a total of 62 parents from 31 nests. We included several nests that were conversely excluded for the brood size manipulation due to time and experiment-derived constraints.

We used a multiple linear regression approach to assess the relationships between PSi scores and several related variables. We applied backward stepwise procedures until only significant interactions remained. The dependent variable was PSi scores and independent variables were the number of prey types in nestling diet, brood size (number of nestlings during recording of control days), date (number of days from 1st April), the proportion of *Quercus spp* surrounding nest boxes (to control for habitat quality, see Pagani-Núñez and Senar (2014)), provisioning rates per nestling and mean prey size.

Finally, in order to investigate what prey types were captured together more often, we used a principal components and classification analysis (PCCA). Using a batch of variables, PCCA computes a principal component analysis, and then, graphically shows how these variables are inter-related. This approach was a reliable means to understand how and why parents combine several food sources. We used the numbers of each prey type in each nest as variables for analysis, but we excluded the four least common prey types (*Himenoptera*, *Diptera*, chrysalis and unidentified insects, each one representing around 1% of nestling diet) to increase the statistical power of the PCCA.

Results

Our repeated measures approach showed that parents precisely adjusted their provisioning rates per brood to actual brood size after manipulating the number of nestlings present in the nest (Table 1, Fig. 1). Experimental groups did not differ a priori in provisioning rates. Neither sex nor their interactions showed any effect on provisioning rates per brood. Additionally, we did not find any significant effect of any factor on provisioning rates per nestling (Table 1). The proportion of caterpillars differed between experimental groups prior to experimental procedures (Table 2). We did not find any other significant effect of sex, the experiment or their interactions on the proportion of caterpillars delivered by parents. Females delivered more spiders than males (Table 2), but the proportion of spiders did not show any other significant interaction. The proportion of “others” showed a similar pattern to the proportion of caterpillars, differing between experimental groups prior to the experimental procedures (Table 2). We did not find any other significant effect for “others”. Finally, mean prey size did not show any significant interaction (Table 2).

Caterpillars were the main prey type, representing half of the total food. Spiders were the second type in importance (around 15%), and the remaining prey types ranged from 1% to 5%. However, nestling diet was extremely variable among territories. For instance, caterpillars ranged from 5% to 95% and not all prey types were present in all nests (see Appendix A1). That is, different pairs selected different combinations of prey types. The similarity index score (SI, population mean of PSi) was 0.72, with PSi scores for each pair ranging from 0.53 to 0.84 (Fig. 2). Mean pairwise overlap was 0.63. We found that pairs displaying a pattern of prey choice most similar to the population mean delivered a higher proportion of caterpillars, but there was no significant interaction with the proportion of spiders, the most relevant prey types within our study population (Fig. 3). This means that more generalist pairs delivered more caterpillars. PSi scores showed a marginally significant negative correlation with brood size (r = -0.33, p = 0.07; Fig. 4), suggesting that breeding pairs with more specialized diets compared with the whole population more frequently had higher brood sizes. The number of prey types, date, the proportion of *Quercus spp* surrounding nest boxes, provisioning rates per nestling and mean prey size did not correlate with PSi scores (Table 3).

The principal component and classification analysis explained 50.73% of the variation in nestling diet (Component axis 1: 27.55%, Component axis 2: 23.17%; Fig. 5). The first component had positive weighting for all prey types. Only stick-insects showed no interaction, and moths and butterflies showed a negative interaction with the other prey. The second component had positive weighting for caterpillars, fruits, and "other” *larvae*, no interaction for spiders and their eggs, and negative weighting for grasshoppers, stick-insects, moths and butterflies, beetles, and formless remains. Thus, there were three main assemblages among prey types, although two of them, stick-insects and moths and butterflies, could be segregated in a fourth group (Fig. 5). Parents showed the tendency to select food sources with similar characteristics. For instance, they delivered together easy taking food items such as caterpillars, fruits and "other" *larvae.* They also combined spiders and their eggs. Additionally, we found that those pairs delivering more items from the first group (caterpillars, "other" *larvae* and fruits), included more prey types in the nestling diet (Fig. 6).

Discussion

- Framing individuals’ foraging behaviour in a population context

Assessing individual trophic niches provides clues of great interest to disentangle trophic webs either at the species or community level (Hespenheide 1971, Cody 1974, Alatalo 1982, Díaz et al. 1998, Newsome et al. 2009, Atiénzar et al. 2013). Previous studies have highlighted that inter-individual variation in foraging strategies may also have great relevance for population dynamics (May and Mac Arthur 1972, Bolnick et al. 2003, Estes et al. 2003, Bolnick et al. 2011). In this work we found that great tit parents, irrespectively of their sex, rapidly modified their behaviour to adjust the number of feeding actions to the number of nestlings in their nest after experimental manipulation of brood size. In other words, they showed an equitable strategy when feeding their offspring. This result is coherent with previous findings (Neuenschwander et al. 2003). However, and in spite of the great variability in prey choice made by parents within this population, breeding pairs did not modify prey proportions in function of the new rate of work. That is, they showed great short-term consistency (Pagani-Núñez and Senar 2013). We also found that the high niche breadth at the population level was composed of multiple, narrower niches of different pairs (Bolnick et al. 2003, Newsome et al. 2009). PSi scores did not correlate with the number of prey types in nestling diet. Therefore, rather than selecting many different prey types, the main cause of the low between-pair similarity we recorded is that parents relied on alternative (and complementary) combinations of prey items with respect to the population mean. This heterogeneous trophic structure fits the diverse but not particularly abundant prey distribution characteristic of the Mediterranean area (Blondel et al. 2010). In line with our findings, previous research reported a trade-off between prey availability and trophic divergence among breeding pairs within a given population (Lewis et al. 2001, Villegas-Amtmann et al. 2013). Thus, our results suggest that the high consistency in their trophic preferences was a means to avoid intra-population niche overlap (Grémillet et al. 2004, Tinker et al. 2008). Consequently, we think that Mediterranean great tit parents may be considered as specialists from this perspective, or more concretely, that in the Mediterranean area, the great tit behaves as a generalist species composed of specialist individuals, a finding observed in several species (Estes et al. 2003, Woo et al. 2008, Vander Zanden et al. 2010, Matich et al. 2011, Polidori et al. 2011, Quiroga et al. 2011).

- Framing Mediterranean Great tits' foraging behaviour in a continental scale

It is commonly assumed that great tits (and their close relatives' blue tits (*Cyanistes caeruleus*)) adjust their time of breeding to the peak availability of caterpillars, their preferred prey (Naef-Daenzer et al. 2000, Tremblay et al. 2003, Blondel 2007, Eeva et al. 2009). Several papers have reported a strong date-related pattern of variation in prey choice and breeding fitness related to the high seasonality of peak abundance of caterpillars (Wilkin et al. (2009), García-Navas and Sanz (2011); but see Pagani-Núñez and Senar (2014)). In keeping with this observation, it has been suggested that northern mid-boreal great tits are constrained by their decisions when breeding, more appropriate to Central and Western Europe (Sanz 1998, Rytkonen and Orell 2001). The main argument used to support this view is that they are excessively dependent on caterpillars, which are scarce in coniferous mid-boreal forests, and are unable to find profitable alternative prey (Rytkonen and Krams 2003). Nevertheless, mixed forests within the Mediterranean area may be considered hotspots of biodiversity that provide multiple ecosystem functions (Pasari et al. 2013). For example, at a continental scale, spider species richness increases southwards, a trend also found in several other animal groups, along with plant species richness (Finch et al. 2008). We think, in consequence, that in Mediterranean mixed forests, where there is generally a great diversity of arthropods and fruits, great tit parents may be able to partly avoid those constraints that limit their fitness in northern Europe. In this regard, we can not consider great tits simply as caterpillar specialists. Individual specialization in this prey type (considering also caterpillar availability) is dependent on the capacity to exploit alternative and suitable prey, such as spiders (Pagani-Núñez and Senar 2014). This ability is especially determinant to maintain reproductive success over a reasonable threshold in evergreen forests within the Mediterranean area (Blondel et al. 1991, Bańbura et al. 1994, Ziane et al. 2006, Pagani-Nuñez et al. 2011). It is of note that great tits (and also blue tits) show a highly plastic foraging behaviour among populations and individuals that is learned in the first stages of their life (Slagsvold and Wiebe 2011). Therefore, the capacity to exploit alternative food sources to caterpillars is not innate to this species and individuals have to learn successful hunting skills. We have previously shown that in our study area more ornamented fathers delivered more spiders than less ornamented fathers, and that nestlings receiving a higher proportion of spiders had a better body condition (Pagani-Núñez and Senar 2014) and a brighter colour (Pagani-Núñez et al. 2014a). In the present work we have also shown that more specialized parents with respect to the population mean showed a tendency to raise higher brood sizes. These parents delivered the lowest proportion of caterpillars. Our findings therefore strongly suggest that Mediterranean great tits evolved to maximize their fitness on the basis of the exploitation of multiple food sources.

- On the relativity of the concept of foraging specialization

Previous works reported contrasting results when evaluating fitness between and within high and low quality habitats and in function of latitude (Sanz 1998, Tremblay et al. 2003, Mägi et al. 2009, Atiénzar et al. 2010). This pattern is probably due to the fact that parents compensate for these extrinsic factors that constrain their reproductive success and fix their foraging strategy in function of the moment of the season, prey availability, and brood size. Moreover, given the high short-term consistency of parental trophic preferences, the selection of a determined strategy should have a strong impact on their performance. We consider, in consequence, that parental foraging strategies should be assessed with caution when linking habitat quality, parental investment, and fitness. For instance, a generalist or specialist strategy may be regarded as the most optimal under different circumstances. That is, individual foraging behaviour should be placed in context with respect to the whole population. This notion is especially relevant when individuals can select prey from among several optimal options that maximize their success (Bolnick et al. 2003, Raubenheimer 2011), because being either generalist or specialist is not necessarily based on the quantity of prey types. In this particular case, it is generally assumed that breeding great tits are caterpillar specialists (Naef-Daenzer et al. (2000), Tremblay et al. (2003), Blondel (2007), Eeva et al. (2009); but see Pagani-Núñez et al. (2011), Pagani-Núñez and Senar (2014), and Pagani-Núñez et al. (2014b)). Interestingly, in our study population the highest proportion of caterpillars was delivered by the most generalist pairs. Parents showed the tendency to specialize on certain combinations of prey types which they considered could maximize their fitness. To successfully exploit all alternative trophic resources available in the environment it therefore seems highly relevant to maintain a stable equilibrium at the population level (Tinker et al. (2009), Křivan (2010); but see Blondel (2007)). Accordingly, the best option was to specialize in several prey types and optimally exploit them according to the ability of individuals and to arthropod availability, rather than specializing in only one prey type. This finding stresses the relevance of considering the effect of the combination of several food sources on fitness (Raubenheimer (2011); see Fig. 6). Those pairs that combined prey proportions in the most efficient manner and that contrasted more with the whole population had more nestlings. The great diversity of nestling diet connects therefore with the great diversity of arthropod species in our area. Consequently, the heterogeneous and diverse life-histories displayed by Mediterranean birds should not be regarded simply as suboptimal contexts compared to populations inhabiting deciduous forests of Central Europe.

- Conclusions

In summary, we found that great tit parents displayed a heterogeneous trophic structure that fits the diverse but scarce prey distribution in our area. Our results indicate that the high consistency reported in their preferences was a means to avoid intra-population niche overlap. Niche partitioning operated as an efficient mechanism of trophic segregation, shaping the trophic structure of our study population. From a general perspective, great tits showed a generalist foraging behaviour that varied largely among individuals and populations. Conversely, most individuals behaved as specialists, and we found that the most specialized individuals showed a tendency to have more nestlings when compared to the whole population. This high behavioural plasticity is probably one of the reasons for their great success in colonizing Europe and Asia (Kvist et al. 2007). In future research it would be interesting to perform an inter-specific comparison on the use of the total population niche between great tits and related species breeding in the same area under different specific constraints. It would also be useful to investigate the effect of aging on parental foraging strategies, and to assess individual repeatability of trophic niches between years in different environmental conditions.

Acknowledgements

We thank Sergio Hernández-Gómez for his help in the field and Jaime Resano-Mayor for his advice to improve an earlier version of the manuscript. We also thank Carolyn Newey for editing a version of the English, Llüisa Arroyo her help in the lab, and the Gil family, owners of Can Catà, for allowing us to work on their property. This study was funded by CGL-2012-38262 research project to J.C.S. and by the FPI grant BES2010-040359 to E.P.N., from the Ministry of Science and Innovation, Spanish Research Council. Birds were handled with the permission of the Departament de Medi Ambient, Generalitat de Catalunya. Rings were provided by the Catalan Ringing Office (ICO).

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Table 1. Repeated measures analysis of variance using provisioning rates per brood of 19 pairs of great tit *Parus major* parents as the dependent variable, the experimental group (experiment: “reduced” or “increased”) as the within-subject factor , and sex (male or female) as the between-subject factor. We did the same using provisioning rates per nestling as the dependent variable. Significant interactions are highlighted in bold.

Provisioning rates per brood

	$F_{1,34}$	P
Sex	1.77	0.19
Experimental group	2.01	0.17
Provisioning rates per brood	0.49	0.49
Sex*Experiment	0.12	0.73
Provisioning rates per brood * Sex	0.01	0.91
Provisioning rates per brood * Experiment	**17.54**	**< 0.01**
Provisioning rates per brood * Sex * Experiment	0.09	0.76

Provisioning rates per nestling

	$F_{1,34}$	P
Sex	1.74	0.20
Experimental group	0.07	0.79
Provisioning rates per nestling	0.59	0.45
Sex*Experiment	< 0.01	0.95
Provisioning rates per nestling * Sex	0.17	0.68
Provisioning rates per nestling * Experiment	0.53	0.47
Provisioning rates per nestling * Sex*Experiment	1.38	0.25

Table 2. Repeated measures analysis of variance using the proportion of caterpillars delivered by 19 pairs of great tit *Parus major* parents to their nestlings as the dependent variable, the experimental group (experiment: “reduced” or “increased”) as the within-subject factor, and sex (male or female) as the between-subject factor. We did the same using the proportion of spiders, the proportion of others, and mean prey size as dependent variables. Significant interactions are highlighted in bold.

% Caterpillars		
	$F_{1,34}$	P
Sex	1.82	0.19
Experimental group	**4.67**	**0.04**
% Caterpillars	0.02	0.90
Sex * Experiment	0.01	0.94
% Caterpillars * Sex	0.55	0.46
% Caterpillars * Experiment	0.06	0.81
% Caterpillars * Sex * Experiment	0.07	0.80
% Spiders		
	$F_{1,34}$	P
Sex	**8.19**	**0.01**
Experimental group	0.17	0.68
% Spiders	0.07	0.80
Sex * Experiment	0.56	0.46
% Spiders * Sex	0.25	0.62
% Spiders * Experiment	0.82	0.37

% Spiders * Sex * Experiment	0.03	0.86
% Others		
	$F_{1,34}$	P
Sex	< 0.01	0.99
Experimental group	**5.36**	**0.03**
% Others	0.01	0.94
Sex * Experiment	0.01	0.92
% Others * Sex	1.31	0.26
% Others * Experiment	2.06	0.16
% Others * Sex * Experiment	0.10	0.75
Mean prey size		
	$F_{1,34}$	P
Sex	0.05	0.82
Experimental group	2.53	0.12
Prey size	0.45	0.51
Sex * Experiment	2.75	0.11
Prey size * Sex	1.52	0.23
Prey size * Experiment	1.47	0.23
Prey size * Sex * Experiment	0.18	0.68

Table 3. Multiple linear regression using proportional similarity index scores (PSi) of 31 breeding pairs of great tits *Parus major* as the dependent variable, and brood size, the number of prey types in nestling diet, provisioning rates per nestling, mean prey size, date (to control for phenology, measured as the number of days from 1st April), and the proportion of *Quercus spp* surrounding nest-boxes (to control for habitat quality) as independent variables. We used backward stepwise procedures until only significant variables remained ($P < 0.10$). $R^2 = 0.11$; $F_{1,29} = 3.46$; $P < 0.07$.

Variables in the model			
	t_{29}	Partial correl.	P
Brood size	-1.86	-0.33	0.07
Variables out of the model			
	t_{28}	Partial correl.	P
Number of prey types	0.04	0.01	0.97
Provisioning rates per nestling	0.16	0.03	0.88
Mean prey size	-0.14	-0.03	0.89
Date	-0.15	-0.03	0.88
% *Quercus spp*	0.97	0.18	0.34

Figure legends

Fig 1 Changes in provisioning rates per brood in natural conditions and after the experimental procedure of increasing or decreasing the number of nestlings in the nest of 19 pairs of Mediterranean great tit *Parus major*. Filled circles correspond to reduced broods, while empty squares correspond to increased broods.

Fig 2 Histogram showing the distribution of proportional similarity index scores within our study population. Data correspond to 31 pairs of Mediterranean great tits *Parus major* and are based on natural brood sizes.

Fig 3 Relationships among the proportion of caterpillars (right y-axis) and spiders (left y-axis) delivered to nestlings by 31 Mediterranean great tit *Parus major* pairs in natural conditions, and their proportional similarity index scores (x-axis).

Fig 4 Relationships between proportional similarity index scores (y-axis) and natural brood size (x-axis) at the moment of recordings of 31 pairs of great tit *Parus major*.

Fig 5 Relationships among the ten most important prey types delivered to nestlings by 31 Mediterranean great tit *Parus major* pairs in natural conditions based on principal components and classification analysis. Cat = caterpillars, Fru = fruits, Lar = “other” *larvae*, Spi = spiders, Egg = spider eggs, Ort =

grassopphers, Col = beetles, Pha = stick-insects, M&B = moths and butterflies and Rem = formless remains.

Fig 6 Equilateral mixture triangle with a quadratic fit type based on prey proportions of the three main assemblages among prey types in function of the number of prey types in the nestling diet (see Fig. 5; Cat/Lar/Fru: caterpillars, “other” *larvae* and fruits, Spi/Egg: spiders and their eggs, Others: the rest of prey types). Black colours represent eight prey types or more, dark grey seven types, pale grey six types, and white colours five or less prey types.

Fig 1

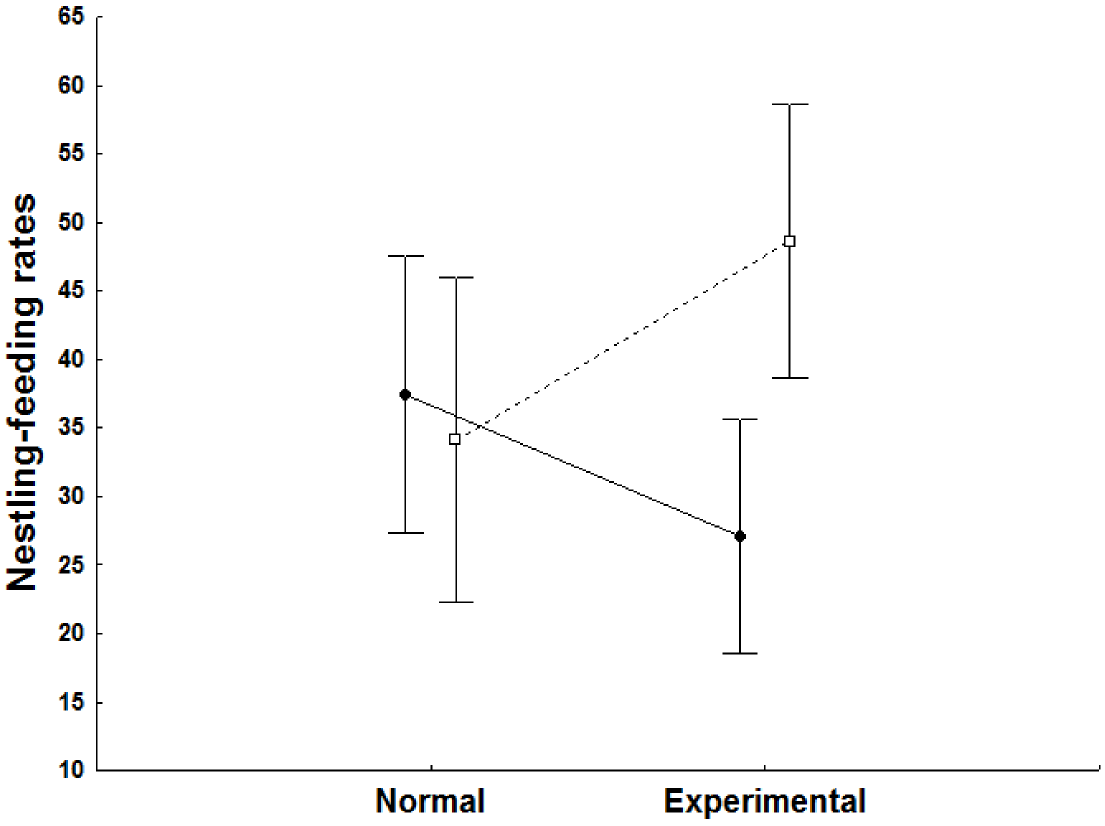

65
60
55
50
45
40
35
30
25
20
15
10
Nestling-feeding rates
Normal
Experimental

Fig 2

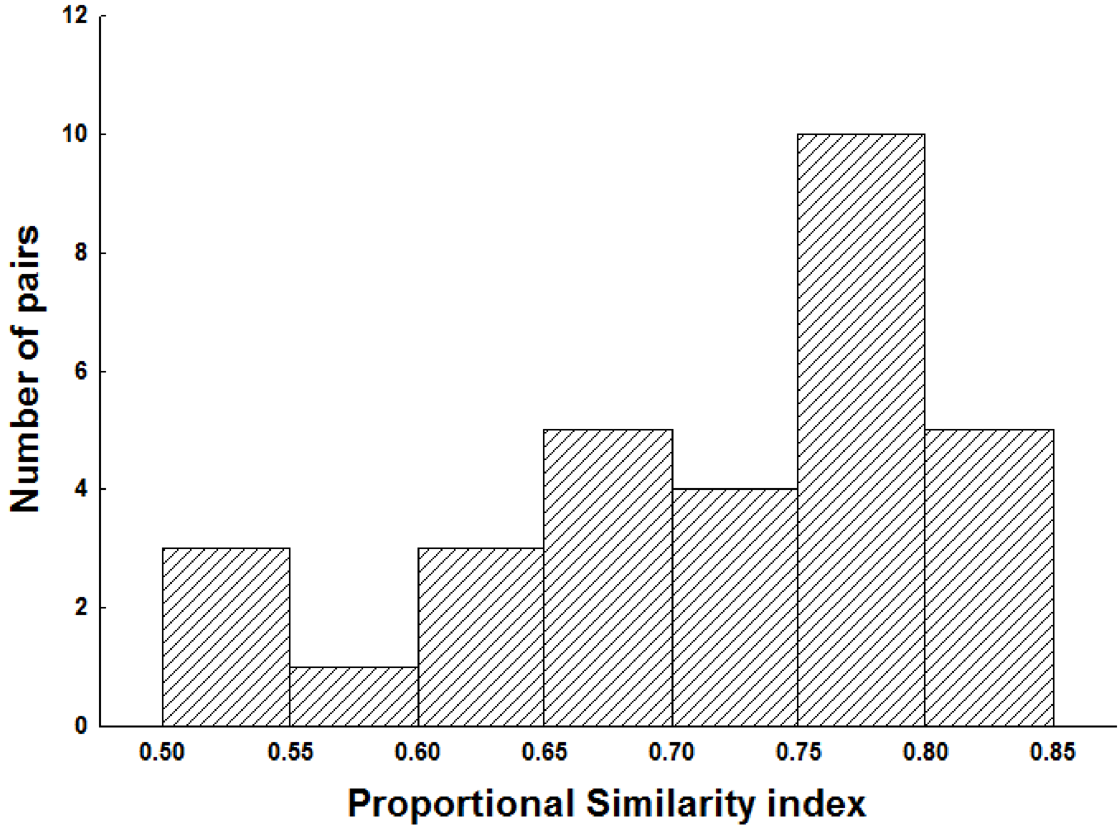

12
10
8
6
4
2
0
Number of pairs
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
Proportional Similarity index

Fig 3

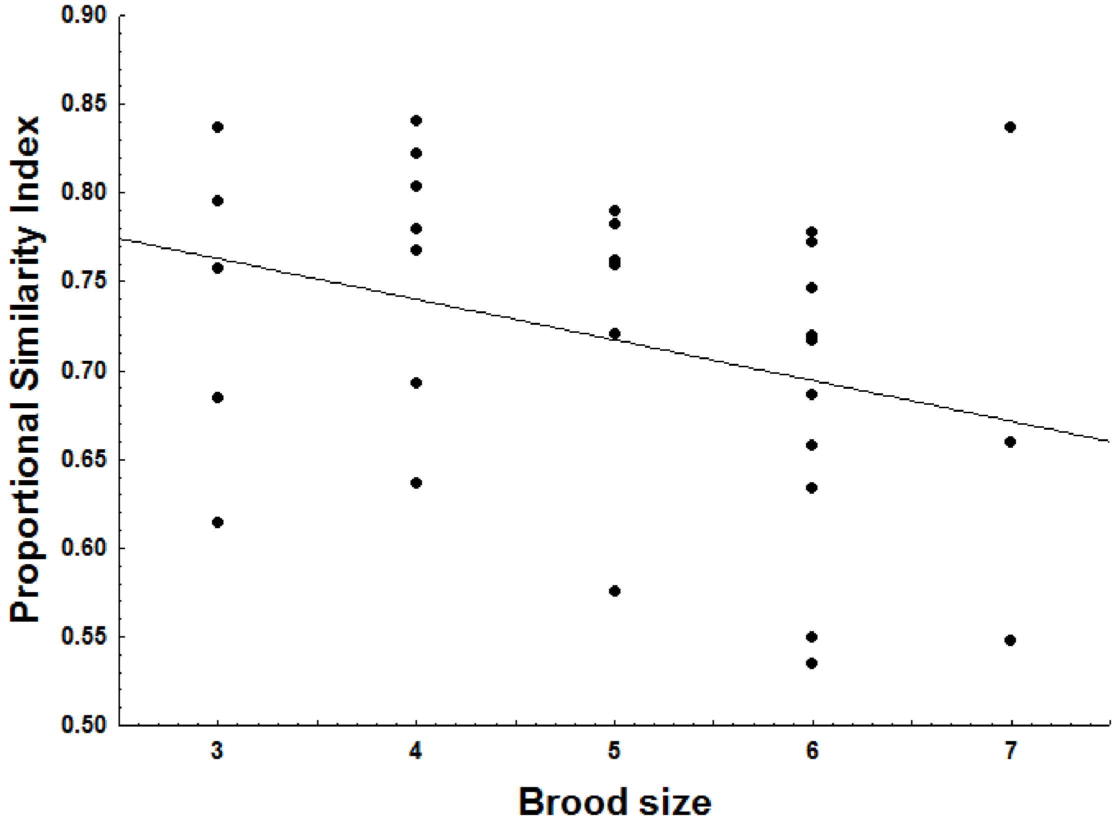

Proportional Similarity Index
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
3
4
5
6
7
Brood size

Fig 4

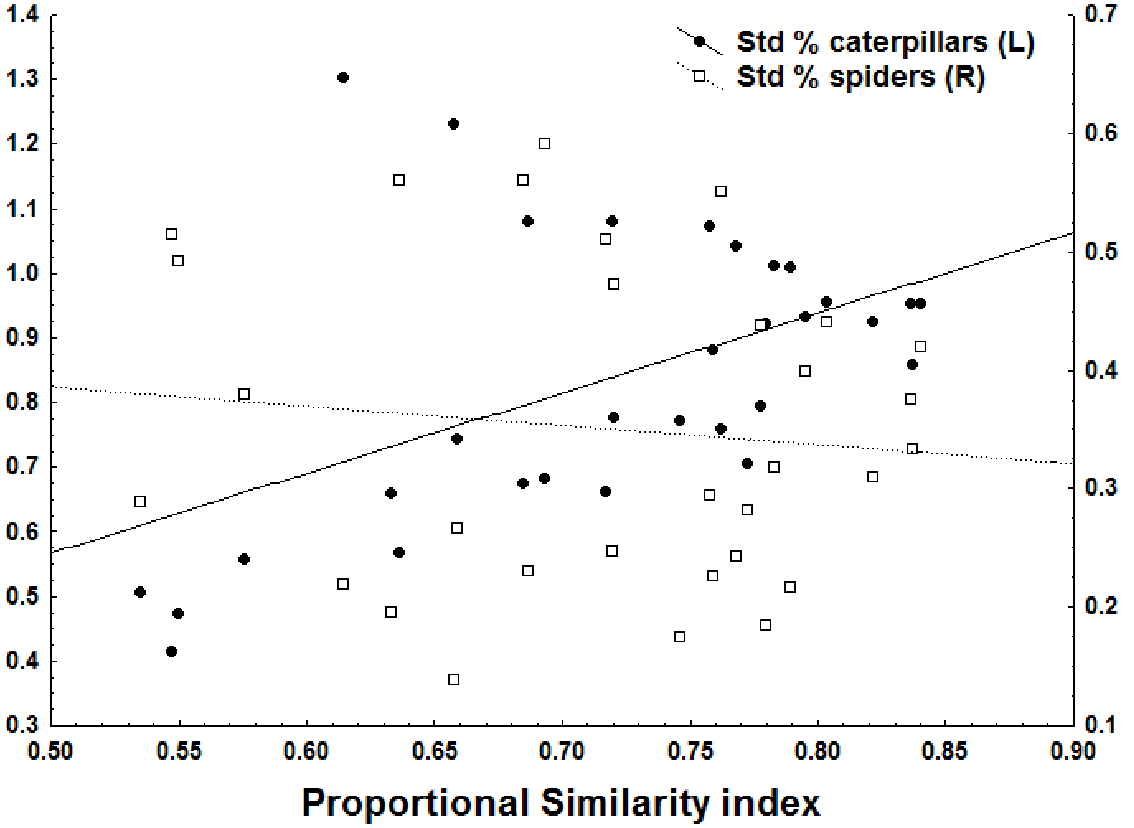

1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
0.90
Std % caterpillars (L)
Std % spiders (R)
Proportional Similarity index

Fig 5

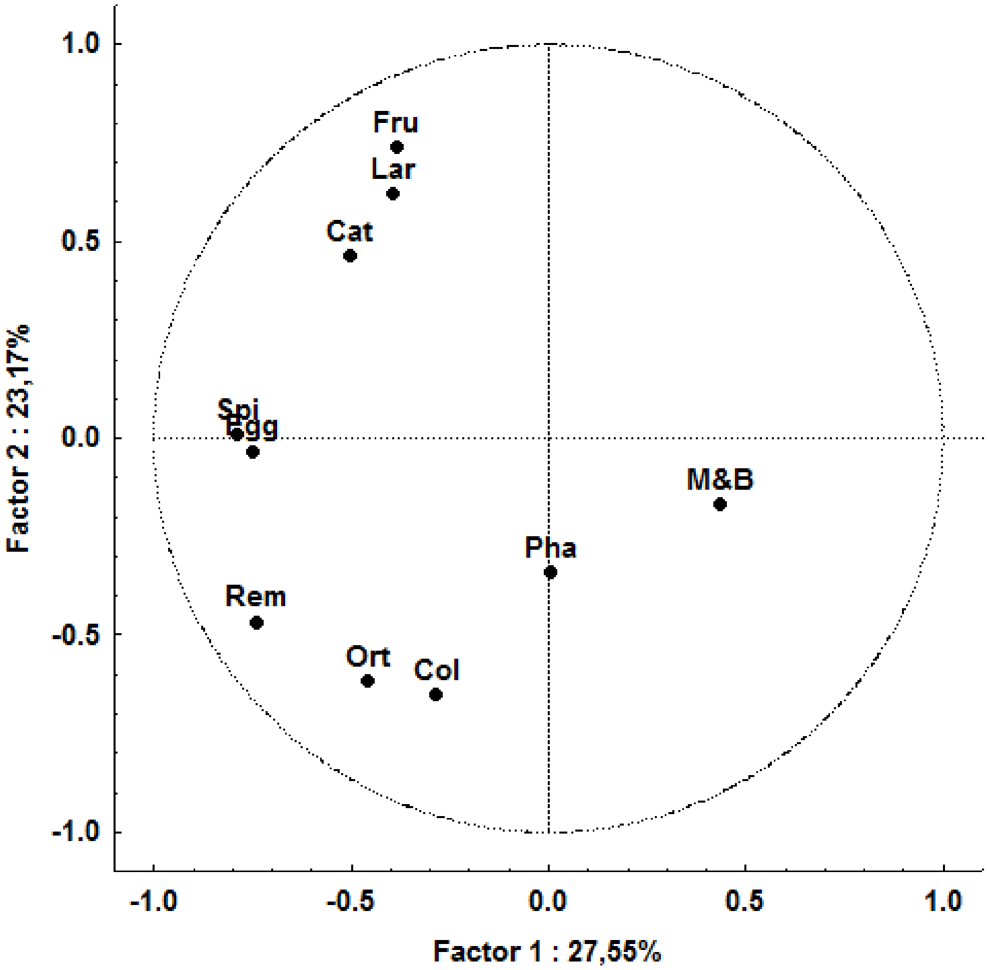
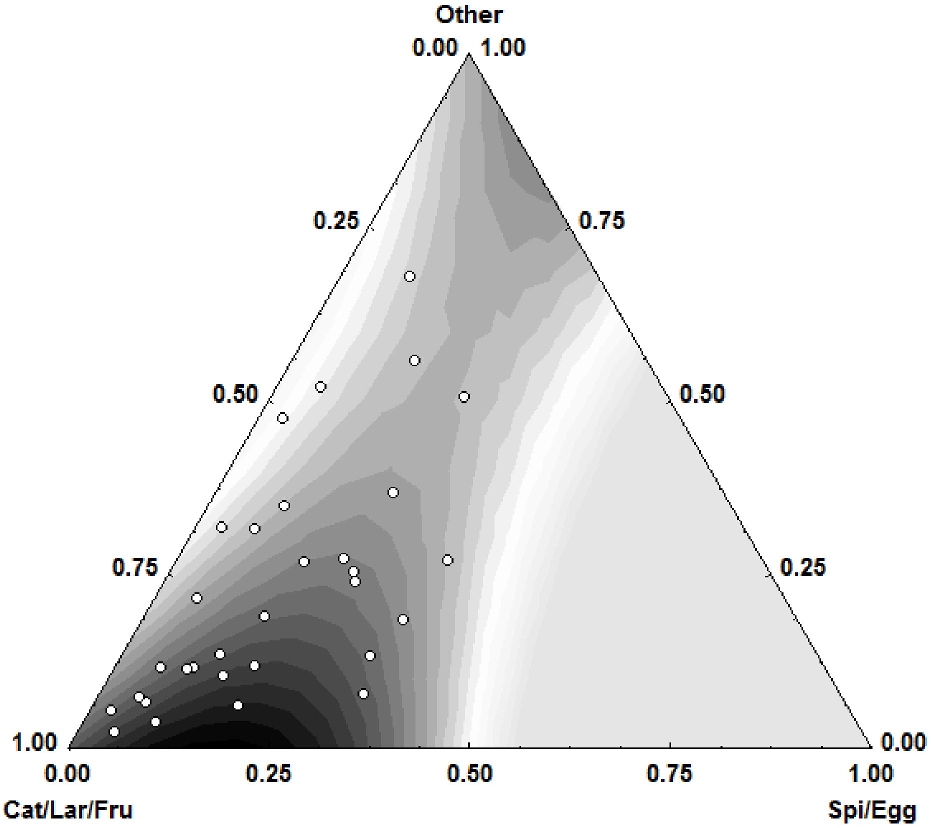

1.0
0.5
0.0
-0.5
-1.0
Factor 2 : 23,17%
-1.0
-0.5
0.0
0.5
1.0
Factor 1 : 27,55%
Fru
Lar
Cat
Spi
Egg
M&B
Pha
Rem
Ort
Col

Fig 6

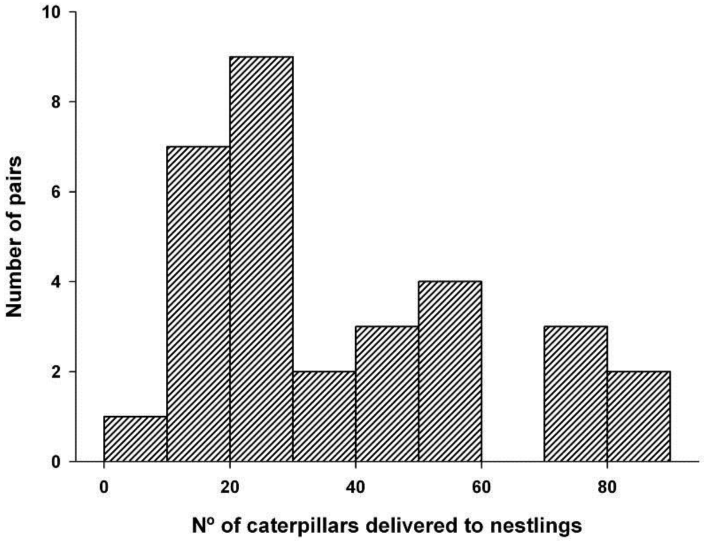

Other
0.00
1.00
0.25
0.75
0.50
0.50
0.75
0.25
1.00
0.00
0.00
0.25
0.50
0.75
1.00
Cat/Lar/Fru
Spi/Egg

624

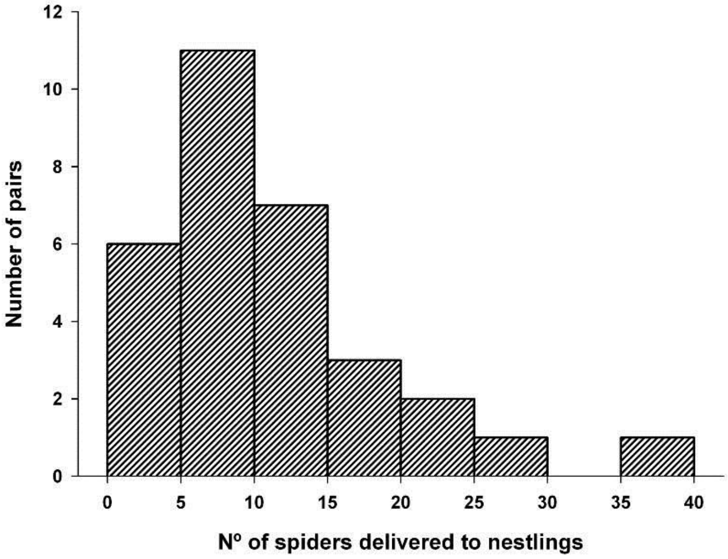
Appendix A1

Histograms based on the distribution of frequencies of several prey types in the nestling diet (caterpillars, spiders, fruits and grasshoppers). They show that some pairs relied strongly on certain prey items (that is, they specialized in this prey type). For instance, some pairs delivered up to 90 caterpillars or 40 spiders to their nestlings within five hours.

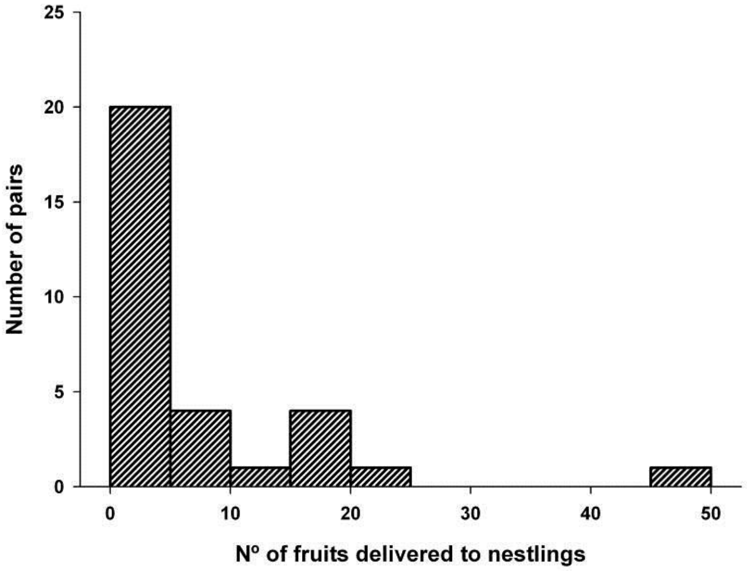
- Nº of caterpillars:



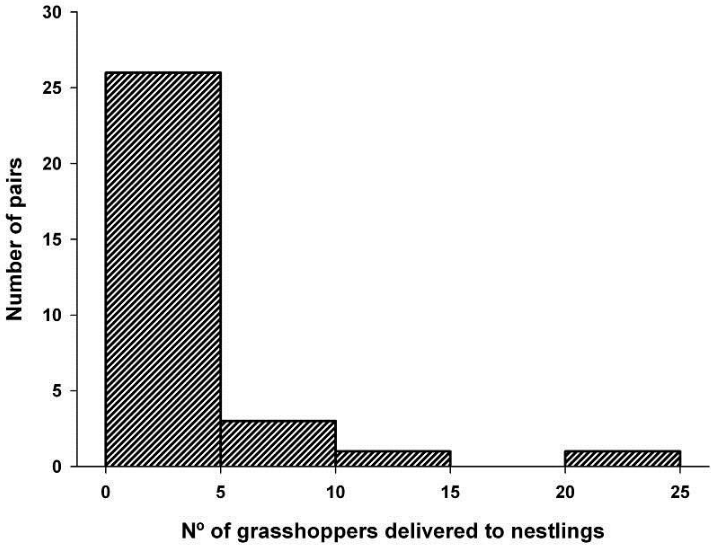
- Nº of spiders:



- Nº of fruits:



- Nº of grasshoppers:



Capítulo 6

Pagani-Núñez, E. & Senar, J. C. 2014. Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality. ***Acta Oecologica***, 55, 23-28.

Acta Oecologica 55 (2014) 23–28

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Are colorful males of great tits *Parus major* better parents? Parental investment is a matter of quality

Emilio Pagani-Núñez*, Juan Carlos Senar

Evolutionary and Behavioural Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n, 08003 Barcelona, Spain

ARTICLE INFO

Article history:
Received 16 June 2013
Accepted 4 November 2013
Available online

Keywords:
Arachnids
Carotenoids
Evergreen forests
Nestling diet
Ornaments
Parental investment

ABSTRACT

Given the known influence of parental investment on breeding success of great tits *Parus major*, females should be expected to use male parental quality as an essential criterion in mate choice. Since parental quality cannot usually be observed directly at the time of pairing, it has been suggested that females rely on male ornaments as indicative of their ability to provide parental care. This hypothesis, called the good parent hypothesis, has been tested repeatedly assessing only parental effort as the number of feedings made by parents. However, in evaluating parental investment, the focus should also be on the quality of prey captured rather than only on its quantity. We analyzed feeding rates and the provisioning of different prey in relation to both male yellow carotenoid-based breast coloration and the size of the black melanin-based stripe in a Mediterranean great tit population. We predicted that more carotenoid ornamented individuals would feed nestlings with a diet consisting of a higher proportion of caterpillars. However, and contrary to predictions, we found that males with higher values of hue in the yellow breast feathers, fed their offspring with a lower proportion of caterpillars and a higher proportion of spiders. In addition, nestlings that received a higher proportion of spiders showed an improved body condition after controlling for tarsus length and other variables. Male feeding rates correlated positively with brood size and tended to correlate negatively with date, although we did not find any effect of male coloration. Our data therefore support the good parent hypothesis, insofar as parental investment is also a matter of quality, and that, at least in the Mediterranean area, caterpillars are not the only key food source.

1. Introduction

Parental investment is a major determinant of breeding success. As a consequence, in species in which males contribute substantially to rearing of offspring, we should expect females to use male parental quality as an essential criterion for the choice of their mate (Danchin et al., 2008). Since parental quality cannot usually be observed directly at the time of pairing, it has been suggested that females may rely on male ornaments as indicative of male ability to provide parental care, referred to as the “Good Parent Hypothesis” (Hoelzer, 1989; Price et al., 1993; Andersson, 1994; Wolf et al., 1997).

Carotenoid-based plumage coloration is generally considered a good candidate to assess individual quality, since animals can only obtain carotenoids through food ingestion. Consequently, this coloration might function as an honest signal of an individual's ability to find food (Hill and McGraw, 2006). Supporting this view, carotenoid-based plumage coloration has been linked to nutritional condition estimated by the rate of tail growth (Hill and Montgomerie, 1994; Senar et al., 2003) and to the ability of the individual to find food and to collect carotenoids (Senar and Escobar, 2002; Ferns and Hinsley, 2008; Senar et al., 2008; García-Navas and Sanz, 2011; Mateos-González et al., 2011; García-Navas et al., 2012). The link between carotenoid-based ornaments and parental investment has been supported by higher provisioning rates by more ornamented males (Hill, 1991; Linville et al., 1998; Préault et al., 2005; Germain et al., 2010; García-Navas et al., 2012). Nevertheless, different patterns may arise, as, for instance, some recent research that has found a negative correlation between plumage coloration and provisioning rates (Mitchell et al., 2007), and some work that has also pointed out a sex-dependent functionality of plumage ornaments (Griggio et al., 2010). This contrasting results also appears in relation to structural and ultraviolet plumage coloration (Balenger et al., 2007; Limbourg et al., 2013).

When trying to relate plumage coloration to parental investment, most previous studies have estimated the quality of parental

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* Corresponding author. Tel.: +34 932562210.
E-mail address: emipanu@gmail.com (E. Pagani-Núñez).

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http://dx.doi.org/10.1016/j.actao.2013.11.001

care from feeding rates or nest attendance. However, this measure does not take into account the quality of prey items, and in consequence, it does not directly assess foraging ability (Royama, 1966; Sætre et al., 1995; García-Navas et al., 2012). More recent work using chick development as a proxy of the quality of the food provided by parents found that father coloration was related to chick development and hence to parental investment (Senar et al., 2002). Nevertheless, with this approach it is not feasible to separate the contributions of the male and the female parent. A more suitable approach to analyze this particular aspect of parental investment should also consider the quality of prey delivered to nestlings (Catoni et al., 2008; Arnold et al., 2010; García-Navas et al., 2012, 2013). Unfortunately, this has rarely been attained due to the difficulty in identifying what prey could be considered high quality and what could be low quality (see Casagrande et al. (2006)).

Our aim was to test for a relationship between male plumage coloration, nestling-feeding rates and the relative amount of both caterpillars and spiders provided to nestlings in an evergreen forest, as a direct measure of parental quality. We analyzed this in a Mediterranean great tit *Parus major* population where birds rely heavily on both kinds of prey as their main food source (Pagani-Núñez et al., 2011; Banbura et al., 1994). We also studied the relationships between nestling growth and parental provisioning (both feeding rates and prey composition). Based on previous findings (Slagsvold and Lifjeld, 1985; García-Navas et al., 2012), we predicted that more ornamented individuals would feed nestlings a higher proportion of caterpillars. However, and contrary to predictions, spiders seemed to be preferably selected by more ornamented fathers.

2. Materials and methods

The study was carried out during the 2011 breeding season at Can Catà field station, in a predominantly evergreen Mediterranean forest (Barcelona, Northeast Spain; see Pagani-Núñez et al. (2011) for details of the area). A total of 182 nest boxes were checked twice a week to determine nest building state, laying date, hatching date, and brood size. Once we determined the hatching date, nests were visited as minimal as possible.

We filmed inside the nest boxes using digital micro-cameras (Mini Colour Sony IR Camera SK-C170IR) attached to the nest-box cover and focused on the entrance. These cameras are provided with an infrared view and a motion sensor: when movement is detected, the camera starts filming until the movement stops. We filmed all nests when the chicks were 10–16 days old to obtain information about nestling provisioning on the period of their highest energetic demands (Naef-Daenzer and Keller, 1999). To minimize the possible effects produced by the installation of the camera, two days before recording we faked an external device by installing a tube on top of the nest cover, and we camouflaged it with branches and vegetation. Furthermore, we installed and activated cameras at 13 h on the first day. Parents readily continued their usual behavior after cameras were installed. For our analysis, we used the recordings obtained during the first 7 h after sunrise only from the second day. We excluded the period between dawn and 7 a.m. to homogenize our sample and avoiding problems with individuals that may start provisioning later than at dawn, so that we used full clock hours from 7 a.m. to 2 p.m.

Most birds had been marked during the previous winter with numbered PVC rings that could be read in the recordings, allowing us to easily recognize each individual. Sexes were also easily recognized in the recordings mainly based on the shininess of the black cap, given the high intensity of sexual color dichromatism in this species, accentuated under infra-red light conditions. For each feeding action recorded we determined the sex of the parent, prey type and exact time. Prey were classified into three categories: caterpillars, spiders, and others. The different kinds of prey were easily identified in the recordings. To analyze the data (203 h of recordings from 29 pairs), we computed the number of feeding actions and the proportion of spiders fed by each individual at each nest box. We calculated proportions as the number of feeding actions of each prey item divided by the total number of feeding actions.

Chicks, and parents that were not captured during winter and did not have PVC rings to allow identification from the recordings, were trapped in the nest-box after the recordings, between the 15th and the 17th day after hatching (Quesada and Senar, 2007). We recorded tarsus length (mm) and mass (g) of every nestling, and standardized them to the age of 16 days. Age and sex of the parents were determined according to Svensson (1992). The area of the black breast stripe was measured from digital pictures (Figuerola and Senar, 2000; Quesada and Senar, 2007) using the program ImageTool 3.00 (Texas, USA). A portable colorimeter Minolta CR200 (Minolta Corporation, 1994) was used to obtain hue, chroma and lightness of the yellow plumage of breast (Figuerola et al., 1999). Hue corresponds to wavelength, which may be considered as the color tone, and is expressed in degrees. In the case of the yellow breast coloration of great tits, low hue values correspond to a more orange tone, whereas high values correspond to a greenish tone. Hue values are positively correlated to carotenoid content in feathers (Senar et al., 2008). Chroma corresponds to color purity, and is measured in a continuous scale ranging from 0 to 100. Lightness corresponds to light intensity of color and is also expressed in a continuous scale from 0 to 100. Given that color measurements were taken both in winter and spring, we standardized color values by date using the protocol described in Figuerola and Senar (2005). Colorimeters provide these measurements automatically, without the need to recompute or transform the data obtained. Color measurements were taken with the colorimeter perpendicular to and making contact with the surface of the feathers patch. We made three measurements of the yellow patch to obtain a reliable mean of male breast coloration. Repeatability for color measurements was high (Figuerola et al., 1999; Quesada and Senar, 2006).

We used a Multiple Linear Regression (MLR) approach. All the proportions were arcsine-root transformed and categorical variables (age and rain) were coded as dummy 0–1 variables. The model included proportion of caterpillars as the dependent variable. As independent variables we used age of the father, proportion of Oak trees within 25 m of the nest box (to control for habitat variability; see Pagani-Núñez et al., 2011), date of recording (to control for phenology), mean daily temperature (taken from a nearby official meteorological station) and presence or absence of rain on the day of the recording, brood size, feeding rates per hour of the father, proportion of caterpillars delivered by the female (to control for female investment), color (lightness, chroma and hue) of the yellow breast of the father (standardized for seasonal effects according to Figuerola and Senar (2005)), and size of the black breast tie of the father. The same method was used when analyzing as dependent variables proportion of spiders and feeding rate.

In order to relate nestling condition to food provided by the parents we used an index of body condition computed as the standardized residual from the regression of mass against tarsus length ($F_{1,30} = 5.03$, $P = 0.03$, $N = 32$, mean values per nest). Although there are alternative methodologies (Tinbergen and Boerlijst, 1990), this approach is the best proxy of nestling lipid stores (Ardia, 2005), and is consistent with previous work of our team (Senar et al., 2008). This index of body condition was our dependent variable. As predictors we included proportion of Oak trees within 25 m of the nest box, hatching date, presence of rain (to control for its effect on the foraging behavior of fathers), brood size, proportion of spiders delivered by the male, proportion of spiders delivered by the female, and male feeding rate. We also carried out sample size calculations for each model to assess whether our sample was enough to detect an effect of interesting size. We found that the sample size needed to obtain a power of 0.90 was 32, 21, 19 and 54 for models 1–4, respectively. These results indicates that sample size was appropriate for the three first models, although was rather limited for the last one.

3. Results

The number of provisioning visits per nest by the male, on a seven-hour period, correlated positively with brood size and tended to correlate negatively with date (Table 1). We did not observe any effect of other environmental variables. Also, we did not find any effect of male coloration or female investment on male feeding rate.

In relation to prey composition, males with higher values of hue of the yellow breast delivered an almost significant lower proportion of caterpillars and a higher proportion of spiders to the chicks than less colorful birds (Tables 2 and 3; Fig. 1). We did not find that other components of carotenoid-based feather coloration, such as lightness and chroma, age of the father, black tie size, or the proportion of prey delivered by females, had any significant effect on male provisioning behavior (Tables 2 and 3). In relation to environmental variables, males provided chicks with more spiders at the beginning of the breeding season and in nest boxes more heavily surrounded by Oaks (Table 3; Fig. 2). The rainy weather caused a significant decrease in the proportion of caterpillars delivered to chicks and an increase in the proportion of spiders (Tables 2 and 3). We did not detect any effect of mean temperature or brood size on provisioning chicks with caterpillars or spiders. Apart from caterpillars and spiders, which ranged from 64% to 100% of total food provisioned when considered together (Fig. 2), male great tits delivered other kinds of prey such as fruits, grasshoppers and stick-insects. Male coloration was not related to the proportion of Oaks surrounding nest-boxes (Fig. 3).

Nestling body condition (mass residuals standardized by tarsus length) was marginally positively related in the global model to the proportion of spiders that the father delivered to the nest, regardless of environmental factors and feeding rates (Table 4). When reducing degrees of freedom by eliminating from the model variables which were clearly no related to the body condition of the chicks, proportion of spiders that the father delivered to the nest reached significance (Reduced model; % of spiders: $r = 0.45$, $t_{27} = 2.4$, $P = 0.02$; date: $r = 0.36$, $t_{27} = 2.0$, $P = 0.06$; rain: $r = -0.34$, $t_{27} = 1.9$, $P = 0.06$; Fig. 4).

Table 1
Results from the Multiple Linear Regression (MLR) relating feeding rates of the fathers to their age, to the proportion of Oaks surrounding the nest, date, temperature and rain, brood size, female feeding rates, and male plumage coloration (lightness, chroma and hue of the yellow breast and black tie size). Regression summary: $R^2 = 0.54$, $F_{11,17} = 1.81$, $P < 0.13$.

	t_{17}	Partial correlation	P
Age	−0.08	−0.02	0.94
%Quercus	0.72	0.17	0.48
Date	−1.87	−0.41	0.08
Temperature	0.08	0.02	0.93
Rain	0.05	0.01	0.96
Brood size	2.19	0.47	0.04
Female feeding rates	−1.13	−0.26	0.27
Yellow lightness	0.58	0.14	0.57
Yellow chroma	−0.47	−0.11	0.65
Yellow hue	−1.68	−0.38	0.11
Black tie size	−1.30	−0.30	0.21

Table 2
Results from the Multiple Linear Regression (MLR) relating the proportion of caterpillars delivered to the chicks by fathers to males age, proportion of Oaks surrounding the nest, date, temperature and rain, brood size, proportion of caterpillars delivered by females, male feeding rates and male plumage coloration (lightness, chroma and hue of the yellow breast and black tie size). Regression summary: $R^2 = 0.78$, $F_{12,16} = 4.86$, $P < 0.01$.

	t_{16}	Partial correlation	P
Age	−1.19	−0.28	0.25
%Quercus	−1.94	−0.44	0.07
Date	0.98	0.24	0.34
Temperature	−1.35	−0.32	0.20
Rain	−2.39	−0.51	0.03
Brood size	0.55	0.14	0.59
Female % caterpillars	1.56	0.36	0.14
Male feeding rates	−1.99	−0.45	0.06
Yellow lightness	0.13	0.03	0.90
Yellow chroma	−0.35	−0.09	0.73
Yellow hue	−2.07	−0.46	0.06
Black tie size	0.16	0.04	0.88

4. Discussion

Previous studies reported that individuals showing the higher degree of carotenoid-based ornamentation invested more in reproduction, either having a higher feeding rate or providing their offspring with the higher proportions of caterpillars (Slagsvold and Lifjeld, 1985; Hill, 1991; García-Navas et al., 2012). Contrary to predictions, however, our results showed that hue of the carotenoid-based yellow feathers of the breast of male great tits was negatively related to the proportion of caterpillars and positively related to the proportion of spiders delivered to their nestlings. It has been stated that tits fit their timing of reproduction to the peak of caterpillar availability (Naef-Daenzer et al., 2000). Nonetheless, in some cases caterpillars become less important or available (Blondel et al., 1991; Banbura et al., 1994). Thus, individuals less dependent on caterpillar phenology and feeding on a greater variability of trophic resources, some of which may be main sources of scarce and limited nutrients, should be at advantage (Banbura et al., 1994; Arnold et al., 2010). Arachnids are likely one of these high quality alternative resources. Several previous studies have already noted the value of spiders in the diet of nestlings since they contain high levels of certain amino acids (Ramsay and

Table 3
Results from the Multiple Linear Regression (MLR) relating the proportion of spiders delivered to the chicks by fathers to males age, proportion of Oaks surrounding the nest, date, temperature and rain, brood size, proportion of spiders delivered by females, male feeding rates and male plumage coloration (lightness, chroma and hue of the yellow breast and black tie size). Regression summary: $R^2 = 0.87$, $F_{12,16} = 9.19$, $P < 0.01$.

	t_{16}	Partial correlation	P
Age	0.60	0.15	0.56
%Quercus	3.92	0.70	<0.01
Date	−2.67	−0.55	0.02
Temperature	1.73	0.40	0.10
Rain	3.44	0.65	<0.01
Brood size	−1.09	−0.26	0.29
Female % spiders	0.47	0.12	0.65
Male feeding rates	1.73	0.40	0.10
Yellow lightness	−1.19	−0.28	0.25
Yellow chroma	1.09	0.26	0.29
Yellow hue	2.58	0.54	0.02
Black tie size	−0.65	−0.16	0.53

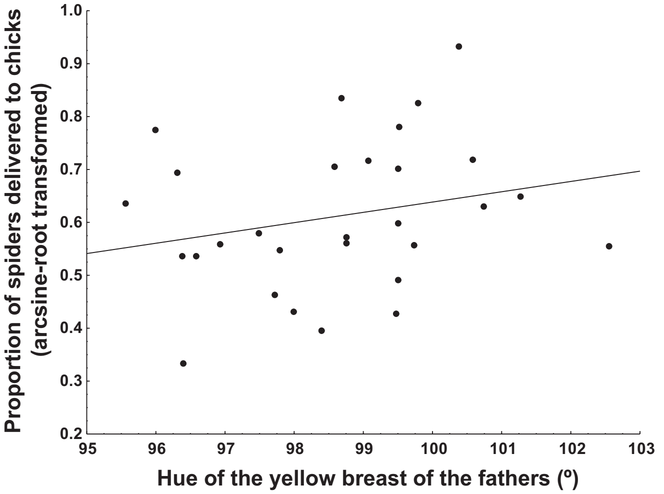

Fig. 1. Relationship between the proportions of spiders (arcsine-root transformed and standardized by the variables showing significant interactions in the model included in Table 3) delivered to their chicks and the hue of the yellow carotenoid-based breast (degrees) of great tit fathers. $R = 0.48$, $P = 0.04$, $N = 29$.

Houston, 2003) that seem to play a key role in nestling development (Arnold et al., 2007, 2010; García-Navas et al., 2013). Spiders are quite similar to caterpillars from a nutritional perspectives, but they have up to fifty times more of taurine, an amino acid which significantly improved spatial learning abilities in hand-raised blue tit *Cyanistes caeruleus* nestlings (Arnold et al., 2007). The results from Magrath et al. (2004) support this view. They showed that male nestlings of brown songlark *Cinclorhamphus cruralis* were fed more spiders than their female siblings. At least in this species, male nestlings are considered of higher reproductive value than females, but they need a greater amount and higher quality of food than females for their development (Danchin et al., 2008). Therefore, the fact that parents provided male nestlings with a higher proportion of spiders strongly suggests that spiders are truly a high quality food source (Magrath et al., 2004). Recent work by García-Navas et al. (2013) has also found a positive correlation between the tarsus length of nestling Blue tits and the proportion of spiders provisioned by their parents. We have found additional support for this idea. Despite of the great number of factors affecting physical condition of great tit nestlings, those receiving a higher proportion of spiders from their fathers showed an improved body condition. Hence, we suggest that more ornamented (higher hue) males are displaying their higher foraging ability at exploiting alternative high quality prey (i.e.: arachnids). The lack of correlation between the proportion of spiders delivered by females and nestling condition would be due to sex-related differences in prey delivering, because females show less plasticity in their foraging behavior and what makes the difference is the proportions of spiders delivered by males (Pagani-Núñez et al., 2011). Anyway, we may not exclude an indirect effect produced by the quality of maternal investment of those females paired with more ornamented males, which delivered a high proportion of spiders (Germain et al., 2010). We also should note that the effect of food on nestling fitness is difficult to pin down based on prey proportions because this approach does not take into account chemical composition of prey (Raubenheimer, 2011).

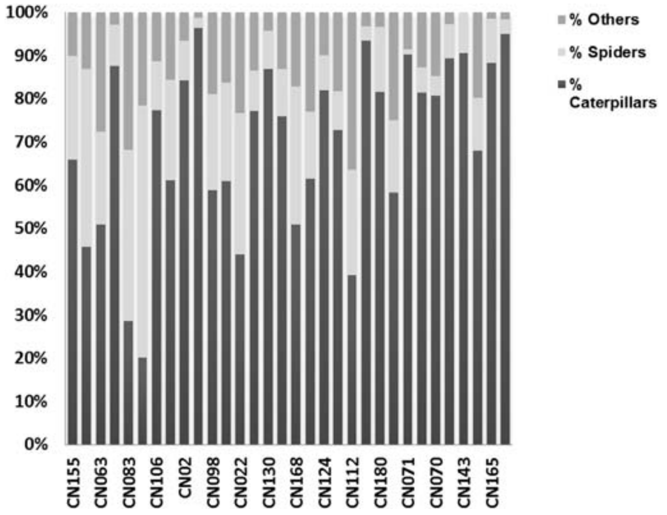

Fig. 2. Proportions of different prey items for all males sampled and ordered by date of recording. We divided prey in caterpillars, spiders and others. $N = 32$.

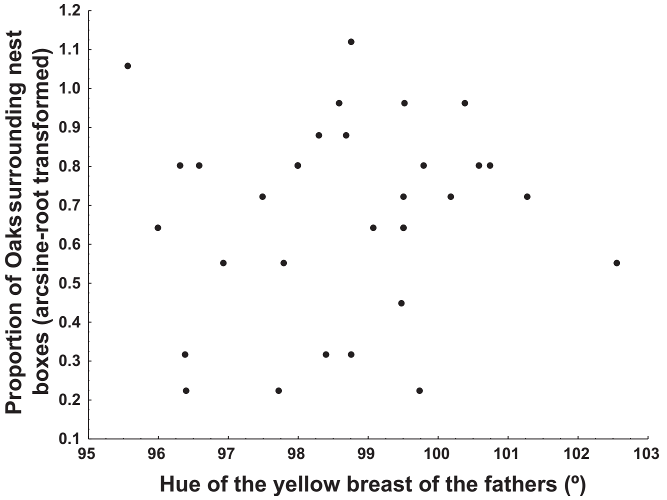

Fig. 3. Relationships between the hue of the yellow carotenoid-based breast (degrees) of Great tit fathers and the proportion of Oaks surrounding nest-boxes within 25 m (arcsin-root transformed). $R = 0.11$, $P = 0.56$, $N = 32$.

The finding that hue relates positively to spider content in diet conflicts with the view that carotenoid-based coloration should relate to caterpillar content in diet (Slagsvold and Lifjeld, 1985; García-Navas et al., 2012). Although spiders contain some carotenoids, their concentration is about one hundred times lower than that in caterpillars (Czeczuga, 1979; Partali et al., 1987; Arnold et al., 2010; Eeva et al., 2010). This apparent contradiction, however, could be explained in different ways. First, we should emphasize that in previous studies conducted with great tits, the predictive

Table 4
Results from the Multiple Linear Regression (MLR) relating nestling body condition, and several environmental factors (proportion of Oak trees within 25 m of the nest box, and brood size, hatching date, rain to control for its effect over parental foraging behaviour) and those variables characterizing parental foraging behaviour (proportion of spiders delivered by males and females, and male feeding rates). Regression summary: $R^2 = 0.30$, $F_{7,23} = 1.43$, $P < 0.24$.

	t_{23}	Partial correlation	P
%Quercus	−0.64	−0.13	0.53
Date	1.50	0.30	0.15
Rain	−1.38	−0.28	0.18
Brood size	−0.65	−0.14	0.52
Male % spiders	1.77	0.35	0.09
Female % spiders	−0.18	−0.04	0.86
Male feeding rates	−0.30	−0.06	0.77

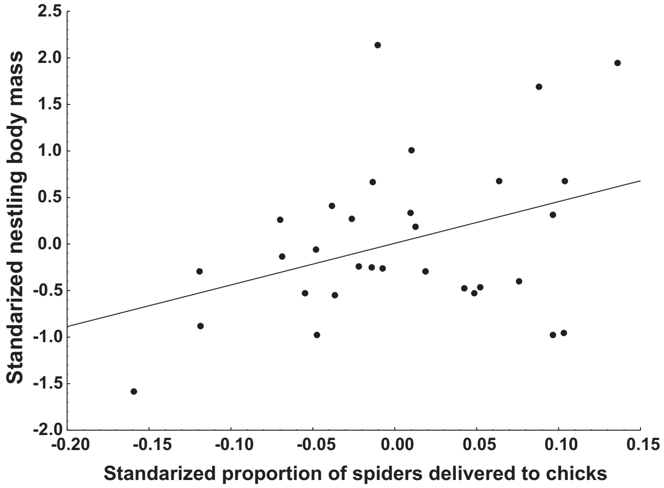

Fig. 4. Relationships between nestling body condition (mass residuals standardized by tarsus length) and the proportions of spiders (arcsin-root transformed and standardized by proportion of oaks surrounding the nest, date and rain, see Table 3) delivered to chicks by fathers. $R = 0.38$, $P = 0.04$, $N = 31$.

value of carotenoid content from plumage hue – although significant – was less than 20% (Senar et al., 2008). Therefore, hue should not be regarded only as a simple measure of carotenoid content. The presence of small amounts of melanin, for instance, could also be partially responsible for shifting the yellow of carotenoids towards the green (Andersson and Prager, 2006). Second, nutritional requirements for plumage development may not be the same for offspring as for adults (Hill, 1992; Sillanpää et al., 2009; Huggins et al., 2010). We have previously shown that an increase in carotenoid-based coloration is related to the ability to solve foraging problems (Mateos-González et al., 2011) or to the ability to detect food resources rather than relying on local enhancement (Senar and Escobar, 2002). Hence, we suggest that carotenoid plumage coloration reflects ability to find key resources, taken as a general measure of foraging ability, rather than the ability just to find caterpillars (Casagrande et al., 2006).

We found that several environmental variables were related to the parental delivery of prey to chicks. First, and interestingly, we found that the proportion of prey delivered by males to the nest was not correlated to that of females, so that sexes seem to show different foraging strategies or respond differently to environmental factors (Banbura et al., 1994; Radford et al., 2001; Pagani-Núñez et al., 2011). We also observed that great tit males in territories heavily surrounded by Oak trees provided nestlings with relatively more spiders. The higher availability of spiders in these trees than in pines would account for this difference (Suorsa et al., 2003). However, our data showed that more ornamented males fed preferentially on spiders regardless of habitat quality, since male coloration and the proportion of Oaks surrounding nest-boxes were not correlated (Fig. 3). Therefore, our finding should not be considered as a sub-product of the differential occupation of better territories by better individuals. We also found that a higher proportion of spiders were delivered in the early stages of the breeding season, whereas the proportion of caterpillars did not show any seasonal trend. This is to be expected if better parents, which should be able to exploit alternative food resources, breed early in the season (Naef-Daenzer et al., 2000; García-Navas and Sanz, 2011). Although it has already been shown that meteorological factors do not heavily affect male great tit foraging behavior (Radford et al., 2001), we found that spiders were more predominant than caterpillars in rainy weather. We think that this increase in spider delivery is a consequence of drastic changes in relative abundance of prey, given that we did not detect any effect of rainy weather on absolute feeding rates. As a consequence, the fact that spiders were the predominant prey in rainy weather could be explained either by a decrease in the availability of caterpillars in poor meteorological conditions (Moss, 1933) or by an increase in the availability of spiders due to their higher mobility in wet conditions (Parry, 1954; Figueroa et al., 2010).

A topic of great interest in the past has been to relate male ornamental characteristics as indicator of parental quality to chick feeding rates. However, contrasting patterns have been reported, and previous literature has either found (Norris, 1990; Sætre et al., 1995) or not found (Rohde et al., 1999; Fitze et al., 2003) a relationship between these two variables. Results from great tits in our paper did not support this relationship. The close to significance negative correlation we found between feeding rates and the proportion of caterpillars provided to chicks may be attributed to either environmental or prey availability effects (Blondel et al., 1991). Consequently, higher feeding rates need not necessarily be associated with a better quality diet (Perrins, 1979; García-Navas et al., 2012), stressing again the need to focus also on quality of diet rather than only on quantity. Moreover, parental care should not be regarded as a static or univocal trait. It has to be assessed from several perspectives, such as the study of incubation or nest-defence, complementary but not necessarily correlated aspects of the same feature (Pilastro et al., 2003; Matessi et al., 2009).

To conclude, our data showed a positive correlation between the proportion of a high quality prey (i.e.: spiders) and nestling physical condition. Moreover, we found a positive relationship between the hue of carotenoid-based ornaments and the proportion of this prey in the nestling diet. Regardless of the intensity of parental work, successful fathers displayed an efficient strategy based on the exploitation of alternative trophic resources to caterpillars. Thus, our results support the good parent model of sexual selection (Hoelzer, 1989; Wolf et al., 1997), stressing that parental investment in great tits is also a matter of quality.

Acknowledgments

We want to thank to Margarida Barcelò, Irene Campderrich, Lluïsa Arroyo, Miguel Cativiela, Vanessa Toribio, Sandra Blanco, Jana Bermúdez, Rubén Belilles and Ramón Muñoz for their assistance during the field work. We would also like to thank María Sabater, Neus Pérez, Marta Gómez and Inés Sánchez for their help analyzing the recordings, and Lluïsa Arroyo for her help in the lab. In another vein, we thank three anonymous referees for their suggestions, which significantly improved an earlier version of the manuscript. The present study was funded by CGL2009-10652 and CGL2012-38262 research projects to J.C.S. and by the FPI grant BES2010-040359 to E.P.N., from the Ministry of Science and Innovation, Spanish Research Council. Birds were handled with the permission of the Departament de Medi Ambient, Generalitat de Catalunya. Rings were provided by the Catalan Ringing Office (ICO).

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Capítulo 7

Pagani-Núñez, E., Uribe, F., Hernández-Gómez, S., Muñoz, G. & Senar, J.C. 2014. Habitat structure and prey composition generate contrasting effects on carotenoid-based colouration of Great tit *Parus major* nestlings. ***Biological Journal of the Linnean Society***. En prensa.

The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2014, ••, ••–••. With 4 figures

Habitat structure and prey composition generate contrasting effects on carotenoid-based coloration of great tit *Parus major* nestlings

EMILIO PAGANI-NÚÑEZ*, FRANCESC URIBE, SERGIO HERNÁNDEZ-GÓMEZ, GUILLERMO MUÑOZ and JUAN CARLOS SENAR

Evolutionary Ecology Associate Research Unit (CSIC), Natural History Museum of Barcelona, Psg. Picasso s/n., 08003 Barcelona, España (Spain)

Received 8 April 2014; revised 26 May 2014; accepted for publication 26 May 2014

Carotenoid-based coloration of nestling plumage is generally considered a reliable signal of quality and has consistently been related to habitat structure. The main hypothesis proposed to explain this correlation is that high quality habitats contain high quality food, which in return affects the expression of carotenoid-based plumage. It therefore assumes that, at the population level, the link between habitat structure and food composition is consistent and more relevant than inter-individual differences in foraging ability or parental investment. In addition, it is assumed by default that food and habitat produce concordant effects on nestling coloration. In this work we evaluated habitat structure and prey composition in addition to several measures of parental investment. We investigated their relative effect on carotenoid-based plumage coloration (lightness, chroma and hue) of great tit *Parus major* nestlings. We found a low correlation between carotenoid-based coloration of nestlings and that of their parents. Nestling coloration, especially lightness and chroma, increased with the intake of more spiders. The time of breeding was positively correlated with lightness and chroma and negatively correlated with hue. Finally, the maturity of oak trees surrounding nest-boxes correlated negatively with lightness, and the size of all tree species surrounding nest-boxes correlated positively with hue of chick plumage. Our findings support the view that habitat structure and prey composition may produce divergent effects on feather pigmentation, and that prey proportions and variables related to parental investment should be assessed when considering carotenoid-based coloration of chicks. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, ••, ••–••.

ADDITIONAL KEYWORDS: carotenoids – coloration – food – great tit – habitat – nestlings – quality.

INTRODUCTION

Animals can only obtain carotenoids through the ingestion of food. Hence, it is generally assumed that carotenoid-based coloration functions as an honest signal of the ability of the individual to find carotenoid-rich food (Hill & McGraw, 2006). Accordingly, carotenoid-based plumage coloration has been linked to nutritional condition (Hill & Montgomerie, 1994; Senar, Figuerola & Domènech, 2003) and foraging ability (Senar *et al.*, 2008; Mateos-González, Quesada & Senar, 2011; García-Navas, Ferrer & Sanz, 2012). A direct association between carotenoid-based ornaments and parental investment has also been supported by higher provisioning rates (Hill, 1991; Linville, Breitwisch & Schilling, 1998; Préault *et al.*, 2005; Germain *et al.*, 2010) or higher food quality (García-Navas *et al.*, 2012; Pagani-Núñez & Senar, 2014) delivered by more ornamented fathers.

By extension, the rearing environment should influence carotenoid-based coloration of nestlings (Evans & Sheldon, 2012; Matrková & Remes, 2012). Several studies support this view, finding a consistent correlation between father coloration, provisioning behaviour and offspring fitness (Senar, Figuerola & Pascual,

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*Corresponding author. E-mail: emipanu@gmail.com

2002; García-Navas *et al*., 2012; Pagani-Núñez & Senar, 2014) and between father and nestling coloration (Tschirren, Fitze & Richner, 2003; Isaksson, Uller & Andersson, 2006). It has been suggested that the mechanism underlying these correlations is the quality of the food delivered by parents (Senar *et al*., 2002). However, detailed analysis of the effect of food quality on nestling coloration has produced contradictory results, with some studies showing evidence of a robust interaction between food quality and carotenoid-based plumage of nestlings (Fitze, Tschirren & Richner, 2003a; Eeva, Sillanpää & Salminen, 2009; Isaksson, 2009), while others found no effect of food quantity on this trait (Fitze, Kölliker & Richner, 2003b). Additionally, parents have been reported to be able to compensate for low food quality by increasing food quantity (Isaksson & Andersson, 2007).

In addition to diet, and regardless of the functional meaning of carotenoid-based coloration for nestling passerines (Tschirren, Fitze & Richner, 2005; Galván, Amo & Sanz, 2008), the expression of this coloration has also been broadly related to habitat structure (Arriero & Fargallo, 2006; Galvan, Diaz & Sanz, 2009; Evans & Sheldon, 2012). However, although food quality is considered to be the main factor driving this interaction, food composition delivered to nestlings by parents has not been systematically assessed (Arriero & Fargallo, 2006; Galvan, Diaz & Sanz, 2009). These approaches emphasise population-level trends versus inter-individual variability, and as recent research has stressed (Bolnick *et al*., 2003), this common axiom may lead to erroneous interpretations. In our opinion, irrespectively of the heritable component of this trait (Evans & Sheldon, 2012), to assess the relative effect of habitat structure and food composition on nestling carotenoid-based coloration, both groups of factors should be studied together. Unfortunately, only the interactions between pollution and plumage coloration have been studied in this manner (Eeva *et al*., 2009; Isaksson, 2009), with the exception of the early work of Slagsvold & Lifjeld (1985).

The aim of this study was to assess the relative effect of habitat structure and prey composition on carotenoid-based plumage coloration in nestlings. We performed this study in a Mediterranean great tit *Parus major* population inhabiting a heterogeneous mixed forest (Pagani-Núñez *et al*., 2011). In this population, parents rely on a wide array of prey items (Pagani-Núñez *et al*., 2011) and more ornamented fathers deliver better food (more spiders) to their nestlings (Pagani-Núñez & Senar, 2014). This high environmental and behavioural variability should therefore help to accurately assess the relative influence of each factor on each parameter of colour considered.

METHODS

DIET RECORDING

We monitored 182 nest-boxes twice a week during the 2011 breeding season at Can Catà field station, located in a Mediterranean mixed forest in Barcelona, northeast Spain. We determined nest building state, laying date, hatching date, and brood size. Nests were visited for as little time as possible to minimize disturbances occasioned to breeding birds. We used digital micro-cameras located inside nest-boxes to estimate provisioning rates and to identify prey items (see Pagani-Núñez & Senar (2014) for a detailed description of the cameras and of filming procedures). We filmed across 7 hours, from 7 am to 2 pm, and we computed the total number of feedings and number of prey items of each type delivered by parents. We divided prey into three groups: caterpillars, spiders, and others (see Pagani-Núñez *et al*. (2011) and Pagani-Núñez & Senar (2014) for more information about prey characteristics and prey availability in our area). We also estimated prey size by means of a semi-quantitative scale of three levels (little = 1, medium = 2, large = 3) based on Barba, Lopez & Gil-Delgado (1996), and we calculated mean prey size for each parent.

NESTLING AND PARENTAL COLORATION

Nestlings were trapped in the nest-box between the 15th and 17th day of life (Quesada & Senar, 2007). We recorded tarsus length (mm) and mass (g) of each chick and we standardized these to the age of 16 days. We used mass residuals standardized by tarsus length as a proxy of body condition (term used in the following to refer to this trait) because they optimally reflect nestlings' lipid stores (Ardia, 2005). Most parents had been previously captured during the winter and had numbered PVC rings to identify them, so we only had to trap a number of them in the nest-box at this stage. Age and sex of the parents were recorded according to Svensson (1992). We used a portable colorimeter Minolta CR200 (Minolta Corporation, 1994) to obtain lightness, chroma and hue (LCH) of the yellow carotenoid-based plumage of breast of both nestlings and adults (Figuerola, Pascual & Senar, 1999). In this context, lightness corresponds to the physical light intensity, indicating to which point the plumage is white. It is expressed on a continuous scale from 0 for black to 100 for white and has primarily been related to the achromatic structural component of colour that affects the expression of carotenoid-based ornaments (Shawkey & Hill, 2005), but it has also been linked to melanin content in feathers (Isaksson *et al*., 2008). Chroma, on the other hand, relates to colour purity, or colour saturation, and is measured on a continuous scale from 0 to 100. Some research has related chroma to carotenoid content in feathers (Isaksson *et al*., 2008), although, alternatively, it has been argued that it is mainly determined by the body condition of the individual (Senar *et al*., 2008). Hue, in contrast, corresponds to wavelength. It is expressed in degrees and considered the colour tone (the colour in a broader sense). Several previous studies have found a consistent correlation between carotenoid content in feathers and hue (Shawkey *et al*., 2006; Ferns & Hinsley, 2008; Senar *et al*., 2008), while another study did not find this (Isaksson *et al*., 2008). In the present study we computed LCH values using the 1976 CIE Lab Uniform Colour Space standard algorithms, which are implemented in our device (Minolta Corporation, 1994; Fairchild, 2005). CIE Lab uses a uniform colour space based on lightness variable L* and chromaticity indices a* and b*. Here, the lightness variable L* is $L^* = 116(Y/Y_n)^{1/3} - 16$, while chromaticity coordinates a* and b* are $a^* = 500[(X/X_n)^{1/3} - (Y/Y_n)^{1/3}]$ and $b^* = 200[(Y/Y_n)^{1/3} - (Z/Z_n)^{1/3}]$. X, Y and Z are tristimulus values of the specimen, while X_n, Y_n and Z_n refer to a perfect reflecting diffuser. The LCH (L*c*h*) colour space uses the same diagram although with cylindrical coordinates. L* is the same than in the L*a*b space, while chroma is $C^* = [(a^*)^2 + (b^*)^2]^{1/2}$, and hue is $h = \tan^{-1}(b^*/a^*)$ [degrees].

Given that colour values of many parents were taken in the previous winter, we standardized their values by date using the protocol described in Figuerola & Senar (2005). Colorimeters provide these data without the need to recompute or transform the values obtained. Colour measurements were taken using the colorimeter perpendicular to and in contact with the surface of the feathers. This device is configured to automatically perform three measurements and compute the mean. The repeatability of colour measurement of the yellow breast is high (lightness: $r_i = 0.85$; chroma: $r_i = 0.87$; hue: $r_i = 92$; $P < 0.001$) in all three cases; Figuerola *et al*., 1999; Quesada & Senar, 2006).

We studied the correlation between carotenoid-based coloration of parents (sexes separately) and that of their nestlings, and also between the components of nestling coloration, by means of Spearman correlations between both batches of parameters. We also performed a multiple linear regression using body condition as the dependent variable and the three components of nestling colour as factors.

HABITAT STRUCTURE

We assessed vegetation surrounding nest-boxes occupied by great tits during the breeding season. Based on previous estimations of territory size of our model and similar species (Royama, 1966; Krebs, 1971; Tremblay *et al*., 2005), we focused on a circular area of 25 m of radius using the nest-box as the midpoint. Hereafter, we refer to this area as the patch or the breeding patch. We carried out this work during the winter of 2011–2012 following two standard protocols: ‘The field manual for describing terrestrial ecosystems’ (British Columbia Ministry of Forests and Range, British Columbia Ministry of Environment, 2010) and the ‘Singular forest inventory of Catalonia’ (CREAF – Centre de Recerca Ecològica i Aplicacions Forestals, 2013). We computed the number of tree species within each patch. To be included in the analysis the diameter at breast height had to have a minimum of 5 cm. We distinguished between pines (mainly *Pinus halepensis*), oaks *Quercus cerrioides*, holm oaks *Quercus ilex*, and the other tree species (which were considered together). We also included the variable total number of trees for each patch. We measured and computed patch means for diameter and height of the three main tree classes. We carried out four orthogonal transects, at 90° of each other, to assess shrub density and composition within the patch. Based on these measurements, we computed the number of species of plants (shrubs and trees) and shrub density (calculated from orthogonal transects) in each patch. Finally, we measured the height above sea level of nest-boxes using a GPS. Using this dataset of 14 variables, we performed a principal components analysis (PCA) to summarize this information. We obtained three components, which were used as factors in subsequent analyses.

The PCA on habitat structure provided three components that summarize all the information gathered. The first component (PC1) increased along with the height of pines, oaks and holm oaks within the patch with the diameter of pines and oaks, and decreased with altitude (Table 1). For this reason we labelled PC1 as tree size. The second component (PC2) increased along with total number of trees and number of ‘other’ tree species within the patch (Table 1). We labelled PC2 as tree density. The third component (PC3) increased along with the mean diameter of oaks and holm oaks (Table 1), and we labelled it as oak maturity. Therefore, habitat variation was primarily related to forest structure rather than to tree composition.

STATISTICAL ANALYSES

To assess the relative effect of habitat structure and parental investment on nestling feather coloration we performed a multiple linear regression (MLR) approach. We followed backward stepwise procedures until we had only significant variables. We obtained three more models using the three components of

Table 1. Principal component analysis using a set of fourteen variables to characterize habitat quality. We recorded this information within a circle of 25 m of radius surrounding nest-boxes occupied by great tits during the breeding season. $N = 30$

	PC1 tree size	PC2 tree density	PC3 oak maturity
Meters above sea level	**−0.74**	−0.04	0.45
Total number of trees	0.10	**0.95**	0.08
Number of pines	−0.47	0.63	0.16
Mean height of pines	**0.71**	0.24	−0.22
Mean diameter of pines	**0.76**	−0.34	−0.15
Number of holm oaks	0.59	0.38	−0.15
Mean height of holm oaks	**0.86**	−0.03	0.29
Mean diameter of holm oaks	0.60	−0.41	**0.56**
Number of oaks	0.21	0.21	−0.32
Mean height of oaks	**0.79**	0.25	0.33
Mean diameter of oaks	**0.72**	0.01	**0.56**
Number of other trees	−0.19	**0.81**	0.30
Number of species	0.59	−0.16	−0.31
Shrub density	0.58	0.53	−0.33

yellow carotenoid-based coloration (LCH) as dependent variables. We included brood size (number of nestlings present during recordings), date (measured as the number of days from 1st April until the day of recordings), mean provisioning rates per hour and nestling of the pair, mean prey size of the pair, number of caterpillars, spiders and 'others' per nestling, and the three components describing habitat structure as factors. Data used in this work are available under request.

RESULTS

Carotenoid-based coloration (LCH) of parents showed no significant interactions with nestling coloration. All correlation values were below 0.33, and were remarkably low in general terms. We also assessed the interactions between the three components of nestling coloration: LCH. We found lightness and chroma of nestlings' plumage were intercorrelated ($r = 0.69$, $P < 0.01$). Hue did not correlate with lightness (−0.11), and it correlated negatively with chroma (−0.45, $P < 0.01$). Nestling body condition did not correlate with any parameter (LCH) of nestling coloration (all $P > 0.10$).

Lightness of carotenoid-based plumage coloration of nestlings showed multiple and contrasting effects. We found that nestling lightness increased with the time of breeding and with the number of spiders per nestling delivered by parents, and decreased with PC3 – tree maturity (Table 2, Figs 1, 2). Chroma of nestling coloration showed a similar pattern, increasing with date and with the number of spiders per nestling delivered by parents (Table 2 and Fig. 2). Hue, however, was positively correlated to PC1 – tree size

Table 2. Results of the backwards stepwise multiple linear regression using nestlings' lightness, chroma and hue of carotenoid-based plumage as dependent variables, and date, the three components describing habitat quality, mean feeding rates of the pair, mean prey size of the pair, and the number of caterpillars, spiders, and others per nestling delivered by parents as factors. We only show significant interactions. Within brackets we provide statistics for each model

Lightness ($R^2 = 0.37$; $F_{3,26} = 5.13$; $P < 0.01$)	t_{26}	Partial correlation	P
PC3 – oak maturity	−2.70	−0.47	0.01
Date	2.59	0.45	0.02
No. spiders per nestling	2.61	0.46	0.01
Chroma ($R^2 = 0.32$; $F_{2,27} = 6.38$; $P < 0.01$)	**t_{27}**	**Partial correlation**	**P**
Date	3.42	0.55	< 0.01
No. spiders per nestling	3.02	0.50	0.01
Hue ($R^2 = 0.38$; $F_{3,26} = 5.27$; $P < 0.01$)	**t_{26}**	**Partial correlation**	**P**
PC1 – tree size	2.27	0.41	0.03
Date	−3.52	−0.57	< 0.01
No. others per nestling	−1.88	−0.35	0.07

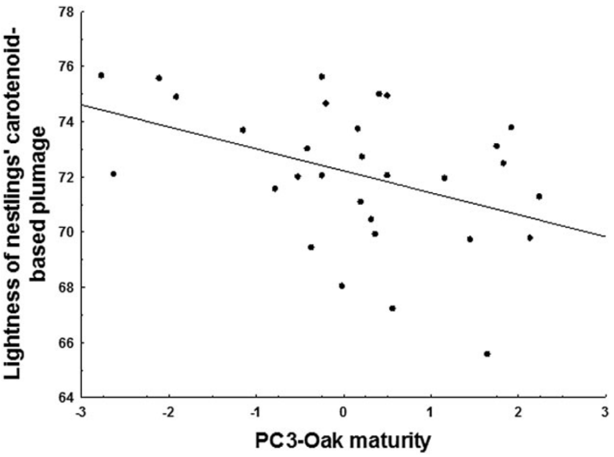

Figure 1. Scatterplot showing the contrasting relationships between lightness of carotenoid-based plumage of great tit *Parus* major nestlings and the component tree maturity (PC3 – tree maturity) characterizing vegetation surrounding nest-boxes.

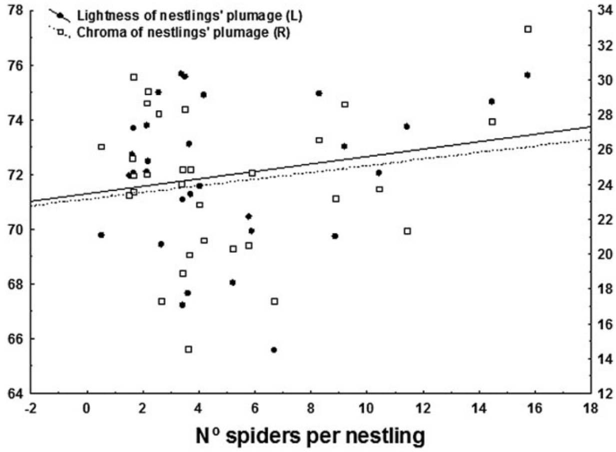

Figure 2. Scatterplot showing the relationships between the number of spiders per nestling delivered by parents, and lightness and chroma of carotenoid-based plumage of great tit *Parus major* nestlings.

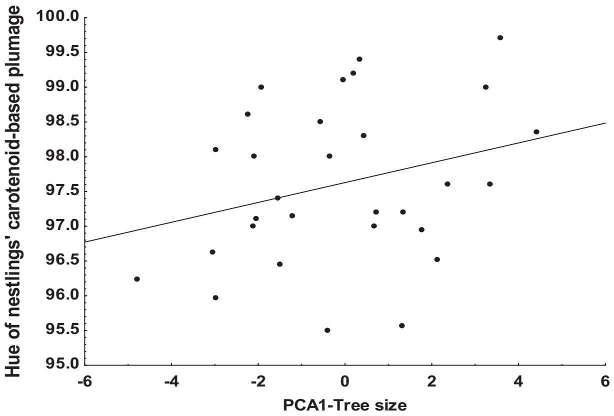

Figure 4. Scatterplot showing the relationships between the first component (PC1 – tree size) characterizing vegetation surrounding nest-boxes and hue of carotenoid-based plumage of great tit *Parus major* nestlings.

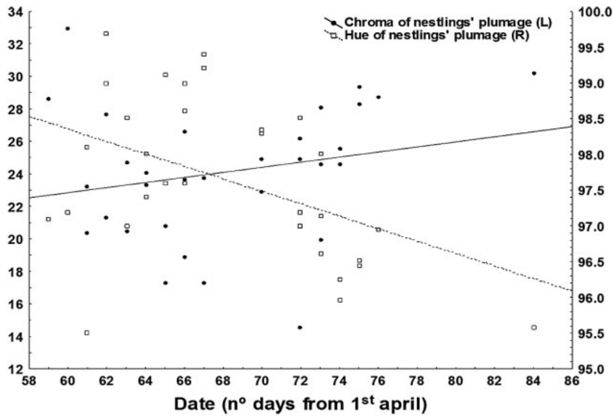

Figure 3. Scatterplot showing the relationships between date of breeding and two aspects, chroma and hue, of carotenoid-based plumage of great tit *Parus major* nestlings.

and negatively correlated to date and to the number of other prey per nestling delivered by parents (Table 2, Figs 3, 4). We did not find any significant effect of mean prey size, mean feeding rates, PC2 – tree density, or brood size on nestling coloration.

DISCUSSION

As our results show, prey composition and habitat structure produced contrasting effects on nestling coloration. Plumage lightness correlated positively with the intake of spiders and negatively with PC3 – oak maturity, while plumage hue correlated positively with PC1 – tree size and negatively with the intake of other prey (opposed to caterpillars and spiders). Moreover, different prey items produced different effects on nestling coloration according to the time of breeding. Lightness and chroma increased across the season with increasing intake of spiders, while hue decreased across the season with intake of other prey. We also recorded a surprisingly low correlation between parent and offspring coloration [see, e.g. Evans & Sheldon (2012)]. Taken together, our data support the view that we can not establish a direct link between habitat structure, food composition and nestling coloration [see also Zabala & Zuberogoitia (2014)]. Slagsvold & Lifjeld (1985) were the first authors to relate carotenoid-based plumage coloration to habitat structure. Later work on nestling coloration supported this early finding (Arriero & Fargallo, 2006; Galvan *et al.*, 2009; Evans & Sheldon, 2012). Nonetheless, it is not new that parents are able to influence coloration of their offspring through their breeding performance (Fitze *et al.*, 2003a & 2003b; Isaksson *et al.*, 2006; Evans & Sheldon, 2012; García-Navas *et al.*, 2012; Matrková & Remes, 2012; Pagani-Núñez & Senar, 2014). In this regard, parental investment is known to be a key factor to influence the carotenoid-based coloration of their nestlings (Senar *et al.*, 2002; Isaksson & Andersson, 2007). This pattern is probably stronger in Mediterranean ecosystems. In our area, prey densities are lower and highly variable across time and space compared with that of Central Europe [Blondel *et al.* (2010); see also Banbura *et al.* (1994) and Pagani-Núñez *et al.* (2011)]. Accordingly, parents show great consistency (Pagani-Núñez & Senar, 2013) and great inter-individual variability in prey choice (Pagani-Núñez & Senar, 2014). Our findings stress, therefore, that it is necessary to investigate parental performance in addition to habitat structure to obtain a complete picture of the main determinants of offspring fitness.

From a traditional perspective, caterpillars have been regarded as the most profitable prey and the main source of carotenoids for feather pigmentation (Slagsvold & Lifjeld, 1985; Isaksson, 2009; Sillanpää, Salminen & Eeva, 2009). However, our current and previous works provide a completely different pattern for Mediterranean tits (Barba & Gil-Delgado, 1990; Blondel *et al*., 1991; Banbura *et al*., 1994; Pagani-Núñez *et al*., 2011), with a positive correlation between carotenoid-based coloration and the intake of spiders by nestlings, as opposed to other prey [see also Pagani-Núñez & Senar (2014)]. This apparently striking result, however, could probably be expected. In the last decade, many researchers have reported the positive effect of spider intake on nestling fitness, mainly as the result of their high content of amino-acids such as taurine (Ramsay & Houston, 2003; Magrath *et al*., 2004; Arnold *et al*., 2007; Wiesenborn, 2012; García-Navas, Ferrer & Sanz, 2013; Pagani-Núñez & Senar, 2014). The underlying mechanism driving this correlation, however, is not yet clear. Recent research has shown multiple and complex interactions between carotenoid availability, anti-oxidative response, and feather coloration of nestlings (Alonso-Álvarez *et al*., 2004; Costantini, Fanfani & Dell'Omo, 2007a; Isaksson & Andersson, 2008). Some works have even suggested a trade-off between the use of carotenoids as feather pigments and their use as anti-oxidants, reporting detrimental effects of carotenoids above certain thresholds (Bertrand *et al*., 2006; Hõrak *et al*., 2006; Fitze *et al*., 2007; Costantini *et al*., 2007b; Isaksson *et al*., 2008; Huggins *et al*., 2010). The relative significance of carotenoids and anti-oxidants for nestling coloration thus remains a controversial issue.

We found that time of breeding had a great effect on the carotenoid-based plumage coloration of nestlings, with both lightness and chroma increasing across the breeding season, while hue decreased. An effect of date on nestling coloration was expected given the relevance of the time of breeding for parental performance, reported many years ago (Perrins, 1970). Hue decreased across the season and with the intake of other prey (as grasshoppers, moths and stick-insects), so that we suggest that it may be considered to be a reliable signal of environmental availability of carotenoids (Isaksson, Von Post & Andersson, 2007; Ferns & Hinsley, 2008; Senar *et al*., 2008; Arnold *et al*., 2010; del Val, Negro & Senar, 2013). It is usually assumed that better parents breed earlier (García-Navas & Sanz, 2011; Pagani-Núñez & Senar, 2014). Consequently, parents were likely prone to breed in the early stages of the season to exploit this high availability of carotenoids. Interestingly, our data signal a trade-off in function of date between lightness, the structural component of coloration, and hue, which is mainly related to carotenoid intake. This finding is in line with previous research. It has been stated that early growth condition determines the structural component of carotenoid-based coloration, while carotenoid availability determines its chromatic aspect (Jacot *et al*., 2010; Matrková & Remes, 2012). It is possible that nestlings allocated more resources to improve feather quality, compensating for the decrease in carotenoid availability across the season (Galvan, Diaz & Sanz, 2009). Alternatively, an increase in mean temperatures across the season could increase feather quality (Dawson, Lawrie & O'Brien, 2005). In any case, the selection of spiders as a main food source seems to impact strongly on the ecology of our model species (Catoni, Peters & Schaefer, 2008). This finding likely signal the importance of considering complex interactions between several food sources (Raubenheimer, 2011), as opposed to the more simplistic traditional view derived from the optimal foraging theory (Charnov, 1976; Pyke, Pulliam & Charnov, 1977).

Why habitat structure produced a direct effect on certain parameters of nestling coloration remains unanswered. We recorded a negative interaction between lightness and PC3 – oak maturity, and a positive interaction between hue and PC1 – tree size. Both correlations are in line with previous findings (Arriero & Fargallo, 2006; Ferns & Hinsley, 2008; Galvan *et al*., 2009). We think that the positive effect of PC1 – tree size on hue may be related to a higher availability of carotenoids in all trophic levels in the most structured patches of the forest (Isaksson, 2009). The negative interaction between PC3 – oak maturity and lightness would be because in areas of low carotenoid availability, where oaks and holm oaks are less mature, nestlings likely increase their investment in feather quality (Galvan, Diaz & Sanz, 2009). Chroma and lightness correlated positively between them, while chroma correlated negatively with hue. Consequently, our findings support the consideration of hue as a reliable signal of carotenoid content in feathers [Senar *et al*. (2008), but see results of Shawkey *et al*. (2006)]. On the other hand, nestlings' body condition did not correlate with their own coloration. In line with our results, it has been suggested that nestlings' body condition and their carotenoid-based coloration may be determined by different pathways (Hõrak *et al*., 2000; Galvan *et al*., 2009). Also, it is known that great tit nestlings may differ in their coloration in function of sex (Slagsvold & Lifjeld, 1985). Given that we computed mean coloration within each nest, sex-ratio could hide the interaction between nestlings' body condition and their coloration. The fact that we did not find a positive correlation at the nest-level does not rule out the possibility that this correlation could be positive in some cases at an individual level (Galvan *et al*., 2009).

To conclude, we found prey composition had a large effect on nestling coloration. These results support the view that, when assessing nestling coloration in relation to habitat, we cannot establish a direct link between habitat and food and it is advisable to combine the assessment of both groups of parameters. Moreover, we found for the first time a positive effect of spider intake on nestling coloration. Finally, and in line with previous studies, we found a correlation between habitat structure and nestling coloration, although this can not be directly attributed to prey composition. Further research is needed to adequately explain this complex issue.

ACKNOWLEDGEMENTS

We thank María Sabater, Neus Pérez, Inés Sanchez, Marta Gómez, Josep Piqué, Miguel Prieto and Jordi Agulló for their help in the fieldwork regarding habitat description. We also thank Lluís Comas for his advice in assessing habitat structure. We thank Llüisa Arroyo her help in the laboratory, Caroline Newey for revising an English version, and the Gil family, owners of Can Catà, for allowing us to work on their property. Two anonymous referees helped to improve an earlier version of the manuscript. This study was funded by CGL-2012–38262 research project to J.C.S and F.U and by the FPI grant BES2010-040359 to E.P.N., from the Ministry of Science and Innovation, Spanish Research Council. Birds were handled with the permission of the Departament de Medi Ambient, Generalitat de Catalunya. Rings were provided by the Catalan Ringing Office (ICO).

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