UNIVERSIDAD COMPLUTENSE DE MADRID

FACULTAD DE CIENCIAS BIOLÓGICAS

Departamento de Biología Animal I (Zoología)

MIGRACIÓN Y SEDENTARISMO EN LOS PASERIFORMES FORESTALES IBÉRICOS: PERSPECTIVAS ECOLÓGICAS Y EVOLUTIVAS

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

Javier Pérez Tris

Bajo la dirección del doctor

José Luis Tellería Jorge

Madrid

DEPARTAMENTO DE BIOLOGÍA ANIMAL I (ZOOLOGÍA)

FACULTAD DE CIENCIAS BIOLÓGICAS

UNIVERSIDAD COMPLUTENSE DE MADRID

MIGRACIÓN Y SEDENTARISMO EN LOS PASERIFORMES FORESTALES IBÉRICOS: PERSPECTIVAS ECOLÓGICAS Y EVOLUTIVAS

JAVIER PÉREZ TRIS

TESIS DOCTORAL

FEBRERO DE 2001

Migración y Sedentarismo en los Paseriformes Forestales Ibéricos:

Perspectivas ecológicas y evolutivas

Diseño y maquetación: Javier Pérez Tris
Ilustraciones: © Txuso García

NOTA IMPORTANTE:

Esta Memoria de Tesis Doctoral es una colección de manuscritos en diferentes estados de publicación, cada uno de los cuales ha dado lugar a un bloque temático independiente con categoría de capítulo.

El bloque titulado* <u>Introducción general</u> y conclusiones*, que constituye la Tesis en sí, revisa el estado actual del tema y sitúa el trabajo realizado en su contexto teórico, planteando los <u>objetivos</u> de la Tesis; presenta los resultados obtenidos realizando una <u>discusión integradora</u> de los artículos que componen la Tesis, y expone sus <u>conclusiones</u>, así como las perspectivas que abren estos estudios para futuras líneas de investigación.

El resto de los capítulos reproduce el texto íntegro de los manuscritos de que consta la Tesis. Por esa razón, se han presentado en el idioma en que, en su día, fueron publicados o enviados para su publicación. En cualquier caso, todos los capítulos van acompañados de un resumen en castellano.

Índice

*Agradecimientos**

Y por fin, después de tanto tiempo, llega el momento de agradecerles su apoyo a las personas que han hecho posible esta Tesis. En primer lugar, creo que es importante destacar que todo esto es el resultado de la colaboración entre los miembros de un magnífico equipo. Han sido muchos los días de trabajo en el campo con Roberto Carbonell, Álvaro Ramírez y José Luis Tellería, como muchas han sido las discusiones de sobremesa con ellos y con Rocío Baquero, Pepe Díaz, Esteban Fernández-Juricic, Txuso García, Tomás Santos y Emilio Virgós. Todos ellos, sin lugar a dudas, han contribuido a que este trabajo llegara a ser lo que es hoy.

A José Luis Tellería, mi director, quiero agradecerle su confianza desde el primer momento, su ánimo contagioso y, sobre todo, su trato de igual a igual. Él ha sido mi mejor escudo frente a los golpes y el mejor compañero con quien compartir los éxitos, especialmente cuando ha sido delante de una buena urta (o al menos de un montaíto del Pasillo tarifeño). Telle, no cambies de vida.

Las Tesis Doctorales no salen de la nada. Roberto Carbonell inició los estudios de currucas capirotadas que, pasado el tiempo, se continuaron con estos que nos traemos ahora juntos entre manos. De hecho, Roberto tomó muchos de los datos que se presentan aquí, algunos incluso antes de que yo empezara mi Tesis. Pero me apetece más recordar todos esos buenos momentos campeando entre Vitoria y Tarifa, en su Gallegos del alma, en Lerma o simplemente de cañas con Roberto *Corazón de Hornazo*.

¡Qué habría sido del trabajo de campo sin Álvaro Ramírez! Supongo que me habría olvidado de tomar la mitad de las medidas de cada pájaro, y que a estas alturas habría perdido ya todas las redes por el monte. Menos mal que, a fuerza de calorías moriónicas, Álvaro consigue mantenerse siempre espabilado, que si no... Pero hubo otras personas que arrimaron el hombro en el campo, como Rocío, que me echó un cablazo una vez que estaba sólo ante el peligro. Y recuerdo también algunas apariciones estelares de Elena, Mónica, Pepe, Tomás y Txuso.

Tomás ha tenido que aguantar la ocupación de su despacho durante unos añitos. Bueno, eso dice él, pero yo estoy seguro de que me echaba de menos durante mis ausencias. Eso sí, ha soportado como un santo la lectura, y peor aún, la redacción de mis manuscritos (aunque creo que se ayudó de la guía de Santa Teresa y los consejos del Cardenal Mendoza para poder atravesar semejante peladal Pampero). Como Pepe, que si trepase a los árboles igual que inventa esas memorables frases finales... En fin, él siempre se ganó a pulso su ración de ortiguitas al yodo.

**Esta Tesis Doctoral ha sido financiada por el Ministerio de Educación y Ciencia (Proyecto PB92-0238 de la Dirección General de Investigación Científica y Técnica: "Relaciones entre fragmentación forestal y biología de vertebrados forestales") y por el Ministerio de Educación y Cultura (Proyecto PB97-0325: "Biología de poblaciones marginales de aves forestales"). Sus métodos (en lo referente a la manipulación de aves) fueron autorizados por las Consejerías de Medio Ambiente de la Diputación Foral de Álava, Comunidad de Madrid y Junta de Andalucía. Durante su elaboración, el autor disfrutó una Beca Predoctoral de la Universidad Complutense de Madrid.*

Quizás alguien se haya preguntado qué pudo impulsarme a dedicar mi tiempo al estudio de esos pajarillos. Parte de la respuesta podría estar en las magníficas acuarelas de Txuso, que por si fuera poco las hizo con la mano medio rota. ¿Para cuándo esos judiones?

Sagrario, Cosme, Tere, Esther y Raúl, mi familia, me han dado su apoyo incondicional. Hay que estar ahí para llevar con tanta serenidad toda una prole de bio-quimio-geólogos, y mis padres han pasado con sobresaliente. Espero poder corresponderles.

A mis compañeros y amigos Álvaro, Pepe, Roberto, Rocío, Telle, Tomás y Txuso, por todo lo aprendido juntos. A Maite, Sergio y María por seguir ahí. A Jesús (*Glorioso*), Ana, Javi (*Ringer King*) y a todos los amigos de Monticola, por crear al biómetra e inyectarle moral a chorros. A Rocío por ser tan deliciosamente pesada. A Elena por animarme siempre, a favor y contra corriente. A Manolo por haber podido contar siempre con su colaboración. A Staffan por confiar en mis posibilidades, abrirme la puerta y enseñarme tanto. A Ana y Debora por conjurar el desánimo a base de Brownies y canela (tack!). En definitiva, ya casi sin aliento, a todos los que me habéis hecho pasar estos buenos años,

Muchas gracias

A mis padres

Migración y sedentarismo en los paseriformes forestales ibéricos: perspectivas ecológicas y evolutivas

Javier Pérez-Tris*

La migración es una respuesta de las aves ante la estacionalidad de sus áreas de distribución. En el Paleártico, donde la estacionalidad aumenta con la latitud, muchas especies son totalmente migradoras en áreas norteñas, pero paulatinamente van adoptando un comportamiento más sedentario hacia el sur. Sin embargo, en la región Mediterránea, la existencia de montañas y mesetas da lugar a marcados contrastes de estacionalidad relacionados con la altitud que podrían alterar este patrón geográfico. Esta Tesis analiza la variación en el comportamiento migrador de los paseriformes forestales (distintos miembros de las familias Turdidae, Sylviidae y Paridae) asociada a los cambios de estacionalidad en la península Ibérica, y las consecuencias que dicha variación tiene sobre la demografía, ciclo vital y morfología de las aves. En estas especies, el comportamiento migrador se acentúa en las regiones más estacionales de la Península (las mesetas y montañas de la mitad norte), y desaparece en las zonas menos estacionales del sur peninsular. La mayor movilidad de las poblaciones de la meseta norte se detecta a escala poblacional mediante una disminución de su abundancia durante el invierno, y a escala individual por una menor constancia de las aves en sus áreas de cría. Estos cambios llevan asociadas variaciones en los ciclos vitales y la morfología de las aves: las poblaciones más migradoras muestran una mayor fecundidad pero una menor supervivencia, y presentan rasgos relacionados con la optimización de la migración más acentuados (alas más largas y apuntadas y cola más corta). Esta covariación entre estacionalidad, migratoriedad, fecundidad, mortalidad y morfología de las aves, nunca antes ilustrada a nivel intraespecífico, tiene importantes implicaciones. Desde una perspectiva aplicada, plantea la conveniencia de revisar los criterios de conservación de especies ampliamente distribuidas, que deberían tener en cuenta la posible diferenciación local de sus poblaciones. Desde una perspectiva evolutiva, la diferenciación entre migradores y sedentarios se mantiene a pesar de que ambos invernan en simpatría. Dado el desequilibrio numérico entre ambas poblaciones y la mayor fecundidad asociada con el aprovechamiento de áreas de cría estacionales, los sedentarios podrían extinguirse si su invernada transcurriese en igualdad de condiciones que la de los migradores. Esto podría evitarse si migradores y sedentarios seleccionasen diferentes recursos o tipos de hábitat, lo que impediría su competencia durante el invierno. Sin embargo, estudios realizados en el Campo de Gibraltar con petirrojos (*Erithacus rubecula*) y currucas capirotadas (*Sylvia atricapilla*) muestran que los sedentarios cuentan con ventajas competitivas sobre los migradores durante el invierno. Este resultado permite responder preguntas centrales en la teoría de la evolución de la migración a partir de poblaciones sedentarias, como de qué modo los procesos dependientes de la densidad de población pudieron estar implicados en la dispersión de los primeros migradores fuera de sus áreas de cría, qué importancia tiene la competencia invernal como un coste de la migración, o cómo han conseguido subsistir los sedentarios a pesar de su menor fecundidad y su convivencia con los migradores durante buena parte del año.

Muchas veces nos hemos preguntado por qué migran las aves, qué les lleva a desplazarse lejos de sus áreas de cría, exponiéndose al cansancio, la desorientación, la impredecibilidad de las condiciones meteorológicas y el acecho de los depredadores. Cuando consideramos el significado de la migración, normalmente pensamos sólo en una huida de la dureza del invierno, de la escasez de alimento, en un viaje hacia zonas más benignas que puedan garantizar la supervivencia de las aves. Pero no siempre consideramos que ese movimiento también tiene unos costes que deben ser compensados de algún modo. La mayor probabilidad de sobrevivir en ambientes más favorables consti-

---

**Este capítulo sitúa la Tesis en su contexto teórico, plantea sus objetivos, resume sus principales resultados y expone sus conclusiones y perspectivas.*

tuye un beneficio obvio, pero no es suficiente para sustentar la migración como una estrategia estable. De hecho, podemos dar la vuelta a nuestra pregunta: si las áreas de reposo ocupadas fuera de la estación reproductora son tan adecuadas, ¿por qué abandonarlas para criar en áreas lejanas? En definitiva, ¿por qué debiera un ave exponerse a los riesgos de la migración pudiendo ser sedentaria?

Para las especies o poblaciones migradoras, las áreas de cría y de reposo siguen ritmos complementarios de producción primaria, como resultado de la estacionalidad de, al menos, una de ellas (Bernis 1966, Alerstam & Högstedt 1982). Desde la perspectiva de las aves, la estacionalidad se manifiesta mediante la alternancia de períodos favorables y desfavorables a lo largo del año, midiéndose la adecuación de cada uno de ellos por su producción primaria (Mooney 1981, Alerstam 1990). Por ejemplo, puede existir una estación húmeda oponiéndose a una seca, como sucede en zonas tropicales; o una cálida frente a una fría, como ocurre en la zona templada. En esta última zona, la primavera es la estación favorable, durante la cual el aumento de la longitud del día y la temperatura favorecen la producción primaria. En invierno, sin embargo, los días son cortos y las temperaturas bajas, de modo que la producción primaria alcanza su nivel mínimo (Alerstam 1990). Este contraste entre primavera e invierno se acentúa con la latitud. A medida que nos aproximamos a los polos, la primavera se va haciendo más corta y el invierno más largo, con lo que la producción primaria anual se concentra en un período más corto de tiempo. Hacia el ecuador, por el contrario, la producción primaria se reparte cada vez más a lo largo del año, hasta que el límite entre primavera e invierno se difumina en las latitudes más bajas (Herrera 1978).

Aprovechando su facilidad de movimiento, las aves pueden beneficiarse de la concentración productiva primaveral desplazándose para criar a latitudes altas (Ricklefs 1980). Por otro lado, aumentando su reclutamiento, compensan los costes de su obligado desplazamiento a zonas meridionales durante el invierno (Alerstam 1990, Berthold 1993). A menores latitudes, los beneficios reproductivos de la migración disminuyen hasta que, pasado cierto umbral, dejan de compensar sus costes, y el sedentarismo aparece como una opción más ventajosa (Greenberg 1980). Este balance entre costes y beneficios da lugar a una enorme variación en el comportamiento migrador de las aves. En primer lugar, la proporción de especies migradoras en las comunidades de aves aumenta con la latitud (MacArthur 1959, Herrera 1978, Newton & Dale 1996). Por otro lado, el comportamiento migrador de una determinada especie puede variar notablemente a medida que nos desplazamos por su área de distribución, desde la migración total y de larga distancia en latitudes altas hasta el sedentarismo en las zonas menos estacionales, pasando en muchos casos por todos los grados posibles de migración parcial (Berthold 1999). Estas variaciones inter e intraespecíficas en la intensidad del comportamiento migrador a escala

Figura 1. Distribución de las principales áreas montañosas del Paleártico occidental (en negro) y de las regiones con clima Mediterráneo cálido (en gris, según Aschmann 1971). El fuerte contraste entre las zonas elevadas, de marcada estacionalidad, y las zonas más atemperadas, más adecuadas para la invernada, sugiere el potencial para el desarrollo de movimientos por parte de las poblaciones mediterráneas de aves.

continental se traducen, además, en cambios en la morfología de las aves. La migración implica fuertes presiones selectivas tendentes a minimizar los costes del desplazamiento en todas sus formas posibles (tiempo invertido, energía consumida, exposición a los depredadores, etc.; Alerstam & Hedenström 1998). En este sentido, tener alas largas y apuntadas aumenta la resistencia durante los vuelos largos y sostenidos, y una cola corta supone un ahorro energético en este tipo de desplazamientos. Como consecuencia, las especies de aves migradoras tienden a acentuar estos rasgos, presentando alas largas y apuntadas y colas cortas, a pesar de que esto disminuye su capacidad de maniobra (Winkler & Leisler 1992, Mönkkönen 1995). Los mismos cambios morfológicos ocurren dentro de una determinada especie cuando su comportamiento migrador varía a lo largo de su área de distribución (Tellería & Carbonell 1999).

El Mediterráneo y la altitud a bajas latitudes

Dentro del Paleártico occidental, la región Mediterránea se caracteriza por una producción primaveral alta –pero interrumpida por una intensa sequía estival–, unida a un invierno templado y moderadamente productivo (Mooney 1981). Además, el otoño es un período de producción elevada debido a que en él coincide la vuelta de las lluvias tras el estío con un ambiente razonablemente térmico (Lautensach 1967). En este momento, que por su intensidad productiva y concentración temporal se ha denominado “otoñada”, fructifican muchas especies vegetales y recuperan su actividad muchos invertebrados. A lo largo del invierno, la productividad se atenúa pero se mantiene a niveles suficientemente altos como para permitir la invernada de enormes poblaciones de aves procedentes del Paleártico (Moreau 1972, Tellería 1988). Ante este panorama de bondad climática, y de acuerdo con el patrón geográfico descrito más arriba, cabría esperar que las migraciones de las aves mediterráneas fuesen de escasa envergadura. De hecho, si excluimos las especies migradoras transaharianas (que invernan en el centro y sur de África; Bernis 1966, Moreau 1972), la región Mediterránea es mucho más rica en especies o poblaciones sedentarias que las áreas más septentrionales del Paleártico (véanse los estudios interespecíficos de Herrera 1978 y Newton & Dale 1996, y varios ejemplos a nivel intraespecífico en Cramp 1992).

Sin embargo, la región Mediterránea no es homogénea en sus condiciones ambientales. El Mediterráneo es el sector del Paleártico occidental con más sistemas montañosos y, por ende, el de mayor contraste altitudinal a escala regional (Fig. 1). El efecto de la altitud en esta región es similar al de la latitud a escala continental, de forma que la estacionalidad puede acentuarse mucho en sus zonas más elevadas (Aschmann 1971). De hecho, las mesetas y montañas mediterráneas presentan unos niveles mayores de productividad primaveral –pero condiciones más rigurosas durante el invierno–, que las tierras bajas costeras de la región, niveles que son comparables a los de zonas más norteñas (Aschmann 1971; Fig. 2 y 3).

Dada esta variación ambiental tan pronunciada, y teniendo en cuenta lo reducido de su escala geográfica, resultaría muy interesante determinar hasta qué punto las aves se ajustan a las variaciones de estacionalidad en el área mediterránea modificando su comportamiento migrador y, como consecuencia, su dinámica poblacional, ciclo vital y morfología. Amparándose en las predicciones del patrón latitudinal, numerosos tratados sobre migración han asumido que las poblaciones mediterráneas de muchas aves son principalmente sedentarias (Alerstam 1990, Berthold 1993). Su argumento es que si ciertas especies mantienen poblaciones sedentarias en áreas tan norteñas como las islas Británicas o las costas de Europa occidental (por ejemplo, Adriaensen & Dohnt 1990), resultaría sorprendente que mantuviesen poblaciones migradoras en áreas más meridionales. Pero a pesar de lo razonable que, a primera vista, pudiera resultar esta postura, la envergadura de los movimientos que realizan las poblaciones de aves mediterráneas dista mucho de estar clara (Harrison 1982, Purroy 1997, Tellería *et al*. 1999). Y todavía se

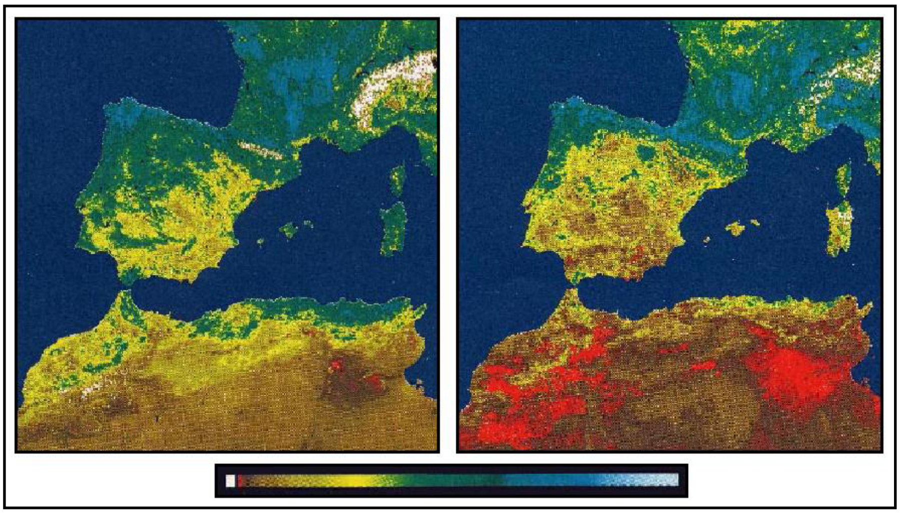

Figura 2. Niveles de producción primaria en la península Ibérica y áreas circundantes, medida mediante el índice de vegetación "diferencia normalizada" (NDVI, obtenido por los satélites de la NOAA; Gutman *et al.* 1995). Los gráficos representan la situación en primavera (izquierda) y verano (derecha). El índice toma valores entre 0 (rojo fuerte) y 1 (azul claro), de acuerdo con la escala de color mostrada al pie de la figura.

sabe mucho menos sobre los efectos que pudieran tener dichos movimientos sobre la biología de estas poblaciones de aves.

Un caso particularmente interesante: los paseriformes forestales ibéricos

Esta Tesis reúne parte de los resultados de una línea de investigación sobre las implicaciones ecológicas y evolutivas que tiene la existencia de poblaciones sedentarias y migradoras de paseriformes forestales en la península Ibérica. El área geográfica escogida es particularmente adecuada para este tipo de estudios debido a su gran extensión (compárese con otras áreas mediterráneas en la Fig. 1) que, unida a su diversidad fisiográfica, garantiza una buena representación de zonas con diferentes regímenes de estacionalidad (Font 1983). Por otra parte, se sabe muy poco sobre la migración de los paseriformes forestales ibéricos, probablemente debido al reducido esfuerzo de anillamiento a que han sido sometidas sus poblaciones. La actividad de los anilladores ibéricos se ha concentrado tradicionalmente en aquellas especies, tipos de hábitat y fechas que pudiesen garantizar un elevado número de capturas. De este modo, se ha dedicado mucho esfuerzo al marcaje de grandes aves en nido y al anillamiento de paseriformes en dormideros invernales o en sus pasos migratorios, sobre todo en medios palustres. Sin embargo, el esfuerzo de anillamiento invertido en ambientes forestales ha sido mucho menor, especialmente en época de cría, como demuestra la deficiencia de anillamientos en primavera con respecto a los realizados en invierno para las especies más comunes de aves forestales (análisis inédito del banco de datos de la Oficina de Anillamiento de la Dirección General de Conservación de la Naturaleza). Este hecho, unido al pequeño tamaño de las poblaciones ibéricas –en comparación con las norteñas que llegan a la Península para pasar el invierno (Tucker & Heath 1994)–, ha limitado la información aportada por el anillamiento sobre los movimientos de los paseriformes forestales en este ámbito geográfico.

De acuerdo con la distribución de los bosques en la península Ibérica, los paseriformes forestales ibéricos afrontan diferentes situaciones de estacionalidad (Fig. 4). Sus poblaciones soportan cambios ambientales acusados entre primavera e invierno en las áreas elevadas del centro y norte peninsular, pero disfrutan condiciones mucho más estables en las zonas costeras meridionales (Fig. 3 y 4). En muchas de estas zonas atemperadas, como cabría esperar, dichas especies son estrictamente sedentarias, un hecho comprobado por el control primaveral e invernal de individuos anillados (Finlayson 1981, Tellería *et al.* 1999, datos propios inéditos). No sabemos, sin embargo, si estas poblaciones sedentarias son sustituidas por poblaciones migradoras en las zonas más estacionales de la península Ibérica ni, en caso de ser así, si ese posible comportamiento migrador a tan pequeña escala geográfica tiene implicaciones importantes sobre la ecología y morfología de estas especies.

RESULTADOS Y DISCUSIÓN GENERAL

Consecuencias ecológicas de la migración en la península Ibérica

En el primer capítulo de la Tesis exploramos las evidencias existentes sobre los cambios de intensidad del comportamiento migrador de dos especies comunes en la península Ibérica: el petirrojo (*Erithacus rubecula*) y la curruca capirotada (*Sylvia atricapilla*). Nuestro objetivo fue ilustrar si la diferente estacionalidad de las regiones ibéricas afecta a la migratoriedad de esas especies, y si esto lleva asociados cambios en su fecundidad y esperanza de vida (como reflejo de los beneficios y costes de la migración, Roff 1992). Comparamos tres regiones con diferentes regímenes de estacionalidad (Fig. 4): la meseta norte, el área más estacional de la Península; las tierras bajas mediterráneas, la zona menos estacional, y la cornisa Cantábrica, un área de estacionalidad intermedia entre las dos anteriores. Tras una extensa revisión de estudios de comunidades, y aprovechando la escasa información contenida en los datos de anillamiento y fichas de nido acumulados hasta el momento, encontramos una clara correlación entre estacionalidad y migración. Ésta se manifiesta en las zonas más estacionales por el descenso invernal de las abundancias locales y el acortamiento del período de estancia de los individuos en el área de cría. Además, estos movimientos, probablemente de pequeña escala, parecen afectar al ciclo vital de las aves, con beneficios reproductivos asociados a la migración pero también costes en términos de supervivencia. Así, las poblaciones de estas especies nidificantes en las mesetas presentan una mayor fecundidad, pero una menor esperanza de vida, que las localizadas en zonas menos estacionales del sur peninsular y de la cornisa Cantábrica.

Esta dicotomía entre poblaciones migradoras y sedentarias en los paseriformes forestales ibéricos se da en un contexto biogeográfico interesante, puesto que las poblaciones sedentarias ocupan el borde meridional de la distribución de esas especies. De acuerdo con diferentes modelos teóricos, que predicen el deterioro progresivo de la calidad del hábitat hacia el borde de la distribución de una determinada especie (Brown 1995), podría ocurrir que las poblaciones meridionales, sedentarias, sufriesen algún síndrome de inadaptación a las condiciones locales del sur peninsular. Después de todo, y pese a su bonanza invernal, estos bosques están sometidos a un fuerte estrés hídrico al final de la época de cría de las aves que albergan (Fig. 2). Este síndrome podría manifestarse, por ejemplo, por medio de una disminución paulatina de la densidad de población en zonas cada vez menos adecuadas, cercanas al borde de la distri-

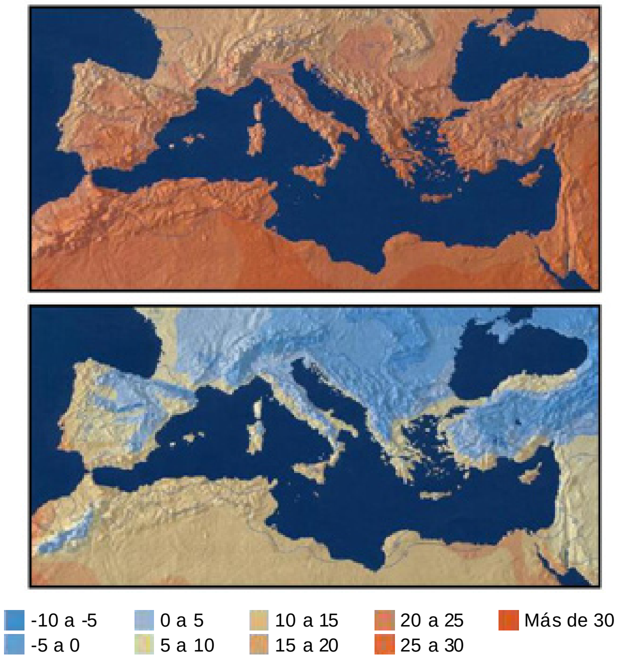

Figura 3. Variaciones de temperatura media en superficie (ºC) en la cuenca Mediterránea, en julio (arriba) y enero (debajo).

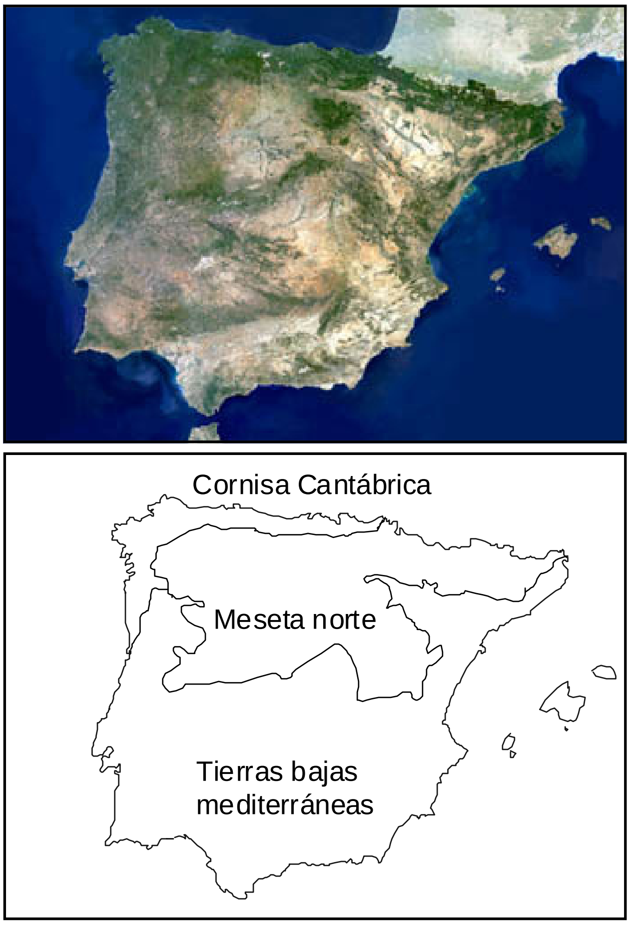

Figura 4. Arriba, una fotografía desde satélite de la península Ibérica en la que se aprecia la distribución de las principales masas forestales, que aparecen en color verde. Existen grandes extensiones boscosas en el norte, pero éstas se van enrareciendo hacia el sur, donde sólo quedan pequeños reductos forestales. Debajo se muestra una división regional de la península Ibérica conforme con sus contrastes de estacionalidad. La meseta norte es la región más estacional, seguida por la cornisa Cantábrica y las tierras bajas mediterráneas. Solapando ambas imágenes se puede apreciar las diferentes situaciones de estacionalidad a que se ven sometidos los paseriformes forestales ibéricos.

bución (Lawton 1993), o mediante una menor calidad fenotípica de los jóvenes nacidos en áreas meridionales (Dias 1996). Alternativamente, las poblaciones meridionales podrían estar aclimatadas, o incluso adaptadas, a sus condiciones locales (Hoffmann & Blows 1994). En este sentido, dado que unas poblaciones son sedentarias y otras son migradoras, su diferenciación morfológica podría ser una buena evidencia de diferenciación poblacional en el borde de la distribución. Efectivamente, se sabe que las aves migradoras presentan alas más largas y apuntadas, así como colas más cortas, que las sedentarias (Fig. 5; Winkler & Leisler 1992, Mönkkönen 1995), y que estos rasgos están determinados genéticamente (Berthold 1996). Por otra parte, estudios previos habían demostrado esta diferenciación morfológica entre las poblaciones migradoras y sedentarias de curruca capirotada en la península Ibérica (Fig. 5; Tellería & Carbonell 1999), así como el deterioro de la condición física en las poblaciones migradoras con el aumento de la xericidad ambiental hacia el sur (Carbonell & Tellería 1998, 1999).

En el Capítulo 2, exploramos los cambios en la abundancia local del petirrojo a lo largo del gradiente ibérico de sequedad creciente hacia el sur, las posibles diferencias morfológicas entre petirrojos migradores y sedentarios, y las variaciones en la condiciones de desarrollo de los jóvenes mediante una combinación de índices de estabilidad durante el desarrollo y estado nutricional (Lindström 1999). Encontramos que, a pesar de disminuir su frecuencia de aparición hacia el sur, los petirrojos mantienen densidades similares en los hábitats que ocupan a lo largo de la península Ibérica, probablemente como resultado de la selección de bosques por encima de cierto umbral de calidad. Además, y pese a estar diferenciados morfológicamente en el sur, empeoran su condición física con respecto a las poblaciones del norte peninsular a medida que la sequía progresa durante el verano. Queda por saber, sin embargo, si esta peor condición física estival pone de manifiesto la inadaptación de los petirrojos sedentarios a sus condiciones locales o si, de acuerdo con los resultados del primer capítulo, estaría evidenciando parte de los beneficios reproductivos de la migración de las poblaciones norteñas.

En el Capítulo 3 estudiamos si esta correlación entre estacionalidad, migratoriedad y morfología es realmente un patrón extendido entre los paseriformes forestales ibéricos. Además del petirrojo y la curruca capirotada, consideramos otras cuatro especies comunes, también migradoras de corta distancia en el Paleártico (mirlo común, *Turdus merula*; reyezuelo listado, *Regulus ignicapillus*; herrerillo común, *Parus caeruleus*, y carbonero común, *Parus major*). Tradicionalmente, estas seis especies habían sido consideradas como principal o exclusivamente sedentarias en la Península (por ejemplo, Purroy 1997). Sin embargo, nuestro estudio permitió establecer un patrón general según el cual la abundancia de estas especies disminuye en las mesetas durante el invierno. Paralelamente a estos cambios en abundancia, los individuos presentan alas más largas y apuntadas, así como colas más cortas, en esas zonas estacionales. La variación en el comportamiento migrador de las poblaciones ibéricas de estas especies explicaría perfectamente esta correlación entre estacionalidad, variación en abundancias y morfología. Esta interpretación se ve reforzada, además, porque el ruiseñor común (*Luscinia megarhynchos*), una especie transahariana y, por tanto, de comportamiento migrador homogéneo en la Península, no satisfizo el patrón definido por las especies migradoras de corta distancia.

La estrategia de los sedentarios

Con todo lo expuesto hasta ahora, podemos concluir que las poblaciones sedentarias del sur peninsular disfrutan de peores condiciones para la reproducción que las migradoras. En primer lugar, consiguen una menor fecundidad al ocupar zonas menos productivas (Capítulo 1). Además, la sequía estival se manifiesta antes en sus áreas de cría, coincidiendo con la emancipación de sus jóvenes y causando un deterioro de su condición física (Capítulo 2). Pero estas poblaciones no se ven perjudicadas únicamente por el impacto negativo que, probablemente, todo esto causa sobre su reclutamiento. Durante el invierno, soportan la ocupación de sus áreas residenciales por los migradores que, en enormes cantidades, llegan al Mediterráneo para invernar. La invernada de ambas fracciones poblacionales en simpatría plantea una situación conflictiva. Los recursos disponibles en las áreas de invernada son limitados, de modo que cabe esperar que, a medida que vayan llegando más y más migradores, las interacciones entre individuos se acentúen (Fretwell & Lucas 1970, Pulliam & Danielson 1991). En este caso, las poblaciones residentes podrían extinguirse si migradores y sedentarios explotasen los mismos hábitats de invernada en igualdad de condiciones (Fig. 6 y 7). El desequilibrio numérico entre ambas poblaciones se iría acentuando progresivamente en favor de los migradores, como consecuencia del mayor reclutamiento que éstos consiguen en sus áreas de cría más favorables (Fig. 6), hasta eliminar cualquier rastro de los residentes, penalizados con una menor fecundidad (Fig. 7; Alerstam & Enckell 1979, Bell 2000).

¿Qué procesos podrían haber permitido solucionar este conflicto haciendo posible la persistencia de poblaciones sedentarias en el sur peninsular? Una primera posibilidad sería que los sedentarios disfrutasen de una mayor supervivencia que los migradores cuando coinciden en áreas de invernada simpátricas. De hecho, en el primer capítulo de la Tesis se puso de manifiesto la mayor

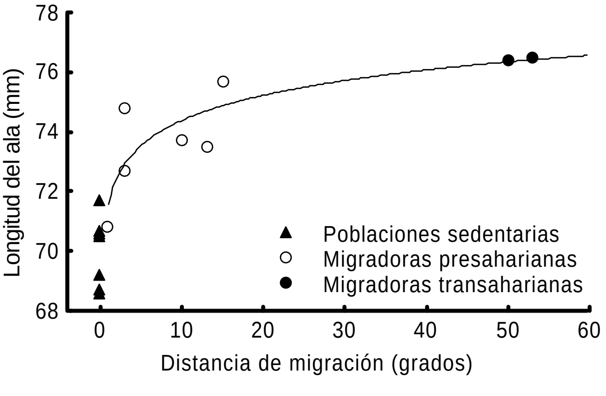

Figura 5. Relación entre la distancia de migración y la longitud del ala (cuerda máxima) en 15 poblaciones europeas de curruca capirotada (*Sylvia atricapilla*). La distancia de migración ha sido medida como la diferencia en grados de latitud entre las áreas de cria y de invernada. La latitud de invernada es la misma que la de cría en las poblaciones sedentarias, 40ºN (la latitud media de los cuarteles de invierno mediterráneos) en las migradoras presaharianas, y 10ºN (la latitud media de los cuarteles de invierno subsaharianos) en las migradoras transaharianas (modificado de Pérez-Tris & Tellería 2001).

esperanza de vida de las poblaciones meridionales. Por ejemplo, debido a su conocimiento previo de la zona, los sedentarios podrían contar con ventajas competitivas que les permitiesen resistir el aluvión de migradores (Cox 1985). Otra posibilidad, sin embargo, sería que migradores y sedentarios prefiriesen diferentes tipos de hábitat, o explotasen diferentes recursos dentro de los mismos hábitats, dando pie a la relajación, o incluso a la eliminación, de su competencia (Rappole 1995). Hasta ahora, sin embargo, la dificultad de identificar individuos migradores y sedentarios en simpatría había hecho imposible este tipo de estudios. Los resultados publicados hasta el momento se refieren a comparaciones de diferentes especies –unas migradoras y otras sedentarias– con diferentes grados de parentesco (Cox 1985, Rappole 1995), o son abstracciones teóricas obtenidas mediante simulaciones (Bell 2000). Dado lo heterogéneo de la información disponible, no resulta sorprendente que, hoy por hoy, tanto el modelo como la intensidad de las interacciones entre migradores y sedentarios en áreas de invernada comunes estén aún sometidos a un intenso debate (Bell 2000).

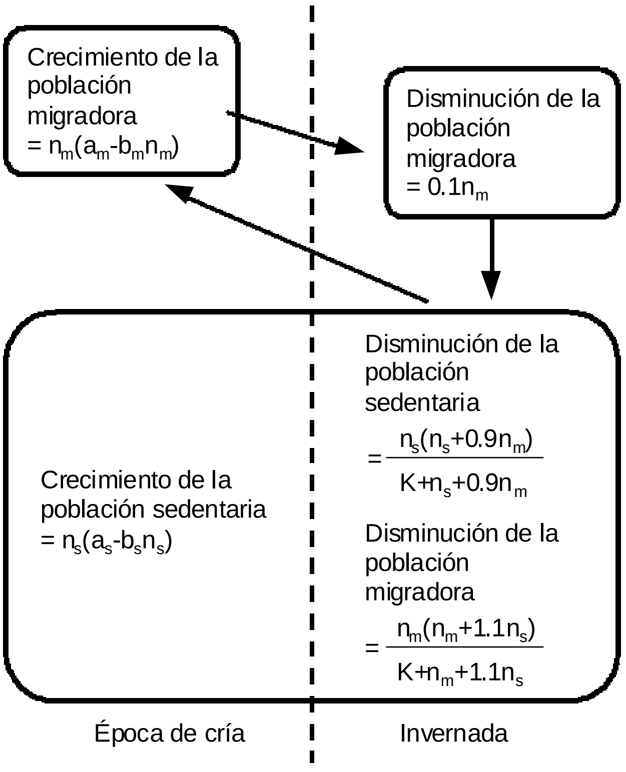

Figura 6. Modelo de cambio de tamaño de poblaciones migradoras y sedentarias a lo largo del ciclo anual. Migradores y sedentarios ocupan diferentes áreas de cría, de modo que el éxito reproductor de cada fracción depende solamente de su tamaño efectivo (n_s: sedentarios, n_m: migradores, a y b son constantes lineares que hacen que la producción de jóvenes per cápita en la población i sea = a_i-$b_i n_i$). Ambas poblaciones invernan en simpatría, y la mortalidad se asocia con el tamaño poblacional (n_s+n_m) de acuerdo con una función hiperbólica simple, de modo que la mitad de la población muere cuando el tamaño poblacional efectivo alcanza K. Se asume que la competencia entre migradores y sedentarios es asimétrica, de forma que el efecto de un sedentario sobre un migrador es 1.1 veces el de otro migrador, y el de un migrador sobre un sedentario 0.9 veces el de otro sedentario. La migración en sí misma da lugar a una mortalidad adicional, independiente de la densidad de población, entre los migradores (modificado de Bell 2000).

A lo largo de nuestra investigación, hemos conseguido reunir una buena cantidad de datos biométricos de las dos especies más comunes en nuestras áreas de estudio: el petirrojo y la curruca capirotada. En estas dos especies, las diferencias morfológicas entre poblaciones migradoras y sedentarias de la península Ibérica son muy acentuadas, tanto más si se combinan distintos rasgos relacionados con la optimización de los vuelos migratorios (longitud y apuntamiento del ala y longitud de la cola). Aprovechando esta variación tan marcada a escala peninsular, y considerando que las aves procedentes de zonas más norteñas tienen rasgos de tipo migrador aún más acentuados (Fig. 5), desarrollamos funciones discriminantes con las que diferenciar individuos migradores y sedentarios durante el invierno (Capítulos 4 y 5), lo cual nos dio la oportunidad de estudiar las interacciones entre ambos grupos de población en sus áreas de invernada comunes. Llevamos a cabo estos estudios en la comarca del Campo de Gibraltar (Cádiz), donde se pueden distinguir dos tipos de hábitat, de diferente calidad y con distinto significado desde la perspectiva de las aves locales y foráneas. En esa región, los petirrojos y currucas sedentarios crían solamente en los bosques (de alcornoque *Quercus suber* y quejigo andaluz *Q. canariensis*), pero no en los matorrales de lentisco (*Pistacia lentiscus*) y acebuche (*Olea europaea sylvestris*) que los rodean (Fig. 8). Durante el invierno, los matorrales son ocupados por grandes poblaciones de estas especies, pero no se sabe hasta qué punto la dispersión de los sedentarios contribuye a esta expansión areal, ni en qué medida los migradores colonizan las sierras donde crían los sedentarios.

Nuestros estudios se centraron en evaluar si los migradores y sedentarios compiten en la ocupación de esos dos tipos de hábitat o si, por el contrario, muestran diferentes preferencias por ellos, dando lugar así a patrones de distribución invernal diferencial. En el Capítulo 6, utilizamos el petirrojo para caracterizar el patrón de ocupación de bosques y matorrales en función de la densidad de población en la región, y para examinar la importancia de la edad y el comportamiento migrador de las aves en el establecimiento de esos patrones. Este estudio permitió mostrar que los petirrojos ocupan los mejores hábitats primero, y sólo colonizan los ambientes menos adecuados cuando su aumento poblacional ha saturado aquéllos. En este escenario, sin embargo, las aves adultas e, interesantemente, las locales, cuentan con prioridad a la hora de instalarse en los mejores ambientes. Si la supervivencia de los individuos dependiese de la calidad de su hábitat (lo cual es un supuesto realista; Sherry & Holmes 1996, Newton 1998), este patrón de ocupación podría constituir un mecanismo de regulación poblacional para el petirrojo durante el invierno. Este mecanismo, además, podría explicar el mantenimiento de la población sedentaria a pesar de sus desventajas reproductivas relacionadas con la sequía estival (véase el Capítulo 2).

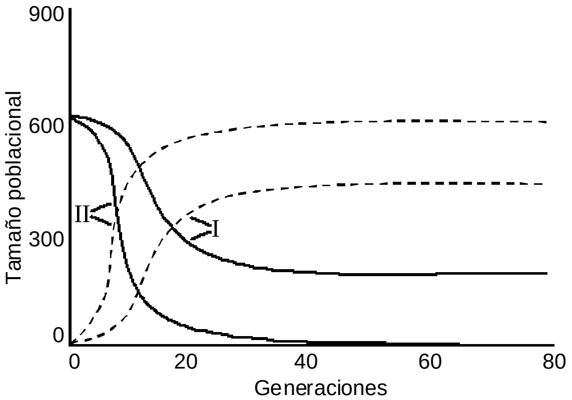

Figura 7. Dos ejemplos de interacciones entre poblaciones migradoras (líneas discontinuas) y sedentarias (se muestra el tamaño poblacional al comienzo de la época de cría) bajo el régimen ilustrado en la Fig. 6. La población residente (inicialmente en equilibrio) sufre la colonización por 3 parejas de migradores (n_m = 6 en el año 0 de la simulación). Los parámetros son $a_s = 3.0$; $b_s = b_m = -0.002$ y $K = 1000$. En el ejemplo I, $a_m = 4.5$; en el ejemplo II, $a_m = 6.0$ (modificado de Bell 2000).

En el Capítulo 7 estudiamos, de un modo más directo, las interacciones intraespecíficas entre migradores y sedentarios, en este caso utilizando la curruca capirotada como modelo. Nuestro objetivo fue determinar cuál es el papel relativo de la competencia y la selección de hábitat como determinantes de la distribución de esta especie entre bosques y matorrales, y qué consecuencias tiene dicha distribución sobre la condición física de las aves en invierno (como indicador de sus probabilidades de supervivencia). En este punto, cabe destacar las importantes implicaciones que tiene el que las interacciones sean de uno u otro tipo sobre la teoría de la evolución de la migración a partir de poblaciones sedentarias. De hecho, se sabe muy poco sobre el papel que pudo jugar la competencia entre migradores y sedentarios o su diferente selección de hábitat en la proliferación de migradores a partir de una población compuesta íntegramente por individuos sedentarios (Rappole 1995).

Como ya se observó en el caso del petirrojo, las currucas sedentarias predominan en los bosques, aunque en este caso están prácticamente ausentes de los matorrales. Entre los individuos migradores, por otro lado, los adultos son más frecuentes en los bosques, y los individuos que ocupan estos hábitats son más grandes, independientemente de su sexo o edad. Asumiendo que ser grande otorga cierta ventaja competitiva, estos resultados sugieren que las currucas capirotadas prefieren los bosques a los matorrales, y compiten por ocuparlos. De hecho, dentro de estos hábitats, sedentarios y migradores rastrean la abundancia de frutos con intensidad, si bien los sedentarios, particularmente los machos, se mantienen en las zonas más adecuadas para la reproducción, quizás para garantizar su éxito reproductor futuro mediante la ocupación temprana de los mejores territorios. No obstante, la preferencia de ambas fracciones poblacionales por los mismos recursos alimenticios desemboca en competencia, de modo que los individuos menos capaces –jóvenes o aves pequeñas– son desplazados a los matorrales, probablemente de menor calidad que los bosques. En este conflicto, los sedentarios, que son más grandes que los migradores, podrían encontrar en su mayor tamaño una nueva ventaja para resistir la llegada de los migradores, junto con las inherentes a su condición de residentes (Cox 1985). No encontramos, sin embargo, diferencias en la condición física de los individuos que ocuparon bosques o matorrales, aunque las aves desplazadas a estos últimos hábitats –cuya cobertura vegetal es mucho menor– podrían sufrir una mayor presión de depredadores. De nuevo, nuestros resultados apoyan la tesis de la ventaja competitiva de los sedentarios como un mecanismo por el cual éstos han conseguido perdurar, a pesar del enorme tamaño de las poblaciones invernantes con las que comparten su hábitat durante buena parte del año.

CONCLUSIONES Y PERSPECTIVAS

Esta Tesis demuestra que la variación en el comportamiento migrador de los paseriformes forestales en la península Ibérica tiene implicaciones ecológicas importantes. En primer lugar, conlleva cambios en fecundidad y mortalidad que, a su vez, implican presiones selectivas lo suficientemente fuertes como para afectar a aspectos tan llamativos como la morfología de las aves. Esta asociación puede resultar trivial a primera vista, pero deja de serlo si tenemos en cuenta lo pequeña que es la escala geográfica de nuestra aproximación. Por otra parte, y hasta donde nosotros conocemos, no existe ningún estudio que haya mostrado la covariación entre estacionalidad, migratoriedad, fecundidad, mortalidad y morfología dentro de una misma especie, a ninguna escala geográfica.

Las diferencias morfológicas y de comportamiento observadas en los paseriformes forestales

Figura 8. Los bosques y matorrales del Campo de Gibraltar constituyen dos tipos de hábitats de diferente calidad para la avifauna forestal. En los bosques (izquierda), la enorme cobertura arbustiva proporciona cobijo frente a posibles depredadores, y la diversidad vegetal garantiza una mayor variedad de frutos. Los matorrales, sin embargo, son medios más expuestos, dominados por el lentisco (*Pistacia lentiscus*) y el acebuche (*Olea europaea sylvestris*), como los de la fotografía de la derecha.

ibéricos coinciden con las antiguas clasificaciones taxonómicas propuestas para muchas de estas especies (por ejemplo, Vaurie 1959). Sin embargo, nunca hasta ahora se había dado un significado ecológico a esta diversidad. Nuestros resultados sugieren de manera evidente que su mantenimiento tiene que ver con el diferente comportamiento migrador de las poblaciones implicadas. En el futuro, resultaría interesante corroborar el mantenimiento de este patrón en otras poblaciones ibéricas. Por ejemplo, ¿qué cabría esperar que pasase con algunas poblaciones catalanas o extremeñas, no contempladas en nuestros estudios, pero sometidas a situaciones de baja estacionalidad? ¿Y con las de Sierra Nevada, localizadas a considerable altitud pero en situación muy meridional? En principio, lo que podríamos denominar "síndrome de migratoriedad" (definido por la covariación de todos los rasgos expresados en poblaciones migradoras) debería seguir un patrón multimodal en la Península, paralelo a las variaciones de estacionalidad entre regiones. Esto significa que, a escala peninsular, la latitud dejaría de ser un buen predictor de la proporción de especies migradoras en las comunidades de aves o la intensidad del comportamiento migrador de una determinada especie (Herrera 1978, Cramp 1992, Newton & Dale 1996), que pasarían a depender de otros factores, principalmente de la altitud. De hecho, nuestros resultados en el Capítulo 1 ya apuntan en ese sentido, dado que las poblaciones cantábricas, más norteñas, muestran al parecer un comportamiento migrador intermedio entre las de la meseta y las de las tierras bajas mediterráneas.

Los resultados de esta Tesis demuestran que la heterogeneidad ambiental de la península Ibérica lleva asociados cambios en la demografía, comportamiento y morfología de sus poblaciones de aves. Queda por aclarar, sin embargo, cómo se mantiene esta variación. Numerosos estudios han mostrado que tanto el comportamiento migrador como la morfología asociada son rasgos determinados genéticamente (Berthold 1996). Sin embargo, aunque las diferencias entre migradores y sedentarios vengan determinadas por sus genes, aún no sabemos qué mecanismos las mantienen. Durante los períodos más fríos del Pleistoceno, las áreas ocupadas actualmente por las poblaciones sedentarias actuaron como refugios para estas especies, desde los que éstas colonizaron regiones más norteñas tras la retirada de los glaciares (Blondel & Mourer-Chauviré 1998, Taberlet *et al.* 1998). La ocupación de zonas estacionales llevó asociada la adopción del comportamiento migrador (Rappole 1995, Safriel 1995, Berthold 1999) y, probablemente, el aislamiento reproductivo entre los individuos sedentarios y los primeros migradores debido a la separación de sus áreas de cría. Este aislamiento podría haber mantenido hasta la actualidad las diferencias morfológicas y comportamentales entre migradores y sedentarios. Sin embargo, dichas diferencias también podrían mantenerse mediante selección, que favorecería la migración o el sedentarismo –y la morfología asociada con cada estrategia– en diferentes situaciones de estacionalidad (Berthold 1999).

Actualmente estamos desarrollando un estudio en el que estimamos el flujo genético entre poblaciones migradoras y sedentarias ibéricas, así como entre éstas y las poblaciones de Suecia, pertenecientes a un sistema migratorio diferente (las currucas escandinavas están al otro lado de la división migratoria existente en esta especie, que separa poblaciones de migración occidental, de paso por Iberia, y oriental, que se dirigen hacia el sureste en otoño; Cramp 1992). Un análisis preliminar de la estructura de la variación genética mitocondrial en este contexto geográfico ha mostrado que las poblaciones ibéricas no están diferenciadas entre sí, pero sí lo están de las escandinavas (J. Pérez-Tris, S. Bensch, R. Carbonell & J.L. Tellería, en prep.). Estas últimas ocuparon, presumiblemente, diferentes refugios durante los períodos más fríos del Pleistoceno, localizados en Europa suroriental y oriente próximo (Taberlet *et al.* 1998). Esto significa que, probablemente, su aislamiento ocurrió hace mucho tiempo, el suficiente como para haber dejado el rastro genético observado (véase Bensch & Hasselquist 1999 para un caso similar con el carricero tordal, *Acrocephalus arundina-*

ceus). Las poblaciones ibéricas, sin embargo, debieron de separarse mucho más recientemente, lo cual explicaría que puedan considerarse panmícticas desde un punto de vista genético. La hipótesis del aislamiento no sirve, por tanto, para explicar la diferenciación morfológica y comportamental de las poblaciones migradoras y sedentarias de curruca capirotada. Sería más parsimonioso pensar que ésta se relaciona con presiones selectivas opuestas dependiendo del nivel de estacionalidad y, por consiguiente, de las ventajas relativas de la migración o el sedentarismo en cada región (Berthold 1999).

Desde un punto de vista evolutivo, y de acuerdo con estos resultados preliminares, la diferenciación entre migradores y sedentarios podría mantenerse por selección natural. Sin embargo, el diferente comportamiento migrador de cada población tiene consecuencias inmediatas en términos de aislamiento reproductivo: migradores y sedentarios no pueden cruzarse, puesto que sus áreas de cría no coinciden. Por ello, el hecho de que no detectemos su aislamiento mediante cambios en las frecuencias genotípicas a escala peninsular podría deberse a que su separación ha sido relativamente reciente. Una forma de aclarar este aspecto sería estudiar la estructura geográfica de la variación genética de estas especies a una escala más amplia, en todo el continente. De acuerdo con la filogeografía molecular de otras especies (Hewitt 1999) y nuestros resultados preliminares para las currucas capirotadas ibéricas, cabría esperar una pérdida de variabilidad genética hacia el norte, en el sentido en que se colonizó el Paleártico occidental a partir de los refugios pleistocénicos ibéricos (Hewitt 1996, Taberlet *et al*. 1998). En este contexto histórico, y conforme con modelos recientes de microevolución del comportamiento migrador (desarrollados además con la curruca capirotada; Berthold 1999), las presiones selectivas relacionadas con la estacionalidad debida a la altitud en las penínsulas mediterráneas podrían haber favorecido el mantenimiento de una frecuencia razonable de migrantes en las poblaciones remanentes durante los máximos glaciares, lo cual habría propiciado una rápida adopción de la migración por las poblaciones que colonizaron el Paleártico posteriormente (Berthold *et al*. 1992, Pulido *et al.* 1996, Berthold 1999). Sin lugar a dudas, esta es una de las líneas de investigación más excitantes que abre esta Tesis.

El interés de las poblaciones ibéricas desde la perspectiva de la evolución de la migración se acentúa si profundizamos en los procesos que, según los diferentes modelos teóricos, propiciaron la aparición del comportamiento migrador en una población originalmente sedentaria (Rappole 1995, Bell 2000). La dispersión de individuos residentes fuera de sus áreas de cría (por ejemplo tras la retirada de los glaciares; Safriel 1995) habría causado, eventualmente, la colonización de ambientes estacionales, donde la migración habría sido favorecida por la selección natural. Sin embargo, estos primeros migradores pagarían su estrategia mediante una menor supervivencia a su regreso a las zonas de origen para pasar el invierno. En esas zonas, la saturación de los mejores hábitats por los sedentarios y los migradores más competentes causaría el desplazamiento de una parte importante de migradores hacia hábitats subóptimos, donde podrían sufrir una mortalidad más alta.

Esta diferente capacidad competitiva de migradores y sedentarios en invierno, aparte de servir para mantener poblaciones estables de ambos tipos, podría haber tenido importantes implicaciones sobre la evolución de los patrones migratorios. Por ejemplo, según el modelo propuesto por Cox (1985), los migradores desplazados fuera del área de invernada podrían encontrar condiciones más favorables si sobrepasasen las zonas ocupadas por los sedentarios, migrando algo más lejos y dando lugar, como consecuencia, a la separación de sus áreas de cría y de invernada. Sin embargo, aunque los resultados de nuestra investigación apoyan hasta cierto punto este modelo de interacciones, todavía existe una notable dispersión invernal de sedentarios fuera de sus áreas de cría, hacia ambientes al parecer menos favorables. No sabemos hasta qué punto un aumento en la afluencia de migradores podría alterar el resultado de estas interacciones (Fig. 6 y 7), dando lugar a situaciones más delicadas para la persistencia de los sedentarios (Alerstam & Enckell 1979, Bell 2000). Sin lugar a dudas, el estudio continuado de las interacciones entre migradores y sedentarios en simpatría permitirá, en el futuro, matizar los modelos teóricos de evolución de la migración y explicar la permanencia de residentes en las áreas de invernada de muchas especies migradoras.

Entre las conclusiones más importantes de esta Tesis destaca la singularidad de las poblaciones de paseriformes forestales del sur peninsular. Aunque las especies estudiadas son muy abundantes y están ampliamente distribuidas en Europa, sus poblaciones mantienen una identidad propia en el sur de Iberia, donde están diferenciadas de las del resto de su distribución. Desde un punto de vista aplicado, su preservación contribuiría sustancialmente al mantenimiento de la diversidad a escala continental (Lesica & Allendorf 1995). La protección de estas poblaciones, por otra parte, también contribuiría a preservar procesos evolutivos (Crandall *et al.* 2000), como los que permitieron la diferenciación entre migradores y sedentarios al final del Pleistoceno, y aún hoy mantienen dicha diferenciación (Safriel 1995, Berthold 1999). Sin lugar a dudas, la preservación de los bosques donde se reproducen estas poblaciones es una pieza clave para su conservación, necesidad que, afortunadamente, queda cubierta por los extensos Parques Naturales de los Alcornocales y de la Sierra de Grazalema. La declaración de estos espacios protegidos, apoyada especialmente en su elevado interés botánico (Costa *et al*. 1990), benefició indirectamente a su fauna, por otra parte poco original si obviamos sus particularidades.

Sin embargo, numerosos estudios han demostrado que los procesos ocurridos fuera de la época de cría pueden ser tan importantes como los que afectan a la reproducción a la hora de determinar el futuro de las poblaciones de aves (Baillie & Peach 1992, Rappole & MacDonald 1994, Sutherland & Dolman 1994, Marra et al. 1998, Newton 1998). En este sentido, la conservación de las poblaciones sedentarias ibéricas podría depender del equilibrio demográfico, tal vez delicado, que mantienen con las migradoras durante el invierno. Por esta razón, sería conveniente proteger no sólo los bosques donde crían estas poblaciones, sino también los matorrales que los rodean. A pesar de que su interés botánico es mucho menor que el de los bosques –son áreas cubiertas casi exclusivamente por lentisco y acebuche–, estas zonas mantienen a la mayor parte de los migradores invernantes en la zona, probablemente reduciendo la presión que, de otro modo, estos ejercerían sobre las poblaciones locales (Fretwell 1980, Ricklefs 1992). Si la modificación del hábitat de la región causase una mayor afluencia de migradores a los bosques, la acentuación de la competencia podría desembocar en un menor reclutamiento de las poblaciones sedentarias (por ejemplo, Goss-Custard *et al*. 1994, Sutherland & Dolman 1994, Newton 1998). Por otra parte, los matorrales también acogen una parte importante de los efectivos locales, que abandonan sus áreas de cría con la llegada de los migradores. Este tipo de dispersiones, más o menos acentuadas según las particularidades ecológicas y comportamentales de cada especie (compárese el petirrojo con la curruca capirotada en los capítulos 6 y 7), podría ser de vital importancia para evitar una drástica reducción del tamaño de las poblaciones locales, ya desfavorecidas por la sequía estival (Winker *et al*. 1997). En el futuro, sería importante determinar hasta dónde llegan las dispersiones de aves sedentarias en la zona de influencia de los bosques gaditanos, así como qué otras poblaciones de especies comunes podrían ser consideradas como ‘unidades evolutivas independientes’ (Moritz 1994, Lesica & Allendorf 1995, Crandall *et al.* 2000) en otros puntos de la Península, a fin de mejorar las bases sobre las que sustentar el desarrollo de estrategias de conservación de la fauna ibérica.

Agradecimientos

Las ideas, comentarios y sugerencias de Ana Alcaide, Roberto Carbonell y José Luis Tellería contribuyeron a mejorar un manuscrito original.

Bibliografía

Adriaensen, F. & Dhont, A.A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology* 59: 1077-1090.

Alerstam, T. 1990. *Bird migration*. Cambridge University Press, Cambridge.

Alerstam, T. & Enckell, P. H. 1979. Unpredictable habitats and evolution of bird migration. *Oikos* 33: 228-232.

Alerstam, T. & Hedenström, A. 1998. The development of bird migration theory. *Journal of Avian Biology* 29: 343-369.

Alerstam, T. & Högstedt, G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scandinavica* 13: 25-37.

Aschmann, H. 1971. Distribution and Peculiarity of Mediterranean Ecosystems. *Mediterranean Type Ecosystems* (eds. F. di Castri & H. A. Mooney), pp. 11-19. Springer-Verlag, Berlin.

Baillie, S.R. & Peach, W.J. 1992. Population limitation in Palearctic-African migrant passerines. *Ibis* 134 (Suppl. 1): 120-132.

Bell, C.P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology* 31: 258-265.

Bensch, S. & Hasselquist, D. 1999. Phylogeographic population structure of great reed warblers: an analysis of mtDNA control region sequences. *Biological Journal of the Linnean Society* 66: 171-185.

Bernis, F. 1966. *Migración en aves. Tratado teórico y práctico.* SEO, Madrid.

Berthold, P. 1993. *Bird migration. A general survey*. Oxford University Press, Oxford.

Berthold, P. 1996. Control of bird migration. Chapman & Hall, London.

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* 70: 1-11.

Berthold, P, Helbig, A.J., Mohr, G. & Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360: 668-669.

Blondel, J. & Mourer-Chauviré, C. 1998. Evolution and history of the western Palaearctic avifauna. *Trends in Ecology & Evolution* 13: 488-492.

Brown, J.H. 1995. *Macroecology*. The University of Chicago Press, Chicago

Carbonell, R. & Tellería, J.L. 1998. Increased asymmetry of tarsus-length in three populations of Blackcaps *Sylvia atricapilla* as related to proximity to range boundary. *Ibis* 140: 331-333.

Carbonell, R. & Tellería, J.L. 1999. Feather traits and ptilochronology as indicators of stress in Iberian Blackcaps *Sylvia atricapilla*. *Bird Study* 46: 243-248.

Costa, M., García, M., Morla, C. & Sáinz, H. 1990. La evolución de los bosques de la Península Ibérica: una interpretación basada en datos paleobiogeográficos. *Ecología* 1: 31-58

Cox, G.W. 1985. The evolution of avian migration systems between temperate and tropical regions of the new world. *American Naturalist* 126: 451-474.

Cramp, S. (ed.) 1992. *The Birds of the Western Palearctic.* Vol. VI. Oxford University Press, Oxford.

Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M. & Wayne, R.K. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution* 15: 290-295.

Dias, P.C. 1996. Sources and sinks in population biology. *Trends in Ecology & Evolution* 11: 326-330.

Finlayson, J.C. 1981. Seasonal distribution, weights and fat of passerine migrants at Gibraltar. *Ibis* 123: 88-95.

Font, I. 1983. *Climatología de España y Portugal*. Instituto Nacional de Meteorología, Madrid.

Fretwell, S.D. 1980. Evolution of migration in relation to factors regulating bird numbers. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds. A. Keast & E.S. Morton), pp. 517-527. Smithsonian Institution Press, Washington, D.C.

Fretwell, S. & Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development.

Acta Biotheoretica 19: 16-36.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. le V. Dit, Urfi, J. & West, A.D. 1994. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis* 137 (suppl. 1): 56-66.

Greenberg, R. 1980. Demographic aspects of long-distance migration. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds. A. Keast & E.S. Morton), pp. 493-504. Smithsonian Institution Press, Washington, D.C.

Gutman, G., Tarpley, D., Ignatov, A. & Olson, S. 1995. The enhanced NOAA global land dataset from the Advanced Very High Resolution Radiometer. *Bulletin of the American Meteorological Society* 75: 1101-1111.

Harrison, C. 1982. *An Atlas of the Birds of the Western Palaearctic*. Collins, London.

Herrera, C.M. 1978. On the breeding distribution pattern of European migrant birds: MacArthur's theme reexamined. *Auk* 95: 496-509.

Hewitt, G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58: 247-276.

Hewitt, G.M. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68: 87-112.

Lautensach, H. 1967. *Geografía de España y Portugal*. Vicens-Vives, Barcelona.

Lawton, J.H. 1993. Range, population abundance, and conservation. *Trends in Ecology & Evolution* 8: 409-413.

Lesica, P. & Allendorf, F.W. 1995. When are peripheral populations valuable for conservation? *Conservation Biology* 9: 753-760.

Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* 14: 343-348.

MacArthur, R.H. 1959. On the breeding distribution pattern of North American migrant birds. *Auk* 76: 318-325.

Marra, P.P., Hobson, K.A. & Holmes, R.T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282: 1884-1886.

Mönkkönen, M. 1995. Do migrant birds have more pointed wings?: a comparative study. *Evolutionary Ecology* 9: 520-528.

Mooney, H.A. 1981. Primary production in Mediterranean-climate regions. *Ecosystems of the World* (eds. F. di Castri, D.W. Goodall & R.L. Spetch), pp 249-255. Elsevier Scientific Publications, Amsterdam.

Moreau, R. E. 1972. *The Palearctic-African bird migration systems*. Academic Press, New York.

Moritz, C. 1994. Defining 'evolutionary significant units' for conservation. *Trends in Ecology & Evolution* 9: 373-375.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego.

Newton, I. & Dale, L. 1996. Relationship between migration and latitude among west European birds. *Journal of Animal Ecology* 65: 137-146.

Pérez-Tris, J. & Tellería, J.L. 2001. Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *Journal of Avian Biology* 32: 000-000.

Pulliam H.R. & Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137 (Suppl.): 50-66.

Purroy, F.J. 1997. *Atlas de las aves de España (1975-1995)*. SEO/BirdLife, Madrid.

Rappole, J.H. 1995. *The Ecology of Migrant Birds: A Neotropical Perspective*. Smithsonian Institution Press, Washington, D.C.

Rappole, J.H. & MacDonald, M.V. 1994. Cause and effect in population declines of migratory birds. *Auk* 111: 652-660.

Ricklefs, R.E. 1980. Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 101: 498-506.

Ricklefs, R.E. 1992. The mega-population: a model of demographic coupling between migrant and resident landbird populations. *Ecology and Conservation of Neotropical Migrant Landbirds* (eds. J.M. Hagan & D.W. Johnston), pp. 537-548.

Smithsonian Institution Press, Washington, D.C.

Roff, D.A. 1992. *The evolution of life histories. Theory and analysis.* Chapman & Hall, New York.

Safriel, U.N. 1995. The evolution of Palearctic migration – The case for southern ancestry. *Israel Journal of Zoology* 41: 417-431.

Sherry, T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

Sutherland, W.J. & Dolman, P.M. 1994. Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. *Proceedings of the Royal Society of London B* 255: 133-138.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cosson, J.F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7: 453-464.

Tellería, J.L. 1988. Invernada de aves en la península Ibérica. SEO, Madrid.

Tellería, J.L., Asensio, B. & Díaz, M. 1999. *Aves Ibéricas. Vol. 2. Passeriformes*. J.M. Reyero, Madrid.

Tellería, J.L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology* 30: 63-71.

Tucker, G.M. & Heath, M.F. 1994. *Birds in Europe: their conservation status*. BirdLife International, Cambridge.

Vaurie, C. 1959. *The birds of the Palearctic fauna. Passeriformes.* H.F. & G. Witherby Ltd, London.

Winker, K., Escalante, P., Rappole, J.H., Ramos, M.A., Oehlenschlager, R.J. & Warner, D.W. 1997. Periodic migration and lowland forest refugia in a “sedentary” neotropical bird, Wetmorte’s Bush Tanager. *Conservation Biology* 11: 692-697.

Winkler, H. & Leisler, B. 1992. On the ecomorphology of migrants. *Ibis* 134 (Suppl. 1): 21-28.

Efectos de la variación regional de la estacionalidad sobre el comportamiento migrador y el ciclo vital de dos paseriformes mediterráneos

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Pérez-Tris, J. & Tellería, J.L. Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines (manuscrito enviado).

RESUMEN

Las aves migradoras se benefician de una mayor fecundidad desplazándose para criar hacia áreas estacionales, pero a la vez sufren una mayor mortalidad como consecuencia de los costes que implica dicho desplazamiento. No obstante, la covariación entre estacionalidad, migratoriedad y ciclo vital debería cambiar entre especies cuyas particularidades ecológicas supusiesen una distinta constancia espacial, supervivencia o fecundidad. En paseriformes frugívoros, por ejemplo, el comportamiento migrador podría ser más acentuado en las especies que rastrean recursos durante el invierno que en las especies territoriales, dado que el nomadismo invernal podría favorecer la realización de movimientos de mayor envergadura. Sin embargo, las aves frugívoras territoriales podrían sufrir una mayor mortalidad que las nómadas, debido a que las últimas evitan enfrentarse a la escasez de alimento (que eventualmente puede tener lugar en territorios discretos dada la impredecibilidad de la producción de frutos) mediante la prospección de diferentes parches de hábitat. En este trabajo, estudiamos la variación de la distribución espaciotemporal, esperanza de vida y tamaño de puesta en petirrojos (*Erithacus rubecula*) y currucas capirotadas (*Sylvia atricapilla*) distribuidos en tres regiones ibéricas con diferentes niveles de estacionalidad (bajo en las tierras bajas mediterráneas, medio en la cornisa Cantábrica y alto en la meseta Norte). En la península Ibérica, estas dos especies son las que aprovechan los frutos de modo más intensivo en las comunidades de aves invernantes. Sin embargo, los petirrojos son territoriales, mientras que las currucas rastrean la disponibilidad de frutos en sus cuarteles de invierno. En la región más estacional de la península (la meseta Norte), tanto petirrojos como currucas disminuyeron su abundancia de primavera a invierno y mostraron una menor constancia en sus áreas de cría, menor esperanza de vida y mayor tamaño de puesta. En las zonas menos estacionales, por el contrario, todos estos rasgos siguieron el patrón de covariación opuesto. Sin embargo, las currucas capirotadas manifestaron un comporta-

miento migrador más intenso que los petirrojos en todas las regiones ibéricas, con cambios de abundancia más acentuados (de hecho, las currucas abandonan completamente la meseta Norte) y menor constancia en las áreas de cría incluso en las áreas menos estacionales. A pesar de su comportamiento migrador más acentuado, que debería incrementar los costes y beneficios de la migración, las currucas capirotadas mostraron una mayor esperanza de vida y un menor tamaño de puesta que los petirrojos en todas las regiones. Estos patrones de covariación entre migratoriedad y ciclo vital, discrepantes a nivel intra e interespecífico, están en consonancia con nuestras predicciones sobre el papel que podría jugar el rastreo de frutos o la territorialidad como moduladores del balance entre supervivencia y fecundidad en estas especies. En los petirrojos, el comportamiento territorial podría implicar una menor supervivencia media invernal, al obligar a los individuos subordinados a permanecer como flotantes sin territorio o a ocupar ambientes de menor calidad. Sin embargo, la supervivencia diferencial de individuos dominantes podría aumentar la fecundidad media durante la siguiente primavera, durante la cual la población reproductora estaría constituida por los individuos más competentes. Por contra, las currucas se beneficiarían de la explotación de los hábitats más favorables durante el invierno, lo que aumentaría su reclutamiento permitiéndoles mantener una población estable sin necesidad de un esfuerzo reproductor tan alto como el de los petirrojos. En conjunto, nuestros resultados muestran que los cambios en el grado de estacionalidad a escala regional pueden afectar a la migratoriedad de las aves, pero de modo diferente dependiendo de la idiosincrasia de cada especie.

Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines

Javier Pérez-Tris & José Luis Tellería*

Migratory birds may improve fecundity by moving to seasonal breeding areas, but may also suffer higher mortality rates as a cost of movement. However, the covariation among seasonality, migratoriness and life-history traits should change between species with differing ecological features that may affect site-tenacity, survival or fecundity. In frugivorous birds, for example, wandering in search for fruits may trigger broader migrations than territorial defence, and may also improve nonbreeding survival by preventing food shortages that eventually happen in discrete territories. We studied the variation in spatio-temporal distribution, life expectancy and fecundity in robins *Erithacus rubecula* and blackcaps *Sylvia atricapilla* distributed in three Iberian regions with a low, mid or high degree of environmental seasonality. In the Iberian Peninsula, robins and blackcaps are the two most intensive frugivores in winter; however, robins are territorial while blackcaps track fruit abundance among habitat patches. In the most seasonal area, robins and blackcaps decreased abundance in winter and showed a lower breeding-site tenacity, a shorter life expectancy and a larger clutch size. However, blackcaps tended to be more migratory than robins in all regions. Despite their stronger migratory behaviour, blackcaps showed a longer life expectancy and a smaller clutch size than robins in all regions. In robins, winter territoriality could decrease non-breeding survival but also improve fecundity, because survivors are dominant and hence more efficient breeders. In blackcaps, by contrast, the use of the most profitable habitat patches could increase non-breeding survival, thereby allowing a similar recruitment than in robins with a lower reproductive investment. These results support the idea that regional-scale changes in seasonality may affect migratory behaviour and hence the trade-off between reproduction and survival in birds, doing so differently depending on the idiosyncrasy of each species.

Migration is a strategy of seasonal exploitation of habitats through which migratory birds benefit from abundant but transitory resources by increasing offspring production (Bernis 1966, Greenberg 1980, Alerstam & Högstedt 1982). However, migration also involves important costs related to energy consumption, exposure to predators or unpredictable food shortages, which cause that migratory birds have a lower non-breeding survival than residents (Alerstam 1990, Berthold 1993). It has long been thought that migration is only possible when the benefits of being migratory may balance its costs (Greenberg 1980, Cox 1985, Gauthreaux 1982, Alerstam & Hedenström 1998), and that migratory behaviour has played an important role in the evolution of different avian life histories by adjusting the trade-off between fecundity and survival (Greenberg 1980, O'Connor 1990, Bell 1996, Young 1996). However, because of the great difficulty of studying survival and fecundity in populations differing in migratory behaviour, these predicted effects of migration on avian life histories have received little empirical support (Alerstam & Hedenström 1998). To our knowledge, there are no studies that have illustrated the covariation among seasonality, migratoriness, survival and fecundity within species.

The extent to which a species responds to variations in seasonality of its habitats by changing migratoriness should depend on particular biological features. For example, different aspects of the non-breeding ecology of each species may determine the intensity of their migratory behaviour (Rappole 1995). One such aspect may be site tenacity during the non-breeding season, which has been particularly studied in relation to food-tracking in frugivorous species because of the low predictability of fruits compared to other food re-

---

**Manuscrito enviado.*

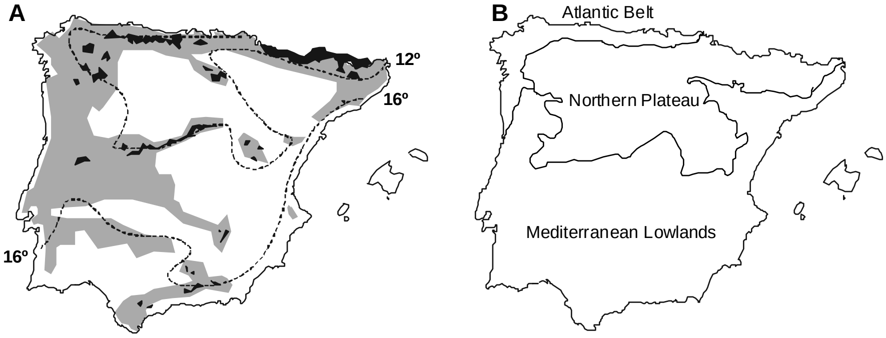

Figure 1. A. Environmental variation in the Iberian Peninsula. Dashed lines represent the mean annual temperature isotherms for 12ºC and 16ºC, and shaded areas correspond to those with mean annual precipitation over 600 mm. Mountain systems above 1500 m (in black) are also shown. B. Regional division of the Iberian Peninsula used in this study. Seasonality in Iberia primarily depends on altitude and continentality (Lautensach 1967), so that it is lowest in the Mediterranean Lowlands and highest in the Northern Plateau, whereas the Atlantic Belt reaches a mid level of seasonality.

sources (Levey & Stiles 1992, Chesser & Levey 1998). While leaf production is essential for a plant to obtain energy, the production of fruits is not necessary for self-maintenance and rather depends on energy surpluses that vary from patch to patch, season to season and year to year. This means that frugivorous birds may improve non-breeding survival by tracking fruit availability across wide areas (Herrera 1985, Levey & Stiles 1992, Rey 1995). Given that vagrant birds are also prone to colonise new breeding grounds (Rappole 1995), it has been postulated that the degree to which different frugivorous species track food resources may have affected the extent of their movements up to have triggered, in species that originally wandered more intensely, the evolution of migratory behaviour between different regions (Levey & Stiles 1992, Chesser & Levey 1998). However, in spite of the survival benefits accrued to vagrant frugivorous birds by tracking the most rewarding habitats for feeding, some frugivores are territorial in winter. Site constancy in winter territories is likely to expose birds to eventual food shortages, and involves the competitive exclusion of subordinates to poorer habitats causing a stronger population limitation than the experienced by resource-trackers, which better follow an ideal free distribution (Fretwell & Lucas 1970, Pulliam & Danielson 1991, Newton 1998). The relevant question at this point is whether the dichotomy between vagrancy and territoriality in frugivorous species not only involves a different migratoriness, but also differences in non-breeding mortality and hence in reproductive investment of birds that follow each strategy (Roff 1992, Stearns 1992).

We studied the covariation among seasonality, migratoriness, survival and fecundity in three Iberian populations of robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*). It is known that these species are sedentary in southern Iberia (Pérez-Tris *et al*. 1999, 2000a, 2000b, Tellería *et al*. 2000), but at the time being the migratory behaviour of most Iberian populations of robins and blackcaps is far from well established (Tellería *et al*. 1999). However, the winter ecology of both species in the Mediterranean zone has been widely documented. Although in the breeding season they feed on invertebrates (Cramp 1988, 1992), they shift to a nearly strict frugivorous diet outside the breeding season, to the point that these two species have been considered to be the most intensive frugivores in the Iberian winter bird communities (Herrera 1984, 1998). However, robins are territorial in wintering grounds (Cuadrado 1995), a behaviour that is more related to anti-predatory defence than to the control of food resources (Cuadrado 1997). Indeed, fleshy fruits may become scarce in robin territories, forcing them to rely on other resources –like ants or oak acorns– which are comparatively more predictable (Cramp 1988, Jordano 1989). In addition, the likely increase in mortality related to food shortages may be emphasised because robins distribute according to an ideal despotic distribution in wintering grounds, through which the most dominant individuals monopolise the best habitats and displace subordinates to poorer sites (Tellería *et al*. 2000). By contrast, wintering blackcaps closely track fruit availability across habitat patches without defending territories (Jordano and Herrera 1981, Debussche and Issenmann 1984, Herrera 1985, 1998, Rey 1995), and in so doing they adjust an ideal free distribution (J.L. Tellería and J. Pérez-Tris in prep.). We have studied whether the variations in seasonality among Iberian regions may affect the migratory behaviour and hence the life history of robins and blackcaps. In a complementary way, given that these two species are similar in most aspects of their breeding and wintering biology (body size, mating system, migratory pattern, year-round habitat preferences, diet and so on; Cramp 1988, 1992) but differ in the way they exploit winter resources, we predicted different population dynamics for each one in relation to vagrancy or territoriality, which led to the following hypotheses:

Variation in the seasonal occupation of habitats

Increasing seasonality implies an uneven temporal distribution of food resources, which affects the length of the period birds will spend outside their breeding areas. This period will be as short as environmental conditions may allow, since the early occupation of breeding sites improves breeding success (von Haartman 1968, Smith & Nilsson 1987). Therefore, we expect that birds show a higher breeding-site tenacity in the less seasonal regions, but leave their breeding areas for a longer time with increasing seasonality. However, if wandering in search for fruits is related to a lower site tenacity in blackcaps (Herrera 1985, Levey and Stiles 1992), then we expect that they perform broader migrations than robins.

Covariation between migration, life expectancy and fecundity

The trade-off between current and future reproduction causes clutch size to be inversely related to life expectancy (Roff 1992, Stearns 1992). Migration could affect this trade-off because migratory populations are likely to achieve a greater fecundity in the most seasonal breeding areas but also are likely to experience a lower survival due to the costs of migration (Greenberg 1980). Therefore, increasing seasonality of Iberian habitats should be coupled with a shorter life expectancy and an enhanced fecundity of robins and blackcaps. However, this trade-off may also be modulated by species-specific features. Particularly, if robins suffer a higher mortality in winter than blackcaps as a consequence of their winter territoriality, this effect should be counterbalanced by interspecific fecundity adjustments in the opposite direction (Roff 1992, Stearns 1992).

METHODS

Study area

The Iberian Peninsula is located at the southern edge of the Western Palearctic, between 36ºN and 43ºN. The gradually decreasing oceanic influence towards its southeastern half, together with elevation in its Northern plateau, makes it possible to differentiate three contrasting regions (Fig. 1, see also Lautensach 1967, Font 1983). The Atlantic Belt has fresh summers and mild winters, as well as abundant rainfall all around the year. The Northern Plateau (mean elevation around 800 m) shows a marked contrast between temperate summers and harsh winters. The Mediterranean Lowlands have hot summers but temperate and rainy winters (Fig. 1). Therefore, these Iberian regions define a non-linear gradient of seasonality, in which primary production –and hence food availability– follow a complementary spatio-temporal distribution (Lautensach 1967, Herrera 1985). The two northernmost regions, especially the Northern Plateau, are

Table 1. Regional variation in breeding phenology of robins and blackcaps. The mean breeding times (referred to as $\bar{B}$ in the text), with standard errors in days and sample sizes in brackets are shown.

	Robins	Blackcaps
A. Belt	17 May ± 2 (107)	25 May ± 3 (46)
N. Plateau	1 June ± 3 (51)	31 May ± 2 (62)
M. Lowlands	6 May ± 3 (6)	8 June ± 6 (15)

summer habitats for migratory birds, while the Mediterranean Lowlands become the most suitable wintering areas for many Palearctic passerines (Tellería 1988). During winter, the harsh Northern Plateau contrasts greatly with the Mediterranean Lowlands, which have a peak of primary production and maintain many insects and large stocks of fleshy fruits available for wintering birds (Lautensach 1967, Herrera 1985, Tellería 1988, Fuentes 1992). The Atlantic Belt shows an intermediate level of primary production during winter that allows invertebrate activity and a moderate fruit production, which sustain small populations of wintering passerines (Lautensach 1967, Guitián 1985, Herrera 1985, Tellería 1988, Fuentes 1992).

Seasonal occupation of habitats

We used two complementary approaches to evaluate the intensity of migratory behaviour of robins and blackcaps in the Iberian Peninsula. The first one, at the population level, consisted of an analysis of seasonal changes in abundance of each species in each Iberian region. The second one, at the individual level, studied the variation in breeding-site tenacity between species and regions.

We studied the spatio-temporal variation in abundance of Iberian robins and blackcaps using 66 published bird censuses, scattered across the Iberian Peninsula (reviewed by Tellería *et al.* 1999). We only considered censuses performed in forested habitats (forests, scrublands, olive growths, etc.), where both species may occur along the year (Cramp 1988, 1992, Tellería *et al.* 1999). All these data were obtained by means of line-transect counts, and all of them were repeated in spring and winter by the same authors to describe the structure of particular Iberian bird communities. This allowed us to test for seasonal changes in abundance among regions controlling for site-specific habitat characteristics.

We used ringing recoveries (available from the Spanish Ringing Scheme) to study the regional variation in breeding-site tenacity of robins and blackcaps. We explored these data to find out native individuals, which were those labelled as local, nesting or nestling (see ringing codes in EURING 1979). We also considered birds ringed or recaptured between April and August (both included), when no migration of these species takes place across the Iberian Peninsula (Cantos 1995, Bueno 1998). Following these criteria, we considered 126 robins (recaptured between 1962 and 1996) and 287 blackcaps (1967-1996). A strong breeding-site fidelity was the rule among these birds since everyone, except a single robin that was excluded, were always recaptured at the same breeding site.

We considered breeding-site tenacity as the time birds remain in the breeding site outside the nesting period. Because the timing of breeding may change among regions or between species, we controlled breeding phenology when estimating breeding-site tenacity. Data on breeding times were obtained from 164 nest-record cards of robins (spread between 1969-1996) and 123 of blackcaps (1970-1992) available from the Spanish Ornithological Society. Because of irregularities in the frequency of visits, we could not determine the laying date accurately in many nests. However, given the broad scale of our comparison, to know the exact laying dates is not necessary to describe breeding phenology in this study. Therefore, we used the average between the dates of the first and the last visit to each nest as measures of breeding time. We found that breeding phenology is similar among regions in blackcaps, but robins breed earlier in southern Iberia than in the other regions (Table 1). This could be a way to avoid extending the breeding season into the summer drought period. Indeed, it has been shown that the summer drought negatively affects the reproductive output of south Iberian robins (Pérez-Tris *et al.* 2000b).

We estimated site tenacity (T) of each local bird i as $T_i = \left|\overline{B} - D_i\right|$, where $\overline{B}$ is the mean breeding time value for the species and the region to which the bird i belongs (given in Table 1), and D_i is the farthest calendar date from $\overline{B}$ in which the individual was recorded at the breeding site, regardless this date corresponds to the ringing or to one of the bird's recaptures. To avoid using birds captured during the nesting period in the analysis of site tenacity, we did not consider time lags shorter than 60 days, which is a safe interval according to the duration of the breeding period –from arrival in spring to departure in autumn– in these species (Cramp 1988, 1992). This measure of site tenacity assumes that the probability of recapture in the breeding area does not change among regions or species. Both species show similar habitat preferences during the breeding season: they defend territories of similar size, moving into low and dense vegetation which makes them easily capturable in mist-nets (the main trapping method used by ringers). In addition, their migratory populations stay in breeding territories until departing once completed the post-nuptial moult, which takes place at a similar time in both species (Cramp 1988, 1992). Therefore, it is very unlikely that the probability of recapture of robins or blackcaps shows different seasonal changes among regions, unless their populations actually differ in breeding-site tenacity.

Regional and interspecific variation in life expectancy and fecundity

We estimated life expectancy of each bird as the minimum number of calendar years it survived until its last recapture in the breeding area. Although we considered the age at ringing of individuals (whether they were first-year birds or older), we nonetheless underestimated life expectancy. However, this happened in both species and in all regions, so it could not have affected regional nor interspecific variation in life expectancy. Nevertheless, in order to avoid further bias of life-expectancy estimates we did not consider individuals ringed after 1992, a safe boundary according to the variation in life expectancies observed in these species (Cramp 1988, 1992, Cuadrado 1994). We could not analyse survival more thoroughly because the number of birds ringed in each region during the study period was not available. Nevertheless, life expectancy in calendar years may be a suitable measure of survival in studies of passerines. Calendar years reflect very adequately the number of breeding opportunities in these species, as their mortality rates usually peak in autumn migration and then decline (Greenberg 1980, Pienkowski & Evans 1985).

We studied regional and interspecific variation in clutch size as a surrogate of fecundity (Stearns 1992). We recorded clutch size from nest record cards considering only accurately complete clutches, which we recognised by their constancy over several days along the incubation period. Regional and interspecific variation in clutch size could be affected by changes among regions or species in nesting success; for instance, egg hatchability rates or fledging rates are known to influence clutch size (Lundberg 1985, Martin 1995). To examine the possibility that the patterns of clutch-size variation were confounded by nesting success, we conducted two-way ANCOVAs on the number of hatched eggs and fledged young, controlling for the covariates clutch size or brood size, respectively. Because of irregularities in the frequency of visits, the number of hatched eggs and fledged young were rarely reported in the Mediterranean Lowlands (two nests for each species), so we restricted these comparisons to the two northern regions.

We transformed variables to meet the statistical assumptions of parametric statistics. Square-root transformation was applied to clutch sizes, brood sizes and fledgling number, and log-transformation to the remaining variables. All tests were two tailed, and *a posteriori* differences among groups were assessed using Tukey's tests.

RESULTS

Seasonal occupation of habitats

Both robins and blackcaps showed different patterns of seasonal distribution among regions in the Iberian Peninsula (Table 2). Thus, the abundance of both species decreased in the Northern Plateau (the most seasonal region) and increased in the Mediterranean Lowlands (the less seasonal region) outside the breeding period (Fig. 2). Obviously, the sharp increase in abundance in the Mediterranean Lowlands is mainly due to the arrival of individuals from central and northern Europe (Cantos 1995, Bueno 1998), but our results suggest that the arrival of migrants from the most seasonal areas in the Iberian Peninsula could also contribute to this increase. According to our predictions, blackcaps displayed a more seasonal pattern of distribution than robins. Blackcaps abandoned the Northern Plateau completely and sharply decreased in abundance in the Atlantic Belt, concentrating themselves in the Mediterranean Lowlands during winter (Fig. 2). In robins, however, the populations that remained during winter in both northern regions were larger, and only the Northern Plateau showed a significant decrease in abundance (Fig. 2).

Both species showed less breeding-site tenacity in the Northern Plateau than in the other two regions, and robins spent more time in their breeding areas than blackcaps (Fig. 3). Interspecific differences were more intense in the Atlantic Belt, although not significantly so, perhaps because blackcaps behave as partial migrants while robins are more sedentary in this region (two-way ANOVA: regions $F_{2,305} = 7.03$, $P < 0.001$; species $F_{1,305} = 14.99$, $P < 0.0001$; region × species $F_{2,305} = 2.77$, $P = 0.064$).

Table 2. Results of two-way repeated measures ANOVAs on spatio-temporal differences in abundance of Iberian robins and blackcaps. Since each forest was sampled both during the spring and the winter, 'season' has been considered as a repeated measures factor.

Robins:	*F*	d.f.	*P*
Region	3.22	2,63	0.047
Season	0.03	1,63	0.863
Region × season	22.82	2,63	< 0.0001
Blackcaps:	*F*	d.f.	*P*
Region	2.17	2,63	0.123
Season	3.94	1,63	0.051
Region × season	6.37	2,63	0.003

Patterns of life expectancy and fecundity

Both species had a significantly shorter life expectancy in the most seasonal region, where birds were found to be more migratory. Nevertheless, according to the predicted benefits of wandering compared to territory defence in winter, blackcaps survived more years than robins in all regions (two-way ANOVA: regions $F_{2,337} = 5.47$, $P < 0.01$; species $F_{1,337} = 21.22$, $P < 0.0001$; region × species $F_{2,337} = 3.04$, $P = 0.050$; Fig. 4). Consistent with these results, both species had a greater clutch size in the most seasonal region, but robins laid larger clutches than blackcaps in all regions (regions $F_{2,257} = 21.27$, $P < 0.0001$; species $F_{1,257} = 54.07$, $P < 0.0001$; region × species $F_{1,257} = 0.25$, $P = 0.78$; Fig. 4). It is unlikely that the small sample size in the area with lowest seasonality affected the reliability of these results, as regional and interspecific effects were both large (an average difference of one egg) and highly significant. At a given clutch size, neither regional nor interspecific variation in number of hatched eggs was significant (two-way ANCOVA: northernmost regions $F_{1,190} = 0.0001$, $P = 0.99$, species $F_{1,190} = 1.08$, $P = 0.30$, region × species $F_{1,190} = 0.09$, $P = 0.77$; covariate clutch size: $F_{1,190} = 4.89$, $P < 0.05$). The number of fledged young at a given brood size did not vary either between regions or between species (northernmost regions $F_{1,81} = 0.0005$, $P = 0.98$, between species $F_{1,81} = 0.45$, $P = 0.50$, region × species $F_{1,81} = 0.24$, $P = 0.62$; covariate brood size: $F_{1,81} = 86.40$, $P < 0.001$). No test of parallelism was significant in these ANCOVAs (all $P > 0.77$ and $P > 0.41$, respectively). According to these results, we can consider that regional and interspecific variations in clutch size were not affected by nesting success.

DISCUSSION

Seasonality, migratory behaviour, and life history traits of robins and blackcaps

So far, the migratory behaviour of Iberian robins and blackcaps had been considered to be nearly homogeneous. Thus, sedentariness would be the most spread strategy among Iberian populations, which would only shift to partial migration in mountainous areas (e.g. Cramp 1988, 1992, Purroy 1997). This view, principally based on the predictions of large-scale latitudinal gradients of migratoriness in the Palearctic, ignores the strong variation in environmental conditions related to elevation in low-latitude areas. In the Mediterranean zone, altitude resembles the effect of latitude, causing similar variations in seasonality at a much smaller geographic scale (Lautensach 1967, Font 1983). Consequently, in the Iberian Peninsula robins and blackcaps tend to be sedentary in the less seasonal areas but migratory in the most seasonal regions, reproducing in a small area their variations in migratoriness with increasing seasonality in the Palearctic (Cramp 1988, 1992). Apart from these intraspecific patterns, we found different responses to seasonality in blackcaps and robins. In the Mediterranean Lowlands (the less seasonal area of all), blackcaps show a slightly smaller breeding-site tenacity than robins, which could be the outcome of spatio-temporal variations in fruit availability which robins do not track (Herrera 1985, Rey 1995). Blackcaps show more seasonal patterns of occurrence in the Atlantic Belt (an area of mid seasonality), where fleshy fruits shift from abundant in late summer to scarce during winter. Meanwhile, robins –which are less dependent on fruit seasonality– could be there as sedentary as in the Mediterranean Lowlands, or engage in regional-scale movements (Guitián 1985). Finally, blackcaps abandon the most seasonal Iberian area (the Northern Plateau) completely during winter, when fleshy fruits are absent there, while robins likely behave as partial migrants in that region. In summary, our results not only reveal the predicted increase in migratoriness of Iberian birds with increasing seasonality, but also support that this association may be modulated by other factors, which in turn will determine the extent to which each species responds to environmental instability by leaving their breeding areas. In our study, interspecific differences in the response to seasonality are consistent with the predicted higher site-constancy in territorial robins if compared to vagrant blackcaps (Herrera 1985, Levey 1988, Levey and Stiles 1992).

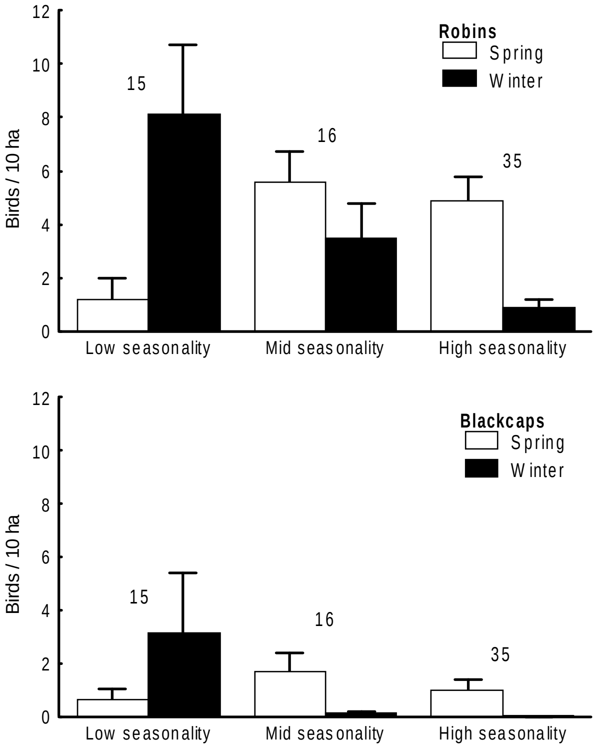

Figure 2. Spatio-temporal patterns of variation in abundance of robins and blackcaps according to the changing degree of seasonality in the Iberian Peninsula. The levels of seasonality correspond to the regions shown in Fig. 1. Means, standard errors and sample sizes are shown.

Our results support the idea that migration affects reproductive trade-offs in Iberian robins and blackcaps. Some studies have found a correlation between migratoriness and clutch size (Bell 1996), or between migratoriness and life expectancy (Cuadrado 1994), but so far no one has illustrated the covariation among migratory behaviour, fecundity and survival in a gradient of increasing seasonality. In Iberian robins and blackcaps, life expectancy decreases and clutch size increases with increasing migratoriness in the Northern Plateau, the most seasonal environment. In this area, primary production concentrates in a shorter breeding season and reproductive restrictions related to the summer drought are less pronounced than in Mediterranean Lowlands (Pérez-Tris *et al.* 2000b). These environmental conditions could allow birds to lay larger clutches (Sæther 1994), which might counterbalance mortality associated to the costs of migration by increasing offspring production (Young 1996, Pérez-Tris *et al.* 2000b). On the other hand, the reduced residual reproductive value due to lower survival chances would also mitigate the importance of reproductive costs, inducing a higher reproductive investment in migratory populations (Roff 1992, Stearns 1992). Other factors may influence changes in clutch size among regions, which could affect mortality rates by modifying reproductive effort. For example, the decrease in clutch size with decreasing seasonality could be explained by a parallel increase in nest-predation rates in the less seasonal areas (Slagsvold 1982, Lundberg 1985, Martin 1995). It is difficult to value *a posteriori* the extent to which predation pressure could influence life history variation among robins and blackcaps in the Iberian Peninsula. The few studies that have evaluated nest-predation rates in these species suggest that they are homogeneous both between species and among Iberian regions (de la Puente and Yanes 1995, Yanes and Suárez 1995), so nest predation is unlikely to have affected the patterns of clutch size variation that we found.

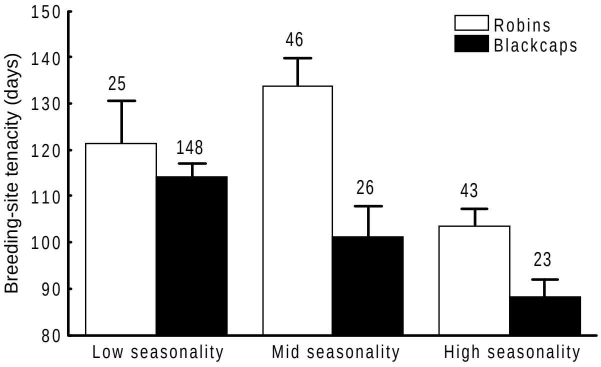

Figure 3. Regional and interspecific variation in the breeding-site tenacity of robins and blackcaps (means, standard errors and sample sizes), in relation to the changing degree of seasonality in the Iberian Peninsula. The levels of seasonality correspond to the regions shown in Fig. 1. In both species, site tenacity was smaller in the region with the highest seasonality than in the other two regions (Tukey's test, $P < 0.005$).

It has been claimed that two-species comparisons cannot provide reliable conclusions about interspecific patterns (see discussions in Harvey and Pagel 1991, Garland and Adolph 1995). However, a multispecies approach is not always feasible given the difficulty to gather information for several species. In our study, to obtain enough data of seasonal variation in abundance, ringing recoveries and nest records for a number of vagrant and territorial species would be simply unworkable: this information does not exist. When faced with these limitations, two-species comparisons may give biologically relevant results provided that independent predictions for between-species differences are formulated *a priori*. In this case, the probability that all differences are in the predicted directions will be given by the combination of probabilities that each individual difference fits such predictions (Garland and Adolph 1995). In this study, the probability of obtaining the four predicted interspecific patterns (spatio-temporal distribution, site tenacity, life expectancy and clutch size) by chance is $P = 0.5^4 = 0.063$, which is nearly significant. To improve the reliability of our results we have selected the best model species available. They are the commonest in the Iberian forest bird communities (Tellería *et al.* 1999), the most representative among vagrant and territorial frugivores (Herrera 1998), and the ones for which a larger body of empirical research has been accumulated so far (Cramp 1988, 1992).

Despite these methodological shortcomings, our results suggest that differences in winter ecology of robins and blackcaps may modulate the effect of migration on the trade-off between fecundity and survival in these species. This would have caused that, while increasing migratoriness involved a higher fecundity and a shorter life expectancy within species, the most migratory species (the Blackcap) showed a lower fecundity and a longer life expectancy than the most sedentary species. These contrasting patterns of covariation within and between species are consistent with the costs of territorial behaviour in terms of survival, which would cause a stronger population limitation in winter (Fretwell & Lucas 1970, Pulliam & Danielson 1990, Newton 1998). These costs could be counterbalanced, however, by an increased fecundity of survivors. In partially migratory robins, winter territoriality may favour breeding success of dominant, highly qualified individuals (Adriaensen & Dhont 1990). In the migratory fraction of the population, dominants may improve survival because they occupy the best habitat patches in non-breeding grounds (Tellería *et al*. 2000). The same happens in the resident fraction, in which survivors benefit from an early occupation of the best breeding territories (von Haartman 1968, Smith and Nilsson 1987, Adriaensen and Dhont 1990). This might constitute a feedback mechanism that could enhance population recruitment although average winter survival is low, since the most qualified individuals would make up the breeding population year after year (Rodenhouse *et al.* 1997). Blackcaps, however, effectively track food resources during winter (Fouarge 1981, Herrera 1982, 1985, Rey 1995), doing so according to an ideal free distribution (J. L. Tellería and J. Pérez-Tris, in prep.). If this improves survival (Jordano 1988), winter vagrancy could enable blackcaps to achieve a similar lifetime breeding output than robins without the increased effort associated with large clutches. Obviously, robins and blackcaps are two particular cases in a continuous series of winter behaviours, and evolutionary history, physiology and many other factors may have influenced the evolution of their life histories. Although this makes our results hardly general to other species, they support our predictions and provide an empirical background for future studies on the role that winter ecology and behaviour may play in shaping the covariation among migration, fecundity and survival of birds.

The migrations of Iberian robins and blackcaps in the Palearctic context

The increase of seasonality with increasing latitude likely triggered the evolution of migration in most Palearctic birds (Moreau 1972, Alerstam & Högstedt 1982). Thus, migration is a common strategy among birds of highest latitudes that progressively declines southward, both within and among species (Moreau 1972). Resembling this latitudi-

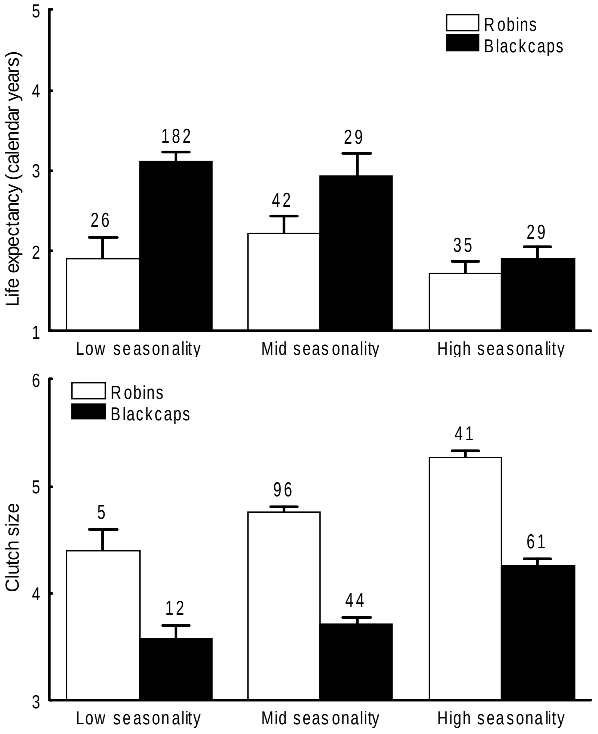

Figure 4. Regional and interspecific variation in life expectancy and clutch size of robins and blackcaps (means, standard errors and sample sizes), in relation to the changing degree of seasonality the Iberian Peninsula. The levels of seasonality correspond to the regions shown in Fig. 1. In both species, means were smaller in the region with the highest seasonality than in the other two regions (Tukey's test: life expectancy $P < 0.05$, clutch size $P < 0.005$).

nal trend, increasing seasonality with elevation should have induced the evolution of migration in mountains and highlands at middle and low latitudes. Our results show that regional differences in the extent of environmental seasonality across the temperate zone may be large so as to cause not only migratory movements, but also life-history adjustments. A number of studies have found morphological differences among Iberian populations of robins and blackcaps that are consistent with this variation in migratory behaviour (Pérez-Tris *et al*. 1999, 2000a, 2000b, Tellería and Carbonell 1999), suggesting that migration actually constitutes a relevant selective pressure for these populations. Moreover, the morphological variation found between populations in the very same geographical context is much larger in blackcaps than in robins (Pérez-Tris *et al*. 1999, 2000a), supporting a stronger response of the former to changes in seasonality.

Operating at the regional scale, the tendency to move of blackcaps could have favoured the development of their complex migratory system in the Palearctic, where several migratory directions have evolved including a pattern of leap-frog migration with sub-Saharan wintering grounds (Cramp 1992). Indeed, the rapid evolution of new migratory directions in European blackcaps (Berthold *et al*. 1992) underlines their plasticity to track newly available wintering areas. By contrast, robins are sedentary or partially migratory in many parts of their range, and do not show so contrasting patterns of distribution between breeding and wintering ranges in the Palearctic (Cramp 1988). According to our results, the higher site constancy of robins compared to blackcaps likely affects the way each species exploit seasonal environments, which could have constrained the evolution of their migratory patterns.

Acknowledgements

The Spanish Ringing Scheme (Oficina de Anillamiento, Dirección General de Conservación de la Naturaleza) and the Spanish Ornithological Society (SEO/BirdLife) kindly provided the data to carry out this work. Elena Arriero and Roberto Carbonell helped us to collect these data. Comments from Roberto Carbonell, José A. Díaz, Pedro Jordano, Juan Moreno and Tomás Santos improved an early version of the paper. Bruno Bruderer, Paul Hamel, Jeffrey F. Kelly and John Wiens also gave valuable ideas for discussion. Financial support was provided by the Spanish Ministerio de Educación y Cultura (project PB97-0325) and a FPI Grant from the Universidad Complutense (to J.P.-T.).

References

Adriaensen, F. & Dhont, A.A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology* 59: 1077-1090.

Alerstam, T. 1990. *Bird migration*. Cambridge University Press, Cambridge.

Alerstam, T. & Hedenström, A. 1998. The development of bird migration theory. *Journal of Avian Biology* 29: 343-369.

Alerstam, T. & Högstedt, G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scandinavica* 13: 25-37.

Bell, C.P. 1996. The relationship between geographic variation in clutch size and migration pattern in the Yellow Wagtail. *Bird Study* 43: 333-341.

Bernis, F. 1966. *Migración en aves. Tratado teórico y práctico*. SEO, Madrid.

Berthold, P. 1993. *Bird migration. A general survey*. Oxford University Press, Oxford.

Berthold, P., Helbig, A.J., Mohr, G. & Querner, U. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360: 668-669.

Bueno, J.M. 1998. Migración e invernada de pequeños turdinos en la península Ibérica. V. Petirrojo (*Erithacus rubecula*). *Ardeola* 45: 193-200.

Cantos, F.J. 1995. Migración e invernada de la curruca capirotada (*Sylvia atricapilla*) en la península Ibérica. *Ecología* 9: 425-433.

Chesser, R.T. & Levey, D.J. 1998. Austral migrants and the evolution of migration in New World birds: Diet, habitat, and migration revisited. *American Naturalist* 152: 311-319.

Cox, G.W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. *American Naturalist* 126: 451-474.

Cramp, S. (ed.) 1988. *The birds of the Western Palearctic.* Vol. V. Oxford University Press, Oxford.

Cramp, S. (ed.) 1992. *The birds of the Western Palearctic.* Vol. VI. Oxford University Press, Oxford.

Cuadrado, M. 1994. Site-tenacity and life-time expectancy of resident and over-wintering Blackcaps *Sylvia atricapilla* in the Mediterranean. *Ringing & Migration* 15: 58-59.

Cuadrado, M. 1995. Territory characteristics and the attacks against intruders in migrant robins *Erithacus rubecula* wintering in the mediterranean area. *Ardeola* 42: 147-160.

Cuadrado M. 1997. Why are migrant Robins (*Erithacus rubecula*) territorial in winter?: the importance of the anti-predatory behaviour. *Ethology, Ecology & Evolution* 9: 77-88.

De la Puente, J. & Yanes, M. 1995. Tasas de depredación en nido de paseriformes ibéricos nidificantes por encima del suelo. *Ardeola* 42: 139-146.

Debussche, M. & Issenmann, P. 1984. Origine et nomadisme des fauvettes à tête noire (*Sylvia atricapilla*) hivernant en zone méditerranénne française. *Oiseau* 54: 101-107.

EURING 1979. *Code manual: New EURING*. British Trust for Ornithology, Tring.

Font, I. 1983. *Climatología de España y Portugal.* Instituto Nacional de Meteorología, Madrid.

Fouarge, J. 1981. La Fauvette á tete noire (*Sylvia atricapilla*). Exploitation des donnes belges de baguage. *Gerfaut* 71: 677-716.

Fretwell, S. & Lucas, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.

Fuentes, M. 1992. Latitudinal and elevational variation in fruiting phenology among western European bird-dispersed plants. *Ecography* 15: 177-183.

Garland, T. Jr. & Adolph, S.C. 1995. Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiological Zoology* 67: 797-828.

Gauthreaux, S.A. Jr. 1982. The ecology and evolution of avian migration systems. *Avian Biology* 6: 93-168.

Greenberg, R. 1980. Demographic aspects of long-distance migration. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds. A. Keast & E.S. Morton), pp. 493-504. Smithsonian Institution Press, Washington, D.C.

Guitián, J. 1985. Datos sobre el régimen alimenticio de los paseriformes de un bosque montano en la Cordillera Cantábrica occidental. *Ardeola* 32: 155-172.

Harvey, P.H. & Pagel, M.D. 1991. *The comparative method in evolutionary biology.* Oxford University Press, Oxford.

Herrera, C.M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63: 773-785.

Herrera, C.M. 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs* 54: 1-23.

Herrera, C.M. 1985. Habitat-consumer interactions in frugivorous birds. *Habitat selection in birds* (ed. M.L. Cody), pp. 341-365. Academic Press, London.

Herrera, C.M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68: 511-538.

Jordano, P. 1988. Diet, fruit choice and variation in body condition of frugivorous warblers in Mediterranean scrublands. *Ardea* 76: 193-209.

Jordano, P. 1989. Variación de la dieta frugívora otoño-invernal del Petirrojo (*Erithacus rubecula*): efectos sobre la condición corporal. *Ardeola* 36: 161-183.

Jordano, P. & Herrera, C.M. 1981. The frugivorous diet of Blackcap populations *Sylvia atricapilla* wintering in southern Spain. *Ibis* 123: 502-507.

Lautensach, H. 1967. *Geografía de España y Portugal.* Vicens-Vives, Barcelona.

Levey, D.J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58: 251-269.

Levey, D.J. & Stiles, F.G. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *American Naturalist* 140: 447-476.

Lundberg, S. 1985. The importance of egg hatchability and nest predation in clutch size evolution in altricial birds. *Oikos* 45: 110-117.

Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101-127.

Moreau, R. E. 1972. *The Palearctic-African bird migration systems.* Academic Press, New York.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego.

O'Connor, R.J. 1990. Some ecological aspects of migrants and residents. In *Bird migration: physiology and ecophysiology* (ed. E. Gwinner), pp. 175-182. Springer-Verlag, Berlin.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 1999. A method for differentiating between sedentary and migratory blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia. *Bird Study* 46: 299-304 (*Capítulo 4*).

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000a. Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. *Ardeola* 47: 9-18 (*Capítulo 5*).

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000b. Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. *Journal of Biogeography* 27: 879-888 (*Capítulo 2*).

Pienkowski, M.W. & Evans, P.R. 1985. The role of migration in the population dynamics of birds. In *Behavioural Ecology. Ecological Consequences of Adaptive Behaviour* (eds. R.M. Sibly & R.H. Smith), pp. 331-352. Blackwell, Oxford.

Pulliam, H. R. & Danielson, B. J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137 (Suppl.): 50-66.

Purroy, F.J. 1997.*Atlas de las aves de España (1975-1995).* SEO/BirdLife, Madrid.

Rappole, J.H. 1995. *The Ecology of Migrant Birds: A Neotropical Perspective.* Smithsonian Institution Press, Washington, D.C.

Rey, P.J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* 76: 1625-1635.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78: 2025-2042.

Roff, D.A. 1992. *The evolution of life histories. Theory and analysis.* Chapman and Hall, New York.

Sæther, B-E. 1994. Food provisioning in relation to reproductive strategy in altricial birds: a comparison of two hypotheses. *Evolution* 48: 1397-1406.

Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54: 159-169.

Smith, H.G. & Nilsson, J-Å. 1987. Intraspecific variation in migratory pattern of a partial migrant, the Blue Tit (*Parus caeruleus*): an evaluation of different hypotheses. *Auk* 104: 109-115.

Stearns, S.C. 1992. *The evolution of life histories.* Oxford University Press, Oxford.

Tellería, J.L. (ed.) 1988. *Invernada de aves en la Península Ibérica.* Monografías 1. Sociedad Española de Ornitología, Madrid.

Tellería, J.L., Asensio, B. & Díaz, M. 1999. *Aves Ibéricas. Vol. 2. Passeriformes.* J. M. Reyero, Madrid.

Tellería, J.L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology* 30: 63-71.

Tellería J.L., Pérez-Tris J., Ramírez A., Fernández-Juricic E., Carbonell R. 2000. Distribution of Robins (*Erithacus rubecula*) in wintering grounds: effects of conspecific density, migratory status and age. *Ardea* 00: 000-000 (*Capítulo 6*).

von Haartman, L. 1968. The evolution of resident versus migratory habit in birds. Some considerations. *Ornis Fennica* 45: 1-7.

Yanes, M. & Suárez. F. 1995. Nest predation patterns in ground-nesting passerines on the Iberian Peninsula. *Ecography* 18: 423-428.

Young, B.E. 1996. An experimental analysis of small clutch size in tropical House Wrens. *Ecology* 77: 472-488.

Capítulo 2

Distribución de abundancias, variación morfológica y condición juvenil de los petirrojos *Erithacus rubecula* (L.) en el borde de su área de distribución mediterránea

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000. Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. *Journal of Biogeography* 27: 879-888.

RESUMEN

Se ha sugerido que las poblaciones de una determinada especie deberían estar peor adaptadas cerca del borde de su distribución, donde sus hábitats son cada vez menos adecuados. En ocasiones, sin embargo, las poblaciones periféricas podrían aclimatarse, o incluso adaptarse, a las condiciones locales. En este trabajo estudiamos petirrojos ibéricos para evaluar si las poblaciones periféricas meridionales son más restrictivas al seleccionar sus hábitats, están localmente diferenciadas o muestran alguna evidencia de inadaptación. Dividimos la Península Ibérica en tres regiones (Eurosiberiana y Supramediterránea en el norte, y tierras bajas mediterráneas en la mitad meridional), que definen un gradiente de xericidad creciente hacia el sur. En cada región, seleccionamos una localidad representativa donde capturamos petirrojos durante tres años de estudio. Revisamos 72 estudios de comunidades para examinar si los petirrojos ocupan menos bosques y disminuyen su abundancia hacia el sur en Iberia. Dado que los petirrojos son sedentarios en la región meridional, pero abandonan en gran medida las regiones norteñas, estudiamos la variación interpoblacional en rasgos relacionados con la migración para examinar la diferenciación de las poblaciones periféricas. Para evaluar la respuesta de las poblaciones a las variaciones ambientales, estudiamos cuatro índices de condición física de los juveniles (asimetría fluctuante, tamaño corporal, ptilocronología y peso corregido por el tamaño), cada uno de ellos relacionado con el estado nutricional de los individuos en un momento concreto entre su desarrollo temprano y su emancipación. Aunque los petirrojos restringieron su distribución hacia el sur, su abundancia local no varió entre regiones. Los petirrojos meridionales, de acuerdo con su comportamiento sedentario, presentaron alas más cortas y redondeadas que los norteños, aunque no encontramos diferencias de tamaño corporal. La asimetría fluctuante y el tamaño de los volanderos no reflejaron un mayor estrés durante el desarrollo de los petirrojos en las poblaciones meridionales, si bien éstos mostraron una peor condición física durante su emancipación (medida mediante la ptilocronología y el peso residual). La distribución de abundancias observa-

da indica que los petirrojos ibéricos podrían seleccionar los hábitats que superasen un cierto umbral de calidad. Además, las poblaciones meridionales parecen estar diferenciadas en el borde de la distribución, de acuerdo con la variación morfológica asociada al comportamiento migrador de cada población. Esto introduce la posibilidad de que las variaciones interpoblacionales de condición juvenil reflejen en realidad las ventajas reproductivas que los petirrojos migradores obtendrían ocupando hábitats estacionalmente productivos, en lugar de la inadaptación de las poblaciones sedentarias periféricas. Desde este punto de vista, y de acuerdo con los patrones de distribución y variación morfológica observados, los petirrojos del sur ibérico podrían constituir poblaciones independientes, localmente adaptadas en el borde de la distribución de la especie.

Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary

Javier Pérez-Tris, Roberto Carbonell & José Luis Tellería*

It has been suggested that populations nearing the border of a species' range should be maladapted because they occupy progressively less suitable environments. In some instances, however, peripheral populations might acclimate or even be adapted to local conditions. We studied Iberian robins to evaluate whether southern, peripheral populations become more restrictive in selecting their habitats, are locally differentiated or show evidence of maladaptation. We divided the Iberian Peninsula into three regions (the Eurosiberian and Supra-Mediterranean regions in northern Iberia, and the Mediterranean Lowlands in southern Iberia), which define a gradient of increasing dryness southwards. In each region, we selected one representative locality, where we captured individuals during three study years. We reviewed 72 community studies to test whether Iberian robins occupy fewer forests and decrease in abundance southwards. Because robins are sedentary in the southernmost region, but largely abandon both northern areas in winter, we analysed the variation in migration-related morphology to test for population differentiation in the range boundary. To examine how populations cope with environmental variation, we studied four indices of juvenile condition (fluctuating asymmetry, fledgling size, ptilochronology and size-corrected body mass), each related to nutritional conditions in a particular stage of growth, from early development to independence. Although robins restricted their range southwards, there was no change in local abundance between regions. Southernmost robins, consistent with their sedentary behaviour, had shorter and more rounded wings than northern robins, although the populations did not differ in terms of body size. Fluctuating asymmetry and fledgling size did not evidence a higher developmental stress in peripheral populations, although southernmost robins had a lower juvenile condition during their independence (as shown by ptilochronology and residual body mass). The distribution of abundance found in this study supports that Iberian robins could select habitats above a somehow restrictive threshold of quality. In addition, morphological correlates of migratory behaviour provided evidence of population differentiation at the range edge. This introduces the possibility that among-region variations in juvenile condition actually reflect reproductive benefits for migrants, related to the occupation of seasonally productive habitats, rather than the maladaptation of sedentary, peripheral populations. From this perspective, and in view of the patterns of distribution and morphology that we found, southern Iberian robins might be independent populations locally adapted in the range boundary.

Many studies have proposed that the well being of populations should decrease towards the border of a species' range. The niche hypothesis, for example, suggests that habitat suitability decreases from the core areas causing a decrease in both the abundance and fitness of populations nearing the species border (Brown 1984, 1995, Lawton 1993). However, peripheral populations may either acclimate or adapt to local conditions, or even have an evolutionary history that is independent of the main population (Caughley *et al.* 1988, Blondel *et al.* 1993, Hoffmann & Blows 1994). In any case, either phenotypic plasticity or population differentiation would allow peripheral populations to avoid maladaptation (Hoffmann & Blows 1994).

European forest passerines seem to face a decreasing habitat suitability in the Mediterranean region. However, there is little empirical evidence illustrating how populations respond to changing environmental conditions in peripheral areas. In the Iberian Peninsula, for example, it is known that

---

**Journal of Biogeography 27: 879-888.*

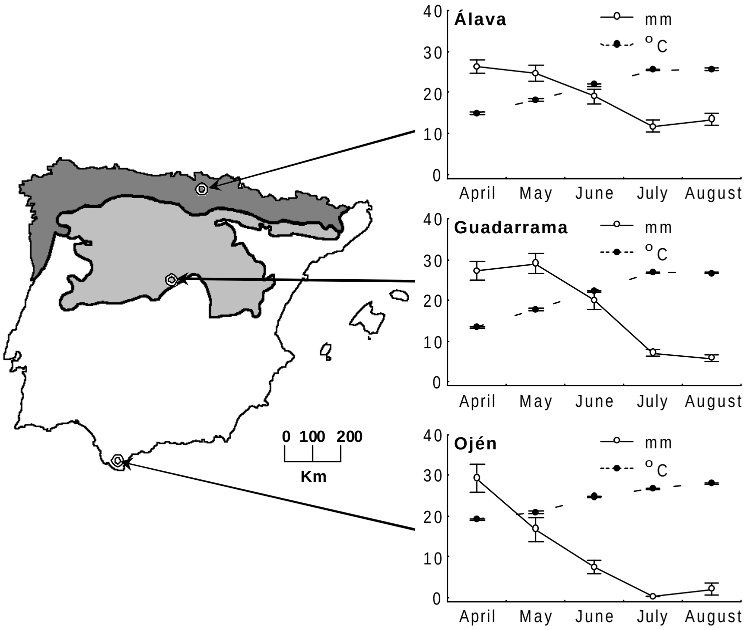

Figure 1. Regional division of the Iberian Peninsula: Eurosiberian Region (dark grey), Supra-Mediterranean Region (light grey) and Mediterranean Lowlands (white). The diagrams show the monthly variation in precipitation (mm) and maximum temperature (ºC) for the period April-August (measured from 1986 to 1997) in the study localities selected in each region (means and standard errors are shown).

they have a more fragmented distribution southwards (Santos & Tellería 1995, Tellería, Asensio & Díaz 1999), and several studies have found a lower body condition in populations occupying some marginal, dry environments (Carbonell & Tellería 1998, 1999). However, this does not necessarily apply to all peripheral Iberian populations. In fact, there are moist forests in the southernmost point of Iberia whose avifauna is similar, both in richness and abundance, to the one recorded in northern Iberia (Santos & Tellería 1995). Moreover, some passerines are known to be sedentary in these forests and to be morphologically differentiated from their north-Iberian migratory counterparts (Tellería & Carbonell 1999). The existence of these peculiar bird communities introduces the possibility that the Iberian peripheral populations of some bird species are locally adapted.

In this paper, we study the variation in some population traits of robins (*Erithacus rubecula* [L.]) distributed along a north-to-south gradient of increasing dryness in the Iberian Peninsula. The robin has a wide distribution in the Western Palearctic (Cramp 1988), and it is also widespread in northern Iberia, but its distribution becomes patchy from there southwards (Tellería & Santos 1994, Tellería *et al.* 1999). Therefore, it is a suitable model for studying the biology of a typical European forest passerine nearing the boundary of its Mediterranean range. We evaluate whether robin populations acclimate to their environments, are differentiated or show evidence of maladaptation in the southernmost Iberian breeding grounds from three complementary perspectives:

Patterns of abundance distribution

If robins actually occupied progressively worse environments across the Iberian gradient, the fragmentation of the species' range southwards should involve a parallel decrease in abundance in the occupied forests (Lawton 1993, but see also Blackburn *et al.* 1999). However, robins may occupy only suitable habitats regardless the distance to the species' border, thereby preventing their maladaptation in the range boundary. If robins actually selected habitats above some threshold of quality, we should find a similar density across the Iberian gradient.

Morphological differentiation

The adaptation of peripheral populations to local conditions may be prevented by gene flow from central, densely populated sectors (Holt & Gomulkiewicz 1997, Kirkpatrick & Barton 1997). In some instances, however, isolation in the range border may preclude this interchange and hence allow local differentiation (Hoffmann & Blows 1994). It has been suggested that Iberian robins belong to the nominate subspecies *E. r. rubecula* (L.) but grade in the south into *E. r. witherbyi* Hartert (Cramp 1988). However, the possible differentiation of southern populations has never been studied, although it is known that they are sedentary whereas northern populations are partially or totally migratory (Tellería *et al.* 1999). In many bird species, migratory populations differ from their sedentary counterparts in that they have longer and more pointed wings, as well as a shorter tail (e.g. Leisler & Winkler 1985, Norberg 1995, Tellería & Carbonell 1999). In contrast, the different use of habitats by migrant and sedentary populations may also involve variations in diet, and hence in its related morphology (Carrascal *et al*. 1990, Tellería & Carbonell 1999). The existence of these morphological correlates of migratory behaviour would be a good evidence of population differentiation, as long as it has been demonstrated that these traits are controlled genetically in robins (Biebach 1983, Berthold 1991).

Juvenile condition

If robins were unable to acclimate or adapt to peripheral conditions (see above), they should achieve a lower fitness near the range boundary (Caughley *et al*. 1988, Hoffmann & Blows 1994, Brown 1995). Juvenile survival is a major component of the variation in fitness among bird populations (Newton 1989), and is determined largely by the body condition of juveniles between early development and independence (Lindén *et al*. 1992, Møller 1997, Lindström 1999). Therefore, a lower juvenile condition in peripheral populations could be a fair surrogate of lower fitness in the range boundary.

METHODS

Study area

The environmental variation that robins meet in the Iberian Peninsula can be summarized into three main regions (Fig. 1; see Lautensach 1964, Font 1983, Tellería *et al*. 1999). In each region, we selected one study site at which both precipitation and temperature were close to the regional average values (Lautensach 1964, Font 1983). The Eurosiberian Region constitutes the non-Mediterranean sector of the Iberian Peninsula, where robins are widespread and abundant. In this region, we captured robins in mixed oak forests (*Quercus faginea* Lam., and *Q. robur* L.) in Álava (42º55'N 2º29'W; 620-m elevation). The Supra-Mediterranean Region is a plateau above 800 m elevation where robins occupy mild areas in mountains and plains. This region is characterised by a marked contrast between a highly productive spring and a very harsh winter. There, we captured robins in Sierra de Guadarrama (40º54'N 3º53'W; 1100-m elevation), in mixed forests (*Quercus pyrenaica* Willd., *Fraxinus excelsior* L., and *Alnus glutinosa* [L.]) interspersed with meadows. Finally, the Mediterranean Lowlands represent the typical dry Mediterranean climate, characterized by an intense summer drought. Well-developed forests are lacking across this region except in some moister mountain and coastal sectors, which are the only sites where robins may be found. We sampled mixed oak forests (*Quercus suber* L., and *Q. canariensis* Willd.) in Sierra de Ojén, in the southernmost point of Iberia (36º01'N 5º36'W, 250-m elevation).

Previous studies have shown that robins are sedentary in southern Iberia, but largely abandon the northernmost regions during winter. Thus, despite the arrival of robins from central and northern Europe for winter in northern Iberia, there is a

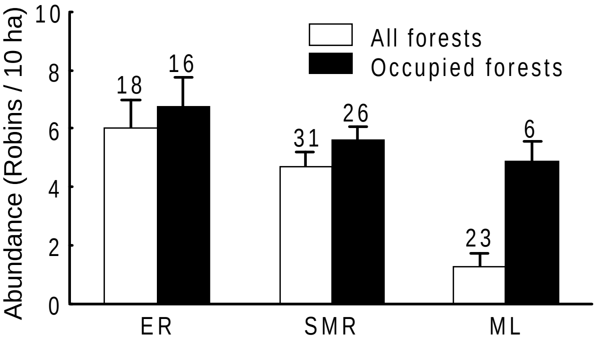

Figure 2. Abundance distribution of robins in the Iberian Peninsula. Mean densities, standard errors and sample sizes are shown (ER, Eurosiberian Region; SMR, Supra-Mediterranean Region; ML, Mediterranean Lowlands).

clear spring-to-winter decrease in robin abundance in both the Eurosiberian Region (where robin density decreases by 37%) and, most especially, in the Supra-Mediterranean Region (where abundance decreases by as much as 82%). Meanwhile, the species increases its abundance in the Mediterranean Lowlands during winter (696% higher), which is greatly influenced by the arrival of foreign robins (Tellería *et al.* 1999, Pérez-Tris & Tellería submitted). In addition, ringing recoveries support the idea that robins are sedentary in southern Iberia, as shown by own recaptures of the same individuals in spring and winter, but also that they spend a shorter time in their northern breeding areas than in the southern ones (Pérez-Tris & Tellería submitted).

Abundance distribution

We reviewed 72 studies of Iberian forest bird communities, in which estimates of breeding abundance of all the species present in each community were obtained using line-transect counting (see Tellería *et al.* 1999 and references therein). Because none of these studies was specifically designed to assess robin abundance, they may be considered as a random sampling of the species distribution along the Iberian Peninsula. We used these censuses to evaluate: (1) the variation in density of robins among Iberian regions (mean densities in all sampled forests), (2) the proportion of forests occupied, and (3) the mean densities in the occupied forests in each region. We also evaluated the mean abundance of robins in our study localities to assess whether they deviate from the average values in each region, for which we censused robins in 1996 in several 500-m long by 50-m wide line transects.

Capture and measurement of robins

In 1996, we sampled our study localities early in the breeding season (in May). In 1997 and 1998, however, we captured robins after fledgling independence (June-July), in order to capture yearlings. In these two years, localities were visited successively from south to north, during the peak of the fledging season. Along the three study years, we trapped 61 adults and 134 juveniles mainly using mist-nets, but also with netted claptraps, which did not influence estimates of body condition based on body mass (ANOVA with body mass: locality $F_{1,113} = 13.22$, $P < 0.001$, capture method $F_{1,113} = 0.01$, $P = 0.92$, locality×method $F_{1,113} = 0.11$, $P = 0.74$). All robins were ringed before being released to avoid repetition. We took standard measurements of the length of both tarsi, bill length and bill height using a 0.01-mm precision digital calliper. We also recorded wing maximum chord and tail length, both to the nearest half millimetre. In 1997 and 1998, we measured the distances between the wing tip and the tip of the nine long primary feathers (primary distances, see Svensson 1992 for details about all measurements). Robins were weighed using a 0.1-g precision digital balance. Finally, we pulled the right fifth rectrix feather to measure its length and the width of ten growth bars in the centre of its vane (Grubb 1995), for which we used a 0.01-mm precision digital calliper. Several missing values led to different sample sizes in our analyses.

Morphological variation among populations

We studied the variation in wing, tail, tarsus and bill measurements among robin populations (see an example with blackcaps *Sylvia atricapilla* [L.] in Tellería & Carbonell 1999). In order to summarize the variation in morphological traits of robins, we first performed a PCA with all body traits except bill measurements, as juveniles did not have a full-grown bill when we captured them. Thus, we tested for overall among-population differences in morphology taking into account the possible differences between age classes, but we only studied bill morphology of adults. To analyse the variation in wing-shape among populations, we conducted a PCA with primary distances for deriving indices of wing shape (Chandler & Mulvihill 1988, Lockwood *et al.* 1998). We measured primary distances in very few adults (five, six and five in the northern, central and southernmost populations, respectively) because most of them were moulting the innermost primaries, so we only studied wing shape of juvenile robins. We did not consider the sex of birds in these analyses because sexing robins is too difficult after females have lost their brooding patch. Nonetheless, sexual dimorphism of robins should not confound among-population variation unless sex-ratios were strongly and differentially biased in each population, which is unlikely.

Indices of juvenile condition

We studied four different indices of juvenile body condition, each related to the nutritional stress that robins experienced during a different stage of development. We used fluctuating asymmetry of tarsus length and juvenile size as two independent correlates of environmental stress early in life (Garnett 1981, Møller 1997, Sanz 1997, Lindström 1999). We also analysed ptilochronology (the width of growth bars in the tail feathers, which measure the amount of feather material that has been produced per day, Grubb 1995) as an index of the nutritional conditions that juveniles experienced during the latest nesting period and soon after fledging, as they do not grow the tail completely until some days after leaving the nest. Finally, we utilised body mass relative to body size (Brown 1996) as a measure of the body condition of juveniles at the moment of their capture, when most of them were already independent of their parents.

We compared juvenile condition among populations during 1997 and 1998, taking into account the different confounding variables that may affect our results. To make sure that juvenile robins had the same, very low age in all three localities, we checked the degree of completion of their post-juvenile moult (Bensch & Lindström 1992). This was at the earliest stages in all individuals, and indeed had not started in most of them. When analysing ptilochronology, we included feather length as a covariate of the width of its growth bars (excluding individuals without a full-grown tail), thereby controlling for the effect of feather final size on feather growth rate (Grubb 1995).

Finally, we evaluated the extent to which the particular environmental conditions in each study year could have influenced the juvenile condition of robins. To do so, we studied the variations in mean precipitation and maximum temperature in our study localities during both breeding seasons.

RESULTS

Abundance distribution

The average density of robins decreased southwards in the Iberian Peninsula (Fig. 2; ANOVA: $F_{2,69} = 12.78$, $P < 0.001$), this being coupled with a decrease in the proportion of forests occupied in the southernmost region (chi-square test with frequencies given in Fig. 2; $\chi^2_2 = 24.97$, $P < 0.001$). However, we did not find significant differences between regions when comparing the densities in the occupied forests (Fig. 2; $F_{2,45} = 0.33$, $P = 0.72$). Although the scarcity of occupied sites in the Mediterranean Lowlands could have affected the power of this analysis, comparison of its significance value with that obtained previously (with not many more degrees of freedom) supports the interpretation that robins actually maintain similar local den-

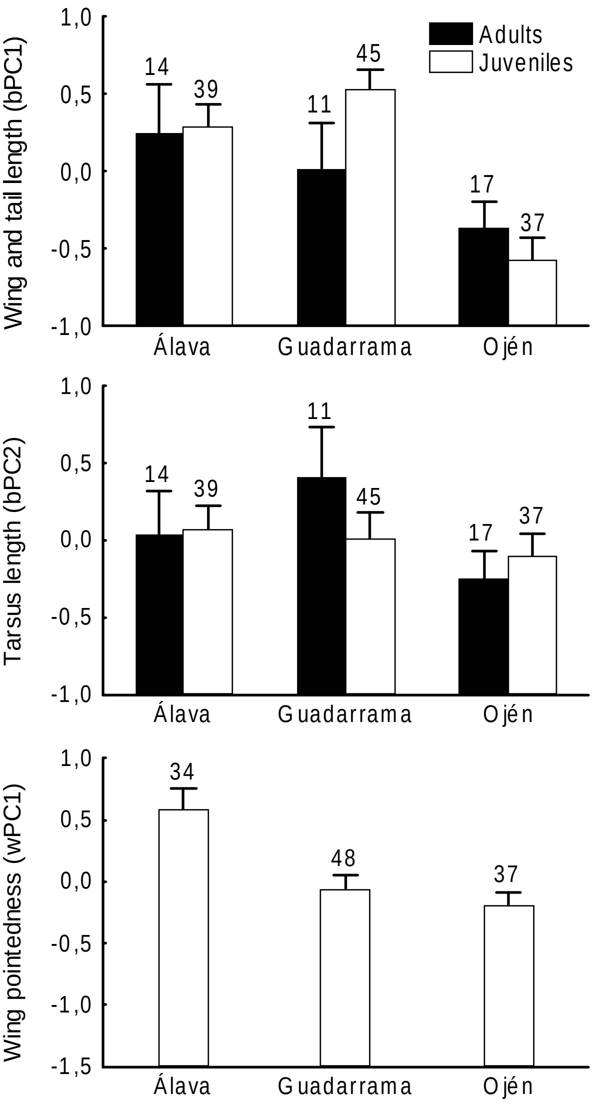

Figure 3. Variation among robin populations in wing and tail length (bPC1 scores), tarsus length (bPC2, a measure of body size) and wing pointedness (wPC1 scores, which were only analysed in juveniles). Means, standard errors and sample sizes are shown.

sities across regions. Moreover, differences between regions explained 27% of variation in robin abundance when all forest were considered, but < 2% when only the occupied forests were analysed. The mean densities in our study sites did not differ from the regional means in the occupied forests (one-sample *t*-tests: Álava t_{15} = 0.92, *P* = 0.37; Guadarrama t_{25} = 0.83, *P* = 0.82; Ojén t_5 = 0.37, *P* = 0.72), supporting the idea that robin densities in our study sites were close to the regional averages.

Morphological variation among populations

The PCA with body measurements extracted two components of variation in body shape and size of robins (bPC1 and bPC2). Wing and tail length had a high loading in bPC1 (both 0.91, within-factor correlation *P* < 0.001), while tarsus length had a small loading in this component (-0.02, n.s.). However, tarsus length had a high loading in the bPC2 (0.99, *P* < 0.001), in which wing and tail length had a small loading (0.01 and -0.04, respectively, n.s.). A multivariate ANOVA analysing the variation among populations and between age classes in bPC1 and bPC2 together showed that, overall, the populations studied differed in morphology (Wilk's Test, *F*-values obtained through Rao's approximation: population $F_{4,312}$ = 4.52, *P* = 0.0015; age $F_{2,156}$ = 1.79, *P* = 0.17; population × age $F_{4,312}$ = 1.23, *P* = 0.29), between-population differences being significant for bPC1 (univariate population effect: $F_{2,157}$ = 7.55, *P* < 0.001), but not for bPC2 ($F_{2,157}$ = 1.56, *P* = 0.21). Therefore, this analysis shows that robins do not vary in body size as measured by bPC2, the component of morphological variation that is best related to a skeletal trait (the tarsus length, see Rising & Somers 1989, Senar &

Table 1. Results of PCA with primary distances. The correlation of each variable with each component is shown.

	Factor loadings	
Primary distances:	wPC1	wPC2
9th primary	0.21	0.75*
8th primary	-0.002	0.88*
7th primary	0.001	0.73*
6th primary	0.38*	0.05
5th primary	0.66*	-0.01
4th primary	0.92*	-0.10
3rd primary	0.94*	-0.06
2nd primary	0.92*	-0.02
1st primary	0.89*	-0.01
Eigenvalue	3.99	1.88
Variance explained (%)	44.30	20.86

* *P* < 0.001.

Table 2. Variation among robin populations in wPC2 scores of juveniles (means adjusted by wing length) and bill measurements of adults. Means, standard errors and sample sizes are shown.

	wPC2 (Juveniles)		Bill measurements (Adults)		
	Adjusted mean	*n*	Length (mm)	Height (mm)	*n*
Álava	-0.13 ± 0.15	34	14.92 ± 0.11	3.73 ± 0.03	21
Guadarrama	0.05 ± 0.14	48	14.99 ± 0.12	3.76 ± 0.03	12
Ojén	-0.12 ± 0.17	37	14.94 ± 0.09	3.75 ± 0.04	26

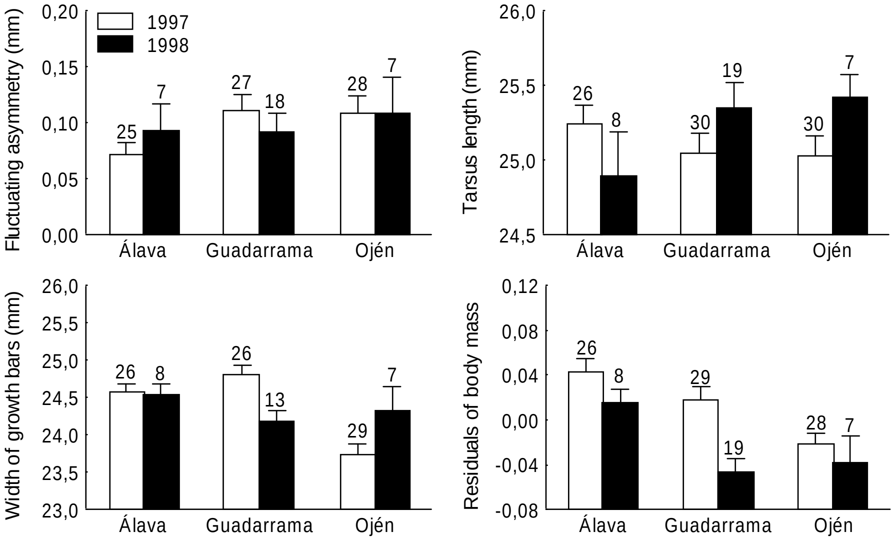

Figure 4. Variation in juvenile condition indices among robin populations in 1997 and 1998. Means, standard errors and sample sizes are shown. Residuals of body mass have been obtained by regressing fledgling mass on tarsus length (both log-transformed).

Pascual 1997). Rather, the populations studied differ in body shape, southernmost robins having shorter wings and tails than their northern counterparts (Fig. 3).

Consistent with the variation in flight-related morphology described above, we also found between-population differences in the wing shape of juveniles. The PCA with primary distances extracted two components (wPC1 and wPC2, Table 1), which described wing pointedness as related to increasing inner (wPC1) or outer (wPC2) primary distances (Chandler & Mulvihill 1988). Overall, robin populations differed in wing shape as described by these components (Multivariate ANCOVA testing for between-population differences in wPC1 and wPC2 together: population $F_{4,260} = 3.89$, $P = 0.0043$; covariate wing length: $F_{2,130} = 26.76$, $P < 0.0001$; test of parallelism: $F_{4,256} = 0.86$, $P = 0.47$). This variation consisted of a decrease of wPC1 scores southwards (Fig. 3; univariate effects: population $F_{2,131} = 7.94$, $P < 0.001$, covariate wing length $F_{1,131} = 42.54$, $P < 0.0001$; test of parallelism: $F_{2,129} = 0.32$, $P = 0.73$), whereas wPC2 scores did not differ between populations (Table 2; population $F_{2,131} = 0.74$, $P = 0.79$, covariate wing length $F_{1,131} = 6.47$, $P = 0.012$; test of parallelism: $F_{2,129} = 1.55$, $P = 0.22$). This result shows that the variation in wing pointedness among Iberian robins consists of changes in length of the inner primaries, but does not affect the outer wing feathers.

Finally, adult robins did not differ among populations in terms of bill length ($F_{2,56} = 0.11$, $P = 0.90$) or bill height ($F_{2,56} = 0.09$, $P = 0.92$; Table 2).

Indices of juvenile condition

Fluctuating asymmetry and body size

Both the tarsus length and its fluctuating asymmetry were highly repeatable (ANOVA: tarsus length $F_{9,17} = 540.80$, $P < 0.0001$, $r = 0.99$; fluctuating asymmetry $F_{9,17} = 44.05$, $P < 0.0001$, $r = 0.94$). Although these estimates were based on a small sample size (because of difficulties in recapturing many individuals), the high level of repeatability obtained suggests that measurement error should not have affected our results (Lessells & Boag 1987). The signed differences between right and left measures fitted a normal distribution (Kolmogorov-Smirnov test: $d = 0.045$, $n = 112$, Lilliefors' $P = 0.2$) whose mean did not differ significantly from zero (one-sample *t*-test: $t_{111} = 1.81$, $P = 0.073$). We normalised the absolute value of these differences (fluctuating asymmetry, FA) through the Box-Cox transformation $FA' = [FA + 0.03]^{0.009}$ (Swaddle *et al*. 1994). Fluctuating asymmetry was not correlated with mean tarsus length ($r = 0.02$, $t_{110} = 0.23$, $P = 0.83$), and did not differ significantly among populations or years (ANOVA: population $F_{2,106} = 0.41$, $P = 0.66$; year $F_{1,106} = 0.02$, $P = 0.89$; population × year $F_{2,106} = 0.50$, $P = 0.61$). This result was unlikely to be due to a low power in detecting a true difference among populations, because the variation of means showed no clear trend (Fig. 4). In contrast, and consistent with this lack of variation in the level of fluctuating asymmetry, juvenile size (measured by the tarsus length, as neither bPC1 or bPC2 arose as a better index of body size) did not change among populations or study years (Fig. 4; ANOVA: population $F_{2,114} = 0.37$, $P = 0.69$; year $F_{1,114} = 0.60$, $P = 0.44$; population × year $F_{2,114} = 2.19$, $P = 0.12$).

Ptilochronology

Feather growth bars were narrower in the southernmost population in 1997 but not in 1998 (Fig. 4), when robins showed even narrower growth bars in the central population than in the southernmost (ANCOVA: population $F_{2,106} = 2.41$, $P = 0.095$; year $F_{1,106} = 0.02$, $P = 0.88$; population × year $F_{2,106} = 3.86$, $P < 0.05$; covariate rectrix length: $F_{1,106} = 6.96$, $P < 0.01$; tests of parallelism: all $P > 0.38$).

Size-corrected body mass

The residuals of body mass on body size (both log-transformed; $r = 0.21$, $F_{1,115} = 5.46$, $P < 0.05$) decreased southwards in both study years (Fig. 4) and were larger in 1997 than in 1998 (ANOVA: population $F_{2,111} = 7.34$, $P < 0.01$; year $F_{1,111} = 8.55$, $P < 0.01$; population × year $F_{2,111} = 1.76$, $P = 0.18$).

The relationship between weather and juvenile condition

Monthly precipitation changed notably between localities and study years, allowing us to detect a significant month by year interaction in a three-way ANOVA (locality $F_{2,60} = 10.79$, $P < 0.0001$; month $F_{4,60} = 7.26$, $P < 0.0001$; locality × month $F_{4,60} = 2.21$, $P < 0.05$; month × year $F_{4,60} = 3.70$, $P < 0.01$; the remaining effects and interactions with $P > 0.20$), even though we had only three precipitation values per month in each locality (one every ten days). Accordingly, maximum temperature increased in the months of lower precipitation, which led to the same pattern and strength of interactions (locality $F_{2,60} = 15.09$, $P < 0.0001$; month $F_{4,60} = 83.14$, $P < 0.0001$; locality × month $F_{4,60} = 2.21$, $P < 0.05$; month × year $F_{4,60} = 7.35$, $P < 0.0001$; the remaining effects and interactions with $P > 0.14$). Because of the nature of the data analysed here, these ANOVA results should be considered to be for guidance only. However, they clearly illustrate that both northern localities suffered a stronger drought in 1998, when they received much less precipitation during June and July, whereas the southernmost locality supported its habitual hot and dry summer in both years (cf. Fig 1 and Table 3).

DISCUSSION

Our study of robin distribution showed that the restriction of the species' range southwards does not relate a parallel decrease in density in the occupied habitats. It has been suggested that a decrease in abundance of birds towards the range edge is most likely to be detected when studying either the whole species' range or a narrow area immediately adjacent to the border (Blackburn *et al*. 1999). The progressive fragmentation of the range of robins southwards in Iberia shows that we are in the latter situation. However, we still failed to detect a lower local abundance in the southernmost region. This supports the idea that

Table 3. Precipitation (mm, left) and maximum temperature (°C, right) by months in the three study localities during the years in which we measured juvenile condition of robins. Data are means by periods of 10 days, so *n* = 3 in all cases.

	Álava		Guadarrama		Ojén	
	1997	1998	1997	1998	1997	1998
April	5.9 / 18.6	29.9 / 14.3	14.3 / 18.2	58.6 / 11.4	16.9 / 20.1	10.4 / 18.4
May	22.2 / 22.2	25.0 / 18.6	54.7 / 17.5	48.4 / 17.0	7.4 / 22.1	12.7 / 20.7
June	26.7 / 21.6	11.6 / 22.6	15.9 / 20.5	10.2 / 22.3	9.2 / 24.7	1.3 / 24.3
July	32.0 / 22.8	3.3 / 23.9	18.7 / 24.6	4.6 / 27.8	0.9 / 25.6	0.0 / 28.0
August	15.9 / 27.7	3.3 / 25.0	8.0 / 26.6	3.3 / 28.2	0.2 / 27.4	0.0 / 28.2

Iberian robins could select sectors above a somehow restrictive threshold of habitat quality, which means that the species' border would be defined by a steep loss of suitable habitats rather than a gradual increase in environmental restrictions in the occupied sites (Lawton 1993, Blackburn *et al.* 1999 and references therein). It could be argued that an asymmetric flow of individuals from the most populated northern sectors to the unsuitable southern ones may also explain a similar abundance across the gradient. However, such a strong gene flow would swamp any differentiation of southern populations (Holt & Gomulkiewicz 1997, Kirkpatrick & Barton 1997), so that we should not have found morphological correlates of migratory behaviour of robins if directional flow were the factor maintaining similar densities across the Iberian gradient (as the geographical variation in migratory behaviour and its related morphology is unlikely to be the outcome of phenotypic plasticity, Berthold 1999). In the Iberian Peninsula, the frequency of forest occupation by robins is related chiefly to the level of precipitation (Tellería & Santos 1993, 1994), which suggests that environmental moisture could determine a threshold of habitat quality for robins. In fact, the ground runs dry in Mediterranean environments as the summer progresses (Joffre & Rambal 1993), causing a decrease in primary production of pastures that limits the availability of invertebrates in both soil and grass (Herrera 1981, Mooney 1981). Because robins feed principally upon ground invertebrates (Cramp 1988), the need for a high soil moisture throughout the breeding season could constrain their distribution in a gradient of increasing dryness.

Together with this seemingly restrictive habitat selection towards the border, southern Iberian robins could avoid maladaptation in the range boundary by local differentiation. The morphological variation that we found is consistent with the different migration patterns of Iberian robins, and supports the differentiation of populations near the Mediterranean range boundary. That migratory robins do not have a shorter tail, in contrast with the predictions of aerodynamics (Norberg 1995), and the morphological variation observed in other passerine species in the same ecological context (Tellería & Carbonell 1999), could be related to selective forces other than migration. For instance, a shorter tail could be constrained by practical requirements for flying in dense vegetation (Norberg 1995). However, we did not find different feeding-related traits among robin populations, which suggests that feeding behaviour remains similar across Iberia (an example of variation in blackcaps is given in Tellería & Carbonell 1999). Because feeding behaviour is likely to be a major determinant of habitat selection in robins (see above), this result is consistent with the existence of a threshold of environmental moisture below which robins would rarely occur.

The role of precipitation in the life history of robins was illustrated by the variation among populations and years in juvenile condition. The southernmost population begins to face a precipitation deficit from May, while the two northernmost populations will not suffer this stress until June (see Fig. 1 and Table 3). Accordingly, we did not find evidence of increased stress during the early development of southernmost robins, as shown by the homogeneous level of fluctuating asymmetry and body size both among populations and years. However, consistent with a differential accentuation of drought southwards during the postfledging period, juvenile condition decreased in the southernmost population during fledgling independence. Moreover, these differences intensified with increasing differences in environmental conditions among localities. Thus, southern robins faced more difficulties than their northern counterparts for growing the tail feathers in the rainiest year, but this trend disappeared when the northernmost localities received less precipitation. Later in the postfledging period, juveniles evidenced the stronger environmental stress in the southern breeding grounds through a lower body mass. It should be noted that morphological changes could also influence this variation in body mass, as wing load depends on mass and wing shape (Norberg 1995). Consistent with the results of ptilochronology, juveniles were heavier relative to body size in the rainiest year, which supports the idea that environmental conditions played a relevant role in shaping among-population differences in fledgling mass.

In summary, our results suggest that the hardness of the summer drought, probably due to its effect on food availability (Herrera 1981, Mooney 1981), could actually be a major proximate determinant of changes in juvenile condition in robins. Thus, the decrease in environmental moisture throughout the breeding season in southern Iberia could lead to a higher summer mortality of juveniles in these areas (as a consequence of their lower body condition, Brown 1996). However, this does not necessarily mean that the southernmost populations are maladapted. Body condition must be interpreted in the context defined by the abundance distribution and morphological variation found. By means of both restrictive habitat selection and population differentiation, Iberian robins are likely to be adjusted to environmental heterogeneity and, in turn, enjoy similar developmental conditions along the Mediterranean gradient. After independence, juvenile robins benefit from a milder summer in northern Iberia, which translates into enhanced body condition compared to that of southern, more stressed populations. However, this may well be resembling the differing reproductive benefits associated to either migratory and sedentary behaviours, in which case differences in body condition would have no net fitness consequence. Indeed, a higher level of survival in migratory robins late in the breeding season might be balanced by increased mortality due to the costs of migration (Alerstam & Högstedt 1982, Alerstam 1990). In contrast, and given that owner robins have advantages against intruders when defending winter territories (Tobias 1997), sedentary populations could improve recruitment by acquiring the best territories before the arrival of northern conspecifics (Sherry & Holmes 1996). In fact, we found that sedentary populations of robins have a smaller clutch size but a longer life expectancy than their migratory counterparts in the Iberian Peninsula (Pérez-Tris & Tellería submitted). From this perspective, one should be prudent when interpreting the lower juvenile condition of southern robins late in the breeding season as evidence of decreased fitness in the species' border. Southernmost Iberian robins are likely to be differentiated in the range boundary, a pattern that could be extensible to other forest passerines (Tellería & Carbonell 1999, Tellería, Pérez-Tris & Carbonell, submitted). It is possible that, in some instances, both migratory and sedentary populations of robins occur in stressing environments, where they may attain a lower fitness than that achieved in their usual habitats (see some examples in Carbonell & Tellería 1998, 1999), but this will not be the outcome of occupying peripheral areas in the species' range. Rather, our results suggest that environmental heterogeneity may result either in maladaptation or local adaptation depending on the geographical configuration of the habitats and the evolutionary history of the populations inhabiting them.

Acknowledgements

We thank R. A. Baquero, J. A. Díaz, T. Santos and two anonymous referees for valuable comments on the manuscript. The Agencias de Medio Ambiente (Diputación Foral de Álava, Comunidad Autónoma de Madrid and Junta de Andalucía) kindly authorized us to capture robins. This paper was funded by the Ministerio de Educación y Cultura de España (projects PB92-0238 and PB97-0325). During its preparation, J.P-T. was also supported by a FPI Grant from the Universidad Complutense de Madrid.

References

Alerstam, T. 1990. *Bird Migration*. Cambridge University Press, Cambridge.

Alerstam, T. & Högstedt, G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scandinavica* 13: 25-37.

Bensch, S. & Lindström, Å. 1992. The age of young willow warblers *Phylloscopus trochilus* estimated from different stages of post-juvenile moult. *Ornis Svecica* 2: 23-28.

Berthold, P. 1991. Genetic control of migratory behaviour in birds. *Trends in Ecology & Evolution* 6: 254-257.

Berthold, P. 1999. Geographic variation and the microevolution of avian migratory behaviour. *Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms* (eds. S.A. Foster & J.A. Endler), pp. 164-179. Oxford University Press, Oxford.

Biebach, H. 1983. Genetic determination of partial migration in the European robin (*Erithacus rubecula*). *Auk* 100: 601-606.

Blackburn, T.M., Gaston, K.J., Quinn, R.M. & Gregory, R.D. 1999. Do local abundances of British birds change with proximity to range edge? *Journal of Biogeography* 26: 493-505.

Blondel, J., Dias, P.C., Maistre, M. & Perret, P. 1993. Habitat heterogeneity in life-history variation of Mediterranean Blue Tits (*Parus caeruleus*). *Auk* 110: 511-520.

Brown, J.H. 1984. On the relationships between abundance and distribution of species. *American Naturalist* 124: 255-279.

Brown, J.H. 1995. *Macroecology*. The University of Chicago Press, Chicago

Brown, M.E. 1996. Assessing body condition in birds. *Current Ornithology* 13: 67-135.

Carbonell, R. & Tellería, J.L. 1998. Increased asymmetry of tarsus-length in three populations of Blackcaps *Sylvia atricapilla* as related to proximity to range boundary. *Ibis* 140: 331-333.

Carbonell, R. & Tellería, J.L. 1999: Feather traits and ptilochronology as indicators of stress in Iberian Blackcaps *Sylvia atricapilla. Bird Study* 46: 243-248.

Carrascal, L.M., Moreno, E. & Tellería, J.L. 1990. Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. *Holarctic Ecology* 13: 105-111.

Caughley, G., Grice, D., Barker, R. & Brown, B. 1988. The edge of range. *Journal of Animal Ecology* 57: 771-785.

Chandler, C.R. & Mulvihill, R.S. 1988. The use of wing shape indices: an evaluation. *Ornis Scandinavica* 19: 212-216.

Cramp, S. (ed) 1988. *The birds of the Western Palearctic*. Vol. V. Oxford University Press, Oxford.

Font, I. 1983. *Climatología de España y Portugal*. Instituto Nacional de Meteorología, Madrid.

Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major. Ibis* 123: 31-41.

Grubb, T.C. 1995. Ptilochronology. A review and prospectus. *Current Ornithology* 12: 89-114.

Herrera, C.M. 1981. Organización temporal en las comunidades de aves. *Doñana Acta Vertebrata* 8: 79-101.

Hoffmann, A.A. & Blows, M.W. 1994. Species borders: ecological and evolutionary perspectives. *Trends in Ecology & Evolution* 9: 223-227.

Holt, R.D. & Gomulkiewicz, R. 1997. How does immigration influence local adaptation? A reexamination of a familiar paradigm. *American Naturalist* 149: 563-572.

Joffre, R. & Rambal, S. 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74: 570-582.

Kirkpatrick, M. & Barton, N.H. 1997. Evolution of a species' range. *American Naturalist* 150: 1-23.

Lautensach, H. 1967. *Geografía de España y Portugal.* Vicens-Vives, Barcelona.

Lawton, J.H. 1993. Range, population abundance, and conservation. *Trends in Ecology & Evolution* 8: 409-413.

Leisler, B. & Winkler, H. 1985. Ecomorphology. *Current Ornithology* 2: 155-186.

Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116-121.

Lindén, M., Gustafsson, L. & Pärt, T. 1992. Selection on fledging mass in the Collared Flycatcher and the Great Tit. *Ecology* 73: 336-343.

Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* 14: 343-348.

Lockwood, R., Swaddle, J.P. & Rayner, J.M.V. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29: 273-292.

Møller, A.P. 1997. Developmental stability and fitness: a review. *American Naturalist* 149: 916-932.

Mooney, H.A. 1981. Primary production in Mediterranean-climate regions. *Ecosystems of the World* (eds. F. di Castri, D.W. Goodall & R.L. Spetch), pp 249-255. Elsevier Scientific Publications, Amsterdam.

Newton, I. 1989. *Lifetime reproduction in birds*. Academic Press, London.

Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology* 9: 48-54.

Rising, J.D. & Somers, K. 1989. The measurement of overall body size in birds. *Auk* 106: 666-674.

Santos, T. & Tellería, J.L. 1995. Global environmental change and the future of Mediterranean forest avifauna. *Global change and Mediterranean-type ecosystems* (eds. J.M. Moreno & W.C. Oechel), pp 457-470. Springer-Verlag, New York.

Sanz, J.J. 1997. Clutch size manipulation in the Pied Flycatcher: effects on nestling growth, parental care and moult. *Journal of Avian Biology* 28: 157-162.

Senar, J.C. & Pascual, J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea* 85: 269-274.

Sherry, T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

Svensson, L. 1992. *Identification guide to European passerines.* British Trust for Ornithology, Tring.

Swaddle, J.P., Witter, M.S. & Cuthill, I.C. 1994. The analysis of fluctuating asymmetry. *Animal Behaviour* 48: 986-989.

Tellería, J.L., Asensio, B. & Díaz, M. 1999. *Aves Ibéricas. Vol. 2. Passeriformes*. J.M. Reyero, Madrid

Tellería, J.L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology* 30: 63-71.

Tellería, J.L. & Santos, T. 1993. Distributional patterns of insectivorous passerines in the Iberian forests: does abundance decrease near the border? *Journal of Biogeography* 20: 235-240.

Tellería, J.L. & Santos, T. 1994. Factors involved in the distribution of forest birds in the Iberian Peninsula. *Bird Study* 41: 161-169.

Tobias, J. 1997. Asymmetric territorial contests in the European robin: The role of settlement costs. *Animal Behaviour* 54: 9-21.

Capítulo 3

Cambios estacionales de abundancia y morfometría del vuelo sugieren diferentes patrones migratorios en los paseriformes forestales ibéricos

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Tellería, J.L., Pérez-Tris, J. & Carbonell, R. Seasonal changes in abundance and flight-related morphology reveal different migration patterns in Iberian forest passerines (manuscrito enviado).

RESUMEN

Un patrón biogeográfico bien conocido es la acentuación del comportamiento migrador de las aves en áreas septentrionales del Paleártico, como consecuencia del aumento de la estacionalidad con la latitud. Sin embargo, no está tan claro si las aves responden de igual modo a las variaciones de estacionalidad en los sectores más meridionales, donde la existencia de montañas y mesetas da lugar a una elevada heterogeneidad ambiental. Esta escasez de información puede deberse al limitado esfuerzo de anillamiento aplicado al estudio de los movimientos de estas poblaciones de aves, lo que obliga a utilizar aproximaciones alternativas que permitan inferir el alcance relativo de sus movimientos. En este trabajo integramos información procedente de (1) cambios estacionales en la abundancia de los paseriformes forestales entre la mitad norte (montañas y mesetas, adecuadas para la reproducción pero duras en invierno) y la mitad sur (menos elevada y muy adecuada para la invernada) de la península Ibérica y (2) datos procedentes del estudio de algunos rasgos morfométricos relacionados con el comportamiento migrador de las aves. Nuestro objetivo es ilustrar si la migratoriedad de estas especies es más acusada en las mesetas que en las tierras bajas de la mitad sur peninsular. Para ello, estudiamos seis especies comunes de invernada presahariana (petirrojo *Erithacus rubecula*, mirlo *Turdus merula*, curruca capirotada *Sylvia atricapilla*, reyezuelo listado *Regulus ignicapillus*, herrerillo común *Parus caeruleus* y carbonero común *Parus major*), más una especie transahariana, que utilizamos como control dado su comportamiento migrador homogéneo en toda la Península (el ruiseñor común *Luscinia megarhynchos*). Revisamos 67 estudios de comunidades ampliamente distribuidos por la Península, en los que la abundancia de estas especies había sido medida en primavera e invierno. En todas las especies, con excepción del mirlo, la abundancia invernal aumentó en la mitad sur peninsular y disminuyó en las mesetas, aunque en algunos casos este patrón pudo verse afectado por la llegada de invernantes desde áreas más norteñas. Medimos individuos de cada una de estas especies en cinco localidades

diferentes, tres en las mesetas y dos en las tierras bajas meridionales, lo que permitió establecer un patrón común en la morfología asociada con el comportamiento migrador. Controlando el tamaño estructural de las aves, las poblaciones de las mesetas presentaron en general alas más largas y apuntadas (medido el apuntamiento alar mediante la primera componente principal extraída en un ACP con las distancias entre la punta de cada primaria y la punta del ala), así como colas más cortas, que las de las tierras bajas meridionales. La única excepción fue el ruiseñor común, que mostró rasgos similares en ambos sectores, de acuerdo con su patrón migratorio homogéneo en toda la Península. Los cambios estacionales en abundancia y las variaciones morfológicas fueron consistentes, por lo tanto, con una mayor intensidad de los movimientos de las aves de las mesetas. Nuestros resultados confirman la variación intraespecífica descrita para muchas de estas especies en la península Ibérica, y suponen un paso adelante en el conocimiento de dicha variación al darle un significado ecológico, con relación al comportamiento migrador predominante en cada región peninsular. De acuerdo con la distribución de las áreas montañosas en el Paleártico, los movimientos de este tipo – probablemente de corta distancia – podrían estar muy extendidos en la cuenca Mediterránea, solapándose con las migraciones latitudinales de estas especies.

Seasonal changes in abundance and flight-related morphology reveal different migration patterns in Iberian forest passerines

José Luis Tellería, Javier Pérez-Tris & Roberto Carbonell*

Although the attenuation of seasonality southwards in the temperate region is known to be a major determinant of the latitudinal decline in the migratory behaviour of many passerines, the spread of altitudinal migrations in southern areas as a response to similar changes with elevation still remains obscure, principally because no extensive ringing program has been conducted in these areas. Here we use spatio-temporal changes in abundance and variations in flight-related morphology to infer differences in migratory behaviour of forest passerines in the Iberian Peninsula, where the environmental optimum for these species moves seasonally between northern highlands (very suitable for breeding but unproductive in winter) and southern lowlands (less suitable for reproduction but highly productive in winter). According to this pattern of environmental conditions, we predict that migratory behaviour should be more intense in highlands, while sedentariness should be the rule in lowlands. We studied abundance and morphology of several common passerines (Robin *Erithacus rubecula*, Blackbird *Turdus merula*, Blackcap *Sylvia atricapilla*, Firecrest *Regulus ignicapillus*, Blue Tit *Parus caeruleus* and Great Tit *P. major*). In all species except Blackbirds, winter abundance increased in lowlands but decreased in highlands, despite European migrants may arrive at this latter area for wintering. A common pattern of variation in flight-related morphology was found, birds having longer and more pointed wings in highlands. In addition, a trans-Saharan migrant species that we used as a control (the Nightingale *Luscinia megarhynchos*), did not differ in these traits between regions. Both the seasonal changes in abundance distribution and the morphological variations between regions are consistent in signalling an increased migratoriness of birds in highlands compared to lowlands. This kind of movements, likely widespread across the Mediterranean region, are likely to constitute a set up of small-scale, altitudinal migration patterns overlapping the broader latitudinal migratory system in the Palearctic.

Migration is a dynamic response of birds to changing environmental conditions through which many populations and species track seasonal productive outputs across environmental gradients (Baker 1978, Berthold 1996). Seasonal changes in productivity are considered to trigger large-scale migrations (Moreau 1972, Greenberg 1980, Alerstam & Högstedt 1982), which have long been studied by research programs based on the analysis of ringing recoveries (Gauthreaux 1996). Today we have a good knowledge of the migratory patterns of many bird species, including the changing intensity of migratory behaviour across latitudinal gradients (Alerstam 1990, Berthold 1993). North-to-south variation in the extent of migratory behaviour is well-known to be the outcome of increasing spring productivity and decreasing winter suitability with latitude, a correlation which has been profusely studied in almost all latitudinal migratory systems in the world (MacArthur 1959, Willson 1976, Herrera 1978, Newton & Dale 1996ab, Chesser 1998). However, although elevation causes variations in seasonal productivity at middle and low latitudes that are similar to those associated with latitude across the temperate zone, little is known on the relevance of altitudinal migrations in this area (Mead 1983). This gap in our understanding of avian migratory systems is primarily due to the lack of extensive ringing programs applied to the relatively small bird populations breeding in montane areas (Gauthreaux 1996). Because of these

---

*Manuscrito enviado.

limitations in the study of altitudinal migrations, evidence of such movements has been obtained so far in rather scattered work, which in many occasions dealt with other aspects of the biology of birds and only referred to altitudinal movements as a secondary topic in the study (e.g. Czajkowski & Dejonghe 1981, Rabenold & Rabenold 1985, Lo Valvo *et al*. 1988).

In this paper, we have explored the movements of forest passerines in the Iberian Peninsula, where highlands and mountains are surrounded by mild Mediterranean lowlands making up a suitable scenario for the development of altitudinal migrations (Fig. 1). The northern half of Iberia is characterised by plateaux and mountains where forest passerines meet good conditions for reproduction, contrasting with southern Iberian environments where the summer drought prevents reproduction of many of these species (Tellería & Santos 1993, 1994, Tellería *et al*. 1999). The opposite occurs in winter, when the cold makes northern Iberian forests to be less productive, while the southern lowlands and the Mediterranean coasts experience a peaking primary production (Tellería 1988, Tellería *et al*. 1988). Accordingly, these lowlands receive a large number of migrant birds coming from Europe to exploit the vegetation sprouting and the ripening of fruiting shrubs in winter (Herrera 1981, 1998, Tellería *et al.* 1988, Fuentes 1992). One can thus postulate that populations of forest birds breeding in lowlands will rely on these abundant winter resources, while highland populations will be forced to escape the impaired environmental conditions in northern Iberia during winter. However, ringing data are scarce for Iberian forest birds and do not provide conclusive information about seasonal movements (Tellería *et al*. 1999). Because these traditional methods to study bird migration do not allow us to disentangle the possible variations in migratory behaviour of Iberian forest birds, we have addressed the topic by relying on alternative methods based on correlates of migratoriness. Thus, we have inferred the movements of these species in highlands and lowlands using two complementary approaches:

Seasonal changes in abundance

Migratory movements are of prime importance in determining the spatio-temporal structuring of bird communities. In the southern Iberian forests, the arrival of Palearctic migrants for wintering causes a huge increase in both abundance and richness of birds (Herrera 1981, Tellería 1988). Because of the problems outlined above, the possible contribution to this increase of the comparatively small northern Iberian populations remains unknown. However, seasonal changes in abundance can help us unravel the extent to which forest passerines abandon the northern highlands. According to the seasonal variation in environmental conditions in the Iberian Peninsula, we can predict a decrease in abundance in highlands parallel to the increase in lowlands.

Morphological variation

A common pattern in passerines is that differences among populations or species in migratory behaviour are related to differences in flight-related morphological traits (Leisler & Winkler 1985, Winkler & Leisler 1992). These differences have been interpreted as the outcome of migration-related selective pressures opposing manoeuvrability-related selective forces, which would shape different morphological traits depending on the extent of migratory journeys. Longer and more pointed wings improve endurance in long non-stop flights, while short and round wings improve efficacy in take-offs (Pennycuick 1989). Thus, populations that undertake longer migrations usually show longer and more pointed wings than their sedentary counterparts (Rayner 1988, Norberg 1990, Winkler & Leisler 1992). In addition, it is known that a longer tail increases drag during flights, and migratory birds have been observed to have a shorter tail than sedentary ones even at the expense of a somehow impaired manoeuvrability (Winkler & Leisler 1992, Norberg 1995). Therefore, when changes in migratory behaviour among populations of a species cannot be studied directly, the evaluation of changes in morphological correlates of migratoriness may provide a formal way to test for such differences (Wainwright 1994). According to our hypothesis, we predict that highland populations will have longer and more pointed wings, and shorter tails, than lowland populations.

METHODS

The Iberian Peninsula as a study area

The Iberian Peninsula locates at the southern edge of the Western Palearctic, between 36ºN and 43ºN, where environmental variation due to the gradually decreasing oceanic influence towards southeast, together with elevation in plateaux and mountains, makes it possible the differentiation of several bioclimatic sectors (see Font 1983 for details; Fig. 1). Because of the strong oceanic influence, the northern Atlantic belt in the Iberian Peninsula is a rainy sector with mild winters, whose environmental conditions are far from typical in Mediterranean environments and rather resemble the Eurosiberian climate. Because of this, we have not considered this northern Iberian sector in our study. Further inland, the Iberian Central Plateau (highlands in this paper), emerges as a huge extension of more than 80000 km^2 above 600-m elevation. This region has a seasonal pattern of primary production, with a marked contrast between temperate summers and harsh winters (Aschmann 1971, Font 1983). In spring, forest passerines are widespread and abundant in these highlands, making up rich communities in nearly all forested areas in the region (Tellería & Santos 1993, 1994). In contrast, the south-Iberian Mediterranean region (lowlands) is characterised by a strong summer drought, which precludes reproduction of forest birds across the region except in some rainy mountain and coastal sectors (Tellería & Santos 1993, 1994). During winter, however, the temperate and relatively moist winters in these lowlands make it possible an intense production of fruits and the activity of many insects (Herrera 1981, Mooney 1981), which permit the sustenance of huge populations of migratory birds that arrive at the area for wintering (Tellería 1988, Tellería *et al*. 1988, 1999).

The study of abundance

We used the comprehensive review by Tellería *et al.* (1999) of the distribution of bird abundances in the Iberian peninsula. These authors gathered most of the work published so far on the composition and abundance of Iberian bird communities. From this general database, we selected those studies in which bird densities were estimated by line-transect counting on identical itineraries in both spring and winter. By using only the counts that were repeated by the same authors, we were able to control for the within-site changes in abundance when testing for variation between regions. The final data-set was composed of 67 survey sites widely distributed across the Iberian Peninsula (42 in highlands and 25 in lowlands). The species studied were those for which we captured enough individuals to do a sound analysis of morphological variation (see below). For each one, we conducted a two-way ANOVA with the region (highlands vs. lowlands) as a between-subjects factor and the season (spring vs. winter) as a within-subjects factor. In this ANOVA, the interaction will test for the hypothesised seasonal change in the regional distribution of abundance of each species. Only those sites in which the corresponding species was found at least once were used in these analyses.

The localities where birds were captured

During the period May-July between 1995 and 1999 we captured forest passerines in five localities in the Iberian Peninsula (Fig. 1), which were representative of highland and lowland environments (for a detailed description of the study sites see Carbonell & Tellería 1998a):

Highlands

(1) Álava (42º55’N 2º29’W, mean elevation 620 m; mean annual rainfall 1000-1500 mm; mean annual temperature: 12ºC). This site lies on the north-

ern edge of the Iberian highlands, and is covered by mixed oak and maple forests (*Quercus faginea, Quercus robur* and *Acer campestre*). (2) Sierra de Guadarrama (40º54’N 3º53’W; 1100 m; 700-1000 mm; 10ºC), a mountain range covered by *Quercus pyrenaica* and *Pinus sylvestris* forests. Birds were caught in mixed *Fraxinus excelsior, Alnus glutinosa* and *Quercus pyrenaica* forests interspersed with meadows. (3) Madrid (40º30’N 3º4’W, 600 m; 300-500 mm; 14ºC), a set of riparian forests (*Populus nigra*, *Tamarix gallica*, *Salix* spp.) along the Guadarrama and Jarama Rivers, which flow through a cereal-farming landscape.

Lowlands

(4) Sierra de Ojén (36º01’N 5º36’W, 250 m; 1000-1500 mm; 16ºC). Birds were caught in rainy hills covered by mixed *Quercus suber* and *Quercus canariensis* forests. (5) Tarifa (36º01’N 5º36’W; 0-5 m; 700-1000 mm; 18ºC). This sector lies at the foot of the Sierra de Ojén, near the Atlantic coast. Forest birds occupy riverside formations with *Alnus glutinosa*, *Populus nigra* and *Nerium oleander* in the Jara River, which flows through deforested grasslands.

Capture and measurement of birds

Mist-netting was conducted in each locality during a research program originally devoted to the study of morphology and body condition of Blackcaps *Sylvia atricapilla* (Carbonell & Tellería 1998b, 1999, Tellería & Carbonell 1999) and Robins *Erithacus rubecula* (Pérez-Tris *et al*. 2000a), so these two species were the best represented in our dataset. Other birds were not so frequently captured and, because the extensive measuring necessary for a detailed analysis of morphology takes a long

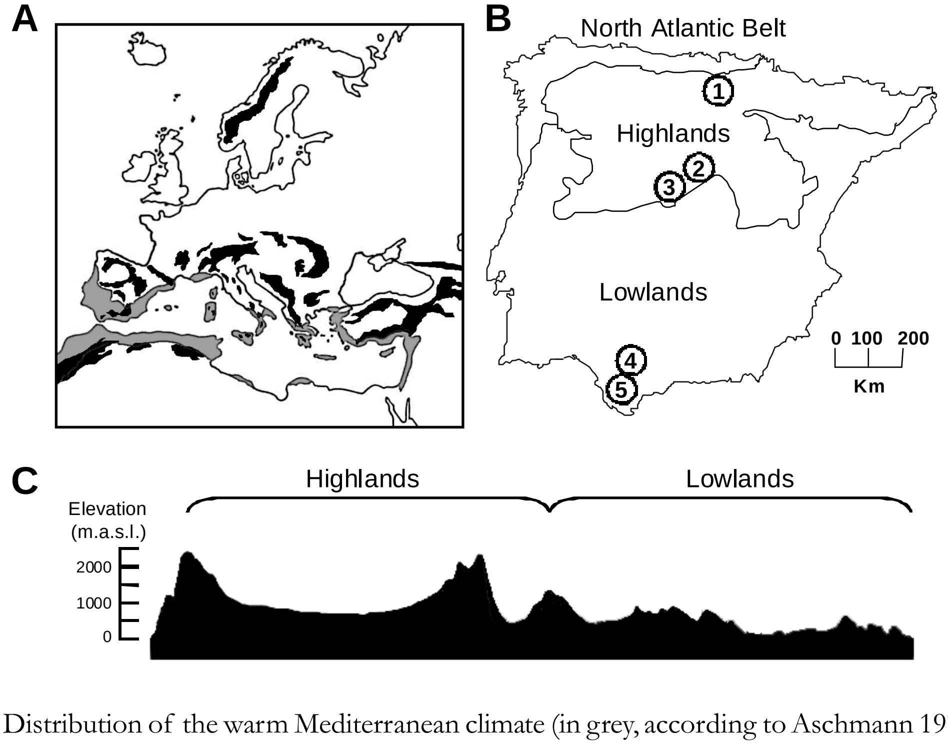

Figure 1. (A) Distribution of the warm Mediterranean climate (in grey, according to Aschmann 1971) and the most important mountains in the Western Palearctic, indicating the potential for altitudinal movements of birds in the Mediterranean zone. (B) Regional division of the Iberian Peninsula in this study. We have differentiated between the northern highlands (very productive in spring but unproductive in winter) and the southern lowlands (with the opposite trend of primary production). The northern, mild Eurosiberian Atlantic Belt has been excluded. The localities where we captured individuals have been labelled: 1 Álava, 2 Guadarrama, 3 Madrid, 4 Ojén and 5 Tarifa. C. North-to-south altitudinal profile showing the contrast in elevation between highlands and lowlands.

time, they were randomly chosen for measuring purposes depending on the time available for safely processing birds other than Blackcaps and Robins. Because of this, a suitable sample size was finally gathered of six species. These were represented by three families of passerines common to European forests: thrushes (Robin and Blackbird *Turdus merula*; F. Turdidae), warblers (Blackcap and Firecrest *Regulus ignicapillus*; F. Sylviidae) and tits (Blue Tit *Parus caeruleus* and Great Tit *Parus major*: F. Paridae). These species differ in most features of ecology and behaviour (diet and feeding strategies, nesting places, social systems, etc.), and may be considered to be potential short-distance migrants as all of them have migratory populations in some part of their range that spend the winter in the Mediterranean (Cramp 1988, 1992, Cramp & Perrins 1993). Together with these six species, we also gathered enough data of one long-distance migrant whose populations spend the winter in sub-Saharan Africa (the Nightingale *Luscinia megarhynchos*; F. Turdidae). This species was regarded as a control of the relationship between flight-related morphology and migratoriness, which we used to rule out the possibility that regional differences were due to unlike productivity, or to any factor other than migration pressures that could affect growth of birds. Thus, according to our hypothesis no morphological change should be found between highland and lowland Nightingale populations, since all of them have a homogeneous trans-Saharan migratory pattern.

Body measurements included the tarsus length (to the last scale before the toes), the length of the straightened tail, the wing maximum chord and the bill height (in the culmen). Bill height was chosen instead of bill length as a measure of the bill size because the latter takes longer for a growing bird to achieve it, and hence most juvenile individuals had not attained its final size at the moment of their capture. We also recorded the wing formula by measuring the distances from the tip of each primary feather 1 to 9 (numbered descendantly) to the wing tip (the so-called primary distances). Measurement methods were the proposed by Svensson (1992), and have been fully described by Tellería and Carbonell (1999). We did not measure wings or tails that were still growing, and our sampling design forced us to discard a complete measurement of some individuals (because of time restrictions). Due to these missing values, sample sizes were heterogeneous in our analyses. A summary of biometrics of the species studied can be found in the Appendix.

We aged individuals according to plumage characters. In all seven species studied, adults undertake a complete post-nuptial moult late in summer, whereas juveniles perform a partial moult which does not affect flight feathers (except in Great Tits, which frequently moult the tail in the post-juvenile moult, Jenni & Winkler 1994, pers. obs.). Thus, in these species one can recognise three age classes in summer before the post-nuptial moult: more than one-year old birds (individuals that moulted completely the previous year and so have a single generation of feathers), one-year old birds (which moulted partially and retained juvenile flight feathers) and fledglings, which have a juvenile plumage in prime condition. Because one-year old individuals have the same flight feathers they had as fledgling, they should be classified as juveniles with regard to flight-related morphology. In our analyses, however, we only distinguished between juveniles (birds that were born in the ongoing study year) and adults (which included birds that were born in the preceding breeding season or before). The reason why we did so is that the change in wing length and shape after the first complete post-nuptial moult (if the juvenile and the adult flight plumages of the same individuals are compared when in prime condition) is negligible compared to the decrease due to one-year feather abrasion in either second-year or older birds (own unpubl. data, for similar results see Flegg & Cox 1969, Francis & Wood 1989). Because it is wear what introduces a noticeable variation in wing morphology in our sample (one-year old and older birds have a very similar morphology at this time of year, which differs from the morphology of juveniles), to take into account the variation due to feather

Table 1. Coefficients of correlation between each body measurement and the principal components of body size extracted by PCA. For the species in which more than one component was extracted, the asterisk indicates the one which was used as an index of structural size.

Species	*n*	Tarsus	Bill	Wing	Tail	Eigenvalue	Variance (%)
E. rubecula	218						
bsPC1		0.11	-0.36	0.87	0.88	1.68	42.08
bsPC2*		0.89	0.46	0.10	-0.02	1.02	25.43
T. merula	58						
bsPC1*		0.01	0.38	0.85	0.85	1.59	39.81
bsPC2		-0.87	0.50	-0.15	-0.07	1.04	25.90
S. atricapilla	515						
bsPC1		0.56	0.47	0.74	0.80	1.73	43.18
R. ignicapillus	20						
bsPC1*		0.62	0.02	0.94	0.85	1.99	49.68
bsPC2		-0.54	0.89	0.02	0.35	1.21	30.31
P. caeruleus	45						
bsPC1		0.67	0.81	0.91	0.79	2.55	63.65
P. major	58						
bsPC1		0.77	0.44	0.86	0.83	2.21	55.28
L. megarhynchos	46						
bsPC1*		0.74	-0.05	0.94	0.88	2.21	55.23
bsPC2		0.43	-0.95	-0.20	-0.20	1.16	28.97

wear (abraded vs. new feathers) instead of the variation due to feather generation (adult vs. juvenile feathers, with the latter mixing new and abraded feathers) will give more reliable results.

Sexing adults was difficult in the sexually monomorphic species (Robins, Nightingales, and the majority of Blue Tits) because many birds had already lost their reproductive characters (brood-patch or protruding cloaca) when we captured them. In addition, no sexual dimorphism takes place in juveniles of any of the species studied that could be utilised for sexing purposes (notice that size-based methods cannot be used in this study). Because of this, we did not consider the sex of birds in our analyses. Although sexual size dimorphism is common among passerines (see Cramp 1988, 1992, Cramp & Perrins 1993 for reviews of the species considered in this paper), it should not have affected our results given that (1) sexual dimorphism concerns to size instead of shape (i.e. proportions), so that no effect of gender should hold once differences in body size among individuals were statistically controlled for in our analyses (see below), and (2) the sex-ratio was homogeneous among populations (minimum *P* value in chi-square tests larger than 0.1, whether sex-ratios were compared among localities or between highlands and lowlands).

The analyses of morphology

When studying the changes between bird populations in flight-related morphology, it is important to control for possible variations in body size that could confound actual variations in body shape between individuals (Norman 1997). We discarded to use the tarsus length for this purpose despite it has been shown to be a good correlate of avian body size (Senar & Pascual 1997), because this trait may well vary between populations independently of body size (Winkler & Leisler 1985, 1992, Tellería & Carbonell 1999). Therefore, our first step was to derive indices of body size for each of the seven species, for which we conducted PCA with body measurements (tarsus length, bill height, wing length and tail length). This method allows one to extract an index of the structural size of individuals (Rising & Somers 1989, Freeman & Jackson 1990), which has been proved effective for measuring the nutrient reserve-independent size of birds (Piersma & Davidson 1991). Usually, every measurement had a high loading in the first component of body size (bsPC1), which sometimes was the only extracted by the PCA. In these cases, bsPC1 was therefore interpretable as a proper index of structural size (Table 1). When the interpretation of principal components was not so straightforward, we chose the index of structural size by first relying on the factor loadings of skeletal measurements (tarsus and bill) in each component and, if still in doubt, by checking the efficacy of each component in predicting body mass (Rising & Somers 1989, Senar & Pascual 1997). Thus, the bsPC1 was considered to be the best index of structural size in all species except in the Robin, for which we used the bsPC2 (Table 1). Differences in body size between populations were examined as a first step in the analysis of morphological variation.

We used PCA with primary distances to obtain wing-shape indices for each species (Chandler & Mulvihill 1988, Lockwood *et al.* 1998). These analyses were consistent among species in extracting a first component of wing shape (wsPC1) in which the innermost primaries had a high loading (Table 2). Therefore, we used the wsPC1 as a proper index of wing pointedness in all species.

Our statistical analyses were designed for specifically testing the hypothesis that highland populations have a morphology that is better suited to long-distance flights than that of lowland populations. In this study, the flight-related morphology is a non-measurable variable defined by the covariation of wing length, tail length, and wing pointedness (in all species studied, these traits correlated to each other more than expected by random, as shown by Bartlett's tests for sphericity with $P < 0.0001$ in all cases). In order to test for changes in flight-related morphology controlling for age and body size, we designed a multivariate general linear model in which locality and age were categorical predictors (factors), the structural size (bsPC1, or bsPC2 in the Robin) was a continuous predictor (covariate), and wing length, tail length, and wing

Table 2. Coefficients of correlation between each primary distance (the distance from the tip of each primary feather to the wing tip) and the first principal component of wing shape extracted by PCA (wsPC1), which we used as an index of wing pointedness. Sample sizes are also shown (*n*). The primaries 6 and 7 showed no variance in Firecrests because they made up the wing tip in all individuals.

	E. rubecula	*T. merula*	*S. atricapilla*	*R. ignicapillus*	*P. caeruleus*	*P. major*	*L. megarhynchos*
(*n*)	200	49	307	14	30	42	22
Primary 9	0.10	0.18	-0.28	0.36	-0.09	-0.32	-0.02
Primary 8	-0.09	-0.22	-0.39	0.44	-0.49	-0.49	0.16
Primary 7	-0.18	-0.22	0.31	–	-0.26	-0.34	0.25
Primary 6	0.44	0.48	0.81	–	0.49	0.71	0.77
Primary 5	0.67	0.89	0.93	0.72	0.76	0.77	0.95
Primary 4	0.91	0.94	0.95	0.89	0.88	0.86	0.98
Primary 3	0.93	0.95	0.95	0.94	0.93	0.89	0.96
Primary 2	0.91	0.95	0.94	0.96	0.90	0.88	0.96
Primary 1	0.91	0.91	0.90	0.99	0.87	0.74	0.90
Eigenvalue	4.04	4.65	5.35	4.43	4.34	4.41	5.18
Var. (%)	44.92	51.70	59.39	63.26	48.24	49.04	57.54

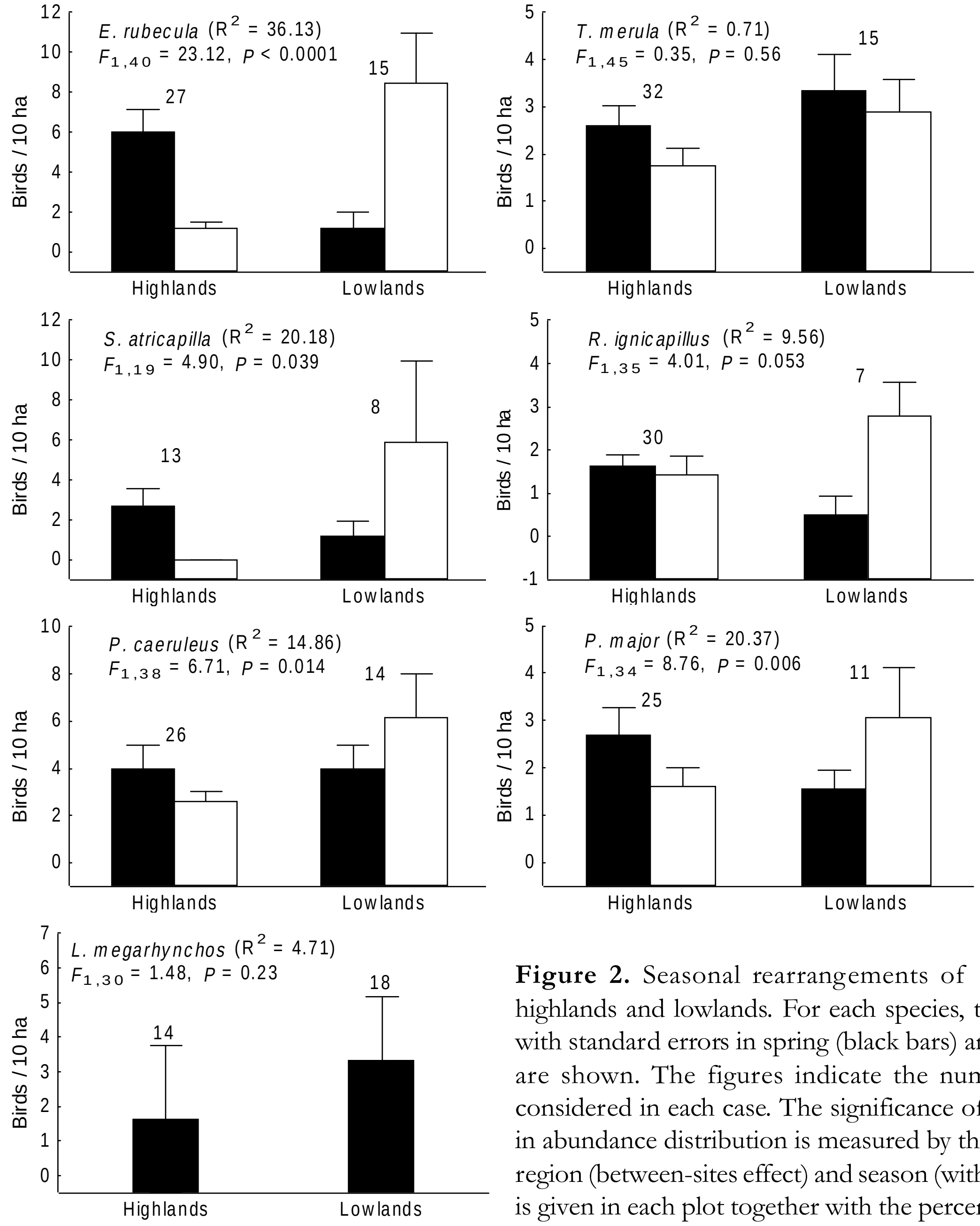

Figure 2. Seasonal rearrangements of abundance between highlands and lowlands. For each species, the mean abundances with standard errors in spring (black bars) and winter (white bars) are shown. The figures indicate the number of survey sites considered in each case. The significance of the seasonal change in abundance distribution is measured by the interaction between region (between-sites effect) and season (within-sites effect), which is given in each plot together with the percentage of variance that it explains (R^2). For Nightingales, which are summer visitors, only the breeding abundances and the results of the corresponding one-way ANOVA are shown.

pointedness (wsPC1) were the dependent variables. First of all, we tested for interactions between the factors and the covariate. Significant deviations from parallelism were only found in Blackcaps, in which the effect of body size changed between age classes. Therefore, in this species we estimated a general effect of body size on flight-related morphology by nesting it within age classes. In the remaining species, the model included the usual terms in a two-way multivariate ANCOVA (the effect of both factors and their interaction, and the effect of the covariate). The corresponding model was then used to test for differences between regions by planning specific comparisons (Lindman 1974) between highland localities (Álava, Guadarrama and Madrid) and lowland localities (Sierra de Ojén and Tarifa). Not all species occurred in all study sites, so different sets of localities were used to compare between highlands and lowlands in each case. In some instances, however, we did not capture either adults or juveniles in some locality, which translated into incomplete designs for some of the species studied. In these cases, a Type IV sum of squares approach was adopted for testing our hypothesis (Goodnight 1980). Once the differences in overall flight-related morphology were evaluated, we conducted univariate analyses (with the same terms as in the corresponding multivariate model designs) to evaluate which particular traits were responsible of the overall effect. For ease of interpretation of our results, we conducted these posterior analyses in all species, whether or not overall differences in flight-related morphology were significant. All the analyses were done with the Visual GLM module implemented in the STATISTICA 5.5 computer program (StatSoft 1999).

The multivariate approach adopted here to assess changes in overall flight-related morphology forces the exclusion of birds without data of every one of the traits considered in the analysis. In Blackcaps and Robins, whose sample sizes were quite large, the loss of power due to this reduction of sample size may actually be considered to be negligible. In the remaining species, however, the multivariate approach should have caused a dramatic decrease in power, related to the reduction of their

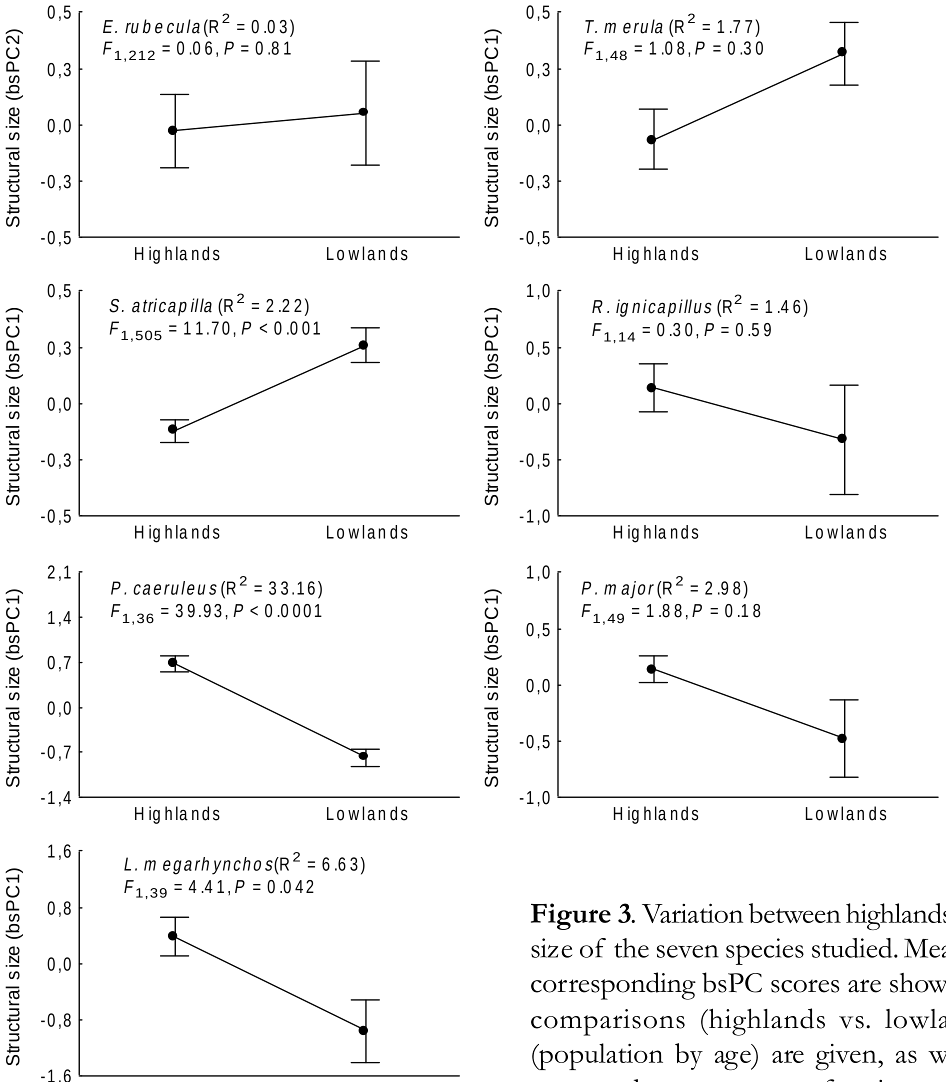

Figure 3. Variation between highlands and lowlands in the structural size of the seven species studied. Means and standard errors of the corresponding bsPC scores are shown. The results of the planned comparisons (highlands vs. lowlands) in a two-way ANOVA (population by age) are given, as well as the size of this effect measured as percentage of variance explained (R^2).

Table 3. Results of planned comparisons testing for differences between highlands and lowlands in flight-related morphology. For each species, it is first shown the sample size (*n*) of adults and juveniles in Álava (locality 1), Guadarrama (2), Madrid (3), Sierra de Ojén (4) and Tarifa (5) (hyphens indicate the absence as breeder of the species from the corresponding locality). Below these, it is shown the contrast vector that defines the comparison between highlands and lowlands in a multivariate general linear model with wing length, wing pointedness (wsPC1, see Table 2) and tail length as dependent variables (whose covariation defines flight-related morphology), population and age as categorical predictors, and body size (bsPC1 or bsPC2, see Table 1) as a covariate. Results are shown, on the right side of the table, for both the regional difference (R) and the effect of body size (BS). See text for a more detailed description of the models tested in each case.

		Adults					Juveniles					Results of the comparison			
		1	2	3	4	5	1	2	3	4	5		*F*	d.f.	*P*
E. rubecula	*n*	11	14	-	18	-	43	53	-	42	-	R	9.27	3,172	< 0.0001
	Contrast vector	1	1		-2		1	1		-2		BS	6.52	3,172	0.0003
T. merula	*n*	6	15	0	5	1	6	10	1	1	2	R	10.11	3,35	< 0.0001
	Contrast vector	4	4	0	-5	-5	4	4	4	-5	-5	BS	172.24	3,35	< 0.0001
S. atricapilla	*n*	27	41	7	47	10	62	28	11	48	20	R	89.09	3,287	< 0.0001
	Contrast vector	2	2	2	-3	-3	2	2	2	-3	-3	BS	467.41	3,287	< 0.0001
R. ignicapillus	*n*	2	2	-	1	-	4	1	-	4	-	R	7.51	3,5	0.027
	Contrast vector	1	1		-2		1	1		-2		BS	12.44	3,5	0.0093
P. caeruleus	*n*	0	3	-	2	0	10	4	-	5	5	R	12.13	3,2	< 0.0001
	Contrast vector	0	1		-1	0	1	1		-1	-1	BS	8.80	3,2	0.0006
P. major	*n*	1	2	0	2	0	20	2	7	3	3	R	1.80	3,29	0.169
	Contrast vector	3	3	0	-5	0	3	3	3	-5	-5	BS	70.28	3,29	< 0.0001
L. megarhynchos	*n*	-	10	4	1	3	-	1	1	0	1	R	0.37	3,11	0.778
	Contrast vector		3	3	-4	-4		3	3	0	-4	BS	123.31	3,11	< 0.0001

already small sample size. In order to check whether our results were affected by small sample sizes, we repeated the univariate analyses for wing length and tail length, this time considering all the birds for which these measurements were available (wing pointedness was the missing value in all cases with incomplete data). We then compared the size and the statistical significance reached by these effects to see whether increasing sample sizes influenced our results.

RESULTS

Seasonal changes in abundance

Four species (Robins, Blackcaps and both tits) of the six passerines for which analyses of seasonal changes in abundance distribution were done (the Nightingale, which is a summer visitor, was obviously excluded) significantly decreased abundance in highlands and increased their numbers in lowlands during winter (Fig. 2). Firecrests showed a similar but not so marked trend, increasing their winter abundance in lowlands but showing only a weak decrease in highlands. Blackbirds did not show any trend that could be interpreted as a seasonal rearrangement of their numbers in the Iberian Peninsula. Finally, the breeding abundances of Nightingales were similar in both Iberian regions (Fig. 2).

Morphological variation

Structural size showed different trends of regional variation in the species studied (Fig. 3). Robins showed a homogeneous body size in both regions.

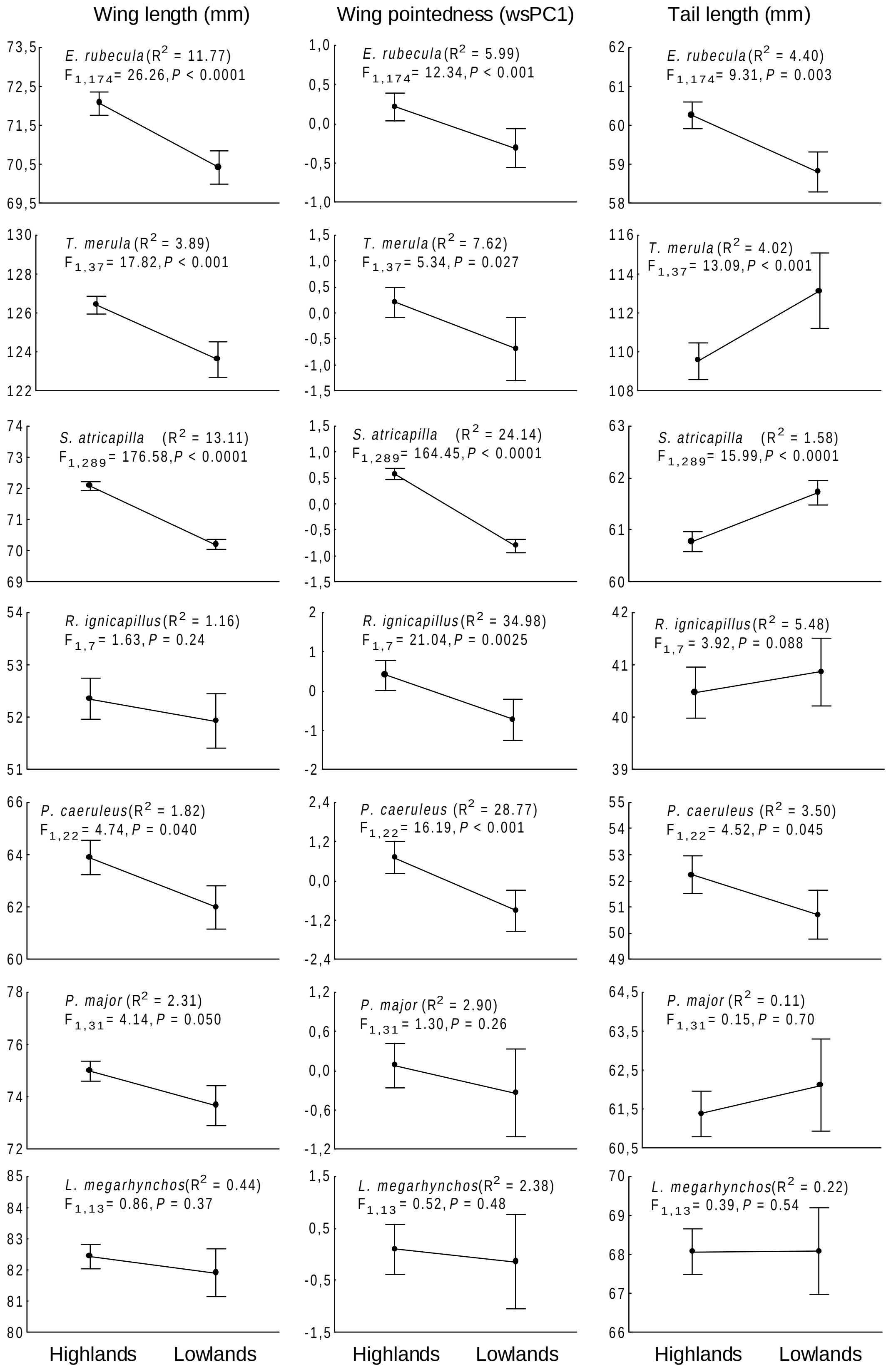

Figure 4. Variation between regions in the three traits that define flight-related morphology. Means adjusted by structural size with standard errors are shown, along with the results of planned comparisons between highlands and lowlands (with the same model as in the multivariate ANCOVA, see Table 3) and the size of this effect (percentage of variance explained, R^2).

Table 4. Results of planned comparisons testing for differences between highlands and lowlands in wing length and tail length, considering all the data available for these traits. Comparisons are the same described in Table 3, although the contrast vectors (not shown) changed in some instances because the increase in sample size filled some cells that were empty in the multivariate design. Only the regional effect and the percentage of variation that it explains (R^2) are shown.

	Wing length				Tail length			
	F	d.f.	*P*	R^2 (%)	*F*	d.f.	*P*	R^2 (%)
E. rubecula	26.50	1,211	0.0001	10.30	12.80	1,211	0.0004	5.23
T. merula	13.89	1,47	0.0005	5.06	9.65	1,47	0.0032	3.49
S. atricapilla	401.33	1,503	0.0001	16.39	23.99	1,503	0.0001	1.37
R. ignicapillus	1.21	1,13	0.291	0.88	5.54	1,13	0.035	4.76
P. caeruleus	5.91	1,35	0.020	1.90	0.01	1,35	0.905	0.01
P. major	6.99	1,48	0.011	2.67	0.12	1,48	0.727	0.05
L. megarhynchos	0.64	1,38	0.429	0.15	1.86	1,38	0.181	0.93

Blackcaps and Blackbirds were larger in lowlands, although this difference was significant only in Blackcaps. In the remaining species, body size was larger in highlands, although differences were significant only in Blue Tits and Nightingales. The small sample size is likely to have reduced the power of these comparisons, although the generalised lack of differences in body size can be also attributable to the fact that these effects were really small (Fig. 3).

Once body size was statistically controlled for in the analyses, we found significant variations in flight-related morphology between highlands and lowlands in five of the six species for which we predicted such a pattern (Table 3). It should be noted that the small sample size decreased the power of these comparisons, so the fact that differences were so significant in these conditions should be interpreted as a further support to the strength of the pattern. The Great Tit was the only species for which we failed to detect a significant trend in flight-related morphology. Actually, Great Tits showed a feeble variation in these traits, which only seemed to affect wing length, so that the lack of differences was attributable to a certainly small regional difference in flight-related morphology in this species (Fig. 4). Finally, as predicted by the homogeneous migratory behaviour of Nightingales, this species showed no difference between regions in flight-related morphology (Table 3, Fig. 4).

Posterior evaluations of the importance of each particular trait in causing the overall differences showed that wing length and wing pointedness were more consistent among species in their regional variation than tail length (Fig. 4). All the five species in which a significant variation in overall flight-related morphology was found showed longer and more pointed wings in highlands. Even Great Tits, for which the overall pattern was not significant, tended to vary in that way. However, the predicted increase in tail length in southern populations only held significant in two species (Blackcaps and Blackbirds), and even tail length varied in the opposite direction in other two (Robins and Blue Tits, Fig. 4).

We obtained very similar results when the analyses of wing length and tail length were done with all data available in our samples (Table 4). Although sample sizes experienced a two or three-fold increase in the species with the smallest initial sample sizes (Firecrests and Nightingales, for example), we did not find significant differences in effect sizes measured as the percentage of variance explained by regional differences (Wilcoxon matched pairs test with species as sample units: wing length $Z = 0.51$, $P = 0.61$; tail length $Z = 0.68$, $P = 0.50$), nor did we find an increase in the statistical significance reached by these differences in the second analyses (wing length $Z = 0.52$, $P = 0.60$; tail length $Z = 0.0001$, $P = 0.99$).

DISCUSSION

Seasonal changes in abundance

Overall, the seasonal abundance distribution of the species studied adjusted the pattern predicted by our hypothesis on the migratory behaviour of Iberian forest passerines. Winter abundance decreased in highlands and increased in lowlands in all these species, with the sole exception of Blackbirds. This species is known to have become sedentary in almost all the southern half of its range during the last century (Berthold 1999), which could partially explain the lack of seasonal changes in its abundance in the Iberian Peninsula. In addition, such changes could be masked by hunting during the autumn-winter period, since the Blackbird is the only game species in our study. This could have caused an underestimation of blackbird densities in Iberian lowlands, where hunting pressure is highest (Santos *et al.* 1988). Despite this fail in our results, the pattern that we have found reflects the complementary role of highlands and lowlands as either breeding or wintering grounds, and supports the effects of different environmental pressures on the movements of Iberian forest passerines. However, such a pattern may be influenced by the arrival of European migrants. Indeed, it is known that the Iberian Peninsula receives during winter a huge amount of Robins, Blackcaps and Blackbirds from central and northern Europe, which principally occupy southern lowlands and coasts (as shown by ringing recoveries, see Santos 1982, Cantos 1995, Bueno 1998). However, although the arrival of extra-Iberian birds is likely to be the main cause of the increase in abundance of these species in lowlands, it seems not to affect their population dynamics in highland forests, where their abundance decreases even after post-breeding recruitment. On the other hand, the arrival of extra-Iberian birds would hardly explain the seasonal changes in abundance of Firecrests and tits: despite the well-known migratory movements of these species in northern and central Europe (Ulfstrand 1962, van Balen & Hage 1989), ringing recoveries do not evidence their regular arrival to Iberia (Tellería *et al.*, 1999). Therefore, our results support the idea that many forest birds leave highlands during winter contributing to the increase in abundance in lowlands during winter. However, these results do not demonstrate the sedentariness of lowland populations, calling for other clues that could corroborate this possibility. In fact, evidence of year-round residence of southern populations has been gathered in some studies. For example, it has been demonstrated that local birds make up an important fraction of the populations wintering in lowland forests, while their overwintering counterparts mainly occupy shrublands, orchards and open forests that are unsuitable for breeding (Pérez-Tris *et al*. 2000b, Tellería *et al*. 2000). In addition, recurrent winter recaptures of locals in their breeding forests of southern Spain further support a low importance of movements in lowland populations (Pérez-Tris *et al*. 1999, 2000b, own unpubl. data). Finally, but not less importantly, we have found morphological differences that may be interpreted as correlates of the unlike migratory behaviour of forest passerines in highlands and lowlands.

Morphological differences

No homogeneous pattern was found among species when comparing body size between Iberian regions. Some species showed an increased body size in highlands, while others tended to be larger in lowlands or showed no change in body size between regions. Although variations in body size were generally small (Fig. 3), the so mixed patterns that we have found are difficult to interpret. Avian body size may be affected by factors such as climate, developmental conditions, migratory pattern, and so on (see some examples in Geist 1989, Baker 1992, Holmgren & Lundberg 1993, Tellería & Carbonell 1999), which may have a different importance in determining changes be-

Table 5. A summary of the taxonomic status of the seven studied species in south-western Europe and north-western Africa, according to different bibliographic sources (Ref. 1: Vaurie 1959, 2: Cramp 1988, 3: Cramp 1992, 4: Cramp & Perrins 1993). The taxonomic ascription (according to these sources) of northern and southern Iberian populations studied in this paper is also indicated.

Species	Ref.	France	Northern Iberia	Southern Iberia	Northern Africa
E. rubecula	1, 2	*E. r. rubecula / E. r. melophilus*	*E. r. rubecula / E. r. melophilus*	*E. r. rubecula / E. r. witherbyi*	*E. r. rubecula / E. r. witherbyi*
T. merula	1	*T. m. merula*	*T. m. merula*	*T. m. merula / T. m. mauritanicus*	*T. m. mauritanicus*
	2	*T. m. merula*	*T. m. merula*	*T. m. merula*	*T. m. mauritanicus*
S. atricapilla	1	*S. a. atricapilla*	*S. a. atricapilla*	*S. a. atricapilla*	*S. a. atricapilla*
	3	*S. a. atricapilla*	*S. a. atricapilla*	*S. a. heineken*	*S. a. heineken*
R. ignicapillus	1, 3	*R. i. ignicapillus*	*R. i. ignicapillus*	*R. i. ignicapillus*	*R. i. balearicus*
P. caeruleus	1	*P. c. caeruleus*	*P. c. caeruleus/ P. c. ogliastrae*	*P. c. ogliastrae*	*P. c. ultramarinus*
	4	*P. c. caeruleus*	*P. c. caeruleus*	*P. c. ogliastrae*	*P. c. ultramarinus*
P. major	1	*P. m. major*	*P. m. major/ P. m. excelsus*	*P. m. major/ P. m. excelsus*	*P. m. excelsus*
	4	*P. m. major*	*P. m. major*	*P. m. corsus*	*P. m. excelsus*
L. megarhynchos	1, 2	*L.m.megarhynchos*	*L.m.megarhynchos*	*L.m.megarhynchos*	*L.m.megarhynchos*

tween Iberian regions in each species. In our study, it is important to know that body size changes between regions because this means that it has to be controlled for in the analyses of flight-related morphology. However, the shape of differences in body size is less important, and its discussion would go beyond the scope of this paper.

After controlling for body size, our results demonstrate the differentiation in flight-related morphological traits between highland and lowland forests passerines. Overall, wing length and wing shape showed a more consistent pattern of regional variation than tail length. Thus, all species showed longer and/or more pointed wings in highlands (or at least tended to do it as we found for Great Tits), and such differences were significant or near significant in almost all cases. For all species differing in flight-related morphology except the Robin, the variation between regions in wing pointedness was stronger than the change in wing length (Fig. 4), which is consistent with the results obtained by Mönkkönen (1995) in a comparative study of the variation in wing shape between migratory and sedentary species. Changes in tail length, however, were less pronounced and even deviated from the predicted direction in two cases (Robins and Blue Tits). Based on the overall pattern of variation in the traits studied, we believe that tail morphology may be affected by migration pressures to a lesser extent than wing shape (see also Winkler & Leisler 1992), and rather be more dependent on other processes related to particular life stiles that could impose different constraints on tail modification in each species (for example, feeding on ground has different manoeuvrability requirements than leaf gleaning, see Leisler & Winkler 1985). However, although these species-specific processes could have caused the observed deviations from the predicted patterns of variation in tail length, any *a posteriori* interpretation of these unexpected trends would be too tentative. What really matters here is the fact that overall changes between regions in flight-related morphology support a more pronounced migratory behaviour in highland populations of forest passerines compared to their lowland counterparts.

It has long been accepted that migrants have longer and more pointed wings, a trend which has been documented both in intraspecific and interspecific analyses (Mulvihill & Chandler 1991, Winkler & Leisler 1992, Mönkkönen 1995). However, differences among populations in wing length and wing pointedness could also result from conflicting selective pressures caused by the requirements of manoeuvrability related to habitat structure or to particular foraging strategies (Leisler & Winkler 1985, Winkler & Leisler 1985, Rainer 1988). We have found that highland populations of several species have longer and more pointed wings than their lowland counterparts, taking into account in our analysis the possible effect of changes in habitat structure among study sites (described by Carbonell & Tellería 1998a). On the other hand, our multispecies study allowed us to control for possible species-specific effects (such as those apparently operating in the case of body size), thus making the proposed role of seasonal movements to be the most parsimonious explanation for the morphological differences described. Two important facts emphasise the soundness of this interpretation. First, despite the species studied show noticeable differences in ecology and behaviour, they define an overall homogeneous trend of variation in wing length and wing shape between highland and lowlands. It should be noted here that we selected these species exclusively because they were the most frequently captured in our study areas, which is unlikely to make them be particularly prone to change between regions in the way described. Second, our interpretation is also supported by the lack of morphological variation in the trans-Saharan migrant species that we used as a control, the Nightingale. As predicted by their homogeneous migratory behaviour, highland and lowland Nightingales showed no difference in flight-related morphology, despite they slightly differed in structural size (like other species studied in this paper), and despite they are certainly similar in most aspects of their ecology and behaviour to some species studied, like Robins or Blackbirds, which did vary in morphological traits between Iberian regions.

In summary, seasonal changes in abundance and differences in morphological traits support that highland and lowland Iberian forest passerines differ in migratory behaviour. We do not know, however, the proportion of highland populations that is involved in these displacements, which no doubt constitute a case of partial migration like the observed in the same species in other parts of their range (Cramp 1988, 1992, Cramp & Perrins 1993).

Conclusions and perspectives

The existence of movements of birds in the Iberian Peninsula can offer a valuable insight into the diversity of migratory strategies in the Western Palearctic. Iberian movements could illustrate that altitudinal migration is a widespread phenomenon, which has probably evolved independently in many species and in many different montane populations around the Mediterranean (Fig. 1). It has been postulated that migratory patterns of European birds could have evolved parallel to the expansion of the breeding ranges of these species in the late Pleistocene (Safriel 1995, Taberlet *et al.* 1998), by first appearing short-distance, partial migratory patterns that would have later derived into total migrations (Berthold 1999). Very likely, the colonisation of highlands had a similar effect at southern latitudes, where regional-scale movements could have evolved increasing the diversity of migratory patterns in the Palearctic migratory system. Nevertheless, phylogeographic studies would be needed to further disentangle the relationships between highland and lowland populations, as well as between Mediterranean and central-European birds.

According to our results, altitudinal migrations are relevant in affecting not only the spatio-temporal structuring of bird communities, but also the morphological traits of the birds involved in these displacements. The morphological differentiation that we found in Iberian populations of forest passerines partially agrees with the taxonomic classifications proposed for these species by early students in Spain and Portugal (Table 5), which considered Iberian populations as intermediate between the central-European ones and those present in northern Africa or in some Mediterranean islands. However, these classifications are imprecise in assessing the morphological differentiation of each species within the Iberian peninsula, and neither they attempted to explain the origin of the observed variations (e.g. the role of seasonality in shaping more or less migratory-like morphs). Furthermore, it has long been accepted that the southern-like morphs of these species occupy almost all the Iberian Peninsula, an incorrect prejudice rooted in the wrong tendency to view the Iberian highlands as a Mediterranean region equivalent to the warm lowlands and coastal areas. Our results go a step further by providing an ecological significance to the differentiation of Iberian populations, which could be determined to a large extent by migration pressures.

Acknowledgements

We thank L.M. Carrascal and J.A. Díaz, whose comments considerably improved an early version. The Agencias de Medio Ambiente (Diputación Foral de Álava, Comunidad Autónoma de Madrid and Junta de Andalucía) kindly authorised us to capture birds. This paper was funded by the Ministerio de Educación y Cultura de España (projects PB92-0238 and PB97-0325). During its preparation, JP-T was supported by a FPI Grant from the Universidad Complutense de Madrid.

References

Alerstam, T. 1990. *Bird migration*. Cambridge University Press. Cambridge.

Alerstam, T. & Högstedt, G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scandinavica* 13: 25-37.

Aschmann, H. 1971. Distribution and Peculiarity of Mediterranean Ecosystems. *Mediterranean Type Ecosystems* (eds. F. di Castri & H. A. Mooney), pp. 11-19. Springer-Verlag, Berlin.

Baker, A.J. 1992. Genetic and morphometric divergence in ancestral European and descendent New Zealand populations of Chaffinches (*Fringilla coelebs*). *Evolution* 46: 1784-1800.

Baker, R.R. 1978. *The evolutionary ecology of animal migration*. Hodder & Stoughton. London.

Berthold, P. 1993. *Bird migration. A general survey*. Oxford University Press. Oxford.

Berthold, P. 1996. *Control of bird migration*. Chapman & Hall. London.

Berthold, P. 1999. Towards a comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* 70: 1-11.

Bueno, J. M. 1998. Migración e invernada de pequeños turdinos en la península Ibérica. V. Petirrojo (*Erithacus rubecula*). *Ardeola* 45: 193-200.

Cantos, F. J. 1995. Migración e invernada de la curruca capirotada (*Sylvia atricapilla*) en la península Ibérica. *Ecología*, 9: 425-433.

Carbonell, R. & Tellería, J.L. 1998a. Selección y uso del hábitat por cinco poblaciones ibéricas de Curruca Capirotada (*Sylvia atricapilla*). *Ardeola* 45: 1-10.

Carbonell, R. & Tellería, J.L. 1998b. Increased asymmetry of tarsus-length in three populations of Blackcaps *Sylvia atricapilla* as related to proximity to range boundary. *Ibis* 140: 331-333.

Carbonell, R. & Tellería, J.L. 1999. Feather traits and ptilochronology as indicators of stress in Iberian Blackcaps *Sylvia atricapilla*. *Bird Study* 46: 243-248.

Chandler, C.R. & Mulvihill, R.S. 1988. The use of wing shape indices: an evaluation. *Ornis Scandinavica* 19: 212-216.

Chesser, R.T. 1998. Further perspectives on the breeding distribution of migratory birds: South American austral migrant flycatchers. *Journal of Animal Ecolology* 67: 69-77.

Cramp, S. (ed.) 1988. *The Birds of the Western Palearctic*. Vol V. Oxford University Press. Oxford.

Cramp, S. (ed.) 1992. *The Birds of the Western Palearctic*. Vol VI. Oxford University Press. Oxford.

Cramp, S. & Perrins, C.M. (eds.) 1993. *The Birds of the Western Palearctic*. Vol VII. Oxford University Press. Oxford.

Czajkowski, M.A. & Dejonghe, J.F. 1981. Sur les mouvements de *Parus ater* et de *Parus montanus* à haute altitude dans les Alpes occidentales. *Alauda* 49: 61-63.

Flegg, J. J. & Cox, C. J. 1969. The moult of British Blue Tit and Great Tit populations. *Bird Study* 16: 147-157.

Font, I. 1983. *Climatología de España y Portugal*. Instituto Nacional de Meteorología. Madrid.

Francis, C.M. & Wood, D.S. 1989. Effects of age and wear on wing length of wood-warblers. *Journal Field Ornithology* 60: 495-503.

Freeman, S. & Jackson, W.M. 1990. Univariate metrics are not adequate to measure avian body size. *Auk* 107: 69-74.

Fuentes, M. 1992. Latitudinal and elevational variation in fruiting phenology among western European bird-dispersed plants. *Ecography* 15: 177-183.

Gauthreaux, S.A. 1996. Bird migration: methodologies and major research trajectories (1945-1995). *Condor* 98: 442-453.

Geist, V. 1989. Bergmann's rule is invalid. *Cannadian Journal of Zoology* 65: 1035-1038.

Goodnight, J.H. 1980. Tests of hypotheses in fixed effects linear models. *Communications in Statistics* 9: 167-180.

Greenberg, R. 1980. Demographic aspects of long-distance migration. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds. A. Keast & E.S. Morton), pp. 493-504. Smithsonian Institution Press, Washington, D.C.

Herrera, C.M. 1978. On the breeding distribution pattern of European migrant birds: MacArthur's theme reexamined. *Auk* 95: 496-509.

Herrera, C.M. 1981. Organización temporal en las comunidades de aves. *Doñana Acta Vertebrata* 8: 79-101.

Herrera, C.M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68: 511-538.

Holmgren, N. & Lundberg, S. 1993. Despotic behaviour and the evolution of migration patterns in birds. *Ornis Scandinavica* 24: 103-109.

Jenni, L. & Winkler, R. 1994. *Moult and ageing of European Passerines*. Academic Press. London.

Leisler, B. & Winkler, H. 1985. Ecomorphology. *Current Ornithology* 2: 155-186.

Lindman, H. R. 1974. *Analysis of variance in complex experimental designs*. Freeman & Co. San Francisco.

Lo Valvo, F., Lo Verde, G. & Lo Valvo, M. 1988. Relationships among wing length, wing shape and migration in Blackcaps *Sylvia atricapilla* populations. *Ringing & Migration* 9: 51-54.

Lockwood, R., Swaddle, J.P. & Rayner, J.M.V. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* 29: 273-292.

MacArthur, R.H. 1959. On the breeding distribution patterns of North American migrant birds. *Auk* 76: 318-325.

Mead, C. 1983. *Bird migration*. Country Life Books. Feltham.

Mönkkönen, M. 1995. Do migrant birds have more pointed wings?: a comparative study. *Evolutionary Ecology* 9: 520-528.

Mooney, H.A. 1981. Primary production in Mediterranean-climate regions. *Ecosystems of the World* (eds. F. di Castri, D.W. Goodall & R.L. Spetch), pp 249-255. Elsevier Scientific Publications, Amsterdam.

Moreau, R.E. 1972. *The Palearctic-African bird migration systems*. Academic Press. New York.

Mulvihill, R.S. & Chandler, C.R. 1991. A comparison of the wing shape between migratory and sedentary Dark-eyed Juncos (*Junco hyemalis*). *Condor* 93: 172-175.

Newton, I. & Dale, L. 1996a. Relationship between migration and latitude among European birds. *Journal of Animal Ecology* 65: 137-146.

Newton, I. & Dale, L. 1996b. Bird migration at different latitudes in eastern North America. *Auk* 113: 626-635.

Norberg, U.M. 1990. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*. Springer Verlag. Heidelberg.

Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology* 9: 48-54.

Norman, S.C. 1997. Juvenile wing shape, wing moult and weight in the family Sylviidae. *Ibis* 139: 617-630.

Pennycuick, C.J. 1989. *Bird flight performance: a practical calculation manual.* Oxford University Press. Oxford.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 1999. A method for differentiating between sedentary and migratory blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia. *Bird Study* 46: 299-304 (*Capítulo 4*).

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000a. Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. *Journal of Biogeography* 27: 879-888 (*Capítulo 2*).

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000b. Identificacion e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. *Ardeola* 47: 9-18 (*Capítulo 5*).

Piersma, T. & Davidson, N.C. 1991. Confusions of mass and size. *Auk* 108: 441-444.

Rabenold, K.N. & Rabenold, P.P. 1985. Variation in altitudinal migration, winter segregation, and site tenacity in two subspecies of Dark-eyed Juncos in the southern Appalachians. *Auk* 102: 805-819.

Rayner, J.M.V. 1988. Form and function in avian flight. *Current Ornithology* 5: 1-66.

Rising, J.D. & Somers, K.M. 1989. The measurement of overall body size in birds. *Auk* 106: 666-674.

Safriel, U.N. 1995. The evolution of Palearctic migration – The case for southern ancestry. *Israel Journal of Zoology* 41: 417-431.

Santos, T. 1982. *Migración e invernada de zorzales y mirlos (Género* Turdus*) en la Península Ibérica*. PhD Thesis. Editorial de la Universidad Complutense. Madrid.

Santos, T., Asensio, B., Bueno, J.M., Cantos, F.J. & Muñoz-Cobo, J. 1988. Distribución y tendencias demográficas de la persecución de paseriformes presaharianos en España.. *Invernada de aves en la península Ibérica* (ed. J.L. Tellería), pp. 167-181. S.E.O. Madrid.

Senar, J. C. & Pascual, J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea*, 85: 269-274.

Statsoft, Inc. 1999. *STATISTICA for Windows (Computer program manual)*. StatSoft, Inc. Tulsa.

Svensson, L. 1992. *Identification guide to European passerines.* 4th ed. L. Svensson. Stockholm.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cosson, J. F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, 7: 453-464.

Tellería, J. L. 1988. Caracteres generales de la invernada de las aves en la península Ibérica. *Invernada de aves en la península Ibérica* (ed. J.L. Tellería), pp. 13-22. S.E.O. Madrid.

Tellería, J. L., Asensio, B. & Díaz, M. 1999. *Aves Ibéricas. Vol. 2. Passeriformes.* J.M. Reyero. Madrid.

Tellería, J. L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology*, 30: 63-71.

Tellería, J. L., Pérez-Tris, J., Ramírez, A., Fernández-Juricic, E. & Carbonell, R. 2000. Distribution of Robins (*Erithacus rubecula*) in wintering grounds: effects of conspecific density, migratory status and age. *Ardea* 00: 000-000 (*Capítulo 6*).

Tellería, J. L. & Santos, T. 1993. Distributional patterns of insectivorous passerines in the Iberian forests: does abundance decrease near the border? *Journal of Biogeography*, 20: 235-240.

Tellería, J. L. & Santos, T. 1994. Factors involved in the distribution of forest birds in the Iberian Peninsula. *Bird Study*, 41: 161-169.

Tellería, J. L., Santos, T. & Carrascal, L. M. 1988. La invernada de los paseriformes (O. Passeriformes) en la península Ibérica. *Invernada de aves en la península Ibérica* (ed. J.L. Tellería), pp. 153-166. S.E.O., Madrid.

Ulfstrand, S. 1962. On the nonbreeding ecology and migratory movements of the Great Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*) in southern Sweden. *Vår Fågelvärld* 3: 1-145.

van Balen, J. H. & Hage, F. 1989. The effect of environmental factors on tit movements. *Ornis Scandinavica* 20: 99-104.

Vaurie, C. 1959. *The birds of the Palearctic fauna. Passeriformes*. H.F. & G. Witherby Ltd. London.

Wainwright, P. C. 1994. Functional morphology as a tool in ecological research. *Ecological Morphology: Integrative Organismal Biology* (eds. P.C. Wainwright & S.M. Reilly), pp. 42-59. University of Chicago Press. Chicago.

Willson, M. F. 1976. The breeding distribution of North American migrant birds: a critique of MacArthur (1959). *Wilson Bulletin* 88: 582-587.

Winkler, H. & Leisler, B. 1985. Morphological aspects of habitat selection in birds. *Habitat selection in birds.* (ed. M.L. Cody), pp. 435-444. Academic Press. New York

Winkler, H. & Leisler, B. 1992. On the ecomorphology of migrants. *Ibis* 134 (Suppl. 1): 21-28.

Appendix. Summary of morphometrics of the seven species studied. Means, standard errors and sample sizes in Iberian highlands and lowlands are shown.

	Tarsus length (mm)			Wing length (mm)			Bill height (mm)			Tail length (mm)			Body mass (g)		
	Mean	s.e.	*n*	Mean	s.e.	*n*	Mean	s.e.	*n*	Mean	s.e.	*n*	Mean	s.e.	*n*
Erithacus rubecula															
Highlands	25.20	0.06	175	71.97	0.13	171	3.63	0.02	173	60.20	0.19	148	15.77	0.12	176
Lowlands	25.10	0.07	91	70.32	0.18	87	3.75	0.02	88	58.81	0.19	75	15.17	0.11	87
Turdus merula															
Highlands	32.40	0.12	60	125.47	0.52	61	7.46	0.07	59	107.90	1.09	50	83.22	0.86	58
Lowlands	33.32	0.24	17	122.94	0.85	18	7.79	0.11	18	114.09	0.74	11	86.36	2.33	17
Sylvia atricapilla															
Highlands	20.14	0.03	383	71.64	0.09	385	3.87	0.01	360	60.45	0.12	356	16.46	0.06	379
Lowlands	20.80	0.05	175	70.24	0.14	169	3.96	0.02	172	61.95	0.17	168	17.32	0.10	174
Regulus ignicapillus															
Highlands	16.81	0.17	16	52.62	0.40	17	2.40	0.04	15	40.40	0.29	15	5.46	0.12	16
Lowlands	16.41	0.26	7	51.07	0.80	7	2.60	0.05	7	40.42	0.58	6	5.71	0.23	7
Parus caeruleus															
Highlands	16.40	0.12	29	65.17	0.32	30	4.34	0.05	27	52.74	0.31	25	10.44	0.16	29
Lowlands	15.76	0.15	24	59.46	0.51	24	4.03	0.05	22	49.02	0.86	25	9.27	0.11	25
Parus major															
Highlands	19.70	0.08	50	75.02	0.30	50	4.55	0.04	50	61.94	0.42	45	16.91	0.38	49
Lowlands	19.35	0.25	14	72.60	0.77	13	4.68	0.07	14	60.75	0.90	14	16.94	0.25	14
Luscinia megarhynchos															
Highlands	26.85	0.13	34	82.38	0.38	38	4.30	0.05	35	68.91	0.39	37	20.40	0.24	37
Lowlands	25.98	0.59	15	78.87	0.67	13	4.17	0.06	15	64.88	0.63	13	20.83	0.54	15

Un método para diferenciar currucas capirotadas *Sylvia atricapilla* sedentarias y migradoras durante su invernada en el sur de la península Ibérica

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 1999. A method for differentiating between sedentary and migratory Blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia. *Bird Study* 46: 299-304.

RESUMEN

Las currucas capirotadas del sur de la península Ibérica son sedentarias, y como consecuencia presentan rasgos morfológicos diferentes de los de las currucas migradoras que ocupan zonas más norteñas; sus alas son más cortas y redondeadas y sus colas son más largas. En este trabajo, aprovechamos esta diferenciación morfológica para desarrollar un método con el que identificar individuos sedentarios y migradores durante su invernada en simpatría en el sur peninsular. Para ello, estudiamos la variación en esos rasgos morfológicos entre cinco poblaciones reproductoras en la península Ibérica, tres migradoras (del norte y centro peninsular) y dos sedentarias (del Campo de Gibraltar, en el sur de Iberia). Utilizamos la longitud de la octava primaria como una medida de longitud alar. Medimos las distancias entre la punta del ala y las primarias primera (P1) y novena (P9, numeradas en orden descendente), y calculamos un índice sencillo de apuntamiento alar (P1-P9). Combinando estas dos medidas con la longitud de la cola, obtuvimos una función discriminante que nos permitió clasificar correctamente en torno al 90% de las currucas reproductoras. Teniendo en cuenta que las poblaciones migradoras del centro y norte de Europa (que constituyen la mayor parte de la población invernante en el Campo de Gibraltar) tienen rasgos morfológicos de tipo migrador aún más acentuados que las poblaciones migradoras ibéricas, este método puede considerarse muy eficaz para identificar individuos migradores durante el invierno. La posibilidad de diferenciar currucas migradoras y sedentarias en sus áreas de invernada simpátricas supone un importante paso adelante en el estudio y conservación de las poblaciones meridionales de curruca capirotada, que probablemente están diferenciadas localmente en el borde de su distribución.

A method for differentiating between sedentary and migratory Blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia

Javier Pérez-Tris, Roberto Carbonell & José Luis Tellería*

We used the morphological differentiation of southern, sedentary Iberian Blackcaps *Sylvia atricapilla* to distinguish them from migratory ones during the winter. To do so, we studied three morphometrical traits during the breeding season (wing length, wing shape and tail length) of three migratory Iberian populations and two sedentary ones. We obtained a discriminant function which allowed us to differentiate both population types (over 90% of correct classifications). We discuss the utility of the method for differentiating between sedentary and migratory Blackcaps in their sympatric wintering areas, as well as the implications of our results for the study and conservation of sedentary, perhaps differentiated Blackcaps in Southern Iberia.

Although the Mediterranean basin is the main wintering ground for most pre-Saharan migrant passerines, it also sustains sedentary populations of many of these species. Despite the interest in differences between migratory and sedentary populations during the winter in traits such as habitat use, diet, body condition or survival, these subjects remain insufficiently understood. Several studies have searched for differences in winter behaviour between subspecies, sexes or age classes, these groups being always easily distinguishable (see Rabenold & Rabenold 1985, Sherry and Holmes 1996 for examples with Nearctic migrants). However, few studies have pointed out how different populations of a given species perform in sympatry during the winter (Finlayson 1981a, Senar *et al*. 1992, Goss-Custard *et al*. 1995), even when these populations may show different morphological traits, possibly related to different patterns of resource exploitation (Finlayson 1981a, Senar *et al.* 1994, Skúlason & Smith 1995, Tellería & Carbonell 1999). Such studies are limited by the lack of suitable methods that allow differentiation between such populations when distinction is not straightforward. In this paper, we use a combination of different morphological traits of Blackcaps *Sylvia atricapilla* to develop a simple procedure for differentiating between sedentary and migratory individuals in the sympatric wintering areas of Southern Iberia. The Blackcap should be a good model to undertake such studies, since most of their Mediterranean breeding grounds receive a considerable influx of migrants in autumn (Cramp 1992, Cantos 1995).

METHODS

During June and July 1997, we mist-netted 146 Blackcaps in five localities distributed along the Iberian Peninsula. We captured 99 young and 47 adult birds (28 males and 19 females). Three of these localities were in the northern half of Iberia (Álava, 42º55’N, 2º29’W, in northern Iberia; Sierra de Guadarrama, 40º54’N, 3º53’W, and Madrid, 40º30’N, 3º40’W, both in central Iberia), and the other two on its southern edge (Sierra de Ojén and Tarifa, 36º01’N, 5º36’W; see Carbonell & Tellería 1998 for details). Blackcap populations are migratory at the northern and central localities, which they abandon during the winter (Tellería & Carbonell 1999). Ringing recoveries show that Blackcaps are sedentary at the southern localities

---

**Bird Study 46: 299-304.*

(Finlayson 1981b, Cuadrado 1994, Cantos 1995). Thus, we grouped these five populations as northern (migratory) and southern (sedentary; Tellería & Carbonell 1999). Since it is known that Blackcaps show migratory polymorphism (Lo Valvo *et al*. 1988, Berthold 1991, Tellería & Carbonell 1999), we used some traits relevant for migratory flight performance (wing length, wing shape and tail length; Norberg 1990, 1995), that could allow us to differentiate such population types in their wintering grounds. Wing maximum chord and length of the 8th primary feather (descendant) were strongly correlated ($r = 0.85$, $n = 146$, $P < 0.001$), thus we selected the latter measurement as related to wing length (Jenni & Winkler 1989). We also considered the difference P1-P9 as an index of wing shape (where P1 and P9 are the distances from the tip of the 1st and 9th primary feathers to the wing tip). In Blackcaps, this difference increases as the wing becomes more pointed (Fig. 1; Kokshaysky 1973, Williamson 1976, Lo Valvo *et al*. 1988, Tellería & Carbonell 1999). Finally, we recorded tail length (straightened), because northern populations have shorter tails than southern ones (Williamson 1976, Tellería & Carbonell 1999). All measurements were recorded by the same person (RC) to the nearest 0.5 mm (see Svensson 1992 for details).

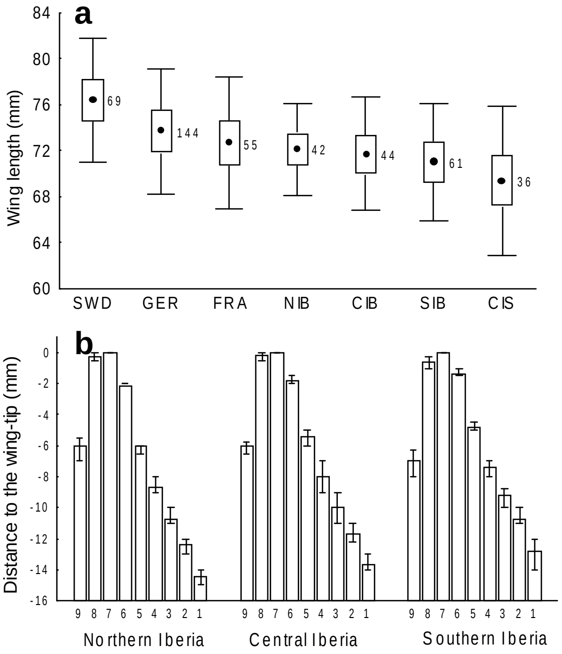

Figure 1. (a) Geographic variation in wing length of European Blackcaps (Mean, standard deviation, theoretical range [mean ± 3sd] and sample size). Measurements are from Sweden (SWD), Southern Germany (GER), South-eastern France (FRA), Northern Iberia (NIB), Central Iberia (CIB), Southern Iberia (SIB), and Canary Islands (CIS). (b) Mean and range of the distances from the tip of each primary feather (1st – 9th, numbered descendantly) to the wing tip of Iberian Blackcaps (we show negative values to simplify the perception of wing shapes). All measurements, except those from Iberia (this study), have been taken from Williamson (1976) and Cramp (1992).

We used discriminant function analysis (hereafter DFA; Manly 1994, StatSoft 1996) to classify birds as migratory or sedentary. Neither sex nor age showed a significant effect on any of the variables we measured (Table 1), so we pooled all sex and age classes in the DFA. Since migratory individuals outnumber residents in wintering areas

Table 1. Results of two-way ANOVAs for between-age (first-year versus adult birds) and between-sex differences for all the variables considered in this study.

	P1-P9		Tail length		Length of 8th primary	
Age (all d.f. = 1,142)	*F*	*P*	*F*	*P*	*F*	*P*
Between-groups	86.06	< 0.001	18.34	< 0.001	30.60	< 0.001
Between-age	0.27	0.61	0.03	0.86	0.66	0.42
Interaction	2.95	0.09	1.30	0.26	0.64	0.42
	P1-P9		Tail length		Length of 8th primary	
Sex (all d.f. = 1,43)	*F*	*P*	*F*	*P*	*F*	*P*
Between-groups	9.60	0.003	6.48	0.01	4.33	0.043
Between-sex	0.001	0.98	0.80	0.38	0.25	0.62
Interaction	1.00	0.32	0.12	0.73	0.06	0.80

(Finlayson 1980), a given Blackcap of unknown origin is, *a priori*, more likely to be migratory than sedentary. However, as the abundance of migratory Blackcaps varies among winters while surely the resident population does not (Finlayson 1980, Rodríguez *et al*. 1986, Rey 1995), we cannot objectively assess the true proportion of sedentary birds in the winter population, so we settled *a priori* probabilities of population membership proportional to sample sizes (Manly 1994, StatSoft 1996). To test the effectiveness of our model, we simulated a series of 50 DFA trials using pairs of half-sample random groups. Thus, for each simulation, we randomly selected two equal groups from the original sample (73 birds in each one) in which all the localities were always equally represented. Then we used one of these groups to develop a discriminant function, with which we attempted to classify the birds of the second group. After repeating the same routine 50 times, we estimated the 95% confidence interval of the mean percentage of correct classifications. If the model was reliable, we could use the first discriminant function, obtained by including all the birds from the original sample, to assign new observations to one or other population.

Once the model was developed, we sampled the southern localities during December 1997 and January 1998, when wintering Blackcaps occur in this region together with residents (Cantos 1995). European Blackcaps, consistently with their migratory behaviour, have more pronounced migratory-type traits than Northern Iberian populations (see Fig. 1; Williamson 1976, Cramp 1992), and are expected to be well-classified by our discriminant function (Manly 1994). If the effectiveness of our model for discriminating Iberian population types is high, we should be able to distinguish resident and migrant birds in their wintering grounds and to estimate their relative numbers in the whole wintering population. Thus, we can obtain the probability of each Blackcap being sedentary (StatSoft 1996), and then use the sample mean (that is, the probability of a given Blackcap of the winter population being sedentary) as an estimate of the proportion of sedentary birds in the whole winter population.

RESULTS

The DFA conducted with the whole spring sample provided a significant function (Wilk's Lambda = 0.39, Rao's approximation: $F_{3,142} = 75.00$, $P < 0.001$; Table 2, see also Fig. 2) whose percentage of correct classifications exceeded 90% (Table 3). About 61% of the variation in the discriminant scores (StatSoft 1996) was accounted for by between-populations differences when all variables were considered together (canonical correlation: $r = 0.78$). Thus, we obtained the following classification functions (StatSoft 1996):

$$M = -696.432 - 6.098\ WS + 4.648\ T + 21.099\ F8$$
$$S = -688.896 - 7.397\ WS + 5.617\ T + 20.018\ F8$$

where WS is the wing-shape index P1-P9, T is the tail length, F8 is the length of the 8th primary feather and M and S are, respectively, the classification scores for migratory and sedentary population types. These functions can be used to classify

Table 2. Descriptive statistics for the variables included in the discriminant function analysis. Pooled within-groups correlations between variables and the canonical discriminant function are also shown.

	Migratory Blackcaps *n* = 85		Sedentary Blackcaps *n* = 61		Correlation with discriminant function
	Mean	sd	Mean	sd	
P1-P9	8.03	1.18	5.79	1.39	-0.70
Tail	60.60	2.15	62.46	2.33	0.33
Eighth primary	54.94	1.55	53.35	1.53	-0.41

Table 3. Classification matrix provided by discriminant function analysis (incorrect classifications in italics), *a priori* probabilities of classification (proportional to sample sizes, *p*), and percentage of correct classifications.

	Actual classifications (*n*)	Predicted classifications Migratory Blackcaps ($p = 0.58$)	 Sedentary Blackcaps ($p = 0.42$)	Correct classifications (%)
Migratory Blackcaps	85	80	5	94.12
Sedentary Blackcaps	61	8	53	86.89
Both groups	146	88	58	91.09

new observations assigning each blackcap to the group for which it has the highest classification score (StatSoft 1996). The model classified first-year birds better than adults (four out of 13 wrong classifications (Table 3) were first-year birds and 9 were adults, $\chi^2_{\text{Yates}} = 7.20$, $P < 0.01$), but both sexes were equally well-classified (5 males and 4 females were misclassified, $\chi^2_{\text{Yates}} = 0.01$, $P = 0.92$). Frequency of misclassifications was also homogeneous for both population types (Table 3, $\chi^2_{\text{Yates}} = 1.49$, $P = 0.22$).

By means of the 50 DFA simulations, our model was effective in differentiating between both population types. We obtained near 90% correct classifications (Table 4), even though we obtained the simulated discriminant functions from reduced samples, which should show less discriminating power (Manly 1994, StatSoft 1996). Once the efficacy of the model was confirmed, we used it to classify Blackcaps captured during the winter. Five out of 36 captured birds were retraps of Blackcaps ringed during the spring at the same locality (13.9%). These birds were not considered for classification as they were not new individuals. Among the remaining 31 birds, 13 (41.9%) were classified as residents. By using the probabilities of each of these 31 Blackcaps being sedentary, we estimated the percentage of residents in the whole winter population, with 95% confidence, as 37.3% ± 16%.

DISCUSSION

In this work, we assessed the utility of DFA as a reliable tool to differentiate between sedentary and migratory Iberian Blackcap populations, which could be employed for differentiating between such populations in sympatric wintering areas (see also Summers *et al.* 1988). Our procedure has important advantages compared with other methods. The use of ringing recoveries, for instance, is often unsuitable for small passerines, due to the difficulty of recapturing enough birds to assess between-population differences that potentially occur at the sympatric wintering areas (see, however, Senar *et al.* 1992). On the other hand, single traits that overlap along the species' range offer limited opportunity to discriminate between birds belonging to dif-

Table 4. Mean, standard error and 95% confidence intervals for the mean percentage of correct classifications obtained after 50 DFA simulations, using pairs of randomly selected half-sample groups (73 individuals in each one).

	n	Observed percentage of correct classifications Mean ± 1 se	 95% confidence interval
Migratory Blackcaps	50	91.78 ± 0.55	90.97 – 92.89
Sedentary Blackcaps	50	87.41 ± 0.74	85.93 – 88.90
Both groups	50	89.95 ± 0.40	89.16 – 90.75

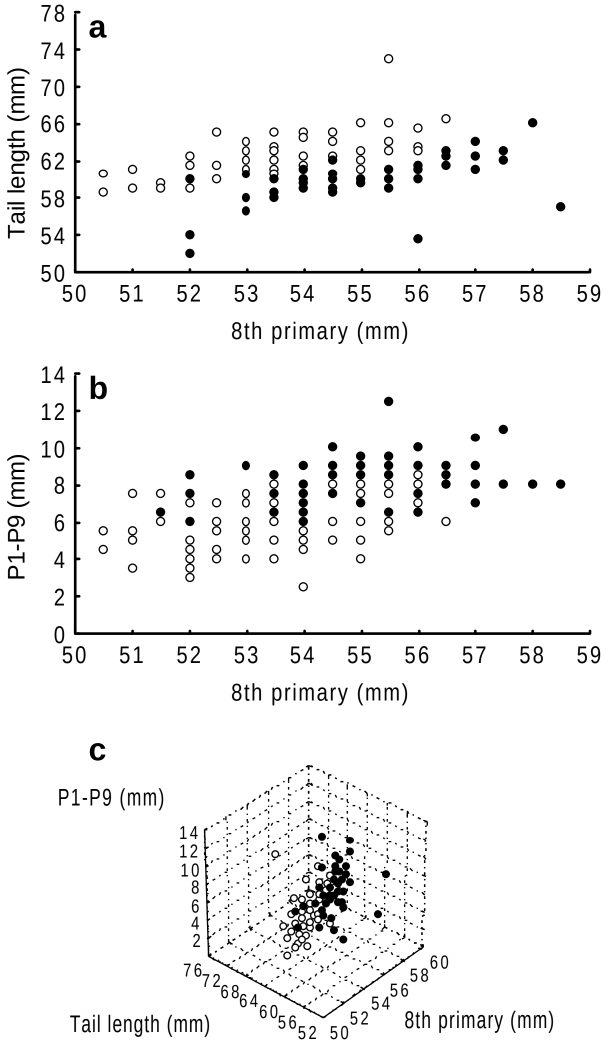

Figure 2. Morphological features of Blackcap population types studied (dots and circles refer to migratory and sedentary birds respectively). Controlling for wing length (measured as length of the 8^{th} primary feather), migratory Blackcaps (*n* = 85) show shorter tails (a) and more pointed wings (b) than sedentary ones (*n* = 61), which makes it possible their near absolute discrimination when all variables are combined (c).

ferent populations. For example, Blackcap is a leapfrog migrant in the western Palearctic (Cramp 1992), so that most birds wintering in the Mediterranean basin will come from mid-latitudes (Cantos 1995), where morphometrical traits largely overlap with those of southern populations (see Fig. 1). Thus, many of these birds would be misclassified as residents if their morphometrical traits (e.g. wing length or wing formula, see Finlayson 1980, 1981a) were considered separately. Moreover, given the difficulty of ageing many Blackcaps during the winter (Jenni & Winkler 1994), our discriminant function showed further advantages since it was suitable to differentiate between local and overwintering Blackcaps independently of their age. The slightly poorer ability of the model to discriminate adult birds in summer is likely due to feather abrasion rather than between-age morphological differences (see Table 1), and hence it will not affect classification during the winter after the complete moult of adults (Svensson 1992, Jenni & Winkler 1994). In fact, it could be suspected that the main shortcoming of our method might be its differential ability to classify Blackcaps of each population type correctly (see Tables 3 and 4). Sedentary birds, for instance, could be more likely to be misclassified and hence their contribution to the whole population could be underestimated. However, this bias does not seem to be too important, since we did not obtain significant between-populations differences in frequency of misclassifications.

Therefore, our results support the view that a high proportion of Blackcaps is sedentary in Southern Iberia (Finlayson 1981b, Cramp 1992, Cuadrado 1994, Cantos 1995). Our recoveries of resident Blackcaps, as well as the high percentage of birds classified as sedentary, support this conclusion. It should be noted, however, that the abundance of migratory Blackcaps varies in relation to food availability, both among and within winters (Finlayson 1980, Rey 1995), and that food resources, especially *Olea europaea sylvestris* olives, were unusually scarce during the 1997-98 winter in which we sampled the mixed population of Blackcaps (pers. obs.). Thus, the proportion of sedentary birds, averaged over a longer period of several years, could be smaller than the estimate we obtained.

Since discrimination depends on the morphological variation existing among Blackcaps, it should be interesting to study potential differences in the use of resources between migratory and sedentary populations during the winter (Skúlason &

Smith 1995, Tellería & Carbonell 1999). Furthermore, as it is known that the migratory behaviour of Blackcaps is heritable (Berthold 1991), it would also be interesting to investigate how these southern birds prevent outbreeding with other surrounding migratory-type individuals which occur at the same wintering areas (Lynch 1991, Hoffman & Blows 1994). In short, the maintenance of characteristic morphological features in Southern Iberian Blackcaps suggests the prospect of differentiated populations (and hence conservation units, Spellerberg 1991, Lesica & Allendorf 1995) locally occurring in the southern edge of the species' range, which may be the subject of fruitful future investigations.

Acknowledgements

José A. Díaz, Esteban Fernández-Juricic, and Emilio Virgós improved early versions of the paper. James D. Rising and Juan Carlos Senar also provided valuable suggestions. We thank the Agencias de Medio Ambiente (Diputación Foral de Álava, Comunidad Autónoma de Madrid and Junta de Andalucía) which authorised us to capture Blackcaps. This is a contribution to the projects PB92-0238 (Dirección General de Investigación Científica y Técnica) and PB97-0325 (Ministerio de Educación y Cultura), and it was developed while J.P-T. was supported by a Predoctoral Grant from the Universidad Complutense de Madrid.

References

Berthold, P. 1991. Genetic control of migratory behaviour in birds. *Trends in Ecology & Evolution* 6: 254-257.

Cantos, F.J. 1995. Migración e invernada de la curruca capirotada (*Sylvia atricapilla*) en la Península Ibérica. *Ecología* 9: 425-433.

Carbonell, R. & Tellería, J.L. 1998. Selección y uso del hábitat por cinco poblaciones ibéricas de Curruca Capirotada (*Sylvia atricapilla*). *Ardeola* 45: 1-10.

Cramp, S. (ed.) 1992. *The birds of the Western Palearctic.* Vol. VI. Oxford University Press, Oxford.

Cuadrado, M. 1994. Site-tenacity and life-time expectancy of resident and over-wintering Blackcaps *Sylvia atricapilla* in the Mediterranean. *Ringing & Migration* 15: 58-59.

Finlayson, J.C. 1980. The recurrence in winter quarters at Gibraltar of some scrub Passerines. *Ringing & Migration* 3: 32-34.

Finlayson, J.C. 1981a. Seasonal distribution, weights and fat of passerine migrants at Gibraltar. Ibis 123: 88-95.

Finlayson, J.C. 1981b. The morphology of Sardinian Warbler *Sylvia melanocephala* and Blackcap *Sylvia atricapilla* resident at Gibraltar. Bulletin of the British Ornithologists Club 101: 299-304.

Goss-Custard, J.D., Clarke, R.T., Durell, S.E.A. le V. dit, Caldow, R.W.G. & Ens, B.J. 1995. Population consequences of winter habitat loss in a migratory shorebird. II. Model predictions. *Journal of Applied Ecology* 32: 337-351.

Hoffman, A.A. & Blows, M.W. 1994. Species borders: ecological and evolutionary perspectives. *Trends in Ecology & Evolution* 9: 223-227.

Jenni, L. & Winkler, R. 1989. The feather-length of small passerines: a measure for wing-length in live birds and museum skins. *Bird Study* 36: 1-15.

Jenni, L. & Winkler, R. 1994. *Moult and ageing of European passerines*. Academic Press, London.

Kokshaysky, N.V. 1973. Functional aspects of some details of bird wing configuration. *Systematic Zoology* 22: 442-450.

Lesica, P. & Allendorf, F.W. 1995. When are peripheral populations valuable for conservation? *Conservation Biology* 9: 753-760.

Lo Valvo, F., Lo Verde, G. & Lo Valvo, M. 1988. Relationships among wing length, wing shape and migration in Blackcap *Sylvia atricapilla* populations. *Ringing & Migration* 9: 51-54.

Lynch, M. 1991. The genetic interpretation of inbreeding depression and outbreeding depression. *Evolution* 45: 622-629.

Manly, B.F.J. 1994. *Multivariate statistical methods. A primer*. 2nd Edition. Chapman & Hall, London.

Norberg, U.M. 1990. *Vertebrate flight*. Springer-Verlag, Berlin.

Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology* 9: 48-54.

Rabenold, K.N. & Rabenold, P.P. 1985. Variation in altitudinal migration, winter segregation, and site tenacity in two subspecies of Dark-eyed Juncos in the Southern Appalachians. *Auk* 102: 805-819.

Rey, P.J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* 76: 1625-1635.

Rodríguez, M., Cuadrado, M. & Arjona, S. 1986. Variation in the abundance of Blackcaps (*Sylvia atricapilla*) wintering in an Olive (*Olea europaea*) orchard in Southern Spain. *Bird Study* 33: 81-86.

Senar, J.C., Burton, P.J.K. & Metcalfe, N.B. 1992. Variation in the nomadic tendency of a wintering finch *Carduelis spinus* and its relationships with body condition. *Ornis Scandinavica* 23: 63-72.

Senar, J.C., Lleonart, L. & Metcalfe, N.B. 1994. Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. *Journal of Avian Biology* 25: 50-54.

Sherry, T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

Skúlason, S. & Smith, T.B. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution* 10: 366-370.

Spellerberg, I.F. 1991. Biogeographical basis of conservation. *The scientific management of temperate communities for conservation* (eds. I.F. Spellerberg, F.B. Goldsmith & M.G. Morris), pp. 293-322. Blackwell, Oxford.

StatSoft, Inc. 1996. *STATISTICA for Windows (Computer program manual)*. StatSoft, Inc., Tulsa.

Summers, R.W., Nicoll, M., Underhill, L.G. & Petersen, A. 1988. Methods for estimating the proportions of Icelandic and British Redshanks *Tringa totanus* in mixed populations wintering in British coasts. *Bird Study* 35: 169-180.

Svensson, L. 1992. *Identification guide to European passerines*. L. Svensson, Stockholm.

Tellería, J. L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology*, 30: 63-71.

Williamson, K. 1976. *Identification for ringers 3. The Genus* Sylvia. Revised Edition. British Trust for Ornithology, Tring.

Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España.

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000. Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. *Ardeola* 47: 9-18.

RESUMEN

En este trabajo desarrollamos un método para diferenciar a los Petirrojos locales de los migradores durante el invierno en el sur de España, con objeto de estimar su contribución relativa a la población invernante en el Campo de Gibraltar durante el invierno 1998-99. Considerando la variación en la longitud y fórmula alar entre dos poblaciones parcialmente migradoras (Álava y Madrid) y una sedentaria (Campo de Gibraltar), desarrollamos una función discriminante que nos permitió clasificar correctamente casi el 80% de los Petirrojos analizados (*n* = 135). La longitud alar (tercera primaria) fue el rasgo de mayor contribución a la diferenciación entre grupos. Utilizando este método, estimamos una proporción de Petirrojos locales en el área del Campo de Gibraltar en torno al 58% (*n* = 134). Esta proporción fue mucho más alta en los hábitats donde cría la especie (70% en bosques) que en los hábitats ocupados sólo durante la invernada (40 % en matorrales), sugiriendo una ocupación diferencial de ambos ambientes por los Petirrojos foráneos y el desplazamiento de parte de la población local fuera de las áreas de cría durante el invierno.

Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España

Javier Pérez-Tris, Roberto Carbonell & José Luis Tellería*

En este trabajo desarrollamos un método para diferenciar a los Petirrojos locales de los migradores durante el invierno en el sur de España, con objeto de estimar su contribución relativa a la población invernante en el Campo de Gibraltar durante el invierno 1998-99. Considerando la variación en la longitud y fórmula alar entre dos poblaciones parcialmente migradoras (Álava y Madrid) y una sedentaria (Campo de Gibraltar), desarrollamos una función discriminante que nos permitió clasificar correctamente casi el 80% de los Petirrojos analizados (n = 135). La longitud alar (tercera primaria) fue el rasgo de mayor contribución a la diferenciación entre grupos. Utilizando este método, estimamos una proporción de Petirrojos locales en el área del Campo de Gibraltar en torno al 58% (n = 134). Esta proporción fue mucho más alta en los hábitats donde cría la especie (70% en bosques) que en los hábitats ocupados sólo durante la invernada (40 % en matorrales), sugiriendo una ocupación diferencial de ambos ambientes por los Petirrojos foráneos y el desplazamiento de parte de la población local fuera de las áreas de cría durante el invierno.

Identification and numerical importance of local Robins Erithacus rubecula *during winter in southern Spain*. Here we develop a method for differentiating between local and migratory Robins during winter in southern Spain, which we applied to estimate their relative proportion in the population wintering in the Campo de Gibraltar area (southern Spain) in 1998-99. To do so, we considered the variation in wing length and wing formula between two partially migratory populations (Álava area, northern Spain, and Guadarrama area, central Spain) and one sedentary population (Campo de Gibraltar). From these, we obtained a discriminant function (Tables 1 and 4) which allowed us to classify correctly almost 80% of the Robins measured (n = 135; Tables 2 and 3). Wing length (third primary) showed the highest contribution to between-group discrimination (Fig. 1). By using this method, we estimated that 58% (n = 134) of the Robins wintering in the Campo de Gibraltar area in 1998-99 belonged to the sedentary population. This proportion was much larger in the breeding habitats of these local populations (70% in forests) than in the habitats that are occupied during the winter only (40% in scrublands), suggesting a differential occupation of both environments by foreign Robins and the displacement of part of the residents away from their breeding areas during the winter.

El estudio de las posibles interacciones entre distintas poblaciones de una misma especie de ave cuando concurren en simpatría en las áreas de migración o invernada es un tema de gran interés teórico y aplicado del que, sin embargo, se tiene escasa información (Ketterson & Nolan 1983, Greenberg 1986, Safriel 1995, Sherry & Holmes 1996). Por ejemplo, y pese a su importancia como área de invernada, todavía se sabe poco sobre las diferencias en la selección de hábitat, rastreo de los recursos, interacciones territoriales, estrategias de acumulación de grasa, gregarismo, etc. entre los paseriformes migradores y los sedentarios en la región Mediterránea (véase, sin embargo, Finlayson 1981, Cuadrado 1994). Esto puede explicarse, en parte, porque la discriminación entre poblaciones locales e invernantes suele ser difícil cuando no presentan diferencias morfológicas obvias. Si, además, no es posible identificar a los individuos mediante el marcado previo en sus áreas de cría, se ha de recurrir a su diferenciación mediante métodos morfométricos o moleculares más o menos

---

**Ardeola 47: 9-18.*

Tabla 1. Función discriminante para la morfología alar de Petirrojos pertenecientes a poblaciones parcialmente migradoras y sedentarias, obtenida a partir de 135 individuos capturados en verano en tres localidades ibéricas. Se muestran los coeficientes de la función, los coeficientes estandarizados, las correlaciones entre las variables y la función (dentro de grupos) y la significación de sus contribuciones individuales.
[Discriminant function for the wing size and wing formula of Robins captured during breeding either in an area where they are sedentary and in two areas (pooled) where they are partillay migratory (n = 135). The figures shown are the function coefficients, the standardized coefficients, the pooled within groups correlations between each variable and the discriminant function, and the significance of the individual contribution of each variable.]

	Coeficientes de la función *[Function coefficients]*	Coeficientes estandarizados *[Standardized coefficients]*	Correlaciones *[Correlations]*	*P*
Constante *[Constant]*	-42.846			
3ª Primaria *[3rd Primary]*	0.776	1.022	0.802	< 0.001
Distancia *[Distance]* P2	0.354	0.404	0.321	0.034
Distancia *[Distance]* P3	0.179	0.106	0.008	0.614
Distancia *[Distance]* P4	-1.401	-0.432	-0.057	0.019
Distancia *[Distance]* P5	-2.394	-0.271	0.055	0.157
Distancia *[Distance]* P6	0.461	0.335	0.216	0.128
Distancia *[Distance]* P7	-0.388	-0.348	0.21	0.288
Distancia *[Distance]* P8	0.895	0.842	0.283	0.063
Distancia *[Distance]* P9	-0.823	-0.795	0.236	0.111
Distancia *[Distance]* P10	-0.049	-0.054	0.183	0.884

elaborados y/o costosos (por ejemplo, Summers *et al.* 1988, Avise 1994, Hobson 1999).

En este trabajo desarrollamos, en primer lugar, un método de diferenciación morfométrica de los Petirrojos *Erithacus rubecula* nativos del Campo de Gibraltar (Cádiz) con respecto a los reproductores en las mesetas y montañas de la mitad norte de la península Ibérica. El área de Gibraltar alberga poblaciones reproductoras de Petirrojos que son mayoritariamente sedentarios (Alonso 1980, Ceballos & Guimerá 1992, datos propios inéditos). Por el contrario, la especie sufre en las mesetas y montañas ibéricas una drástica disminución de su abundancia durante el invierno, abandonando muchas localidades de cría (Tellería *et al.* 1999). Así, a pesar de la llegada de Petirrojos procedentes del centro y norte de Europa para pasar el invierno en las mesetas (Bueno 1998), la abundancia de la especie en esa región disminuye de primavera a invierno en un 82%, mientras que aumenta en un 686% en las regiones más meridionales (algo que está claramente influido por la llegada de individuos migradores, Pérez-Tris & Tellería, en prep.). Por otro lado, el diferente comportamiento migrador de los Petirrojos ibéricos también se hace evidente a escala individual. Las recuperaciones de anillas muestran que la especie es sedentaria en el sur peninsular, como ponen de manifiesto las abundantes recapturas de Petirrojos en el mismo lugar tanto en primavera como en invierno. Pero también que su tenacidad en las áreas de cría (medida como el tiempo que pasan en ellas fuera de la estación reproductora) es allí mucho mayor que en las mesetas, lo que sugiere el movimiento de una parte considerable de los Petirrojos de la mitad norte peninsular (Pérez-Tris & Tellería, en prep.).

Dado el carácter clinal de la morfología alar de esta especie y su relación con el comportamiento migrador de sus poblaciones (Cramp 1988), puede predecirse la existencia de diferencias en la es-

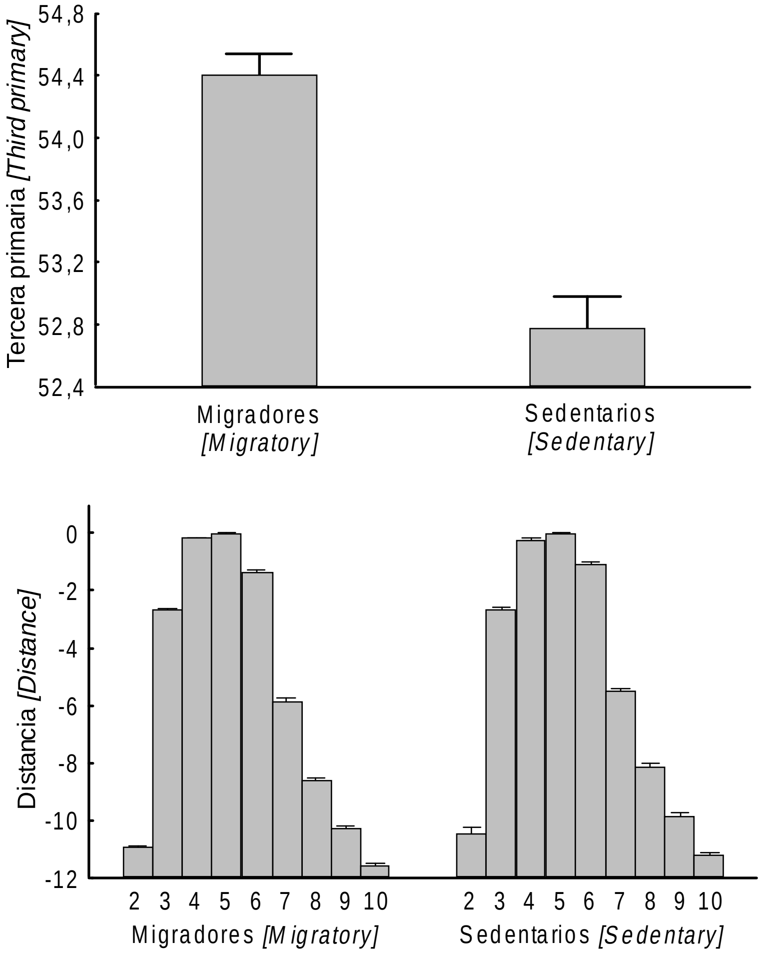

Figura 1. Diferencias entre los Petirrojos ibéricos migradores y sedentarios en la longitud de la tercera primaria y las distancias entre cada primaria y la punta del ala (distancias a las primarias, representadas con valores negativos para facilitar la apreciación de la forma del ala). Se muestran las medias en milímetros y sus errores estándar. Los tamaños muestrales se dan en la Tabla 2.

[Differences between migratory and sedentary Iberian Robins in the length of the third primary and in the distances between each primary and the wing tip (negative values are shown for ease of perception of wing shape). Bars are means (in milimeters) and wiskers are standard errors. Sample sizes are given in Table 2.]

tructura del ala de los Petirrojos de ambas regiones que reflejen el desigual alcance de sus movimientos. Estas diferencias pueden ser útiles para diferenciarlos en aquellas localidades donde coincidan en simpatría durante el invierno. En segundo lugar, utilizaremos esta herramienta para valorar la contribución relativa de los Petirrojos locales a la población invernante en la comarca del Campo de Gibraltar. Ésta recibe durante el otoño grandes aportes de Petirrojos foráneos (Tellería 1981) que aumentan tanto la abundancia como la variedad de ambientes ocupados por la especie (Arroyo & Tellería 1983). No se sabe, sin embargo, si los individuos locales quedan acantonados en los bosques donde crían, tal vez amortiguando la entrada de los migradores, o si se mezclan con estos ampliando su distribución hacia los matorrales de la base de las montañas.

MATERIAL Y MÉTODOS

Durante los meses de junio y julio de 1997 y 1998 capturamos Petirrojos con redes japonesas en tres poblaciones reproductoras diferentes, dos de ellas situadas en la mitad norte de la península Ibérica (Álava, 620 m.s.n.m., 42º55'N, 2º29'O, en el norte de España, y Sierra de Guadarrama, 1100 m, 40º54'N, 3º53'O, en el Sistema Central) y la tercera en el Campo de Gibraltar (Sierra de Ojén, 250 m, 36º01'N, 5º36'O; para una descripción detallada de las áreas de estudio, véase Carbonell & Tellería 1998). En total, se capturaron 135 individuos de los que 119 fueron jóvenes (34, 48 y 37 aves en Álava, Guadarrama y Ojén, respectivamente). Los 16 adultos fueron sexados de acuerdo con la presencia de placa incubadora y la forma de la protuberancia cloacal (Svensson 1996). De estos, 9 (3/3/3) fueron machos y 7 (2/3/2) hembras. Medimos tanto la longitud del ala (cuerda máxima) como la tercera primaria de los individuos capturados, si bien seleccionamos ésta última para diferenciar a las poblaciones por ser más fácil de tomar y, por tanto, más repetible (Jenni & Winkler 1989). Medimos también la distancia entre la punta del ala y cada una de las primarias (distancias a las primarias segunda a décima, numeradas por orden ascendente). Todas las medidas fueron tomadas con 0,5 mm de precisión (véase Svensson 1996 para más detalles). Una vez completa la toma de datos, procedimos al anillamiento y liberación de los Petirrojos.

De acuerdo con nuestra hipótesis de partida, los Petirrojos de Álava y Guadarrama presentaron una tercera primaria significativamente mayor que los de la sierra de Ojén ($F_{2,132} = 22.70$, $P < 0.001$). Un test de Tukey demostró, además, que las dos primeras poblaciones no diferían significativamente entre sí ($P = 0.73$) mientras que sí lo hacían con la de Ojén ($P < 0.001$ en ambos casos). Por esta razón, los individuos de las dos localidades norteñas fueron incluidos en un único grupo. Con estos Petirrojos realizamos un análisis de funciones discriminantes (Manly 1994, StatSoft 1996) para diferenciar a las aves de las mesetas (migradoras, desde ahora) de las del sur (sedentarias). Dado que las proporciones de jóvenes y de adultos de cada sexo fueron homogéneas en estos dos grupos ($\chi^2_2 = 0.04$, $P = 0.98$), se analizaron conjuntamente todos los individuos con el fin de obtener una función igualmente válida para todos los segmentos poblacionales. Todas las variables consideradas fueron incluidas en la función, a pesar de que algunas de ellas no contribuyesen significativamente a la discriminación entre grupos. Esta decisión de utilizar la función saturada se tomó por motivos prácticos, dado que es más sencillo (y por ello ofrece una mayor repetibilidad) medir la fórmula alar completa que medir sólo las distancias a algunas de las primarias por separado. Para examinar la validez de la función discriminante así obtenida, realizamos 50 repeticiones del análisis con pares de grupos de 67 y 68 individuos seleccionados al azar a partir de la muestra original, pero de for-

Tabla 2. Matriz de clasificación proporcionada por la función discriminante detallada en la Tabla 1 (clasificaciones incorrectas en cursiva) y porcentajes de clasificaciones correctas.
[Classification matrix provided by the discriminant function detailed in Table 1 (incorrect classifications are indicated in italics) and percentage of correct classifications.]

	Clasificación observada *[Observed classification]* (*n*)	Clasificación esperada *[Predicted classification]* Migradores *[Migratory]*	Clasificación esperada *[Predicted classification]* Sedentarios *[Sedentary]*	% correctas *[% correct]*
Petirrojos migradores *[Migratory Robins]*	93	73	20	78.49
Petirrojos sedentarios *[Sedentary Robins]*	42	8	34	80.95
Ambos grupos *[Both groups]*	135	81	54	79.26

Tabla 3. Porcentaje medio de clasificaciones correctas, con su error estándar e intervalos de confianza al 95%, obtenido tras realizar 50 repeticiones de análisis del funciones discriminantes descrito en la Tabla 1, con pares de grupos seleccionados al azar a partir de la muestra original (para más detalles véase el texto).
[Mean percentage of correct classifications, with standard errors and 95% confidence intervals, obtained after performing 50 discriminant function analyses as described in Table 1, but using pairs of groups randomly selected from the original sample.]

		Porcentaje observado de clasificaciones correctas *[Observed percentage of correct classifications]*	
	(*n*)	Media ± se *[Mean ± se]*	Intervalo de confianza al 95% *[95% confidence interval]*
Petirrojos migradores *[Migratory Robins]*	50	76.09 ± 1.11	73.86 – 78.32
Petirrojos sedentarios *[Sedentary Robins]*	50	79.64 ± 1.04	77.54 – 81.74
Ambos grupos *[Both groups]*	50	77.21 ± 0.90	75.41 – 79.01

Tabla 4. Ecuaciones de clasificación utilizadas para diferenciar Petirrojos migradores y sedentarios, correspondientes a la función discriminante detallada en la Tabla 1. Los individuos se asignan al grupo para cuya ecuación dan un resultado mayor. Las ecuaciones se resuelven sumando la constante a los productos de multiplicar cada coeficiente por el valor de su correspondiente medida morfológica (StatSoft, 1996).
[Classification equations for both migratory and sedentary Robins, corresponding to the discriminant function described in Table 1. New individuals are assigned to the group for whose equation they give the highest result. Equations are solved by adding the value of the constant to the sum of products of each coefficient multiplied by its corresponding morphological trait (StatSoft, 1996).]

	Coeficientes *[Coefficients]*	
	Migradores *[Migratory]*	Sedentarios *[Sedentary]*
Constante *[Constant]*	-1078.81	-1013.56
3ª Primaria *[3rd Primary]*	39.98	38.77
Distancia *[Distance]* P2	5.09	4.54
Distancia *[Distance]* P3	23.01	22.73
Distancia *[Distance]* P4	-53.94	-51.76
Distancia *[Distance]* P5	-93.34	-89.63
Distancia *[Distance]* P6	13.13	12.42
Distancia *[Distance]* P7	-12.16	-11.56
Distancia *[Distance]* P8	15.81	14.42
Distancia *[Distance]* P9	-33.22	-31.94
Distancia *[Distance]* P10	11.5	11.58

ma que mantuviesen la misma proporción de migradores y sedentarios que ésta. En cada repetición, utilizamos una de las submuestras para generar una nueva función discriminante y la otra para comprobar su eficacia por medio del porcentaje de clasificaciones correctas. Para evitar sesgos debidos a la presencia de un Petirrojo migrador más en los grupos de 68 individuos, generamos de modo sistemático el mismo número de funciones con cada tamaño de submuestra. Una vez realizadas las 50 repeticiones, calculamos el porcentaje medio de clasificaciones correctas y su intervalo de confianza al 95%.

Una vez desarrollado el método de diferenciación, lo aplicamos para obtener la proporción de individuos sedentarios en el invierno de 1998-99 en el Campo de Gibraltar, así como la representación poblacional de los Petirrojos sedentarios y migradores en las áreas de cría de la especie y en aquéllas que sólo son ocupadas en invierno. Durante los meses de diciembre y enero capturamos Petirrojos con redes japonesas en nueve localidades diferentes. Cinco de ellas son lugares de cría (bosques de *Quercus suber* y *Q. canariensis*) mientras que las cuatro restantes sólo son ocupadas durante la invernada (matorrales de *Pistacia lentiscus*, *Olea europaea sylvestris*, etc.). Una vez clasificados los individuos capturados en invierno, estimamos la proporción de Petirrojos sedentarios en la población invernante en el área del Campo de Gibraltar, así como la importancia relativa de cada grupo en los hábitats de cría e invernada teniendo en cuenta el posible nivel de error cometido en la clasificación de los individuos.

RESULTADOS

El análisis de funciones discriminantes realizado con los Petirrojos capturados en verano proporcionó una función significativa (Lambda de Wilk = 0.66, aproximación de Rao: $F_{10,124} = 6.50$, $P < 0.001$, Tabla 1) que permitió clasificar correctamente al 79% de los individuos (Tabla 2). La longitud de la tercera primaria mostró la mayor contribución individual a la diferenciación entre grupos (Tabla 1). Alrededor del 35% de la variación en los valores discriminantes pudo ser explicada por las diferencias entre los migradores y sedentarios, considerando todas las variables combinadas (correlación canónica: $r = 0.59$). La capacidad de clasificación de nuestra función discriminante fue homogénea tanto entre migradores y sedentarios ($\chi^2_{\text{Yates}} = 0.01$, $P = 0.92$; frecuencias en la Tabla 2), como entre clases de edad y sexos (un macho, dos hembras y 25 jóvenes fueron clasificados incorrectamente, $\chi^2_2 = 0.78$, $P = 0.68$), a pesar del conocido dimorfismo sexual del Petirrojo en longitud alar (Cuadrado 1991, Madsen 1997). Por otra parte, y considerando sólo los adultos, el porcentaje de clasificaciones correctas fue homogéneo entre machos y hembras (Test Exacto de Fisher, $P = 0.55$). Este resultado se mantuvo al considerar solamente los individuos capturados en el norte (seis machos y tres hembras correctamente clasificados, Test Exacto de Fisher: $P = 0.18$) y en el sur (2/2, $P = 0.99$). Las 50 repeticiones de análisis realizadas con grupos aleatorios proporcionaron un porcentaje medio de clasificaciones correctas del 77% (Tabla 3), muy próximo al obtenido utilizando la muestra completa. Teniendo en cuenta la menor potencia de estos análisis debida a la reducción a la mitad del tamaño muestral, este resultado confirma la validez de nuestro método.

Una vez desarrollada y examinada la función discriminante, clasificamos los Petirrojos capturados durante el invierno como migradores o sedentarios calculando sus valores de clasificación para cada grupo (Tabla 4). De un total de 134 Petirrojos capturados, cuatro fueron controles de individuos anillados en verano, que no fueron clasificados al tratarse de repeticiones. Utilizando los 130 restantes, obtuvimos un porcentaje de Petirrojos sedentarios en el área del Campo de Gibraltar del 57.91 ± 10.71% (media e intervalo de confianza al 95%; $n = 9$ localidades). Los Petirrojos clasificados como locales dominaron en los hábitats de cría (55 locales frente a 24 migradores), mientras que contribuyeron tanto como los clasificados como foráneos a la ocupación invernal de los matorrales de la periferia de la sierra (27 locales frente a 28 migradores). Dado que la función discriminante clasificó igualmente bien a migradores y sedentarios, es improbable que nuestra estima de la proporción global esté seriamente sesgada por errores de clasificación. Sin embargo, estos errores sí deben ser tenidos en cuenta al estudiar los patrones de ocupación de las áreas de cría y de invernada. Asumiendo un 21% de errores en la clasificación de los individuos (Tabla 2), la representación de cada fracción poblacional en los matorrales se des-

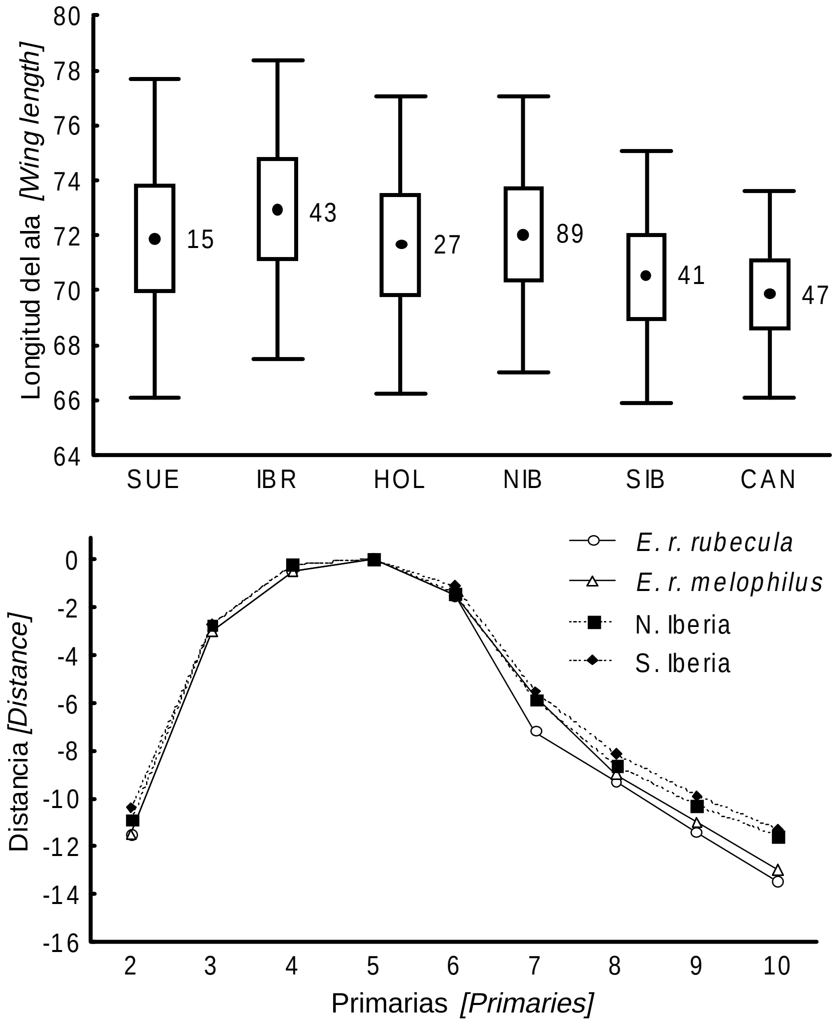

Figura 2. Arriba, variación en la longitud del ala de los Petirrojos en el Paleártico Occidental (medias, desviaciones típicas, rangos teóricos [media ± 3 sd] y tamaños muestrales; SUE, Suecia; IBR, islas Británicas; HOL, Holanda; NIB, norte ibérico; SIB, sur ibérico; CAN, islas Canarias). Abajo, variación entre las subespecies europeas y los Petirrojos ibéricos en la fórmula alar (distancias medias entre cada primaria y la punta del ala, con valor negativo). Los datos para las aves no ibéricas han sido obtenidos de Cramp (1988), interpolando los valores para la 8^a y 9^a primarias. Todas las medidas se dan en milímetros.

[Above, variation in wing length of Robins in the Western Palearctic (means, standard deviations, theoretical ranges [mean ± 3 sd] and sample sizes. SUE, Sweden; IBR, British Islands; HOL, The Netherlands; NIB, Northern Iberia; SIB, Southern Iberia; CAN, Canary Islands). Below, variation among European subspecies and Iberian Robins in wing formula (mean distances between each primary and the wing tip, negative values). Data for non-Iberian Robins have been obtained from Cramp (1988), after interpolating the values for the 8^{th} and the 9^{th} primaries. All measurements are given in milimeters.]

vía significativamente de la que cabría esperar en ausencia de individuos sedentarios ($\chi^2_1 = 23.98$, $P < 0.001$). Sin embargo, la entrada de Petirrojos foráneos en las áreas de cría de los locales es sólo marginalmente superior que la que cabría esperar teniendo en cuenta el nivel de error de nuestra función discriminante ($\chi^2_1 = 3.67$, $P = 0.055$).

DISCUSIÓN

La utilidad del análisis discriminante para identificar individuos de diferentes grupos poblacionales en simpatría ha sido ya demostrada en otras ocasiones (Summers *et al.* 1988, Pérez-Tris *et al.* 1999). Su utilidad práctica radica en su capacidad para diferenciar, de manera inmediata, una gran cantidad de individuos, evaluando además el error que se puede cometer en su identificación. Esto permite evitar el uso de rasgos morfométricos aislados con elevado solapamiento entre grupos. En el caso del Petirrojo, por ejemplo, las diferencias descritas para la estructura y coloración del plumaje entre las distintas poblaciones europeas son solamente apreciables examinando extensas colecciones de ejemplares (Cramp 1988, Svensson 1996). De hecho, aunque existe un gradiente de acortamiento y de aumento de la redondez del ala hacia el sur, el solapamiento entre poblaciones hace imposible la utilización por separado de estos rasgos como criterios únicos de diferenciación (Fig. 2). Es probable que este solapamiento, acentuado en la península Ibérica, limite la capacidad discriminante de nuestro modelo (un 21% de clasificaciones erróneas). En cualquier caso, los Petirrojos de origen escandinavo y centroeuropeo que componen el grueso de la población invernante en el área de Gibraltar (Tellería 1981, véase también Bueno 1998), tienen rasgos de tipo migrador aún más exagerados que los del norte peninsular (Fig. 2; Cramp 1988). Por esta razón, es previsible que estos Petirrojos foráneos sean más fácilmente discriminados por una función capaz de separar a las poblaciones ibéricas y que, como consecuencia, el nivel de error real se reduzca al aplicar el método durante el invierno. Aunque esta aseveración debiera ser confirmada por estudios posteriores, entendemos que asumir un porcentaje de error del 21% durante el invierno es, cuando menos, una estrategia conservadora.

Aunque el porcentaje de Petirrojos no ibéricos invernantes en el sur peninsular puede variar considerablemente entre años (Herrera 1998), los controles de Petirrojos locales durante el invierno (el 9.5% de los 42 marcados durante los dos veranos anteriores como reproductores en el Campo de Gibraltar), junto con el elevado número de individuos clasificados como residentes, apoyan el carácter sedentario de las poblaciones gaditanas y su elevada contribución al conjunto de la población invernante en aquellas áreas donde se encuentran presentes. El Petirrojo cría en los alcornocales y quejigales de las sierras del Campo de Gibraltar en densidades relativamente altas (15 aves/10 ha en la Sierra de Ojén; datos propios inéditos). Estas densidades aumentan durante el invierno, alcanzando valores medios de 17 aves/10 ha en los bosques de la sierra y de 15 aves/10 ha en los matorrales de la periferia (Arroyo & Tellería 1983). A tenor de nuestros resultados, este incremento numérico y la colonización de los matorrales utilizados por la especie durante el invierno parecen deberse tanto al aporte masivo de individuos foráneos (Tellería 1981) como al reclutamiento primaveral de la población local de Petirrojos y su posterior expansión hacia los matorrales de la periferia de las sierras, cuya calidad como área de invernada podría superar a la de los bosques dado que los frutos que consume la especie son más abundantes en esos ambientes (Herrera 1981, Jordano 1989). Sin embargo, el carácter territorial del Petirrojo durante el invierno parece estar más relacionado con la defensa de buenos refugios ante los depredadores que con el monopolio de zonas de alimentación (Cuadrado 1997). Por esta razón, los bosques podrían ser preferidos por el Petirrojo como una zona de invernada más segura que los matorrales, dado que en aquellos los frutos son también muy abundantes y, como en los matorrales, se mantienen disponibles durante todo el invierno (obs. pers.). En este caso, la tenacidad de los Petirrojos sedentarios en sus áreas de cría (lo que les facilitaría el mantenimiento de sus territorios frente a los migradores que fuesen llegando en otoño; Tobias 1997), así como las habilidades competitivas de cada individuo independientes de su origen, favorecerían la exclusión de los individuos migradores y de un porcentaje considerable de los sedentarios, que se verían abocados a ocupar los matorrales de la periferia de las sierras. En cualquier caso, si el ocupar bosques o matorrales se tradujese en diferentes costes y beneficios para los Petirrojos, los patrones de distribución diferencial entre tipos de hábitat que se describen en este trabajo podrían constituir un mecanismo de ajuste demográfico para la especie durante el invierno (Pulliam & Danielson 1991, Sherry & Holmes 1996, Rodenhouse *et al*. 1997).

Agradecimientos

A Álvaro Ramírez por su ayuda en el trabajo de campo. Agradecemos a las Agencias de Medio Ambiente de la Diputación Foral de Álava, Comunidad Autónoma de Madrid y Junta de Andalucía la concesión de los permisos para capturar aves, y a D. Carlos Masaveu Mora-Figueroa las facilidades para trabajar en la finca El Ojén. Mariano Cuadrado, Juan Carlos Senar y un revisor anónimo mejoraron sustancialmente una versión preliminar de este trabajo. Este trabajo ha sido financiado por los proyectos PB92-0238 y PB97-0325 del Ministerio de Educación y Cultura. Durante su desarrollo, J.P-T. disfrutó de una Beca Predoctoral de la Universidad Complutense de Madrid.

Bibliografía

Alonso, J. 1980. *Avifauna del sur de Cádiz, Campo de Gibraltar y comarca de La Janda*. Tesis Doctoral. Universidad Complutense. Madrid.

Arroyo, B. & Tellería, J.L. 1983. La invernada de las aves en el área de Gibraltar. *Ardeola* 30: 23-31.

Avise, J.C. 1994.*Molecular markers, natural history, and evolution*. Chapman & Hall. New York.

Bueno, J.M. 1998. Migración e invernada de pequeños turdinos en la península Ibérica. V. Petirrojo (*Erithacus rubecula*). *Ardeola* 45: 193-200.

Carbonell, R. & Tellería, J.L. 1998. Selección y uso del hábitat por cinco poblaciones ibéricas de Curruca Capirotada (*Sylvia atricapilla*). *Ardeola* 45: 1-10.

Ceballos, J.J. & Guimerá, V.M. 1992. *Guía de las aves de Jerez y de la província de Cádiz. Atlas ornitológico de las especies nidificantes.* Biblioteca de Urbanismo y Cultura. Jerez.

Cramp, S. (ed.) 1988. *The Birds of the Western Palearctic.* Vol. V. Oxford University Press. Oxford.

Cuadrado, M. 1991. Wing length criteria for sex determination of Robins *Erithacus rubecula* wintering in southern Spain. *Ornis Svecica* 1: 55-57.

Cuadrado, M. 1994. Site-tenacity and life-time expectancy of resident and overwintering Blackcaps *Sylvia atricapilla* in the Mediterranean. *Ringing & Migration* 15: 58-59.

Cuadrado, M. 1997. Why are migrant Robins (*Erithacus rubecula*) territorial in winter? The importance of the anti-predatory behaviour. *Ethology, Ecology & Evolution* 9: 77-88.

Finlayson, J.C. 1981. Seasonal distribution, weights and fat of passerine migrants at Gibraltar. *Ibis* 123: 88-95.

Greenberg, R. 1986. Competition in migrant birds in the nonbreeding season. *Current Ornithology* 3: 281-307.

Herrera, C.M. 1981. Fruit food of Robins wintering in southern Spanish Mediterranean scrubland. *Bird Study* 28: 115-122.

Herrera, C.M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68: 511-538.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120: 314-326.

Jenni, L. & Winkler, R. 1989. The feather-length of small passerines: a measure for wing-length in live birds and museum skins. *Bird Study* 36: 1-15.

Jordano, P. 1989. Variación de la dieta frugívora otoño-invernal del Petirrojo (*Erithacus rubecula*): efectos sobre la condición corporal. *Ardeola* 36: 161-183.

Ketterson, E.D. & Nolan, V. Jr. 1983. The evolution of differential bird migration. *Current Ornithology* 1: 357-402.

Madsen, V. 1997. Sex-determination of Continental European Robins *Erithacus r. rubecula*. *Bird Study* 44: 239-244.

Manly, B.F.J. 1994. *Multivariate statistical methods. A primer*. 2nd Edition. Chapman & Hall. London.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 1999. A method for differentiating between sedentary and migratory Blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia. *Bird Study* 46: 299-304 (*Capítulo 4*).

Pulliam, H.R. & Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137: 550-566.

Rodenhouse, H.R., Sherry, T.W. & Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78: 2025-2042.

Safriel, U.N. 1995. The evolution of Palearctic migration – The case for southern ancestry. *Israel Journal of Zoology* 41: 417-431.

Sherry, T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

StatSoft, Inc. 1996. *STATISTICA for Windows (Computer program manual).* StatSoft, Inc. Tulsa.

Summers, R.W., Nicoll, M., Underhill, L.G. & Petersen, A. 1988. Methods for estimating the proportions of Icelandic and British Redshanks *Tringa totanus* in mixed populations wintering in British coasts. *Bird Study* 35: 169-180.

Svensson, L. 1996. *Guía para la Identificación de los Passeriformes Europeos.* Sociedad Española de Ornitología. Madrid.

Tellería, J.L. 1981. *La migración de las aves en el Estrecho de Gibraltar. Vol. II: Aves no planeadoras.* Ediciones de la Universidad Complutense. Madrid.

Tellería, J.L., Asensio, B. & Díaz, M. 1999. *Aves Ibéricas. Vol. II. Passeriformes*. J. M. Reyero. Madrid.

Tobias, J. 1997. Asymmetric territorial contests in the European Robin: The role of settlement costs. *Animal Behaviour* 54: 9-21.

Distribución del petirrojo (*Erithacus rubecula*) en sus cuarteles de invierno: efectos de la densidad de población, el comportamiento migrador y la edad de los individuos

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Tellería, J.L., Pérez-Tris, J., Ramírez, Á., Fernández-Juricic, E. & Carbonell, R. 2000. Distribution of Robins (*Erithacus rubecula*) in wintering grounds: effects of conspecific density, migratory status and age. *Ardea* 00:000-000.

RESUMEN

Este trabajo estudia cómo influye la densidad de población sobre la dinámica de ocupación del hábitat por los petirrojos en un área de invernada del sur de España (Campo de Gibraltar), y cómo la distribución de las aves entre hábitats es afectada por la edad y el comportamiento migrador de los individuos (si son residentes o migradores invernantes). Estudiamos dos tipos de hábitat diferentes: bosques y matorrales. Los bosques son hábitats de alta cobertura vegetal, algunos de los cuales son utilizados por los petirrojos locales durante la reproducción. Los matorrales, sin embargo, son zonas mucho más expuestas, que los petirrojos sólo utilizan durante el invierno. Censamos los petirrojos a intervalos de cuatro días en 21 sitios (10 bosques y 11 matorrales) durante dos inviernos. Encontramos un patrón temporal de ocupación de los hábitats según el cual, a medida que la llegada de petirrojos migradores aumenta la abundancia de la especie en la zona, los parches de hábitat van siendo colonizados secuencialmente, pero de forma que los bosques son los primeros que se ocupan y los últimos que se abandonan (independientemente de si son o no hábitats de cría). Por otra parte, la abundancia de petirrojos disminuyó durante el período otoño-invierno en los parches más densamente poblados, dando lugar a una distribución de los petirrojos entre parches cada vez más homogénea. Los matorrales fueron ocupados principalmente por jóvenes (83% de los individuos), tanto migradores como sedentarios. De todos modos, los petirrojos locales fueron más abundantes que los migradores en los bosques (67% de residentes), aunque también contribuyeron a la colonización de los matorrales, donde integraron el 47% de la población. En conjunto, estos resultados indican que la distribución entre hábitats del petirrojo no sólo depende de la densidad de población, sino también de la edad y la condición migradora de los individuos –locales o invernantes– que intentan hacerse con un territorio invernal. Si los bosques son hábitats de mayor calidad que los matorrales, lo cual es una suposición realista de acuerdo con la biología invernal del petirrojo, los patrones de ocupación que hemos encontrado podrían constituir un mecanismo de regulación poblacional durante el invierno.

Distribution of Robins (*Erithacus rubecula*) in wintering grounds: effects of conspecific density, migratory status and age

José Luis Tellería, Javier Pérez-Tris, Álvaro Ramírez, Esteban Fernández-Juricic & Roberto Carbonell*

This paper studies how population density affects the dynamics of habitat occupation by Robins in a wintering area of southern Spain (Gibraltar area), and how the between-habitat distribution is influenced by the age and migratory behaviour of birds (whether they are year-round residents or overwintering migrants). We studied two different habitat types: forested sites, some of which are breeding habitats of Robins, and shrubland sites, to which Robins spread their range in autumn-winter due to the arrival of migrants. As arriving migrants increased abundance in the area, new habitat patches were sequentially colonised, forested sites being the first to be occupied and the last to be abandoned (regardless they maintained breeding populations or not). In addition, the abundance of Robins tended to decrease along the autumn-winter period in the most densely populated patches, which made the among-site distribution of Robins to be progressively more uniform. Juveniles of both local and migratory populations dominated (83% of individuals) in lowlands. Local Robins were more abundant (67%) than migratory ones in montane forests, although they also contributed to the winter colonisation of lowland habitats (47%). Together, these results support that the between-habitat distribution of Robins depends not only on population density, but also on the migratory status and age of individuals attempting to get a wintering site. Therefore, if winter habitats differed in quality, these factors could influence the mechanisms of regulation of Robin populations in the nonbreeding season.

Winter is frequently regarded as the season in which populations of migratory land birds are most often limited, although the processes underlying nonbreeding limitation are still poorly known (Terborgh 1989, Baillie & Peach 1992, Rappole & MacDonald 1994, Newton 1998). The occupation of habitats of different quality, for instance, has been considered to be one of the most important such processes (Sherry & Holmes 1996, Rodenhouse *et al*. 1997). Since both direct and indirect interactions among individuals attempting to colonise a heterogeneous landscape may produce their sequential arrangement from the most suitable habitat patches to the less suitable ones (Fretwell and Lucas 1970, Pulliam & Danielson 1991), density-dependent habitat selection may well provide a mechanism for population regulation in nonbreeding areas. Arriving migrants may saturate the best patches in wintering grounds, which will cause increasing interactions among conspecifics and, in turn, the occupation of suboptimal patches by surplus individuals. If these dynamics of habitat occupation affected survival rates, wintering populations could be regulated by the availability of suitable habitat patches (Greenberg 1986, Goss-Custard *et al.* 1994, Sutherland & Dolman 1994, Sherry & Holmes 1996, Rodenhouse *et al.* 1997).

This paper studies the effects of population density on the patterns of landscape occupation by Robins *Erithacus rubecula* wintering in the Campo de Gibraltar area, Southern Spain. This area sustains breeding populations of Robins in some montane forests, and receives in autumn a large number of migrants from northern and central Europe (Tellería 1981). The arrival of migrants is coupled with

---

**Ardea 00: 000-000.*

the expansion of the species' range across the area during winter, when Robins occupy shrublands located at the bottom of mountains. But despite there is a sharp difference between forests and shrublands in some features that are certainly relevant from the perspective of Robin preferences (e.g. vegetation cover, see Cuadrado 1997, Johnston 1998), little is known on the numerical rearrangements of Robins among habitat types, or on the way year-round residents and overwintering migrants are distributed in the area. We address these topics in this paper through two complementary approaches:

Patterns of habitat occupation of wintering grounds

We studied how the increase in regional abundance of Robins due to the arrival of migrants influences their dynamics of landscape occupation. If habitat selection depends on density of conspecifics, birds are expected to follow an ordered pattern of occupation of habitat patches according to among-site differences in habitat quality. In this case, it is predicted that the increase in regional abundance will cause the saturation of the most suitable sites before the less suitable ones are occupied (Fretwell and Lucas 1970, Pulliam & Danielson 1991).

Distribution according to migratory status and age

The social status of birds could determine whether they will be able to remain in the best patches or, conversely, will be displaced to worse sites as soon as population density increases in the preferred habitats (Sherry & Holmes 1996). Robins are territorial in winter (Cramp 1988), and exhibit a strong wintering-site fidelity in southern Iberia (Cuadrado 1992), which could involve dominance relationships among individuals. In this case, it could be expected that year-round residents monopolised the best habitat patches by occupying them before the arrival of migrants (Tobias 1997). On the other hand, dominance relationships could also shape the distribution of Robins in relation to age, adults occupying the best patches and causing the displacement of juveniles to the worst sites (Sherry & Holmes 1996). Therefore, we studied the composition of populations during the winter according to the migratory status and age of individuals, to evaluate whether either year-round resident or adult Robins occupy the best habitat patches in the area, and to what extent their distribution affects that of overwintering migrants or juveniles, respectively.

METHODS

Study area

We studied the winter distribution of Robins in an area of about 200 Km^2 located at the northern side of the Gibraltar Strait (36º01'N, 5º36'W). This area is crossed from north to south by several parallel, low-elevation mountain ranges, which are surrounded by shrublands and grasslands that extend westwards to the Atlantic ocean and eastwards to the Mediterranean sea. The influence of humid winds from the Atlantic, together with the north-to-south arrangement of mountains, allow the growth of well-developed forests in the moister ravines in mountains, which are covered by cork-oaks *Quercus suber* mixed with African oaks *Q. canariensis*. These forests sustain breeding populations of Robins and other forest birds, which are increased in winter due to arrival of many overwintering migrants (Arroyo & Tellería 1983, Pérez-Tris *et al*. 1999, Tellería & Carbonell 1999). In the surroundings of mountains, however, the lowland landscape is covered by grasslands, shrublands (*Pistacia lentiscus*, *Olea europaea sylvestris*, *Calicotome villosa*) and some more developed riparian formations (*Nerium oleander*, *Rubus* spp., *Populus nigra*) associated with the rivers that cross the area. In these habitats, the environmental conditions are typical of the dry Mediterranean region, characterised by an extreme summer drought. Because of this, Robins and many other forest birds avoid these habitats for breeding. However, lowland shrublands are colonised in autumn by a large

Table 1 Temporal distribution of Robins across the 19 sites where the species occurred at least once in the study period. Sites have been labelled as high (hs) or low (ls) suitability sites, and those occupied in summer show an asterisk. The matrix takes into account the presence (1) or absence (0) of individuals in every site (columns) and count (rows). To facilitate the perception of the nested pattern of site occupation, both sites and count dates have been sorted by decreasing number of presences (*n*).

Sites	9*	18*	20*	8	15	1	11	21	12	16	13	17	19	4	5	10	14	7	2	
Habitat type	hs	hs	hs	hs	hs	ls	hs	ls	hs	ls	hs	ls	hs	ls	hs	ls	ls	ls	ls	*n*
Census dates																				
November 3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	18
November 7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	17
January 8	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	16
January 4	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	16
November 11	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	16
October 30	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	16
October 26	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	16
October 22	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	0	15
October 18	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	15
October 14	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	12
October 10	1	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	10
October 6	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	6
September 8	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
October 2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
September 12	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
September 28	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
September 20	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
n	16	16	13	12	12	11	11	11	10	10	9	9	9	8	8	8	5	3	1	

amount of Robins and many other birds that arrive at the area for wintering (Tellería 1981, Arroyo & Tellería 1983, Pérez-Tris *et al*. 1999).

Patterns of site occupation

We studied 21 sites representative of the lowland habitats occupied by wintering birds in the study area (Appendix). The variation in abundance of Robins in these sites throughout the autumn-winter periods of 1975-76 and 1976-77 was described by Tellería (1981). Since Robins confer more importance to shelter than to feeding resources when selecting their winter territories (Cuadrado 1997, Johnstone 1998), we considered vegetation cover to be a reliable clue for evaluating the quality of wintering sites. We classified the study sites according to two levels of suitability for Robins (Appendix). High suitability sites (HS) were represented by cleared cork-oak forests with a great cover of bushes (e.g. *Olea europaea sylvestris*, *Crataegus monogyna*, *Pistacia lentiscus*, *Rubus* spp., etc.), and riparian forests (*Alnus glutinosa*) with *Nerium oleander*, *Crataegus monogyna* and *Olea europaea* bushes. Low suitability sites (LS) were represented by a mixture of grasslands (with some sprinkled bushes) and shrublands of *Erica arborea*, *Calicotome villosa*, and *Adenocarpus complicatus* (with some isolated patches of *Pistacia lentiscus* and *Olea europaea sylvestris*). Each study site was censused during one autumn-winter period, either in 1975-76 or 1976-77. The distribution of HS and LS sites was homogeneous between study years, each habitat type making up

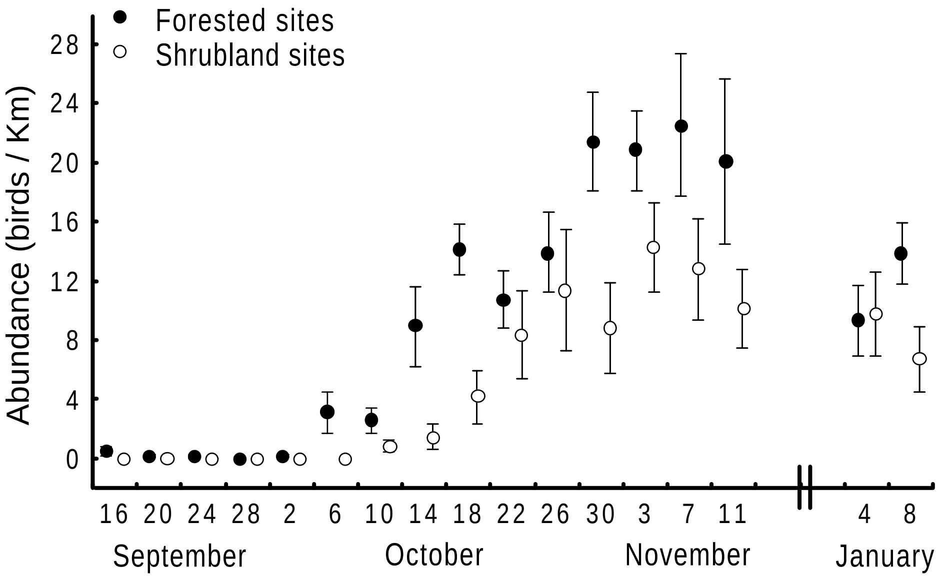

Figure 1. Variation in the regional abundance (mean ± se) of Robins during the study period (both years pooled), in forested sites (high suitability) and shrubland sites (low suitability) of lowlands. Figures in abscissas refer to the first day of each 4-days counting period used for assessing the evolution in Robin abundance.

near 50% of sites censused (Fisher exact test: *P* > 0.99, see Appendix). The seasonal changes in Robin abundance were monitored at the study sites by repeated counting at 4-day intervals from September to mid-November, with two additional counts in January to estimate winter abundances. Counting periods were the same in both study years. Robins were censused by one of us (J.L.T.), by means of transects in which the number of Robins seen or heard was noted. Since the transect lengths changed among sites (Appendix), the abundance of Robins was finally measured in number of birds per Km. It should be noted that we did not include in our analyses two open grasslands with some scattered shrubs (sites 3 and 6 in Appendix) where Robins never occurred.

We compared the abundance of Robins between forested sites and shrubland sites taking into account the between-years variations in abundance and the seasonal changes in Robin density. To do so, we specifically tested for between-habitat differences in abundance (log-transformed) in a three-way ANOVA, in which sites were the sampling units, habitat type and year were between-subjects factors, and counts were the levels of the third (within-subjects) factor. By using this design, the amount of variance that is accounted for by within-site fluctuations in abundance throughout the study period was controlled for when testing for between-habitat differences. Since for such an effect to be properly evaluated it is required that the possible variations in abundance between years do not affect changes between habitats, we also tested for the year effect and the habitat by year interaction in the model. However, we did not test for the remaining effects and interactions, in which the changes in abundance within sites from count to count were involved. Actually, the variation accounted for by within-site fluctuations in abundance is not interesting in this study beyond its utility for computing a more appropriate error term when testing for the relevant hypothesis.

To analyse how regional abundance influenced the distribution of Robins in the study area, we first studied to what extent the eventual increases in Robin abundance along the study period were coupled with a concomitant expansion of the species' range. In this analysis, the mean abundances in the occupied sites at each count were used to estimate the regional abundance of

Robins, whose effect on the number of occupied sites was evaluated by means of regression analysis (Gaston & Lawton 1990). In order to establish whether the expansions or retreats of the range of Robins as a response to fluctuations of regional abundance were random or followed a hierarchical order, we set a matrix tallying the presence or absence of Robins in each site and count, both sorted by decreasing number of presences (Table 1). We compared the number of observed absences in this matrix to the number of expected absences generated at random by the Nestedness Calculator computer program (Atmar & Patterson 1995). This software measures the degree of nestedness (order) in the matrix by means of a metric (the so-called temperature of the system, T) proposed by Atmar and Patterson (1993), which assumes a value between 0 (a perfectly nested matrix) and 100 (a random matrix). The program allows one to contrast the observed T with a Monte Carlo-derived expected value, by means of a *z*-score whose associated probability estimates the likelihood of randomly producing a matrix even more nested than the observed one (Atmar & Patterson 1995). To assess the role of habitat suitability in determining the sequence of occupation of sites, we compared the ranks acquired by HS and LS sites in the matrix by means of a Mann-Whitney U-test.

We used linear regression to model how the among-site abundance distribution in a given month determined the patterns of site occupation in the next one, an approach based in a modification of the isodar method (Morris 1987, 1990). To do so, we obtained the mean abundance in each site (*i*) around September (mean of the first five counts), October (five counts), November (five) and January (two). These data were used to perform simple regression analyses ($x_i = a + b\,x_{i\text{-}1}$) in which the mean abundance in a given month (x_i) was regressed on the mean abundance in the previous one ($x_{i\text{-}1}$). In these relationships, the regression slopes (*b*) will reflect how the patterns of site occupation change from month to month, indicating a similar month-to-month pattern of abundance distribution among sites ($b = 1$), the crowding of the most densely populated sites ($b > 1$), or an increased inter-patch parity ($b < 1$).

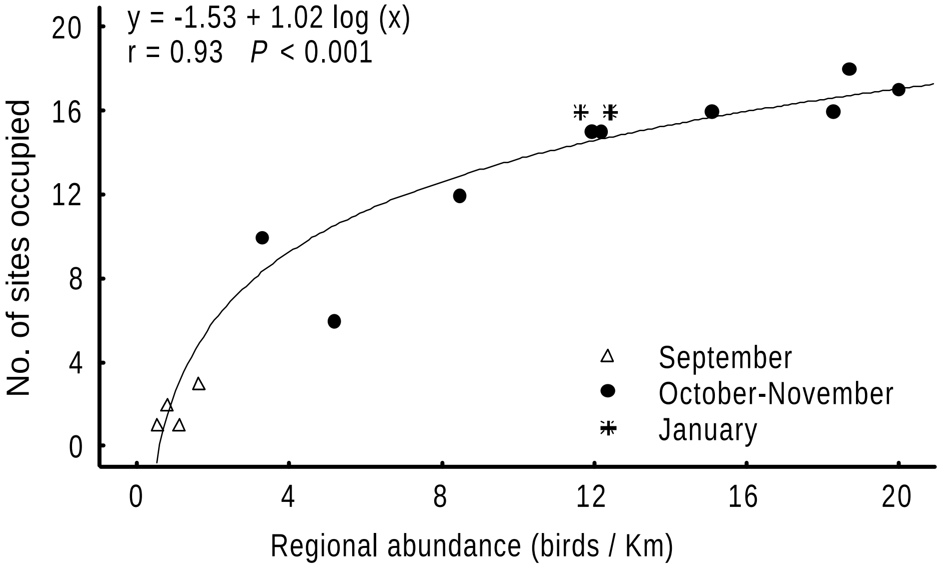

Figure 2. Relationship between the regional abundance (mean abundance in the occupied sites) and the number of sites occupied by Robins through the study period. Censuses have been labelled as late summer (September), autumn (October-November) and winter (January) counts.

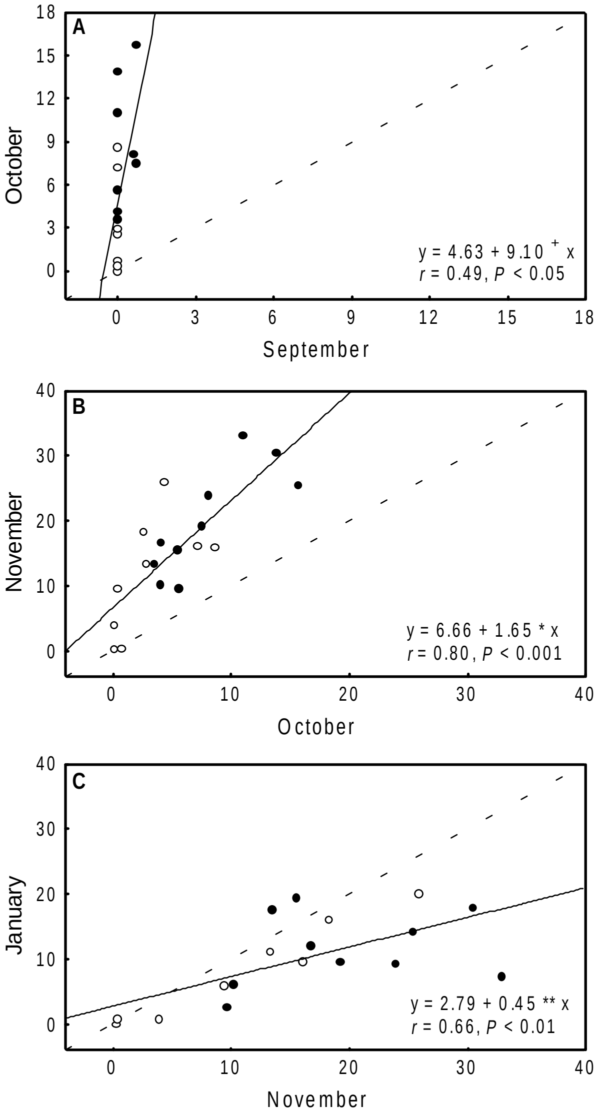

Figure 3. Relationships between abundance of Robins in the occupied sites each month and the abundance in the same sites the previous one. Abundances are given in number of birds per Km. Filled dots refer to forested sites and open dots to shrubland sites. The observed slopes have been labelled to show the significance of their deviations from a slope of 1, represented by the main diagonal in the plot ($^{+}P = 0.05$, * $P < 0.05$, ** $P < 0.001$).

Distribution of Robins according to migratory status and age

During the winters 1997-98 and 1998-99 (from mid December to mid January), we mist-netted Robins in sites No. 8, 12, 13 and 15 (Appendix). We also captured Robins in two other lowland localities (in areas covered by *Pistacia*, *Calicotome* and *Olea* shrubs), and in six other forested sites in the mountains. Robins were aged according to plumage features (Svensson 1992) and measured to identify them as locals or migrants. To do so, we used the discriminant function analysis described by Pérez-Tris *et al.* (2000). This method relies on changes in migration-related morphology (wing length and wing formula) between migratory and sedentary Robins breeding in the Iberian Peninsula, and allows one to correctly classify 80% of individuals. Because of their stronger migratory behaviour, Robins from further north in Europe have longer and more pointed wings than Iberian Robins (Cramp 1988), so they are expected to be accurately classified as migrants by this method. Since foreign Robins make up the bulk of wintering populations in southern Iberia (Bueno 1998), the discriminant function can be so regarded as a reliable clue for differentiating between migratory and sedentary Robins during winter in this area (see Pérez-Tris *et al.* 2000 for further details). We conducted a hierarchical, three-factor log-linear analysis with these birds to compare the proportion of adults and juveniles of both local and migratory populations between montane forests and lowland shrublands.

RESULTS

Patterns of site occupation

The abundance of Robins increased from September to November and decreased from November to January in the study area (Fig. 1). Forested sites were occupied first and consistently showed higher abundances than shrublands, despite variations in abundance both between years and throughout the autumn-winter period (specific effects in a three-way ANOVA with the count date as a controlling factor: habitat type $F_{1,15} = 6.07, P < 0.05$, year $F_{1,15} = 5.09$, $P < 0.05$, habitat × year $F_{1,15} = 2.76$, $P = 0.12$). Although Robins occupied more sites with increasing regional abundance, this relationship was not linear (Fig. 2). Thus, the number of occupied sites sharply increased with increasing abundance at the lowest interval of regional abundance (abscissa in Fig. 2), corresponding to the arrival of the first migrants to the area. By contrast, when regional abundance reached its highest level, larger increases were required for Robins to occupy more sites. This supports the view that Robins increased their abundance to saturation in some sites before colonising others. Consistent with this, the occupation of sites fitted a nested pattern (observed T = 5.47, random generated T after 1000 simulations: 57.94, SD = 5.57, z = -9.41, $P < 0.001$), supporting an ordered advance and retreat from the most frequently occupied sites to the scarcely used ones (Table 1). According to our hypothesis, this sequence of occupation of sites was related to habitat suitability, the most suitable sites being the first to be occupied and the last to be abandoned (U-test comparing the ranks attained by HS and LS sites in Table 1: z = 2.45, n = 19, $P < 0.05$). This pattern remained, although not significantly so, after excluding the three sites that were already occupied in September by local Robins (z = 1.75, n = 16, P = 0.08).

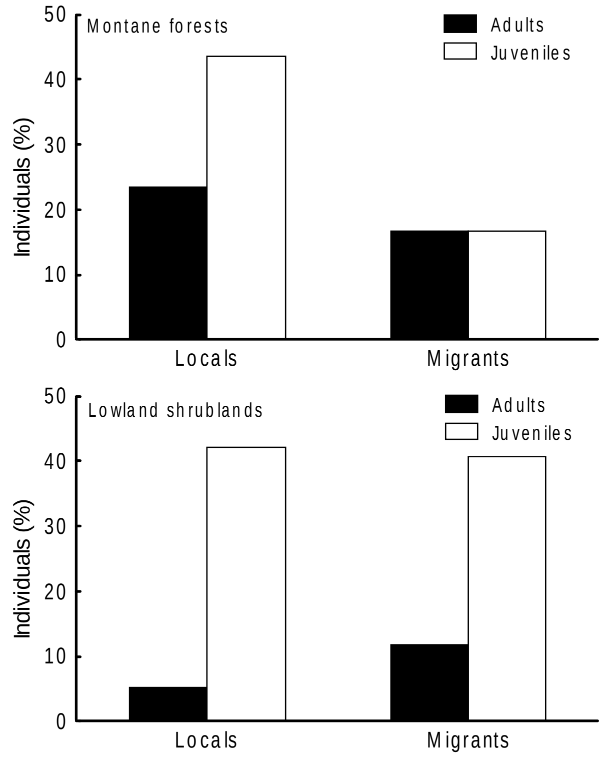

Figure 4. Composition of Robin populations according to migratory status and age in the two winter habitat types that have been considered in this study. The bars show the percentage of individuals belonging to each population fraction, in montane forests (above, n = 85) and in lowland shrublands (below, n = 59).

The month-to-month arrangement of Robin numbers among sites varied along the autumn-winter period (Fig. 3). The first Robins arriving on the wintering grounds sharply increased overall abundance in forested sites (Fig. 3A). During the peak of the autumn movements (October-November), the species tended to show a more parallel interpatch abundance distribution (Fig. 3B), the most densely populated patches in October being also the most densely populated sites in November. However, the abundance of Robins tended to decrease more strongly in the most densely occupied sites during November (Fig. 3C), suggesting a preemptive distribution during winter following the crowding of forests in autumn. According to this, the drop in regional abundance observed in January (Fig. 1) may be interpreted as a decrease in the abundance of Robins in the most suitable sites.

Distribution of Robins according to migratory status and age

The best saturated log-linear model fitting the frequency of Robins in each habitat type according to migratory behaviour and age was the one including all two-way interactions (Maximum-likelihood Chi-square, χ^2_1 = 0.056, P = 0.81). The reduced model resulting from removing the nonsignificant age × migratory status interaction (Marginal association chi-square, χ^2_1 = 1.196, P = 0.27) suitably fitted the contingency table (Maximum likelihood chi-square, χ^2_2 = 3.074, P = 0.22). Regardless the migratory status of Robins, adults were far more frequent in the montane forests than were in the lowland habitats, where wintering populations were almost completely composed of juveniles (Fig. 4; age × habitat type interaction: χ^2_1 = 8.610, P = 0.003). Local individuals, especially juveniles, greatly contributed to the seasonal occupation of lowlands, where they represented almost a half of the whole population. However, migrant Robins were less frequent than locals in the montane forests, representing only 33% of individuals (Fig. 4; migratory status × habitat type interaction: $\chi^2_1 = 5.410$, $P = 0.020$).

DISCUSSION

The arrival of migrant Robins at the Gibraltar area may be regarded as a massive occurrence of individuals, which increases both the regional abundance and the local range of the species across the area. The sequential occupation of wintering sites that we have found is similar to that observed in many bird species whose population dynamics have been monitored in the long-term, in which the species' range in a given area either spreads or retreats following fluctuations of population size (e.g. Newton 1998). Migrant Robins arrive at the Mediterranean wintering grounds at the end of the summer drought, coinciding with the beginning of the intense productive output that characterises these environments during the autumn-winter period (Herrera 1985, Fuentes 1992). At this time, the main food resources that the species exploits during winter experience a notable increase (fleshy fruits, cracked oak acorns, insects; Herrera 1977, 1981, Jordano 1989). This enhancement of the carrying capacity in these habitats could explain the sharp increase of Robin abundance in the study area from September to November (Fig. 1), as well as the time-lag between the increase of regional abundance and the expansion of Robins from the most preferred sites to the less preferred ones (Fig. 2). However, our results show that this enhancement does not rule out the effect of conspecific density on the numerical distribution of birds among the occupied sites. This is supported not only by the sequential occupation of habitats in relation to their suitability (a fair evidence of density-dependence; Brown 1969, Rosenzweig 1981), but also by the between-site arrangement of Robin numbers along the autumn-winter months. In turn, the outcome of these density-dependent dynamics of habitat occupation may well be the displacement of surplus individuals to marginal habitats (Bowers 1994). With the occurrence of many conspecifics in the best patches, increasing intraspecific interactions would cause the rearrangement of birds among sites (Pulliam & Danielson 1991). At the equilibrium, the outcome of these two processes is likely to be a balance between the saturation of a few sites and a homogeneous inter-patch distribution throughout the autumn-winter period. Although this pattern of settlement has been observed in many bird species during spring, little evidence has yet been gathered of this sort of landscape occupation in wintering birds (Newton 1998).

Although some information is available on the segregation mechanisms among migrant and local species in wintering areas, how local populations cope with the arrival of migrant conspecifics on their grounds is not so well-known (Greenberg 1986, Sherry & Holmes 1996). This paper suggests that local Robins prevent a massive irruption of migrants in their breeding sites. Moreover, there are age-related differences in the distribution of individuals, adults tending to occupy the montane forests and juveniles being the most abundant in the lowland shrublands, regardless the migratory status of individuals. According to the distribution of each population fraction between habitat types, a dominance hierarchy seems to rule the Robin populations we have studied, in which the social rank of birds would decrease from adult locals to juvenile migrants. It is likely that adults and locals have priority of access to territories compared to juveniles and migrants, respectively (Tobias 1997). If the latter were more prone to fail when attempting to acquire a winter territory and endured as floaters in the best patches, they could be easily displaced from these habitats to the less suitable ones once circumstances become more difficult for territory owners. It has been suggested that individuals that abandon the breeding habitats in partially migrant populations of Robins are making 'the best of a bad job' (Adriaensen & Dhondt 1990). In our study area, if differences in habitat suitability were related to differential rates of mortality during winter, juveniles and migrants would actually be the population fractions which would suffer the highest mortality (Bowers 1994). In summary, our results put forward that interactions between locals and migrants could be a major determinant of the regulation of Robin populations in wintering areas, where both population fractions are sympatric during almost half of the annual cycle (from September to March). This supports the view that a full understanding of the mechanisms underlying population regulation of birds will require the control of both breeding and wintering processes.

Acknowledgements

We thank J.A. Díaz, M. Cuadrado and two anonymous referees, whose comments improved an early draft. The Agencia de Medio Ambiente (Junta de Andalucía) kindly authorised us to capture and measure Robins. This paper was founded by the Ministerio de Educación y Cultura (project PB97-0325), as well as by Predoctoral Grants from the Universidad Complutense de Madrid (J.P-T.) and the Agencia Española de Cooperación Internacional (Mutis Fellowship; E.F-J.).

References

Adriaensen, F. & Dhondt, A.A. 1990. Population dynamics and partial migration of the European Robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology* 59: 1077-1090.

Arroyo B. & Tellería, J.L. 1983. La invernada de las aves en el área de Gibraltar. *Ardeola* 30: 23-31.

Atmar W. & Patterson, B.D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96: 373-382.

Atmar W. & Patterson, B.D. 1995. *Nested temperature calculator: a visual basic program, including 294 presence absence matices*. AICS Research, University Park, NM and The Field Museum, Chicago.

Baillie S.R. & Peach, W.J. 1992. Population limitation in Palearctic-African migrant passerines. *Ibis* 134 (Suppl. 1): 120-132.

Bowers, M.A. 1994. Dynamics of age- and habitat-structured populations. *Oikos* 69: 327-333.

Brown, J.L. 1969. Territorial behavior and population regulation in birds. *Wilson Bulletin* 81: 293-329.

Bueno J.M. 1998. Migración e invernada de pequeños turdinos en la península Ibérica. V. Petirrojo (*Erithacus rubecula*). *Ardeola* 45: 193-200.

Cramp S. (ed) 1988. *The birds of the Western Paelarctic*. Vol 5. Oxford University Press, Oxford.

Cuadrado M. 1992. Year to year recurrence and site-fidelity of Blackcaps *Sylvia atricapilla* and Robins *Erithacus rubecula* in a Mediterranean wintering area. *Ringing & Migration* 13: 36-42.

Cuadrado M. 1997. Why are migrant Robins (*Erithacus rubecula*) territorial in winter?: the importance of the anti-predatory behaviour. *Ethology, Ecology & Evolution* 9: 77-88.

Fretwell S. & Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.

Fuentes M. 1992. Latitudinal and elevational variation in fruit phenology among Western European bird-dispersed plants. *Ecography* 15: 177-183.

Gaston, K.J. & Lawton, J.H. 1990. Effects of scale and habitat on the relationships between distribution and local abundance. *Oikos* 59: 329-335.

Goss-Custard J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E., Dit, A., Urfi, J. & West, A.D. 1994. Consequences of habitat loss and change to populations of wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis* 137 (Suppl. 1): 56-66.

Greenberg R 1986. Competition in migrant birds in the nonbreeding season. *Current Ornithology* 3: 281-307.

Herrera C.M. 1977. Ecología alimenticia del Petirrojo (*Erithacus rubecula*) durante su invernada en encinares del Sur de España. *Doñana, Acta Vertebrata* 4: 35-59.

Herrera C.M. 1981. Fruit food of Robins wintering in Southern Spanish Mediterranean scrubland. *Bird Study* 28: 115-122.

Herrera C.M. 1985. Habitat-consumer interaction in frugivorous birds. *Habitat selection in birds* (ed. M.L. Cody), pp. 341-365. Academic Press, New York.

Johnstone Y. 1998. Territory structure of the Robin *Erithacus rubecula* outside the breeding season. *Ibis* 140: 244-251.

Jordano P. 1989. Variación de la dieta frugívora otoño-invernal del Petirrojo (*Erithacus rubecula*): efectos sobre la condición corporal. *Ardeola* 36: 161-183.

Morris D.W. 1987. Test of density-dependent habitat selection in a patchy environment. *Ecological Monographs* 57: 269-281.

Morris D.W. 1990. Temporal variation, habitat selection and community structure. *Oikos* 59: 303-312.

Newton I. 1998. *Population limitation in birds*. Academic Press, San Diego.

Pérez-Tris J., Carbonell, R. & Tellería, J.L. 1999. A method for differentiating between sedentary and migratory blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia. *Bird Study* 46: 299-304 (*Capítulo 4*).

Pérez-Tris J., Carbonell, R. & Tellería, J.L. 2000. Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. *Ardeola* 47: 9-18 (*Capítulo 5*).

Pulliam H.R. & Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137 (Suppl.): 50-66.

Rappole J.H. & MacDonald, M.V. 1994. Cause and effect in population declines of migratory birds. *Auk* 111: 652-660.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78: 2025-2042.

Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology* 62: 327-335.

Sherry T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

Sutherland W.J. & Dolman, P.M. 1994. Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. *Proceedings of the Royal Society of London B* 255: 133-138.

Svensson L. 1992. *Identification guide to European passerines.* 4th ed. L. Svensson, Stockholm.

Tellería J.L. 1981. *La migración de las aves por el Estrecho de Gibraltar. Vol. II. No planeadoras.* Editorial de la Universidad Complutense, Madrid.

Tellería J.L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology* 30: 63-71.

Terborgh, J.W. 1989. *Where have all the birds gone?* Princeton University Press, New Jersey.

Tobias J. 1997 Asymmetric territorial contests in the European robin: The role of settlement costs. *Animal Behaviour* 54: 9-21.

Appendix. Brief description of the study sites. Length of transects, classification of sites according to its suitability (HS: high, LS: low suitability), and type of occurrence of Robins at each site (S: Summer presence, W: Winter occupancy only, N: No occurrence) are shown. Sites 1 to 15 were censused in 1976-77, and the remaining in 1977-78. See Tellería (1981) for further details.

No.	Name of site	UTM coord.	Site description	Length (m)	Habitat type	Occurrence
1	Matorral-Playa	30STE594943	Shrubland	1895	LS	W
2	Pastizal-Playa	30STE627923	Sandy grassland, with some scattered shrubs	900	LS	W
3	Valle del Santuario 1	30STE636935	Grassland with scattered shrubs	590	LS	N
4	Valle del Santuario 2	30STE638994	Shrubland	630	LS	W
5	Valle del Santuario 3	30STF606036	Forest	200	HS	W
6	Punta Paloma 1	30STE587956	Grassland with scattered shrubs	390	LS	N
7	Punta Paloma 2	30STE568948	Sandy grassland, with some scattered small trees	590	LS	W
8	Punta Paloma 3	30STE576965	Riparian forest	420	HS	W
9	El Rayo	30STE768984	Forest	1800	HS	S
10	Punta Carnero 1	30STE804965	Shrubland	590	LS	W
11	Punta Carnero 2	30STE811948	Riparian forest	540	HS	W
12	Campamento de Anillamiento 1	30STE637974	Riparian forest	540	HS	W
13	Campamento de Anillamiento 2	30STE637981	Riparian forest	400	HS	W
14	Casa del Cable	30STE645902	Grassland with scattered bushes	554	LS	W
15	El Maestral	30STE633941	Riparian forest	2050	HS	W
16	Molino del Maestral	30STE625937	Grassland	830	LS	W
17	La Peña	30STE606943	Grassland interspersed with shrubland	360	LS	W
18	La Hoya	30STE738937	Forest	1900	HS	S
19	Río Pícaro	30STE796978	Grassland interspersed with shrubland	600	HS	W
20	Arroyo Lobo	30STE797971	Riparian forest	600	HS	S
21	Arroyo Marchenilla	30STE790974	Grassland interspersed with shrubland	415	LS	W

Capítulo 7

Currucas capirotadas migradoras y sedentarias en áreas de invernada simpátricas: implicaciones en la evolución de la migración

Este capítulo reproduce el texto íntegro del siguiente manuscrito:

Pérez-Tris, J. & Tellería, J.L. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration (manuscrito enviado).

RESUMEN

Varias hipótesis han intentado explicar por qué existen poblaciones sedentarias en las áreas de invernada de muchas especies migradoras. Por ejemplo, los residentes podrían superar la invasión de su área de distribución si fuesen mejores competidores que los migradores durante el invierno. Como solución alternativa, cada fracción poblacional podría explotar diferentes recursos o tipos de hábitat. Por ejemplo, los residentes podrían beneficiarse de la constancia en sus territorios de cría, mientras que los migradores podrían preferir rastrear los recursos que necesitan durante el invierno. Para examinar estas hipótesis, estudiamos la distribución de las currucas capirotadas (*Sylvia atricapilla*) migradoras y sedentarias invernantes en simpatría en el Campo de Gibraltar (sur de España). El estudio se realizó durante dos inviernos en dos tipos de hábitat claramente diferentes: bosques, que constituyen los hábitats de cría de la curruca capirotada en la zona, y matorrales, que son ocupados solamente durante el invierno, tras la llegada de los migradores. En cuanto a su calidad como hábitats de invernada, los matorrales presentan una menor cobertura vegetal que los bosques, y cuentan con una mayor abundancia pero una menor diversidad de frutos (la base de la dieta invernal de la curruca capirotada). Estudiamos (1) si las currucas muestran segregación entre hábitats con respecto a su comportamiento migrador, sexo, edad o tamaño corporal; (2) qué recursos utiliza cada fracción poblacional en cada tipo de hábitat (si rastrean la abundancia de frutos o la distribución de los mejores territorios para la reproducción), y (3) qué efectos tiene la ocupación de diferentes hábitats sobre la condición física de los individuos. Los residentes permanecieron prácticamente restringidos a los bosques, mientras que los migradores ocuparon ambos tipos de hábitat. Entre estos últimos, los adultos predominaron en los bosques y los jóvenes en los matorrales, sin que existiese segregación sexual entre hábitats. Las currucas sedentarias mostraron un mayor tamaño corporal que las migradoras, y éstas fueron de mayor tamaño en los bosques que en los matorrales, especialmente entre

los jóvenes. Si las aves grandes son dominantes, estos resultados sugieren que los residentes pueden aguantar en los bosques desplazando a los migradores menos competentes (jóvenes e individuos pequeños) hacia los matorrales. Migradores y sedentarios mostraron patrones de uso de los recursos invernales muy similares. En los bosques, donde coinciden ambas fracciones poblacionales, tanto migradores como sedentarios rastrearon la abundancia de frutos, aunque los últimos tendieron a ocupar zonas más adecuadas para la reproducción. En los matorrales, donde prácticamente sólo existen migradores, estos se asociaron con la abundancia de frutos menos intensamente que en los bosques, reflejando probablemente un rastreo de recursos más cauteloso derivado de la mayor abundancia de frutos y el mayor riesgo de depredación en esos hábitats más expuestos. La segregación entre hábitats no afectó al peso magro de los individuos (corregido por su tamaño), que de hecho acumularon más grasa en los matorrales. Esto significa que las posibles diferencias de calidad nutricional entre bosques y matorrales no sirven para explicar la segregación entre hábitats, con las aves adultas y de mayor tamaño predominando en los bosques. En lugar de estos factores, otros determinantes, como la diversidad de frutos o la exposición a los depredadores, podrían explicar esta distribución. En cualquier caso, nuestros resultados proporcionan un mecanismo para explicar la persistencia de poblaciones sedentarias a pesar de que sus áreas son invadidas por enormes poblaciones de migradores que utilizan los mismos recursos: los residentes pueden enfrentarse a esta invasión porque son mejores competidores. Desde una perspectiva evolutiva, esto muestra que los procesos que tienen lugar durante el invierno pueden ser tan importantes como los ocurridos en época de cría para interpretar la dinámica de las poblaciones migradoras y sedentarias.

Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration

Javier Pérez-Tris & José Luis Tellería*

Several hypotheses have tried to explain why sedentary populations persist in the wintering grounds of many migratory bird species. For instance, residents may overcome the flooding of their range if they are better competitors than migrants. Alternatively, each population fraction may use different resources or even different habitat types, for example because residents reward from site tenacity while migrants reward from resource tracking. To evaluate these hypotheses, we studied the distribution of sympatric migratory and sedentary blackcaps (*Sylvia atricapilla*) in southern Spain during two winters. We distinguished two habitat types: forests, which are used by residents for breeding, and shrublands, to which blackcaps spread in winter with the arrival of migrants. Shrublands are unsheltered habitats that show more abundant but less diverse fruits than forests. We investigated (1) if blackcaps show habitat segregation with respect to migratory behaviour, sex, age and body size, (2) what resources are used by each population fraction within each habitat type, and (3) how habitat occupancy affects the body condition of individuals. Residents were almost completely restricted to forests, while migrants occupied both habitat types. Among migrants, adults predominated in forests and juveniles in shrublands, but no sexual segregation was found. Body size was larger in residents than in migrants, and these were larger in forests than in shrublands (especially juveniles). If larger birds are dominant, these results support the idea that residents may endure in forests and exclude the most subordinate migrants (juveniles and small birds) towards shrublands. Within forests, migrants and residents tracked fruit abundance, but residents were also associated with the most suitable breeding sites. Migrants tracked fruits less closely in shrublands, probably due to a higher fruit abundance and a lower availability of shelter. Habitat segregation did not affect lean body mass corrected by size of migrants, which indeed accumulated more fat in shrublands. Therefore, differences in nutritional quality cannot explain why adult and larger blackcaps predominate in forests. Instead, other factors like food diversity or exposure to predators might account for this distribution. Our results provide a mechanism to explain the persistence of sedentary populations despite migrants overflow their range and use the same resources. Residents may challenge the arrival of conspecifics because they are better competitors. From an evolutionary perspective, this shows that non-breeding processes may be as important as breeding benefits accrued to migrants for explaining the dynamics of migratory and sedentary populations.

Birds are able to seasonally exploit the most suitable habitats at each moment in their life cycle. By moving between highly productive breeding and wintering grounds, they may improve fecundity and non-breeding survival paying a comparatively low cost of movement, which has led to a wide occurrence of migration and a large variety of migratory patterns (Gauthreaux 1982, Alerstam 1991, Berthold 1993). In the temperate zone, for instance, primary production in spring increases with increasing latitude, which is paralleled by a rising proportion of migratory species with respect to residents towards the poles (e.g., Newton & Dale 1996). This also occurs within species, in which migratory behaviour shifts from sedentariness at low latitudes to complete migratoriness at high latitudes (Berthold 1999). As a consequence of this gradation in migratory behaviours, the wintering area of migratory populations overlaps with the range of residents in many species. Because of the much larger breeding range of the migratory populations, in most cases the residents’ range is literally flooded by migrant conspecifics.

**Manuscrito enviado.*

Given the intense limitation to which bird populations are subjected during winter (Newton 1998), the coexistence of migrant and resident conspecifics in non-breeding grounds may be a conflicting state. In absence of resource partitioning between migrants and residents, and assuming that they have a similar success in sympatric non-breeding grounds, a simple matter of numbers would lead to opposite population trends in each population fraction. Year after year, migrants would contribute to the winter population with more individuals than residents, as a consequence of the higher fecundity they may achieve in their very productive breeding grounds (Ricklefs 1980, Alerstam 1991). In the end, this increasing numerical imbalance between the two fractions would put an end to the resident population (Alerstam & Enckell 1979, Fretwell 1980, Ricklefs 1992, Bell 2000). Competition with migrants has long been thought to explain why residents are absent from the wintering areas of many migratory species, despite environmental conditions may apparently favour their existence (Alerstam & Enckell 1979, Bell 2000). However, in many other species residents have somehow overcome the negative impact of life together with migrants, and maintain flourishing populations despite their much lower fecundity. Nowadays, we have a little knowledge of the processes that may have caused that sedentary populations persist in some cases but have gone extinct in others (Bell 2000).

In two influential papers, Cox (1968, 1985) proposed that residents are better competitors than migrants and hence may persist in their range as long as environmental conditions allow their existence. If residents take advantage from prior occupancy, site-tenacity and familiarity with the area, they might endure in their breeding territories expelling arriving migrants once saturation is reached. This may well explain the stable coexistence of both population fractions in non-breeding grounds. On the one hand, competitive advantages would improve non-breeding survival of residents up to counterbalance their comparatively low fecundity; on the other hand, the reproductive benefits accrued to migrants would counteract their lower average non-breeding survival (Greenberg 1980). Although the Cox's hypothesis has constituted the basis of much of the subsequent theoretical work (Rappole 1995, Safriel 1995), the extent to which unequal competitive abilities may account for the coexistence of migrants and residents has long been subjected to discussion. A number of studies have suggested that site-fidelity or familiarity with the area may not have that impact on the outcome of social contests, and prior occupancy by residents cannot preclude that migrants overflow their range (Alerstam & Enckell 1979, Fretwell 1980, Bell 2000). According to this view, whether or not residents may overcome competition with migrants would primarily depend on the size attained by the migratory population instead of the competitive abilities of each population fraction (Bell 2000).

Opposing to these two models of conflicting coexistence of migrants and residents, it has been suggested that competition between migrants and residents may be attenuated through resource partitioning, as a consequence of the preferences of each population fraction for different resources or habitat types. This idea originated from the observation that, opposing resident species, migratory species usually occupy secondary-growth habitats in wintering areas. Alerstam and Enckell (1979) insinuated that this is a result of the lower predictability of these habitats, where residents would loss the advantage of site-tenacity and hence might compete less efficiently. However, migrants and residents may actually have different requirements during the non-breeding season that could affect their habitat preferences. Residents have reproductive interests in their range, where they could try to endure over winter to benefit from an early occupancy of the best territories the next breeding season (Verboven & Visser 1998). Meanwhile, migrants are free of this kind of pressures, so they may track resources that are necessary to secure self-maintenance across the most profitable habitat patches (Herrera 1985, Rey 1995). For them, food and refuge to escape predators are likely to be the main resources (Blem 1990, McNamara & Houston 1990, Watts 1991). If different preferences of migrants and residents involve the selection of different habitat types, the two population fractions would coexist in the same areas without competing for winter resources.

Understanding the way non-breeding interactions between migrants and residents may result in the extinction or the permanence of sedentary populations is crucial in the theory for the evolution of migratory patterns. Based on the former models of interaction between migrant and resident conspecifics, three main hypotheses have tried to explain how migratory behaviour could appear from an otherwise sedentary population, leading to a migratory species with non-overlapping breeding and wintering grounds (Rappole 1995). According to the first hypothesis (Cox 1985), if locals are better competitors the split between breeding and non-breeding areas of migrants could proceed by selection for leap-frogging the residents' range. Leap-frog migration could be favoured because many migrants are obliged to leave the areas already occupied by residents, and birds that move beyond could eventually reach suitable non-breeding habitats without competitors (Cox 1985). However, this cannot account for the final extinction of residents, which has to be explained by advocating other processes like the deterioration of environmental conditions or interspecific competition (Cox 1985).

Contrasting with this hypothesis, the second one is based on the assumption that residents lack advantages upon migrants, so that intraspecific competition may drive sedentary populations to extinction (Alerstam and Enckell 1979, Bell 2000). In this case, the split between breeding and non-breeding areas of migrants would occur through a wave-like latitudinal expansion of their breeding areas caused by a progressively increased fecundity at higher latitudes, combined with the inability of populations to afford flooding by migrants below some fecundity threshold at lower latitudes. According to this model, not only the original resident populations, but also the first migrants would disappear from the areas in which the breeding output were too small to counterbalance mortality due to competition with more northerly migratory populations. If sedentary populations still remain, this would only evidence that migratory populations have not grown up to cause them go extinct through competition (Bell 2000).

Finally, the third hypothesis does not require competition to explain the separation of breeding and wintering grounds of migrants, and suggest that this would be triggered by selection by migrants of resources located outside the residents' range (Chesser & Levey 1998). The first migrants would occupy a sort of 'ecological vacuum' in winter bird communities (Hutto 1980), which would allow them to increase their numbers in a population dominated by sedentary birds (Levey & Stiles 1992). For instance, Levey and Stiles (1992) realised that many temperate migrants are frugivorous and occupy open habitats, two strategies based on the exploitation of unpredictable environments that force birds to track resources, and proposed that wandering movements connected to these strategies would be precursors of true migrations (Levey & Stiles 1992, Chesser & Levey 1998).

Given this state of affairs, any advance in our knowledge of interactions between migrant and resident conspecifics in non-breeding grounds would be of capital relevance in the theory for the evolution of migratory behaviour (Cox 1985, Levey & Stiles 1992, Rappole 1995, Bell 2000). However, the difficulty to distinguish between migrant and resident conspecifics in non-breeding grounds has caused that the shape and intensity of their interactions remain a matter of controversy. To the extent we may be aware, very few studies have tried to analyse these interactions directly (Pérez-Tris *et al.* 2000a, Tellería *et al.* 2000). A larger research effort has been devoted to infer them by studying migratory and sedentary species with different degrees of relatedness (Fretwell 1980, Cox 1985, Ricklefs 1992), or by relying on the patterns of distribution and the relative size of migratory and sedentary populations in the whole species range (Safriel 1995, Bell 2000). In the same way, resource partitioning and habitat preferences of migrants and residents have been studied so far by comparing different species (Hutto 1980, Levey & Stiles 1992, Poulin & Lefebvre 1996, Chesser & Levey 1998), but if migrant and resident conspecifics may have unlike habitat requirements during winter remains unknown.

We have studied sympatric migratory and sedentary blackcaps, *Sylvia atricapilla* (L.), wintering at the northern side of the Strait of Gibraltar (southern Spain). In this region, sedentary blackcaps are abundant breeders in forests, but avoid the neighbouring shrublands for reproduction. When migrant blackcaps coming from northwestern Europe arrive at the area, however, the species spreads across the region. Our aims are (1) to elucidate whether migrant and resident blackcaps have a different habitat distribution, (2) to unravel the role that competition or habitat preferences may play in determining this distribution, and (3) to evaluate if the occupation of one or another habitat type may have an effect on mortality due to starvation. The blackcaps wintering in southern Spain are very appropriate for this study not only because large numbers of individuals may be captured that can be easily sexed and aged, but also because resident birds can be accurately told apart from migrants based on their morphology (Pérez-Tris *et al*. 1999). Therefore, we have an excellent opportunity to test the hypotheses mentioned above, for which we have used four complementary approaches:

Distribution between habitats of migrants and residents

Migrants and residents may show habitat segregation, either due to competition (e.g. Cox 1985, Ricklefs 1992) or to resource partitioning (e.g. Hutto 1980). Alternatively, both population fractions may mix during winter and spread across the area. As a first step, we studied the extent to which migrants occupy the breeding areas of residents, and the extent to which residents disperse towards neighbouring environments during winter.

Social dominance and the distribution of blackcaps between habitats

Even if migrants and residents do not show habitat segregation, competition in a heterogeneous landscape should translate into a biased population composition in each habitat, with dominant individuals occupying the preferred habitat types (Sherry & Holmes 1996). For example, in many migrant bird species social dominance leads to a different distribution of sexes or age classes. Compared to females and juveniles, adult males usually endure in the breeding sites during winter in partial migrants (Adriaensen & Dhont 1990), or remain closer to these sites in differential migrants (Ketterson & Nolan 1983). In completely migratory species, adults and males often occupy the best habitat types in wintering grounds (Marra *et al*. 1993, Sherry & Holmes 1996, Marra 2000). We studied whether the distribution of migrants and residents between forests and shrublands is sex or age biased, thus suggesting the existence of dominance hierarchies in the occupation of wintering habitats.

Another factor that may influence dominance hierarchies in birds is body size, especially in a mixed population in which individuals show a wide range of body sizes (Ketterson 1979). To be large could give subordinate individuals (e.g., females or juveniles) priority of access to the most preferred habitats compared to the smallest subordinates, or even to the smallest dominants (Marra 2000). Hence, to study the variations in body size between habitats would provide further insight into the role of social dominance in the distribution of blackcaps. If competition occurs, subordinate individuals that occupy the dominant-biased habitat should be larger than those obliged to occupy the subordinate-biased habitat.

Resource utilisation by migrants and residents within habitats

A requisite for competition to cause habitat segregation is that contending individuals have the same habitat preferences (Greenberg 1986). Otherwise, segregation could be a by-product of partitioning resources through habitat selection, particularly if the resources preferred by different groups of individuals are unequally distributed between habitat types. We studied the extent to which the abundance of migrants and residents is related to the abundance of food and refuge against predators, the most limiting resources for wintering forest passerines (Blem 1990, McNamara & Houston 1990, Watts 1991). In addition, we evaluated if resident blackcaps are better associated with the distribution of breeding territories, which could also cause their spatial segregation from migrants in winter.

Consequences to individuals of habitat occupancy

Social dominance can only have ecological significance if it adversely affects some fitness component of subordinates, for example survival (Greenberg 1986). In temperate regions, winter survival strongly depends on energy storage, which is necessary for birds to face long cold nights and unpredictable food shortages (Blem 1990). In birds wintering in heterogeneous landscapes, the occupation of poor, subordinate-biased habitats usually translates into an increased physiological stress and an impaired body condition (Sherry & Holmes 1996, Marra & Holberton 1998, Strong & Sherry 2000). Therefore, if there is habitat segregation due to competition, blackcaps occupying the subordinate-biased habitat should have a worse body condition than those occupying the dominant-biased habitat.

METHODS

Study area and sampling of blackcaps

We studied blackcaps during two winters (between 1998 and 2000) in an area of around 200 km^2 in the Campo de Gibraltar region (36º01’N, 5º36’W). In this area, mountain ranges (up to 400-m elevation) retain moisture of oceanic winds and hence receive much more precipitation than the surrounding lowlands, which causes the dissimilarity between the two habitats that we have investigated. On the one hand, the montane valleys are covered by forests (ranging between 100 and 300 masl) dominated by cork-oaks *Quercus suber* and mixed with Mirbeck’s oaks *Q. canariensis*, which constitute the only breeding habitats of blackcaps in the area. On the other hand, largely bare shrublands dominated by lentiscs *Pistacia lentiscus* and wild olives *Olea europaea sylvestris* are the typical lowland landscape. In winter, these environments are occupied by a large number of blackcaps.

We captured blackcaps in forests and shrublands from mid December to mid January, when the species is not migrating through the area (Cramp 1992). To account for within-habitat heterogeneity and avoid an excessive nuisance, we moved among different sites between field sessions. Four sites were sampled in each habitat type, which showed similar shelter, food abundance and migrant-resident ratios as shown by Tukey’s tests in an ANOVA with site as a factor and mist-nets as sampling units (all pairwise within-habitat comparisons with $P >$ 0.05, see methods to measure these variables below). Because of this we did not consider between-site differences in our analyses. We made sure that blackcaps were present as breeders in all forest sites and absent from all shrubland sites by means of an extensive searching in spring (Tellería & Pérez-Tris in prep.). All sites were sampled from dawn to dusk and at least twice in the study period, first in December and later on in January (about three weeks later). Every day we set up four to twelve mist-nets depending on fieldwork circumstances, such as slope inclination, rate of flow of streams, presence of cattle and so on. Nets were placed in randomly selected locations, but avoiding too bare spots to assure them to work.

Mist-nets were visited every full hour, and all individuals collected during the same visit were assigned to the same time of capture. Blackcaps were kept in individual cloth-bags labelled with the time of capture and a mist-net identification. All individuals were processed within one hour after cap-

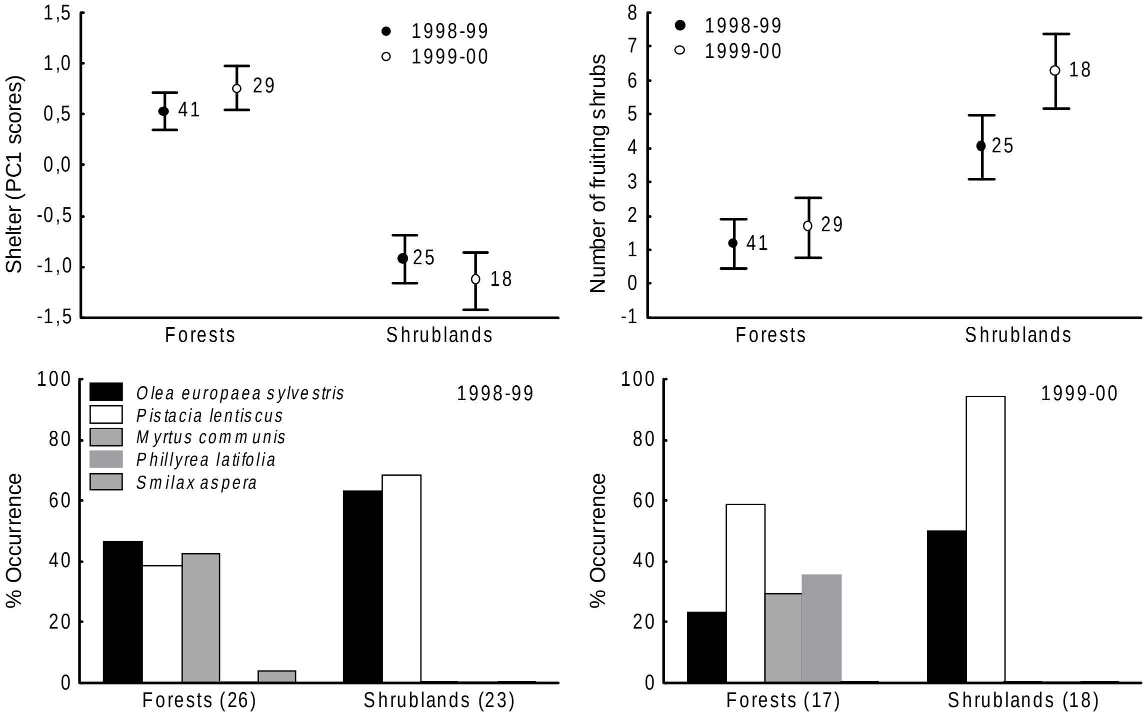

Figure 1. Habitat characteristics of forests and shrublands. Above, variation between habitats and years in shelter (an index obtained by PCA that increases with increasing cover of trees and shrubs) and fruit abundance measured around mist-nets (means ± s.e. and sample sizes). Below, variation between habitats and years in the species composition of fruiting shrubs (frequency of each species in sampling plots with fruits, whose number is indicated in brackets).

ture. Birds were sexed and aged according to plumage characters (Svensson 1992). We distinguished between juveniles (first-winter birds) and adults (older birds whose exact age was unknown). Of 548 blackcaps captured in total, we were unable to age 26 individuals which were excluded from the analyses. We measured the maximum wing chord, the length of the eighth primary feather (primaries numbered from the body to the wing tip), the tail length, and the distance between the wing tip and the tip of each primary feather (from the first to the ninth, hereafter primary distances). All these measurements were taken to the nearest half mm using appropriate rulers. We also recorded the tarsus length (to the last unbroken scale before the toes), the bill length from the skull and the bill height, all of them with a 0.01-mm precision digital calliper. Finally, we estimated visually the size of the subcutaneous fat deposits (according to a nine-value scale; Kaiser 1993) and weighed individuals with a 0.1-g precision digital balance. All the measurements were recorded by the same person (JP-T) to avoid any inter-personal bias. Before being released, every blackcap was marked with a numbered aluminium ring to avoid repetition.

Habitat characteristics of forests and shrublands

For wintering passerines, survival depends on the existence of adequate refuges to escape predators and on the availability of suitable food sources. Blackcaps are forest birds, so they are likely to be more vulnerable to predators in open landscapes (Watts 1991). On the other hand, they are intensive frugivores in winter (Jordano & Herrera 1981, Herrera 1998). Although blackcaps could prefer habitats with abundant fruits, they have been found to feed upon up to nine fruit species in habitats where most fruits are rare and one single species is supplied almost *ad libitum*, which suggests the need of maintaining an adequate nutrient balance in the diet (Herrera 1982, 1985). It is therefore reason-able to think that sheltered environments with a high abundance and variety of fleshy fruits will be the highest-quality wintering habitats for blackcaps.

To evaluate these features, we recorded the percentage of ground covered by trees (vegetation above 2-m height), shrubs (below 2 m) and grass or bare ground in a 50-m diameter circular plot around each mist-net. We also recorded the number and specific composition of shrubs and trees holding ripe fruits in each sampling plot. We only considered the fruits that blackcaps habitually feed upon (according to studies of diet; Jordano & Herrera 1981, own unpublished data). These are all fleshy fruits in the area except *Rosa* spp., *Crataegus monogyna* and *Ruscus aculeatus*, three species with large and very hard berries that we have never found in the diet of these blackcaps (own unpublished data).

Differentiation between sedentary and migratory blackcaps

We used a discriminant function for differentiating between migratory and sedentary blackcaps. The technique is based on three morphological traits: the length of the eighth primary feather, the tail length, and the difference between the primary distances 1 and 9 (a simple index of wing pointedness). When applied to Iberian blackcaps, this method allows the correct classification of 91% of individuals (Pérez-Tris *et al.* 1999). North-western European blackcaps, the main components of populations wintering in our study area, have more pronounced migratory-like traits than Iberian migratory blackcaps (Pérez-Tris & Tellería 2001). Hence, they will be more easily classified by a method that differentiates so finely between Iberian migratory and sedentary populations (for further details see Pérez-Tris *et al.* 1999).

The analysis of distribution between habitats

We conducted a log-linear analysis to investigate the variation in population composition between forests and shrublands in relation to migratory behaviour, sex and age. This method manages multifactor cross-tabulations by partitioning the variation in frequency data into the different factors, allowing one to test for interactions in a way similar to the analysis of variance. The log-linear model is defined by the minimum number of interactions necessary to account for the distribution of frequencies. To obtain this model, we first proceeded hierarchically by fitting all interactions of order n to the correspondent null hypotheses that all of them are simultaneously zero. As soon as the reduction in n caused a lack of fit, we selected the terms of that order or lower which significantly contributed to explain the distribution of frequencies, thus generating the final model that best fitted the data (StatSoft 1999).

The analysis of within-habitat distribution

We used mist-nets as sampling units to analyse whether the abundance of migrant and resident blackcaps is associated with the same or different resources within habitats. However, mist-nets differed in the number of days they were working (because of different alterations including forestry or presence of cattle). To allow proper comparisons, we derived capture indices computed as the number of individuals captured in one net per day activity. Capture indices were computed for each population group, that is, individuals with the same migratory behaviour, sex and age, and were used as measures of abundance in our analyses (after log-transformation to meet normality).

Because the patterns of distribution of different population groups are non-independent, to analyse how they are associated to habitat characteristics one by one would increase the risk of detecting significant effects only by chance. To avoid this, we conducted a PCA with the capture indices of each population fraction and the variables measured to assess habitat characteristics. By doing so, we studied on the one hand if there is a match between the abundance of migrants and residents within habitats, and on the other hand which resources are associated with the distribution of each

Table 1. Log-linear analysis of blackcap frequencies according to population, sex, age, habitat type and year. From top downwards, the fit to the lack of interactions of the corresponding order (only the relevant orders are shown), the goodness of fit of the final model and the contributions of each interaction included in the model are shown. Partial associations are computed by evaluating the gain of fit of the model that includes the corresponding interaction with the model that excludes it. Marginal associations are computed by comparing the fit of the model including all effects of lower order than the one of interest with the model including that interaction instead (StatSoft 1999).

		Maximum likelihood chi-square			
Order of interactions:	d.f.		χ^2	*P*	
No fourth-order interactions	5		2.06	0.840	
No third-order interactions	10		26.35	0.0033	
Test of fit of the final model:	14		6.65	0.948	
		Partial association		Marginal association	
Interactions in the model:		χ^2	*P*	χ^2	*P*
Population × habitat	1	148.80	< 0.0001	154.62	< 0.0001
Age × habitat	1	25.11	< 0.0001	25.30	< 0.0001
Sex × habitat × year	1	8.86	0.0029	9.27	0.0023
Sex × age × year	1	7.02	0.0081	3.68	0.0549
Sex × age × population	1	7.83	0.0051	8.47	0.0036

population fraction at the within-habitat scale, taking into account the possible effects of sex and age. We considered food and vegetation cover to be important resources for all blackcaps regardless of their migratory behaviour. In addition, we used the distribution of breeding resources as possible particular requirements of residents. Breeding territories are characterised by a high cover of Mirbeck's oaks (which are restricted to the moistest sites in forests) and brambles (*Rubus* spp.), a thorny bush commonly chosen by blackcaps to place the nest (Cramp 1992). Indeed, the covers of these two species are the best predictors of the distribution of blackcap breeding territories in our study area (Carbonell & Tellería 1998).

Body size and body condition

In a population composed of individuals with different morphology, single traits like tarsus or wing length are inadequate to measure body size. Because of this, we conducted a PCA with several body dimensions to extract an index of structural size (Rising & Somers 1989). We used the amount of fat stored by blackcaps as a measure of their body reserves. Fat is the main source of energy for wintering birds, and it has been suggested that starvation probabilities decrease exponentially with increasing fat stores (Blem 1990, McNamara & Houston 1990). Visual estimates of fat content have long been used to measure the nutritional condition of birds during winter (Brown 1996). However, the relationship between the amount of fat scored by visual indices and the actual fat content is not linear, but usually better fits a quadratic model (Rogers 1991, Kaiser 1993). Because of this, we used the logarithm of the squared fat scores as a measure of fat content, which was normally distributed and linearly related to body mass (changes in avian body mass are chiefly due to fat mobilisation; Blem 1990). We controlled for daily fat accumulation in the analysis of fat content, but fat storage also depends on other factors which are less easily controlled, such as unpredictable variations in environmental conditions, predation risk or dominance hierarchies (Blem 1990, McNamara & Houston 1990, Witter & Cuthill 1993). Because of this, we also studied the muscular development of individuals, which better measures long-term nutrient reserves (Brown 1996). At a given body size, changes in avian body mass are primarily related to fat accumulation, but after this they principally depend on the development of the large pectoral muscles (Blem 1990). We regressed body mass on structural size and fat content (beta values: size = 0.47, $P < 0.0001$; fat = 0.45, $P < 0.0001$) and used the residuals of this regression as indices of muscular development.

RESULTS

Habitat characteristics of forests and shrublands

A PCA with the arcsine-transformed proportion of ground covered by trees, shrubs and grass in each sampling plot extracted a single component which accounted for 80% of variance, whose scores increased with increasing vegetation cover (eigenvalue = 2.39; factor loading for trees = 0.81, shrubs = 0.91, grass or bare ground = -0.94). Obviously, forests are more sheltered environments than shrublands (Fig. 1; two-way ANOVA: habitat $F_{1,109}$ = 206.53, $P < 0.0001$, year $F_{1,109}$ = 0.003, $P = 0.95$, interaction $F_{1,109}$ = 3.41, $P = 0.068$).

The abundance of fruits, measured as the number of fruit-holding shrubs in each plot, was higher in shrublands than in forests in both years, and slightly increased in the second winter (ANOVA with the log-transformed abundance of fruits: habitat $F_{1,109}$ = 68.46, $P < 0.0001$, year $F_{1,109}$ = 4.25, P = 0.042, interaction $F_{1,109}$ = 1.83, $P = 0.18$; Fig. 1). Two shrub species were by far the most abundant and widely distributed in the area, the lentisc and the wild olive, which were very frequent in both forests and shrublands. However, these were the only species found in shrubland plots, where some scattered *Smilax aspera* observed during the fieldwork apparently made up the rest of available fruits for blackcaps. In forests, by contrast, three other species occurred in sampling plots: *Myrtus communis*, *Phillyrea latifolia* and *Smilax aspera*, the first two being rather common depending on year (Fig. 1). Moreover, we observed some scattered *Rhamnus alaternus*, *Hedera helix* and *Viburnum*

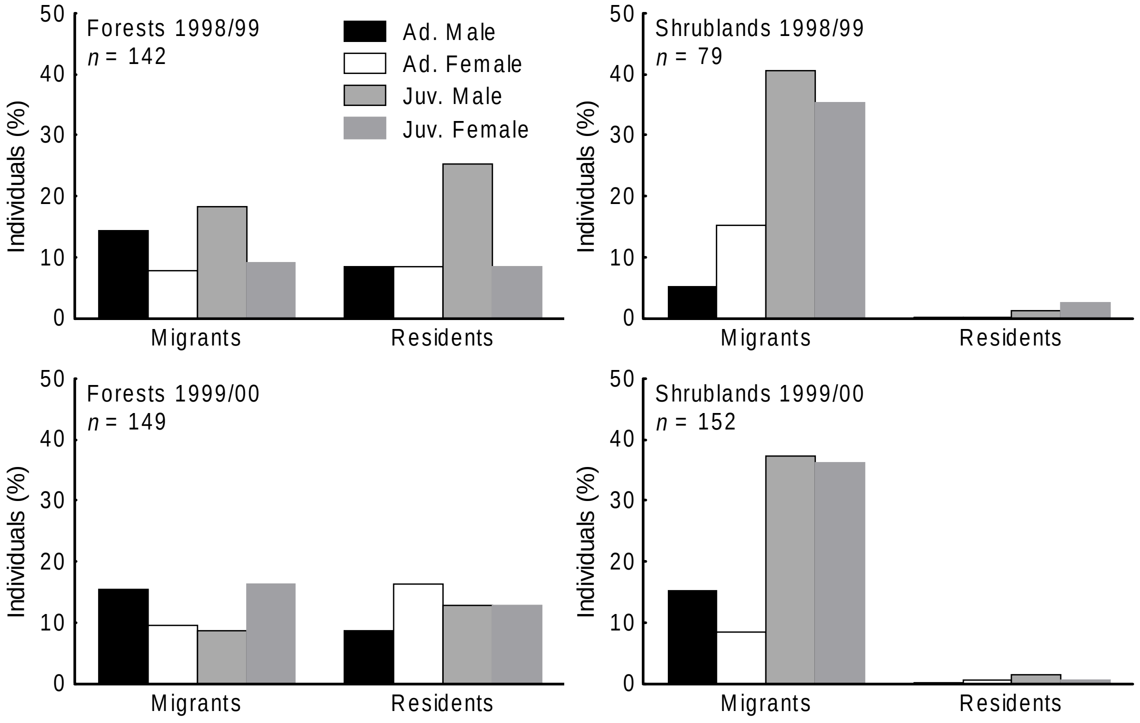

Figure 2. Composition of the blackcap populations wintering in forests and shrublands in each study year, with respect to migratory behaviour, sex and age.

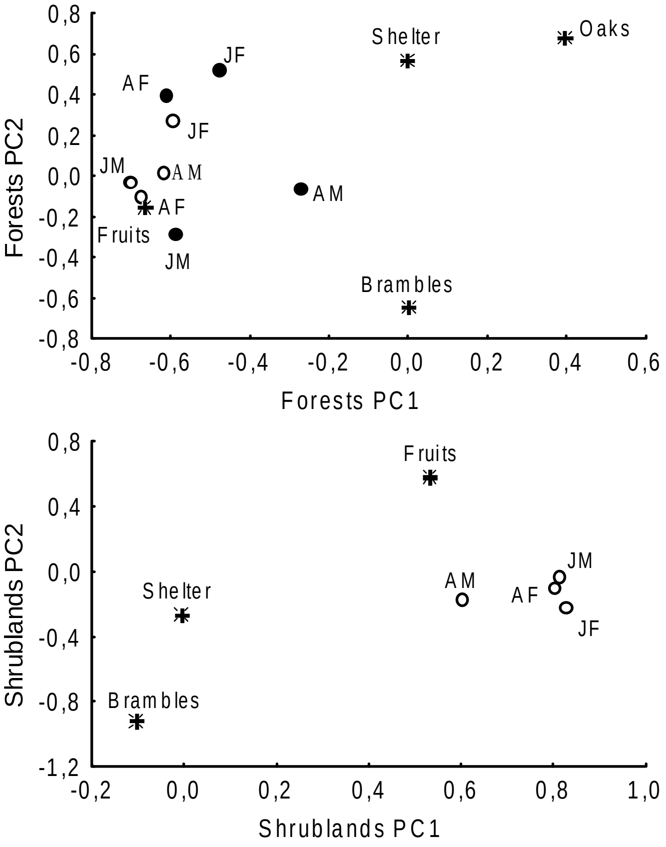

Figure 3. Plot of loadings in the two components extracted by PCA with the capture index of each blackcap population group (open dots: migrants, filled dots: residents) and the variables measured to describe habitat characteristics (cover of Mirbeck's oaks *Quercus canariensis* and brambles *Rubus* spp., and number of fruit-holding shrubs; stars). Labels identify age classes (A: adults, J: juveniles) and sexes (M: males, F: females). Above, residents and migrants in forests; below, migrants in shrublands. Mirbeck's oaks never occurred in shrublands and hence were excluded from the second PCA. Further details on the correlations of each variable with each component are given in Table 2.

tinus in forests during our fieldwork. Therefore, despite fruits are less abundant in forests, these have more diverse fruiting species than shrublands.

Habitat segregation in relation to migratory behaviour, sex and age

The composition of blackcap populations varied between forests and shrublands, and this variation remained similar between study years with only slight changes with respect to sex. The best log-linear model to explain the frequency of each population group in forests and shrublands included five interactions (Table 1, Fig. 2). The first one, between habitat and population, showed that resident blackcaps were almost restricted to forests, while migrants occupied more equally both habitats although were more abundant in shrublands. Adult blackcaps were more frequent in forests while juveniles predominated in shrublands, leading to an interaction between age and habitat type. Males were more frequent than females in forests in the first winter, but this trend disappeared in the second winter causing an interaction between sex, habitat and year. However, this change was not associated to sexual segregation in the first winter. Rather, it was due to a higher proportion of resident juvenile males captured in forests that year, as shown by the significant change between years in the proportions of individuals of each sex and age. Finally, we captured a higher proportion of juveniles of the migratory population, which was especially accentuated in females leading to an interaction between sex, age and population (Table 1, Fig. 2).

Distribution within habitats of migrants and residents

It follows from the former results that the comparison of within-habitat distribution of migrants and residents must be restricted to forests, where both population groups occur in enough numbers. Furthermore, a PCA including forests and shrublands would give a non-realistic picture of the association between breeding resources and the abundance of residents within habitats. Thus, the abundance of residents and Mirbeck's oaks would be associated because they only occur in forests. To avoid these problems, we analysed the associations between migrants, residents and habitat characteristics within forests by means of a first PCA. After this, we checked whether migrants track the same resources in both habitat types by conducting another PCA for shrublands, including only migrants and excluding the cover of Mirbeck's oaks.

The first PCA (with forest plots) extracted two components (Table 2). The PC1 showed that, in general, all blackcaps track the abundance of fruits in that habitat type (Fig. 3). Moreover, because fruits are abundant in forest clearings and very scarce in the most developed areas covered by Mirbeck's oaks, this analysis allowed us to unequivocally discern the generalised preference of blackcaps for fruits above the other resources studied (shelter and breeding territories). Only resident adult males deviated towards a higher preference for these latter resources indicating that they tend to remain in their breeding territories during winter, at least to a greater extent than other resident population groups (Fig. 3). The PC2 defined a gradient of increasing forest development, with highest loadings for oak cover and shelter. However, the cover of brambles (the main nesting substrate of blackcaps in the area) had a very low, negative loading in this component. Interestingly, controlling for the strong effect of fruit abundance in the distribution of blackcaps, resident males tended to be more associated with brambles, while resident females tended to occur in more sheltered sites (Fig. 3). Meanwhile, migrants chiefly lied in the space between, in closer correlation to the abundance of fruits than any of the resident population groups (Fig. 3).

Table 2. Factor loadings in the PCAs evaluating the association between abundance of blackcap population fractions and the variables measured to describe habitat characteristics (cover of Mirbeck's oaks and brambles, number of fruit-holding shrubs, and an index of shelter obtained by PCA from vegetation covers) in forest and shrublands. The significance of each correlation is also shown.

	Forests (n = 70)		Shrublands (n = 43)	
	PC1	PC2	PC1	PC2
Migrants:				
Adult males	-0.614**	0.015	0.608**	-0.172
Adult female	-0.672**	-0.101	0.806**	-0.104
Juvenile male	-0.700**	-0.035	0.816**	-0.037
Juvenile female	-0.593**	0.270*	0.830**	-0.224
Residents:				
Adult males	-0.271*	-0.067	—	—
Adult female	-0.607**	0.390**	—	—
Juvenile male	-0.587**	-0.294*	—	—
Juvenile female	-0.477**	0.520**	—	—
Habitat features:				
Mirbeck's oaks	0.397	0.674**	—	—
Brambles	0.004	-0.646**	-0.102	-0.922**
Fruit abundance	-0.664**	-0.160	0.534**	0.579**
Shelter	-0.001	0.564**	-0.006	-0.267
Eigenvalue	3.283	1.813	2.670	1.349
Variance (%)	27.36	15.11	38.15	19.27

* $P < 0.05$, ** $P < 0.001$

We found sensibly different patterns for migrants when we analysed their distribution in shrublands with the second PCA. This analysis also extracted two components (Table 2). Like in forests, the PC1 showed that migrants tended to be better related to fruit abundance than to any of the other variables measured. However, fruit abundance was a poorer predictor of the abundance of migrant blackcaps in shrublands compared to forests (Fig. 3), suggesting that the distribution of birds in this habitat is affected by other factors. Indeed, in the PC2 all population groups were weighed similarly to vegetation cover (Fig. 3), indicating that shelter is also important in determining the distribution of blackcaps in this habitat type.

Changes in body size and body condition

The PC1 from body dimensions was a good descriptor of body size, as it showed high positive loadings for all body measurements except wing length (eigenvalue = 1.59; factor loading for tarsus length = 0.74, bill length = 0.71, bill height = 0.44, wing length = 0.13, tail length = 0.57). Wing length showed a small loading on this component and was separated on the PC2 together with tail length (eigenvalue = 1.34; tarsus = 0.14, bill length = 0.34, bill height = 0.28, wing = -0.86, tail = -0.62). This was likely due to the strong variation in flight-related morphology in the population, which includes birds from many different origins (Pérez-Tris *et al.* 1999, Pérez-Tris & Tellería 2001).

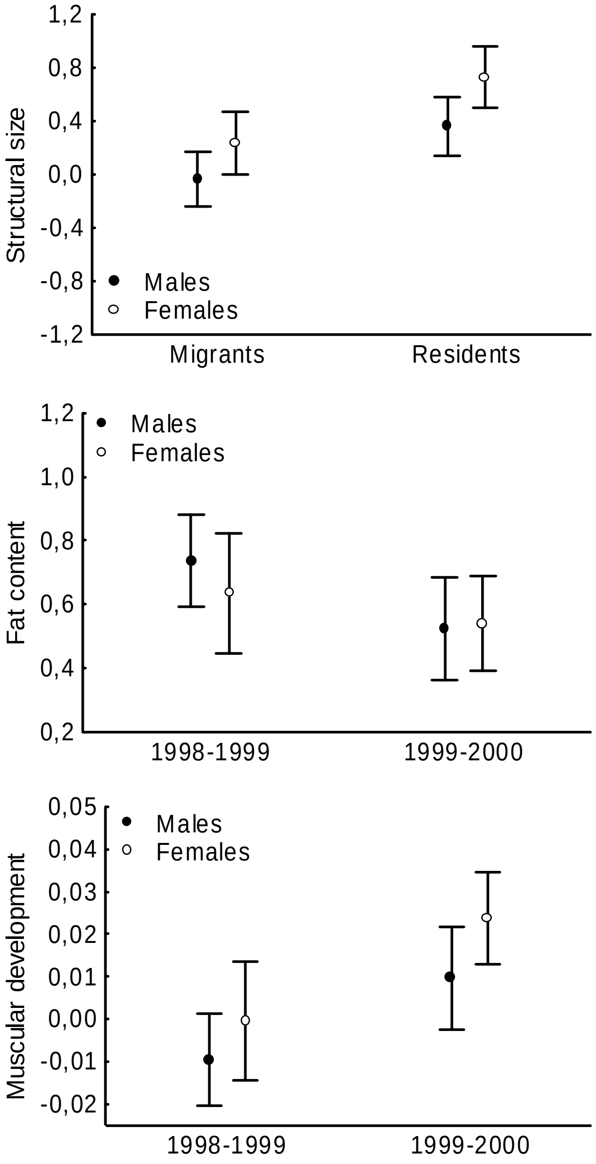

Figure 4. Variations in structural size (scores of the PC1 from body dimensions), fat content (measured as the logarithm of the squared fat scores) and muscular development (residual body mass controlling for size and fat content) among blackcaps wintering in forests (means ± s.e., adjusted by time of day in the case of fat). The relevant comparisons of means according to our results (Table 3) are shown.

The absence of residents from shrublands made it difficult to test for between-habitat variation in body size and body condition. To avoid the confounding effect of an extreme unbalance when conducting ANOVA, we divided our analysis of body size and body condition into two parts. First, we tested for differences between migrants and residents in forests, and then we studied changes between forests and shrublands in migrants.

In forests, body size varied in relation to migratory behaviour and sex (Table 3). Residents were larger than migrants, and females were larger than males (Fig 4). When studying the variation between habitats in body size of migrants, we also found females to be larger than males, although in this case the pattern was not significant (Table 4). Migrant blackcaps were larger in forests compared to shrublands and, on average, adults were larger than juveniles. Interestingly, however, we found significant interactions between age, sex and habitat. Thus, the juvenile migrant males captured in forests were larger than those captured in shrublands. By contrast, no such trend could be detected in migrant females, whose body size was larger in forests regardless of the age of individuals (Table 4, Fig. 5).

Controlling for daily fat storage, we did not find differences in fat content between residents and migrants in forests, nor did we find any significant trend with respect to sex or age (Table 3, Fig. 4). Muscular development, however, significantly increased in the second winter in all population groups. No differences were found between population groups, sexes or age classes, although there was a non-significant trend towards females to be more corpulent than males in both years (Table 3, Fig. 4). When studying the body condition of migrant blackcaps in forests and shrublands, we observed differences between habitats and years. Controlling for time of day, migrant blackcaps

Table 3. Results of analyses of structural size (scores of the PC1 from body dimensions), subcutaneous fat (controlling for time of day) and body condition (residuals of body mass on structural size and fat content) in migratory and sedentary blackcaps wintering in forests. Non-significant interactions have been omitted (all with $P > 0.10$). Sample sizes are the same as in Fig. 2, with some missing values as summarised at the foot of the table.

	Structural size*		Subcutaneous fat		Body condition†	
	$F_{1,274}$	P	$F_{1,274}$	P	$F_{1,273}$	P
Sex	7.95	0.0052	0.27	0.602	3.61	0.059
Age	1.85	0.175	0.50	0.480	0.04	0.847
Population	15.69	0.0001	1.63	0.203	1.02	0.312
Winter	0.49	0.486	3.47	0.064	12.73	0.0004
Time of day §	—	—	108.35	< 0.0001	—	—

*A juvenile resident male without wing length data was excluded.

† Another juvenile resident male (without body mass data) was excluded.

§ The interactions between factors and the covariate were not significant.

stored more fat in shrublands than in forests, and increased fat reserves from the first to the second winter in both habitats (Table 4, Fig. 6). However, muscular development did not vary in the same way. Remarkably, differences between habitats were not significant. As we found in forests, there was a trend to increase protein reserves in the second winter when studying migrants in both habitats, but this change was not significant. In fact, only sexual differences, which were already insinuated in the comparison between migrants and residents in forests, were significant in this analysis, with females being more corpulent than males in both habitat types and in both winters (Table 4, Fig. 6).

DISCUSSION

Despite the importance of conspecific interactions in the theory for the evolution of migration (Cox 1985, Rappole 1995), up to date very little was known on the distribution of migrant and resident conspecifics in wintering grounds, and no attempt had been made to value the relative role of dominance hierarchies and habitat preferences in determining such distribution (Pérez-Tris *et al.* 2000a, Tellería *et al.* 2000). Our results show the arrival of a huge population of migratory blackcaps to spend the winter months in the range of a resident population. Does the existence of these 'remnant' residents mean that they are better competitors than migrants and hence have been able to endure in their habitats (Cox 1985)? Or is it just indicating that migrants have not attained sufficient population size to drive residents to extinction (Bell 2000)? Alternatively, is this one a particular case in which resource partitioning has attenuated competition between migrants and residents (Hutto 1980, Leck 1987)? These are the questions we shall discuss in the light of our results.

Distribution of blackcaps between habitats: a role for dominance

According to our evaluation of habitat characteristics, forests are better environments than shrublands for blackcaps wintering in our study area. In forests, blackcaps will face less difficulties to move into sheltered sites and hence to escape predators. On the other hand, fruits are more diverse in forests, where blackcaps could therefore be allowed to maintain a better nutrient balance. Apparently, the only advantage of shrublands is that they sustain larger fruit crops than forests. Due to the abundance of wild olives and lentisc berries, blackcaps could meet less difficulties to find food in this habitat. Nevertheless, this difference could loss importance because these fruits are not exhausted along the winter in any of the two habitats (they still remain available after the departure of migrants in

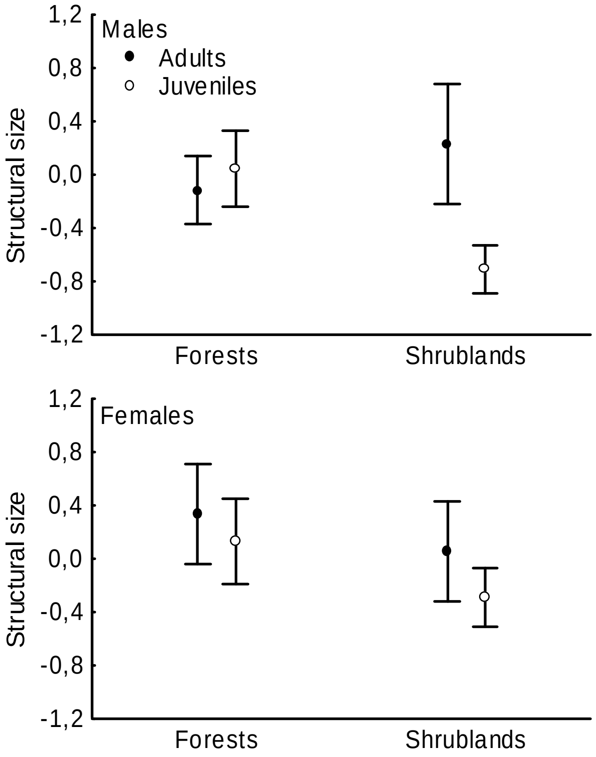

Figure 5. Changes in structural size (scores of the PC1 from body dimensions) between habitat types in migrant blackcaps, according to sex and age (means ± s.e.).

spring, pers. obs.). Actually, if these fruits are supplied *ad libitum* in forests and shrublands, the variety of other fruiting shrubs could make the difference for blackcaps when selecting habitats according to food resources (Herrera 1982, 1985).

In this heterogeneous landscape, residents are almost restricted to forests, while migrants also occupy shrublands. However, this does not necessarily mean that one population fraction, say migrants or residents, is displacing the other one to worse habitats. For example, residents could be enduring in their breeding territories, while migrants could be tracking winter resources that are more uniformly distributed between habitats. Considerable insight on this respect was gained by studying the distribution of blackcaps according to sex, age and body size. Adults were more frequent in forests than juveniles, but no sexual habitat segregation was found. In the majority of species studied so far, males are dominant upon females and hence predominate in the preferred habitat types (e.g. Sherry & Holmes 1996). This trend also holds in partial and differential migrants, in which males make up the bulk of the sedentary fraction or migrate shorter distances than females on average (Ketterson & Nolan 1983, Adriaensen & Dhont 1990). Remarkably, the few studies that have failed to detect dominance of males have dealt with non territorial birds (Myers 1981) or with species in which females are larger than males (Arnold 1991 and references therein). Blackcaps rarely defend winter territories (Cramp 1992), and reversed sexual size dimorphism was revealed by our analysis of body size. Although the non-territorial character of blackcaps could somewhat lessen interactions, these clearly occur between adults and juveniles (see below), and we have no reasons to believe that social contests are feebler between sexes than between age classes (Marra 2000; but see Greenberg 1986). To our view, it is the reversed sexual size dimorphism what most likely accounts for the lack of sexual segregation in blackcaps. In fact, although males could be behaviourally dominant, for example due to the correlation between testosterone levels and aggressive behaviour (Ketterson & Nolan 1992), the larger size of females could buffer this effect leading to a similar distribution of the two sexes.

While sexes do not show different patterns of habitat occupation, age-related habitat segregation is evident in blackcaps. A number of studies have found the same association between age and habitat quality in other species (for a review see Sherry & Holmes 1996), and when its determinants could be experimentally studied (for example by removing territory owners) dominance was proved to cause segregation (Marra *et al.* 1993, Marra 2000). In our study, the variation in body size supports that dominance underlies spatial segregation. Thus, in migrants – the only population fraction for which sample size allowed comparisons – juveniles are larger in the dominant-biased habitat (forests). Moreover, this trend holds in males, the smallest-sized sex, but not in females. This is consistent with a role of body size in determining which individuals remain in forests and which ones are displaced to lowlands. For example, in wintering American redstarts (*Setophaga ruticilla*) sexual habitat segregation has been proved to be mediated by sexual dominance, males are larger and more dominant than females, and females have a larger body size in the male-biased habitat type (Marra 2000). On the other hand, if smaller individuals are subordinates and hence suffer higher mortality rates, selection for a larger body size could explain why adults are larger than juveniles in male migrant blackcaps, as we found in our analyses (Fig. 5).

Based on these results, our study provides a possible explanation for the ability of residents to remain in their breeding range despite this is flooded by migrants. Residents are larger than migrants and, interestingly, migrants are larger in forests than in shrublands on average. If larger birds are dominant in social contests, as it seems likely according to the variation between habitats in body size of juvenile migrant blackcaps, residents could prevent migrants to occupy their range. Once saturation is reached in these habitats, subordinate migrants (juveniles and, among these, small birds) would make up the fraction excluded to shrublands, leading to the differences in body size between habitats that we have found. Among the morphological correlates of migration, the reduction in body size has been interpreted as a way to decrease wing load (Winkler & Leisler 1992). Indeed, migrant blackcaps wintering in our study area are smaller but show much longer and more pointed wings than residents, consistent with selective pressures related to migration (Pérez-Tris & Tellería 2001). According to our results, morphological adaptations of migratory blackcaps could improve migration performance at the expense of reduced competitive ability in wintering grounds.

Within-habitat distribution of migrants and residents

Within forests, the distribution of blackcaps is associated to the distribution of fruits, independently of migratory behaviour, sex or age. The movements of blackcaps tracking fruit crops are well known, especially in migratory populations wintering in the Mediterranean (Herrera 1985, Rey 1995). Our results support that, at a reduced scale compared to migrants, residents also track the availability of fruits within their range. Since migrant and resident blackcaps use the same resources within forests – the preferred habitat type according to the former results – their habitat segregation is unlikely to be caused by different habitat preferences. Instead, the utilisation of common resources within forests could propitiate the interactions that force subordinate migrants to occupy shrublands. Consistent with this interpretation, a year-round monitoring of blackcap abundance in forests and shrublands has found that forests are saturated habitats (where blackcaps hardly increase in abundance

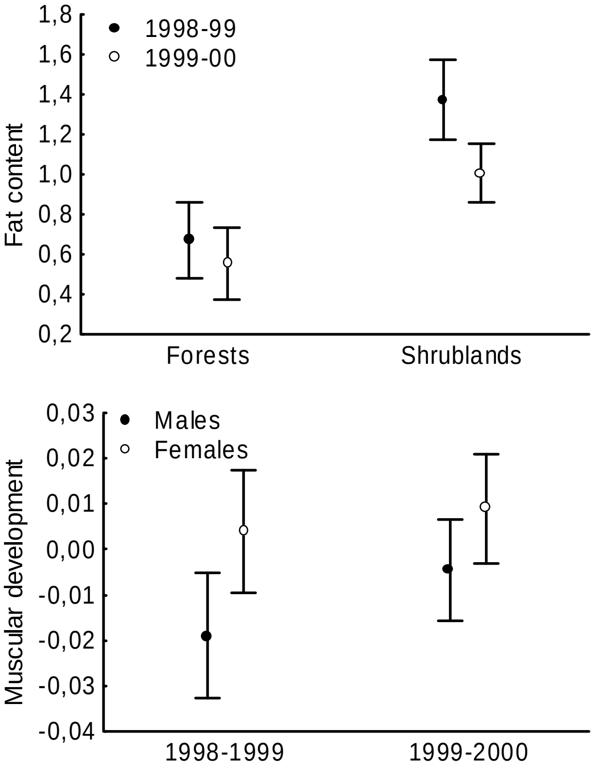

Figure 6. Changes in fat content (measured as the logarithm of the squared fat scores) and muscular development (residual body mass controlling for size and fat content) in migrant blackcaps wintering in forests and shrublands. The relevant comparisons of means according to our results (Table 4) are shown.

Table 4. Results of analyses of structural size (scores of the PC1 from body dimensions), subcutaneous fat (controlling for time of day) and body condition (residuals of body mass on structural size) of migratory blackcaps wintering in forests and shrublands. Non-significant interactions have been omitted (all with $P > 0.14$). Sample sizes are the same as in Fig. 2, with some missing values as summarised at the foot of the table.

	Structural size*		Subcutaneous fat		Body condition†	
	$F_{1,351}$	P	$F_{1,351}$	P	$F_{1,350}$	P
(1) Sex	2.98	0.085	1.91	0.168	7.29	0.007
(2) Age	8.37	0.004	0.00	0.962	0.001	0.977
(3) Habitat	5.98	0.015	40.34	< 0.0001	2.37	0.125
(4) Winter	0.27	0.605	7.97	0.0050	3.44	0.064
2 × 3	7.50	0.0065				
1 × 2 × 3	4.37	0.037				
Time of day §	—	—	134.53	< 0.0001	—	—

*One juvenile female (without bill height data) was excluded.

† Another juvenile female (without body mass data) was excluded.

§ The interactions between factors and the covariate were not significant.

from spring to winter), whose fruits are more intensely depleted in winter if compared to shrublands (Tellería & Pérez-Tris in prep.). In addition, the frequency of singing blackcaps is much higher in forests than in shrublands, suggesting some defence of territories in the former habitat (Tellería & Pérez-Tris in prep.).

Although migrants and residents do not partition resources within forests, their distribution is slightly different in this habitat. Remarkably, resident adult males show a weaker relationship with fruit abundance than the other population groups. In addition, controlling for the strong effect of the abundance of fruits on the distribution of all population fractions, residents tend to be more abundant in areas with abundant shelter, and particularly in sites covered by brambles in the case of males. This association between the abundance of breeding resources – such as brambles – and the abundance of resident males (which take the responsibility to establish territories; Cramp 1992) supports that residents may benefit from site tenacity by increasing the probability of getting a suitable breeding site. This agrees with the view that forests make the best alternative to resident blackcaps, both from the breeding and the non-breeding perspective.

According to the habitat segregation of migrant blackcaps in relation to age and body size, migrants also prefer forests instead of shrublands. This preference is likely due to the higher variety of food resources and availability of shelter in forests compared to shrublands. In relation to the latter possibility, an interesting result in our study is the poorer association between the abundance of migrants and fruits in shrublands if compared to forests. This may be due to the combination of a higher fruit abundance and a lower availability of shelter in shrublands, which could make blackcaps more prudent foragers in this habitat type. Recent theoretical models of optimal foraging suggest that it is better for birds to stay longer at a more dangerous site, feeding with less effort and being more vigilant, compared to feeding more intensely without paying attention to predators and incurring mortality costs (McNamara & Houston 1994). In shrublands, where food abundance is less limiting, blackcaps may well be allowed to forage in relatively sheltered patches, or to move more often between sheltered patches and fruit-rich patches. This would explain why their abundance is weakly related to either food or refuge in shrublands. However, shelter may be found everywhere in forests, where precautions during foraging would loss importance and hence blackcaps may track fruit abundance more closely. In turn, this could counterbalance the lower abundance of fruits in forests and hence emphasize their higher quality compared to shrublands.

Does habitat segregation affect body condition of blackcaps?

In forests, migrants and residents show a similar body condition, as they accumulate a similar amount of fat and do not differ in muscular development. However, migrant blackcaps store more fat in shrublands than in forests. It is hard to believe that this evidences a higher nutritional quality of shrublands, as this would imply that adults and large birds are subordinates displaced to the worst habitats or, alternatively, that dominants prefer the worst habitats. In fact, the variation in fat storage between habitat types was not linked to changes in muscular development, which better measures long-term nutritional reserves. Therefore, fat dynamics are more probably related to more factors than nutritional restrictions. For instance, although putting on fat will reduce the risk of starvation (Blem 1990, McNamara & Houston 1990), heavier birds are known to incur mortality costs because a higher wing load impairs take-offs and hence increases exposure to predators, as shown in several studies including one with blackcaps (Kullberg *et al.* 1996 and references therein). As a consequence of this trade-off, birds administrate their fat reserves at levels that are neither at the physiological nor at the environmental optima. Usually, birds store more fat when, because of some reason, they perceive a lower probability to secure their food or a reduced predation risk (McNamara & Houston 1990, Witter & Cuthill 1993).

Why do blackcaps store more fat in shrublands than in forests? We find several alternatives based on the non-energetic meaning of fat storage. Antipredatory defence may be involved, but it is unlikely that blackcaps put on more fat in shrublands because they perceive a lower predation risk in this habitat type since, *a priori*, blackcaps should be more vulnerable to predators in open environments (Watts 1991). Actually, the amount of fat that birds carry around is likely to be less important for antipredatory defence than vigilance behaviour or the availability of shelter. We found evidences of a more prudent behaviour of blackcaps in shrublands, which might require to spend less time foraging and hence to put on more fat to avoid starvation. Another factor that may influence fat dynamics is the likelihood of finding food, as it has been observed that birds occupying low-quality habitats may store more fat than birds wintering in more predictable environments (Strong & Sherry 2000). In our case, however, this kind of interpretation is very difficult. Fruits could be more predictable in forests because of their higher diversity of fruiting species. Since the production of a single species varies in time and space (Levey & Stiles 1992, Herrera 1998), blackcaps could find more predictable the habitats in which the occurrence of several species may secure a more homogeneous crop due to the partially overlapping fruiting periods of each plant. However, food abundance is higher in shrublands than in forests, which could increase food predictability in this habitat. Alternatively, dominance could also influence fat storage if dominant individuals store less fat than subordinates because they have priority of access to food resources (for a review see Matthysen 1990). In this case, blackcaps displaced to shrublands could put on more fat because they are subordinates and thus perceive a lower probability to secure their food. Finally, differences between habitats in diet composition could also account for fat dynamics to some extent. Lentiscs and wild olives, the unique fruits available in shrublands, are also the fat-richest in the area (Herrera 1982). Thus, an increased fat storage could be a by-product of basing the diet on these fruits. This would mean that in forests, where birds may choose among many more fruits, blackcaps maintain a better nutrient balance than in shrublands (Herrera 1982, 1985). In turn, fat accumulation probably depends on the combination of all these factors, and partialling out their contribution to the variation observed will require experimentation.

Notwithstanding these caveats in our interpretation of the patterns of fat accumulation that we found, the final conclusion is that habitat segregation has no effect on mortality of subordinates due to starvation, as long as fat is the first energy source to be depleted under nutritional stress (Blem 1990). The absence of changes between habitats in muscular development is consistent with this idea. However, the low availability of shelter and the evidences of prudent foraging in shrublands suggest that blackcaps are more exposed to predators in this habitat. If predation rates are higher in shrublands, competition would depress the fitness of individuals displaced out of forests without affecting their body condition (Greenberg 1986). We acknowledge, however, that our study does not conclusively elucidate the consequences to individuals of habitat segregation, for which other methods have to be applied. For example, direct evaluations of stress suffered by birds in different environments based on corticosterone levels have been proved satisfactory in recent studies (Marra & Holberton 1998). At the present time, we are applying these techniques to the study of sympatric migrant and resident wintering blackcaps.

Non-breeding competition and the evolution of migration

This paper presents sufficient evidence to rule out the hypothesis that migrant blackcaps avoid competition with residents by selecting different resources or environments. Several studies of non-breeding bird communities have suggested resource partitioning between migrant and resident species as a way for them to avoid competition (e.g. Hutto 1980), so that the use of resources that are underexploited by residents would make up a 'just better than nothing' alternative for migrants (Poulin & Lefebvre 1996, Strong 2000). Particularly in winter frugivores, migratory species usually occupy secondary-growth, fruit-rich habitats outside the range of residents, which endure in their breeding sites over the winter (Leck 1987, Levey and Stiles 1992). In blackcaps, both the concentration of residents in forests and their distribution within this habitat support this preference for breeding territories. However, habitat selection cannot explain the distribution of migrant blackcaps in our study area. Like in comparative studies, our results show that secondary-growth habitats sustain a large part of the migratory population, yet migrants are also very abundant in forests. Although migrant and resident blackcaps differ in morphology and behaviour (Tellería & Carbonell 1999), this variation has much less ecological significance than interspecific differences and is less likely to cause their segregation. Instead of this, competition in forests may cause the exclusion of subordinate migrants to the less preferred shrublands.

Usually, the role of non-breeding competition in the evolution of migration has been inferred from the distribution of migrants and residents in the whole species range. For example, Bell (2000) proposed that the lack of sedentary populations in adequate areas within the wintering range of migratory species supports their extinction as a result of flooding by migrants. Thus, resident populations would only remain when their breeding success could counterbalance the negative impact of non-breeding competition. In blackcaps, however, it is hard to believe that the low fecundity of sedentary populations may compensate strong mortality due to competition with migrants. In the Iberian Peninsula, sedentary blackcaps have a smaller clutch size than their migratory counterparts (Pérez-Tris & Tellería, submitted). In addition, the lower quality for breeding of the residents' range is accentuated by the summer drought in southern Mediterranean environments, which may reduce fledgling survival as shown in robins breeding in the same area (Pérez-Tris *et al*. 2000b). However, despite sedentary populations face these handicaps, their competitive advantages in winter could well increase their recruitment up to allow their subsistence in Mediterranean environments. Our results in this paper support that residents are better competitors than migrants and this allows them to endure in their breeding habitats, which moreover seem to be also the best wintering sites. Body size, prior occupancy, or the advantages of familiarity with the area could all determine these dynamics of habitat occupation. In robins, indeed, it has been shown that the arrival of migrants is connected to a density-dependent, sequential occupation of habitats of decreasing quality in which residents are better competitors (Tellería *et al.* 2000). Therefore, despite the large population size and the reproductive benefits accrued to migrants may be of crucial importance in determining the population dynamics of migrant and resident conspecifics (Bell 2000), the observation of their interactions in nature supports that their competitive abilities play also a very important role in deciding the future of migratory and sedentary populations.

Acknowledgements

This study would not have been possible without the excellent field assistance from A. Ramírez. Comments by D. Arlt, R. Carbonell and J. A. Díaz considerably improved an early version of the paper. The Consejería de Medio Ambiente (Junta de Andalucía) kindly authorised us to capture and measure blackcaps. Financial support was provided by the Ministerio Español de Educación y Cultura (Project PB97-0325) and a FPI Grant from the Universidad Complutense de Madrid (to JP-T).

References

Adriaensen, F. & Dhont, A.A. 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *Journal of Animal Ecology* 59: 1077-1090.

Alerstam, T. 1991. *Bird migration*. Cambridge University Press, Cambridge.

Alerstam, T. & Enckell, P.H. 1979. Unpredictable habitats and evolution of bird migration. *Oikos* 33: 228-232.

Arnold, T.W. 1991. Geographic variation in sex ratios of wintering American Kestrels *Falco sparverius*. *Ornis Scandinavica* 22: 20-26.

Bell, C.P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology* 31: 258-265.

Berthold, P. 1993. *Bird migration. A general survey*. Oxford University Press, Oxford.

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* 70: 1-11.

Blem, C.R. 1990. Avian energy storage. *Current Ornithology* 7: 59-113.

Brown, M.E. 1996. Assessing body condition in birds. *Current Ornithology* 13: 67-135.

Carbonell, R. & Tellería, J.L. 1998. Selección y uso del hábitat por cinco poblaciones ibéricas de Curruca Capirotada (*Sylvia atricapilla*). *Ardeola* 45: 1-10.

Chesser, R.T. & Levey, D.J. 1998. Austral migrants and the evolution of migration in New World birds: Diet, habitat, and migration revisited. *American Naturalist* 152: 311-319.

Cox, G.W. 1968. The role of competition in the evolution of migration. *Evolution* 22: 180-192.

Cox, G.W. 1985. The evolution of avian migration systems between temperate and tropical regions of the new world. *American Naturalist* 126: 451-474.

Cramp, S. (ed.) 1992. *The birds of the Western Palearctic*. Vol VI. Oxford University Press, Oxford.

Fretwell, S.D. 1980. Evolution of migration in relation to factors regulating bird numbers. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds A. Keast & E.S. Morton), pp. 517-527. Smithsonian Institution Press, Washington, D.C.

Gauthreaux, S.A. Jr. 1982. The ecology and evolution of avian migration systems. *Avian Biology* 6: 93-168.

Greenberg, R. 1980. Demographic aspects of long-distance migration. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds A. Keast & E.S. Morton), pp. 493-504. Smithsonian Institution Press, Washington, D.C.

Greenberg, R. 1986. Competition in migrant birds in the non-breeding season. *Current Ornithology* 3: 281-307.

Herrera, C.M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63: 773-785.

Herrera, C.M. 1985. Habitat-consumer interactions in frugivorous birds. *Habitat selection in birds* (ed M.L. Cody), pp. 341-365. Academic Press, Orlando.

Herrera, C.M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68: 511-538.

Hutto, R.L. 1980. Winter habitat distribution of migratory land birds in western Mexico, with special reference to small foliage gleaning insectivores. *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (eds A. Keast & E.S. Morton), pp. 181-203. Smithsonian Institution Press, Washington, D.C.

Jordano, P. & Herrera, C.M. 1981. The frugivorous diet of Blackcap populations *Sylvia atricapilla* wintering in Southern Spain. *Ibis* 123: 502-507.

Kaiser, A. 1993. A new multicategory classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* 64: 246-255.

Ketterson, E.D. 1979. Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. *Wilson Bulletin* 91: 371-383.

Ketterson, E.D. & Nolan, V. Jr. 1983. The evolution of differential bird migration. *Current Ornithology* 1: 357-402.

Ketterson, E.D. & Nolan, V. Jr. 1992. Hormones and life histories: an integrative approach. *American Naturalist* 140: S33-S62.

Kullberg, C., Fransson, T. & Jakobsson, S. 1996. Impaired predator evasion in fat blackcaps. *Proceedings of the Royal Society of London B* 263: 1671-1675.

Leck, C.F. 1987. Habitat selection in migrant birds: seductive fruits. *Trends in Ecology & Evolution* 2: 33.

Levey, D.J. & Stiles, F.G. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *American Naturalist* 140: 447-476.

Marra, P.P. 2000. The role of behavioural dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11: 299-308.

Marra, P.P. & Holberton, R.L. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116: 284-292.

Marra, P.P., Sherry, T.W. & Holmes, R.T. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American redstarts (*Setophaga ruticilla*). *Auk* 110: 565-572.

Matthysen, E. 1990. Nonbreeding social organization in *Parus*. *Current Ornithology* 7: 209-249.

McNamara, J.M. & Houston, J.A. 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheoretica* 38: 37-61.

McNamara, J.M. & Houston, J.A. 1994. The effect of a change in foraging options on intake rate and predation rate. *American Naturalist* 144: 978-1000.

Myers, J.P. 1981. A test of three hypotheses for latitudinal segregation of sexes in wintering birds. *Canadian Journal of Zoology* 59: 1527-1534.

Newton, I. 1998. *Population limitation in birds*. Academic Press, San Diego.

Newton, I. & Dale, L. 1996. Relationship between migration and latitude among west European birds. *Journal of Animal Ecology* 65: 137-146.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 1999. A method for differentiating between sedentary and migratory blackcaps *Sylvia atricapilla* in wintering areas of Southern Iberia. *Bird Study* 46: 299-304 (*Capítulo 4*).

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000a. Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. *Ardeola* 47: 9-18 (*Capítulo 5*).

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000b. Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. *Journal of Biogeography* 27: 879-888 (*Capítulo 2*).

Pérez-Tris, J. & Tellería, J.L. 2001. Age-related variation in wing shape of migratory and sedentary blackcaps *Sylvia atricapilla*. *Journal of Avian Biology* 32: 000-000.

Poulin, B. & Lefebvre, G. 1996. Dietary relationships of migrant and resident birds from a humid forest in central Panama. *Auk* 113: 277-287.

Rappole, J.H. 1995. *The Ecology of Migrant Birds: A Neotropical Perspective*. Smithsonian Institution Press, Washington, D.C.

Rey, P.J. 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* 76: 1625-1635.

Ricklefs, R.E. 1980. Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 101: 498-506.

Ricklefs, R.E. 1992. The mega-population: a model of demographic coupling between migrant and resident landbird populations. *Ecology and Conservation of Neotropical Migrant Landbirds* (eds J.M. Hagan & D.W. Johnston), pp. 537-548. Smithsonian Institution Press, Washington, D.C., pp. 537-548.

Rising, J.D. & Somers, K.M. 1989. The measurement of overall body size in birds. *Auk* 106: 666-674.

Rogers, C.M. 1991. An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. *Journal of Field Ornithology* 62: 349-356.

Safriel, U.N. 1995. The evolution of Palearctic migration – The case for southern ancestry. *Israel Journal of Zoology* 41: 417-431.

Sherry, T.W. & Holmes, R.T. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77: 36-48.

StatSoft, Inc. 1999. *STATISTICA for Windows (Computer program manual)*. StatSoft, Inc., Tulsa.

Strong, A.M. 2000. Divergent winter foraging strategies of two ground-foraging Neotropical migrant warblers: implications for habitat use patterns. *Auk* 117: 381-392.

Strong, A.M. & Sherry, T.W. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology* 69: 883-895.

Svensson, L. 1992. *Identification guide to European passerines*. L. Svensson, Stockholm.

Tellería, J.L. & Carbonell, R. 1999. Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology* 30: 63-71.

Tellería, J.L., Pérez-Tris, J., Ramírez, A., Fernández-Juricic, E. & Carbonell, R. 2000. Distribution of Robins (*Erithacus rubecula*) in wintering grounds: effects of conspecific density, migratory status and age. *Ardea*, in press (*Capítulo 7*).

Verboven, N. & Visser, M.E. 1998. Seasonal variation in local recruitment of Great Tits: the importance of being early. *Oikos* 81: 511-524.

Watts, B.D. 1991. Effects of predation risk on distribution within and between habitats in savannah sparrows. *Ecology* 72: 1515-1519.

Winkler, H. & Leisler, B. 1992. On the ecomorphology of migrants. *Ibis* 134: S21-S28.

Witter, M.S. & Cuthill, I.C. 1993. The ecological cost of avian fat storage. *Philosophical Transactions of the Royal Society of London B* 340: 73-92.