UNIVERSIDAD COMPLUTENSE DE MADRID
FACULTAD DE CIENCIAS BIOLÓGICAS

TESIS DOCTORAL

Muda y estructura del plumaje en aves de montaña del límite occidental del Paleártico

Moult and plumage structure in mountain birds of the western edge of the Palaearctic

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

Irene Hernández Téllez

Directores

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D9BA - DOCTORADO EN BIOLOGÍA

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Tesis doctoral de:

Irene Hernández Téllez

Directores:

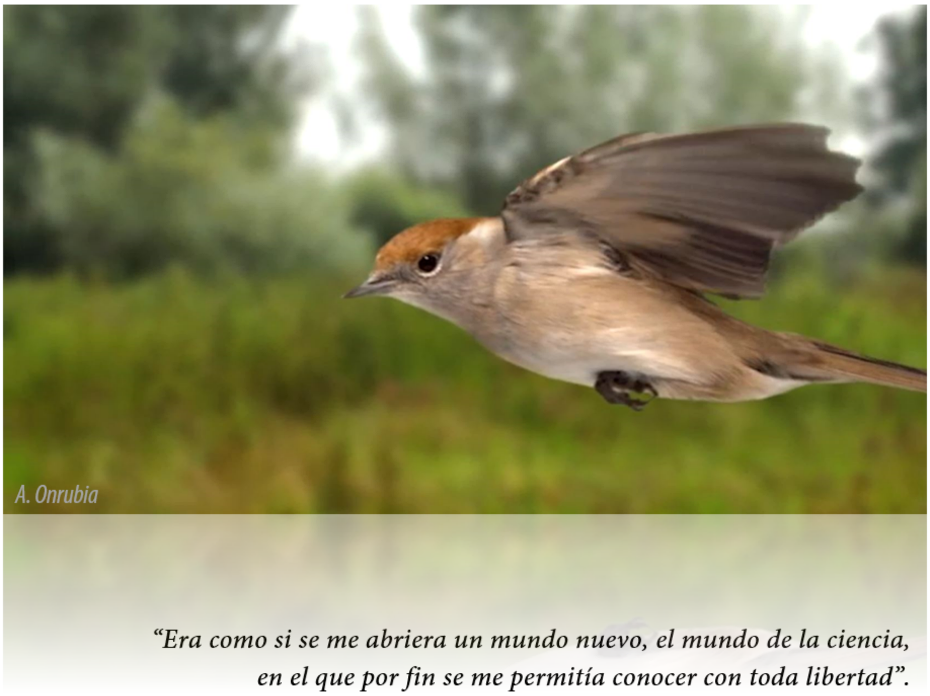
José Ignacio Aguirre de Miguel

José Luis Tellería Jorge

Madrid, 2023

A mi nido...

Las ilustraciones de la portada general y las portadas de los capítulos han sido realizadas por © Laura Hernández Téllez.


A. Onrubia

"Era como si se me abriera un mundo nuevo, el mundo de la ciencia,
en el que por fin se me permitía conocer con toda libertad".

Marie Curie.

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Os quiero y sé que me queréis.

Ahí va la décima de tesis,

To' lo que empieza termina?
qué es principio y qué es final,
festejemos con mezcal
que la vida se camina.
Pongámonos purpurina,
hilemos lo descosido…
Qué alegría haber coincidido,
qué orgullo ser aliadas,
alas al viento o plegadas,
sois mi casa, sois mi nido.

Irene,

El Boalo, 4 de diciembre de 2022

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RESUMEN

MUDA Y ESTRUCTURA DEL PLUMAJE EN AVES DE MONTAÑA DEL LÍMITE OCCIDENTAL DEL PALEÁRTICO

INTRODUCCIÓN

Los balances entre actividades vitales costosas han ido dando forma a las estrategias vitales de los organismos para asegurar su eficacia biológica. Por tanto, estos compromisos pueden ayudar a comprender las trayectorias evolutivas y la variación fenotípica existente en las poblaciones naturales. La muda es un hito importante en el ciclo vital de las aves que interactúa con otros procesos (reproducción, migración) y proporciona plumas que pueden ser útiles para el seguimiento de varios aspectos de la biología de las aves. Varios estudios apoyan la existencia de ajustes durante la muda del plumaje de las aves en respuesta a los requerimientos asociados con la migración pero nuestro conocimiento sigue siendo muy escaso.

Las adaptaciones morfológicas a la migración se han estudiado principalmente en un contexto latitudinal, considerando la selección de muchos rasgos como respuestas programada al aumento en la estacionalidad de los recursos y las severas presiones de tiempo en zonas inestables de mayor latitud. Esto también podría estar ocurriendo a nivel altitudinal, donde se asume una estacionalidad similar pero a escalas regionales. Las aves de montaña se enfrentan a numerosos retos causados por la estacionalidad ambiental producida por la elevación, que puede afectar a su morfología, comportamiento y organización de eventos estacionales. Por ello, las regiones montañosas son ecosistemas complejos de gran valor para la conservación y podrían ser áreas claves para comprender los procesos que determinan la diversificación de las poblaciones de aves.

Esta tesis estudia los determinantes que modulan el crecimiento y los rasgos de las plumas de las aves forestales que habitan las montañas del límite sur del Paleártico para ampliar nuestro conocimiento sobre las presiones de selección que operan durante la muda. El objetivo principal se centra en explorar la existencia de respuestas a la estacionalidad (latitudinal y altitudinal) a través de las características de sus plumas. Más explícitamente, estudiamos si las modificaciones de las plumas asociadas a la migración latitudinal se dan también en respuesta a los movimientos altitudinales de estas poblaciones meridionales.

SÍNTESIS

Los objetivos parciales se organizan en dos bloques compuestos por cuatro capítulos:

Bloque A. Implicaciones de la migración latitudinal en las plumas y efectos de las montañas sobre el comportamiento migratorio.

En el *capítulo 1*, estudiamos la existencia de adaptaciones morfológicas en las plumas asociadas a la migración latitudinal. Los resultados revelan que la distancia de migración no sólo favorece alas más largas y cóncavas, sino que también promueve unas plumas con un raquis más grueso y longitudes de barbas más cortas, lo que a su vez confirió más rigidez de flexión a estas plumas. Estas características podrían reducir los costes energéticos de los vuelos prolongados, por lo que sugerimos que estos ajustes en el plumaje podrían ser una adaptación inadvertida dentro del síndrome migratorio aviar para facilitar la ocupación de entornos estacionales.

En el *capítulo 2*, rastreamos el posible comportamiento migrador de las aves de montaña del suroeste del Paleártico. Los resultados muestran que las poblaciones de aves se desplazan desde las zonas altas a las bajas durante el invierno y esto va acompañado por una configuración de la morfología alar que mejora su capacidad de vuelo. Por tanto, sugerimos un papel potencial de la estacionalidad altitudinal como impulsor de la diversificación regional dentro de las poblaciones de aves de borde que favorecerá su capacidad de adaptación ante los cambios ambientales en curso en esta zona del Paleártico.

Bloque B. Muda y plumaje en aves de montaña.

En el *capítulo 3*, comparamos rasgos de las plumas entre cuatro poblaciones de curruca capirotada que se reproducen en diferentes elevaciones del suroeste del Paleártico. Los resultados revelan que las plumas de las poblaciones de tierras altas (con morfología alar migradora), presentan tasas de crecimiento más rápidas y raquis más anchos que las de las zonas bajas más productivas, debido a las limitaciones de tiempo para la muda y para mejorar la eficacia de vuelo, respectivamente. Por ello, la variación en las características del plumaje se interpreta mejor como respuesta adaptativa a la migración altitudinal que como consecuencia de la disponibilidad regional de alimento.

En el *capítulo 4*, exploramos si estos patrones son generalizables a otras aves, estudiando además la evolución estacional de la temperatura y poniendo a prueba el posible efecto barrera del Estrecho de Gibraltar. Las zonas de montaña muestran ventanas temporales óptimas estrechas y están ocupadas por poblaciones con alas largas y cóncavas y barras de crecimiento amplias. Las plumas más pesadas fueron las del Magreb, por lo que su calidad podría relacionarse con rasgos idiosincrásicos de estas poblaciones periféricas. Por tanto, la selección favorece una tasa de crecimiento del plumaje acelerada y una morfología migratoria en las aves de montaña para hacer frente a la reducción de la ventana temporal óptima a medida que aumenta la elevación, sin repercutir en la calidad del plumaje.

CONCLUSIONES

Esta tesis proporciona información muy valiosa acerca de cómo las aves integran la muda dentro de su ciclo anual. En general, proponemos que la adopción de la migración latitudinal y altitudinal en las historias vitales de las aves no sólo tiene consecuencias generalizadas en su comportamiento y morfología general, sino que sus presiones selectivas también repercutirían en la configuración del plumaje. Por tanto, los efectos de la altitud a escala regional son equivalentes a los de la latitud a grandes escalas geográficas y podríamos estar detectando un síndrome altitudinal sobre el desarrollo y diseño estructural de las plumas. Las montañas del límite sur del Paleártico parecen ser una de las principales fuerzas motrices que promueven la diferenciación poblacional en las aves forestales de borde, que presentan una dinámica regional propia en algunos aspectos clave de su biología (muda, características del plumaje, movimientos). Esto hace que la protección de los hábitats dentro de estos gradientes de altitud sea una estrategia principal de conservación de las poblaciones periféricas de aves.

SUMMARY

MOULT AND PLUMAGE STRUCTURE IN MOUNTAIN BIRDS OF THE WESTERN EDGE OF THE PALAEARCTIC

BACKGROUND

Trade-offs between costly life activities have been shaping the life strategies of organisms to ensure their biological efficiency. These trade-offs can therefore help understand evolutionary trajectories and phenotypic variation in natural populations. Moult is an important milestone in the life cycle of birds that interacts with other processes (reproduction, migration) and provides feathers that can be useful for monitoring various aspects of bird biology. Several studies support the existence of adjustments during the moult of bird plumage in response to the requirements associated with migration but our knowledge remains very scarce.

Morphological adaptations to migration have been studied mainly in a latitudinal contexts, with the selection of many traits being considered as programmed responses to increased resource seasonality and severe weather pressures in unstable, higher latitude areas. This may also be occurring at the altitudinal level, where similar seasonality is assumed but at regional scales. Mountain birds face numerous challenges caused by environmental seasonality due to elevation, which can affect their morphology, behaviour and organisation of seasonal events. Mountain regions are therefore complex ecosystems of great conservation value and could be key areas for understanding the processes that determine the diversification of bird populations.

This thesis studies the determinants that modulate the growth and feather traits of forest birds inhabiting the mountains of the southern Palearctic boundary to extend our understanding of the selection pressures operating during moult. The main objective is to explore the existence of responses to seasonality (latitudinal and altitudinal) through feather traits. More explicitly, we study whether feather modifications associated with latitudinal migration also occur in response to altitudinal movements of these southern populations.

SYNTHESIS

The partial objectives are organised in two sections with four chapters:

Section A. Implications of latitudinal migration on feathers and effects of mountains on migratory behaviour.

In *chapter 1*, we study the existence of morphological adaptations in feathers associated to latitudinal migration. The results reveal that migration distance not only favours longer and concave wings, but also promotes wider rachis and shorter barbed feathers, which in turn confers more bending stiffness to these feathers. These features may reduce the energetic costs of prolonged flight, and we suggest that these plumage adjustments may be an inadvertent adaptation within the avian migratory syndrome to facilitate occupancy of seasonal environments.

In *chapter 2*, we track the possible migratory behaviour of southwestern Palaearctic mountain birds. The results show that bird populations move from high to low altitudes during winter and this is accompanied by a configuration of wing morphology that enhances their flight ability. Therefore, we suggest a potential role of altitudinal seasonality as a driver of regional diversification within edge bird populations that will favour their adaptability to ongoing environmental changes in this Palaearctic area.

Section B. Moult and plumage in mountain birds.

In *chapter 3*, we compared feather traits among four populations of blackcaps breeding at different elevations in the southwestern Palaearctic. The results reveal that feathers from upland populations (with migratory wing morphology), show faster growth rates and wider rachises than those from more productive lowland areas, due to time constraints for moulting and for improving flight efficiency, respectively. Variation in plumage characteristics is therefore better interpreted as an adaptive response to altitudinal migration than as a consequence of regional food availability.

In *chapter 4*, we explore whether these patterns are generalisable to other birds, also studying the seasonal evolution of temperature and testing the possible barrier effect of the Strait of Gibraltar. Mountain areas show narrow optimal temporal windows and are occupied by populations with long and concave wings and large growth bars. The heaviest feathers were those from the Maghreb, so their quality could be related to idiosyncratic traits of these peripheral populations. Thus, selection favours accelerated plumage growth rate and migratory morphology in upland birds to cope with the narrowing of the optimal temporal window as elevation increases, without impacting plumage quality.

CONCLUSIONS

This thesis provides valuable information on how birds integrate moult into their annual cycle. Overall, we propose that the adoption of latitudinal and altitudinal migration in the life histories of birds not only has widespread consequences on their behaviour and general morphology, but that its selective pressures would also impact on plumage configuration. Therefore, the effects of altitude at regional scales are equivalent to those of latitude at large geographic scales and we may be detecting an altitudinal syndrome on feather development and structural design. The mountains at the southern limit of the Palaearctic appear to be one of the main driving forces promoting population differentiation in edge forest birds, which have their own regional dynamics in some key aspects of their biology (moult, plumage characteristics, movements). This makes the protection of habitats within these altitudinal gradients a major conservation strategy for peripheral bird populations.

INTRODUCCIÓN GENERAL

MIGRACIÓN Y MUDA: MARCO CONCEPTUAL

Las estrategias vitales de las poblaciones de organismos están condicionadas por las restricciones impuestas por el ambiente (Stearns, 1992, 2000). Como los recursos son limitados, es frecuente que su adscripción al crecimiento, mantenimiento o reproducción sean objeto de presiones dirigidas a optimizar su rendimiento a lo largo del ciclo anual. De esta forma, los recursos invertidos en unos procesos pueden comprometer el desarrollo de otras actividades dando lugar a balances a veces complejos (Stearns, 1989; Flatt & Heyland, 2011).

Si bien los compromisos relacionados con la inversión reproductiva han recibido una atención especial (Zera & Harshman, 2001; Santos & Nakagawa, 2012), se conocen menos los referentes a la adscripción de recursos entre otras actividades que pueden ser importantes en determinados organismos iteróparos (Cornelius et al., 2011). Este es el caso, por ejemplo, de la migración y la muda del plumaje en las aves, dos procesos que anteceden y siguen a la reproducción en este grupo de organismos (Hedenström, 2008).

La adopción del comportamiento migratorio en las aves como respuesta adaptativa a la estacionalidad ambiental (Berthold, 2001) supone beneficios para las poblaciones implicadas (explotación de pulsos productivos, facilidad para reproducirse, etc.) pero tiene costes asociados a una actividad exigente (largos vuelos migratorios, mortalidad, etc.) que pueden afectar a otros procesos importantes de su ciclo vital, como la muda del plumaje.

Los movimientos de las aves se vinculan a los ambientes estacionales de las regiones templadas surgidos con el retroceso glaciar hace unos 12.000 años (Newton, 2008). En estas nuevas condiciones, la disponibilidad de recursos fluctúa a lo largo del año de tal manera que las aves pueden aprovechar una extraordinaria abundancia de alimento para reproducirse durante un corto periodo estival. Como contrapartida, deben regresar a latitudes más meridionales o atemperadas para evitar las duras condiciones invernales (Chapman et al., 2011). Esto ha permitido que muchas poblaciones de aves colonicen las zonas estacionales más norteñas configurando sus patrones actuales de migración, que han diversificado tanto en movimientos de poco alcance como en espectaculares desplazamientos interhemisféricos o intercontinentales (Berthold, 2001; Somveille et al., 2020).

Las poblaciones implicadas en los movimientos migratorios han sido seleccionadas en aquellos rasgos que les permiten rastrear los cambios estacionales en productividad. Se trata de un conjunto de rasgos integrados (*síndrome de migración*; Piersma et al., 2005; Dingle, 2006) que aumenta la eficiencia de este comportamiento (Hedenström, 2008) y afecta a muchos aspectos de su biología (morfología, fisiología, flexibilidad fenotípica, ajustes de comportamiento, depósito de reservas energéticas, mecanismos de orientación, etc.). Entre todos ellos, los cambios morfológicos han protagonizado muchos de los estudios sobre las adaptaciones de las aves migratorias, ya que mejoran su capacidad de vuelo y se concretan en un "fenotipo migrador". Este se traduce en individuos con alas largas y puntiagudas, patas cortas, colas cortas y cuadradas, cráneos pequeños y planos, picos puntiagudos, esternón y coracoides largos, quillas profundas, baja masa corporal magra o tamaño corporal pequeño (James, 1982; Winkler & Leisler, 1992; Calmaestra & Moreno, 2000; Hedenström, 2002, 2008; Leisler & Winkler, 2003; Winkler & Leisler, 2005; Vágási et al., 2016; Kelsey et al., 2021), que hacen posible diferenciarlos de los individuos sedentarios. Por tanto, estas variaciones fenotípicas pueden utilizarse para estudiar la respuesta migratoria de las aves a las condiciones ecológicas e históricas de un entorno biogeográfico dado (Tellería et al., 2013; Richardson et al., 2014).

La estrategia migratoria de las aves puede interferir en el desarrollo de otras actividades importantes y fisiológicamente costosas, como la muda. La renovación del plumaje es un acontecimiento drástico que sirve para mantener el plumaje en buen estado, algo fundamental para la supervivencia de las aves (p. ej., Lindström et al., 1993). Normalmente, tiene lugar justo después de la reproducción y antes de la migración (Fig. 1), dos procesos muy exigentes para los individuos implicados (Lindström et al., 1994; Nilsson & Svensson, 1996; Dawson et al., 2000; Sillett & Holmes, 2002; Bonier et al., 2007). En este contexto, la migración parece haber influido sobre las estrategias de muda (Jenni & Winkler, 1994; Kjellén, 1994; Barta et al., 2008; Kiat et al., 2019) y, muy especialmente, sobre el crecimiento y la calidad del plumaje (Weber et al., 2009; De la Hera et al., 2009b, 2010; Pap et al., 2015, 2019). En cualquier caso, aunque varios estudios apoyan la existencia de ajustes en la producción del plumaje asociados con la migración, nuestro conocimiento sobre estas posibles interacciones sigue siendo escaso. El objetivo de esta tesis es, por lo tanto, contribuir al conocimiento de los balances entre la migración y la muda de acuerdo con los planteamientos siguientes.

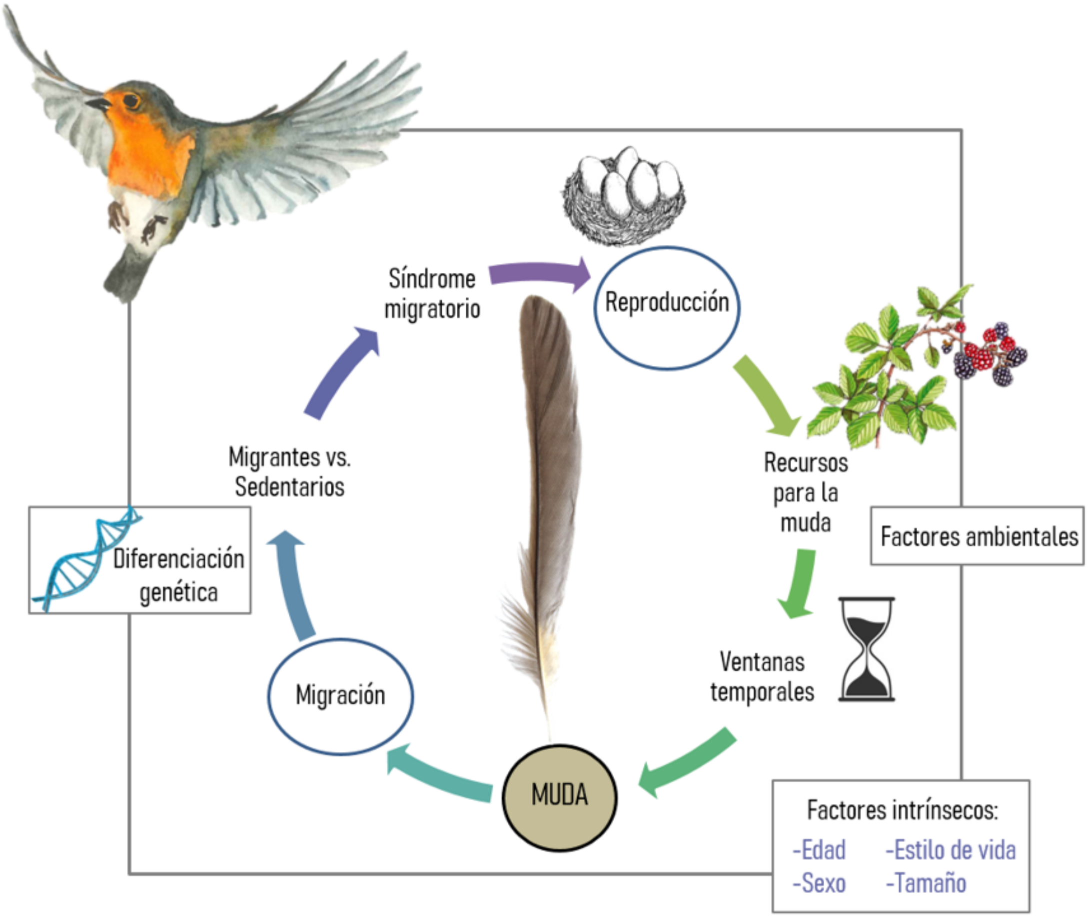

Figura 1. Organización del ciclo anual de las poblaciones de aves migratorias y factores que influyen en el proceso de la muda.

LAS PLUMAS: RASGOS FLEXIBLES

Las plumas, hoy exclusivas de las aves (Subclase Neornithes), se desarrollaron hace 160 millones de años en los saurópsidos terópodos (Clado Pennaraptora; Foth et al., 2014). Cubren una infinidad de funciones (barrera de protección y aislamiento térmico, vuelo, apariencia, sensores táctiles, flotabilidad, producción de sonido, reducción del sonido, ayuda a la audición, soporte mecánico, transporte de agua, defensa y comunicación química; Jenni & Winkler, 2020b) por lo que tienen un papel central en la biología de las aves. No obstante, estas faneras son metabólicamente inertes por lo que se desgastan con el tiempo debido a que la queratina que las compone no se auto regenera. Por lo tanto, necesitan ser renovadas individualmente a través de mudas periódicas a lo largo de la vida de estos animales. La muda es, por tanto, imprescindible para muchos (si no la mayoría) de los aspectos de la vida de un ave.

Siguiendo a Piersma y Drent (2003), la producción de las plumas podría considerarse una subcategoría de plasticidad fenotípica dado que estas estructuras, producidas por cada folículo de cada individuo (Fig. 2), pueden cambiar según las condiciones a lo largo de su vida.

Es importante resaltar que el plumaje reemplazado representa entre el 20 y 35% de la masa corporal seca de un ave (Jenni & Winkler, 2020b) por lo que la renovación de estas estructuras supone un reto metabólico excepcional entre los vertebrados (Murphy, 1996). Este esfuerzo se complica, además, porque durante la muda, las aves tienen que afrontar las restricciones asociadas a su forma de vida habitual. Por ejemplo, la muda limita la distancia de vuelo, la velocidad, la maniobrabilidad, el tiempo de movimiento y la búsqueda de alimento; reduce su masa corporal; aumenta el metabolismo de las proteínas; disminuye la respuesta fisiológica al estrés, etc; Jenni & Winkler, 2020b). Esto explicaría que las aves eviten solapar la muda con otras actividades costosas de su ciclo anual, como la reproducción o la migración.

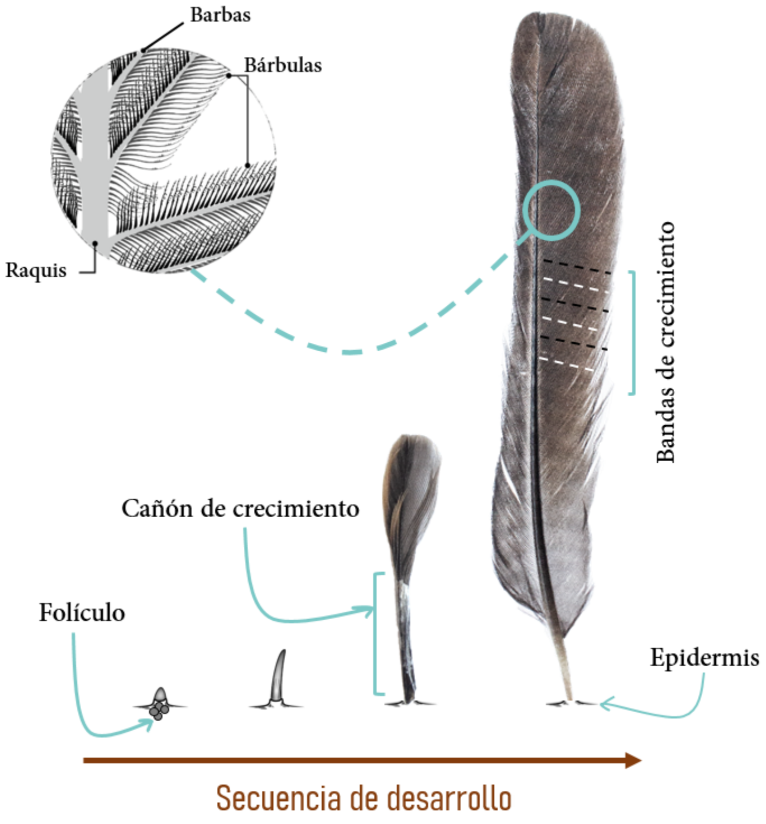

Figura 2. Secuencia del desarrollo de una pluma con detalles de su diseño estructural.

Las condiciones durante el proceso de muda pueden afectar a las características y calidad de las plumas que pueden analizarse por diferentes procedimientos (Jenni & Winkler, 2020b).

La tasa de crecimiento individual de las plumas refleja el incremento diario en longitud de las mismas y es una variable importante que puede emplearse para explorar diferencias en la velocidad de muda (que dependerá, a su vez, de su extensión, duración y de las compensaciones que se den durante el proceso; Jenni et al., 2020). Las plumas crecen a un ritmo similar tanto de día como de noche (Newton, 1968; Murphy & King, 1986; Jovani et a., 2011), lo que da como resultado dos bandas de crecimiento claras/oscuras cada 24 horas debido a la calidad diferencial del material depositado (una banda ligeramente más oscura durante el día y otra ligeramente más clara durante la noche; Broding, 1993; Fig. 2). Estas bandas de crecimiento pueden usarse, por tanto, para evaluar retrospectivamente la tasa de crecimiento de las plumas durante la muda pasada y vincularlo con la disponibilidad de recursos y otros rasgos ambientales que afecten a la muda de las aves (Grubb, 2006).

Por otro lado, la calidad del plumaje se suele analizar mediante la cantidad de material que forma parte de las plumas. Es decir, es un índice de la inversión en la muda y puede estimarse mediante el peso total de las plumas corregido por su tamaño (De la Hera et al., 2012b). En vista de que el reemplazo del plumaje puede venir limitado temporalmente por el inicio de los movimientos postgenerativos al acortarse la ventana de producción óptima, las aves podrían disminuir el tiempo necesario para la muda aumentando la velocidad a la que crecen las plumas individuales (Rhower & Rhower, 2013). Parece, sin embargo, que las mudas rápidas producen plumas de menor calidad (Dawson, 2004), lo que tendría consecuencias sobre su aptitud y la mecánica del vuelo (Hinsley et al., 2003). Por ello, varios estudios sugieren la existencia de un compromiso entre la velocidad de la muda y la calidad de las plumas (Hall & Fransson, 2000; Serra, 2001; Serra et al., 2007) y la necesidad de validar esta relación en diferentes especies, poblaciones y contextos ambientales.

Así, la variación en los rasgos de las plumas puede deberse a una variedad de factores genéticos, intrínsecos y ambientales (Fig. 1). Por consiguiente, podría explicarse por algunos rasgos idiosincrásicos de las especies (p. ej., tamaño, fisiología, dieta), de los individuos (p. ej., sexo, edad), de las escalas de aproximación (dentro o entre poblaciones), de las adaptaciones particulares del ciclo anual (p. ej. migración, reproducción) o de los entornos ambientales (p. ej., disponibilidad de alimento, limitaciones de tiempo, competencia, depredación; véase el capítulo 3.2.7 Jenni & Winkler, 2020). Cabe resaltar que aunque esta tesis no se centra en el estudio de la totalidad de factores implicados, el efecto de muchos de ellos fue controlado durante los análisis.

Estos rasgos del plumaje (tasa de crecimiento y masa) se han considerado rasgos flexibles cuya expresión vendría determinada principalmente por las limitaciones ambientales (Grubb, 2006). Sin embargo, cada vez hay más evidencias que sugieren que los factores genéticos pueden contribuir a la variación fenotípica de las características de las plumas, lo que plantea la posibilidad de que hayan sido moldeadas en parte por presiones selectivas (Piersma et al., 2005; Gienapp & Merila, 2010; de la Hera et al., 2013; Saino et al., 2013; De la Hera et al., 2022).

Además, la complejidad estructural de las plumas (Fig. 2; anchura del raquis, longitud y densidad de barbas, ángulo de inserción de las barbas en el raquis) puede determinar sus propiedades mecánicas (p. ej. su rigidez a la flexión). Por tanto, son esenciales para la ejecución del vuelo (Swaddle et al. 1996) y podrían estar potencialmente bajo selección natural (De la Hera et a., 2010a; Szép et al., 2019). Así, el diseño estructural del plumaje puede estar influido por diferentes factores, a veces contradictorios pero unos pocos estudios recientes sugieren la existencia de adaptaciones a los requisitos de vuelo (Pap et al, 2015, 2019) que permitirían a las poblaciones migradoras producir plumas con mejores propiedades mecánicas que las aves sedentarias.

En este contexto, es importante distinguir entre las aproximaciones dentro de una población, que pueden sugerir diferencias de calidad entre individuos, y las aproximaciones entre especies o poblaciones. Al comparar poblaciones diferenciadas, la variación en la calidad, estructura y producción del plumaje puede indicar diferentes estrategias o limitaciones evolutivas (Van Noordwijk & de Jong, 1986).

MONTAÑAS: POSIBLES IMPULSORES DE DIFERENCIACIÓN POBLACIONAL

Las regiones montañosas ocupan alrededor de una cuarta parte de la superficie de la Tierra (Kapos et al., 2000) y son ecosistemas complejos de gran valor para la conservación (Rahbek et al., 2019). Sus características climáticas difieren fundamentalmente de las de las regiones bajas y pueden albergar comunidades de especies adaptadas a sus gradientes altitudinales (Martin, 2004). Sin embargo, nuestro conocimiento sobre las dinámicas de las poblaciones a lo largo de estos gradientes es todavía muy incompleto (Boyle et al., 2016), a pesar de sus importantes implicaciones biológicas y de conservación (Lundblad & Conway, 2020).

Las aves de las montañas se enfrentan al desafío de hacer frente a las cambiantes condiciones ambientales de los gradientes de altitud (Laiolo & Obeso, 2017; Quintero & Jetz, 2018; Spehn et al., 2019). Esto puede dar lugar a cambios en su morfología, fisiología y configuración de su ciclo anual, aún poco conocidos, ya que muchas poblaciones se ven obligadas a moverse a lo largo del gradiente de elevación para pasar la época no reproductiva en zonas bajas (Boyle et al., 2016; Boyle, 2017; Cheng et al., 2022). De esta forma, su ciclo anual parece estar fuertemente influido por la duración de las condiciones adecuadas para la reproducción y la muda en las áreas de cría altimontanas (Lundblad & Conway, 2020; Grzybowski & Pease, 2005 ; LaBarbera & Lacey, 2018 ; Martin & Wiebe, 2004). En comparación con las migraciones latitudinales, los desplazamientos altitudinales se caracterizan por cubrir distancias más cortas (Cheng et al., 2022) pero puede sugerirse, sin embargo, que las restricciones temporales a la explotación de los recursos de alta montaña podrían aumentar la velocidad de crecimiento y modificar los rasgos de las plumas tal como ocurre con las migraciones latitudinales (De la Hera et al., 2009b). Pese a estas evidencias, ningún estudio ha comprobado si las aves que migran a lo largo de los gradientes altitudinales tienen patrones de muda y configuración del plumaje similares a las que desarrollan movimientos latitudinales.

En esta tesis se estudian los rasgos de las plumas de una serie de poblaciones de aves forestales del Paleártico suroccidental. Las regiones montañosas de la Península Ibérica y el Magreb, parecen un escenario muy adecuado para el estudio de la diferenciación de las poblaciones de montaña y su impacto sobre el plumaje por varias razones. En primer lugar, porque al tratarse de una región montañosa en un intervalo latitudinal relativamente

pequeño nos permite analizar si las adaptaciones relacionadas con la migración altitudinal coinciden o no con las que se dan en los gradientes latitudinales más amplios. En segundo lugar, porque la región ha actuado como refugio de poblaciones de aves sedentarias desde final del Pleistoceno (Hewitt, 2011; Husemann et al., 2014), con las que podemos estudiar su posible diferenciación en formas migratorias relacionadas con los movimientos locales y regionales a lo largo del gradiente altitudinal. Finalmente, estas poblaciones periféricas tienden a reducir sus efectivos en un escenario donde el deterioro ambiental y las dificultades de recolonización de los sectores más meridionales pudieran promover su desaparición, con lo que su estudio es esencial desde una perspectiva conservacionista (Hampe & Petit, 2005; Sexton et al., 2009). Este deterioro ambiental pudiera asociarse, además, con la calidad del plumaje si los recursos alimenticios con los que abordar la muda se vieran disminuidos en estas áreas geográfica y ecológicamente marginales de su área de distribución (Tellería et al., 2021).

ESTRUCTURA, HIPÓTESIS Y OBJETIVOS DE LA TESIS

En esta tesis estudiamos los determinantes que modulan el crecimiento del plumaje y los rasgos de las plumas de las aves forestales que habitan el límite sur del Paleártico para ampliar nuestro conocimiento sobre las presiones de selección que operan durante la muda. El objetivo principal se centra en explorar la existencia de respuestas a la estacionalidad (latitudinal y altitudinal) a través de las características de sus plumas. Más explícitamente, estudiamos si las modificaciones de las plumas asociadas a la migración latitudinal se dan también en respuesta a los movimientos altitudinales de estas poblaciones meridionales. Para ello, hemos organizado esta tesis en dos bloques compuestos por un total de cuatro capítulos interrelacionados.

Bloque A. Implicaciones de la migración latitudinal en las plumas y efectos de las montañas sobre el comportamiento migratorio.

Esta primera parte de la tesis pretende sentar los antecedentes sobre los que se apoyarán los capítulos del siguiente bloque. El objetivo de este bloque es doble: en primer lugar, investigamos si ciertos rasgos de las plumas responden al comportamiento migratorio a escala latitudinal y, en segundo lugar, exploramos la influencia de la estacionalidad altitudinal sobre el comportamiento migratorio de las poblaciones periféricas objeto de

esta tesis. Para llevarlos a cabo, partimos de dos hipótesis en parte ya confirmadas en otros contextos y que aplicamos al entorno del Paleártico suroccidental:

Estacionalidad latitudinal. Las aves están sujetas al efecto de la estacionalidad climática que, a su vez, afecta a su comportamiento migratorio. Esto configura un gradiente latitudinal asociado a mayores distancias de migración hacia el norte en las regiones templadas. En este contexto, diferentes estudios han destacado la importancia de la latitud en la configuración de la morfología alar y el plumaje. En este sentido, como ya hemos comentado anteriormente, las aves que recorren largas distancias presentan adaptaciones morfológicas en el aparato de vuelo y algunas propiedades estructurales de las plumas que determinan el comportamiento mecánico para aumentar la eficacia de vuelo (p.ej. alas más largas y puntiagudas, plumas con mayor rigidez a la flexión; Pérez-Tris et al., 2000; De la Hera et al., 2010a). Asimismo, se han descrito tasas de crecimiento de las plumas más rápidas en latitudes elevadas (Dietz et al., 2015; Terrill, 2018; Horák et al., 2022). Este hecho se interpreta como una consecuencia del rápido acortamiento de las condiciones óptimas de las áreas de cría con la llegada del otoño y/o al aumento del ritmo de vida hacia latitudes más septentrionales. Por lo que tanto las restricciones en los requisitos de vuelo como las restricciones temporales asociadas a la latitud podrían afectar a la morfología y a los rasgos del plumaje (*Hipótesis A1; Fig. 3*). Según esta hipótesis, una morfología alar migradora, una velocidad de la muda acelerada (a costa de la calidad del plumaje) y un diseño estructural que facilite el rendimiento mecánico de las plumas (p. ej. plumas más largas, raquis más ancho y ángulos de inserción de las púas más agudos) se asociaría positivamente con la distancia de migración de las poblaciones estudiadas.

Estacionalidad altitudinal. Como en el caso de los movimientos latitudinales, los cambios ambientales asociados a la altitud podrían propiciar el desarrollo de movimientos estacionales de las aves a escalas locales o regionales (Boyle, 2017; Tellería et al., 2001; Ceresa et al., 2020; Barras et al., 2021). Esto iría acompañado por una diferenciación morfológica para mejorar la eficiencia del vuelo (Tellería et al., 2001; Lundblad & Conway, 2019). Por lo tanto, el patrón espacio-temporal de la idoneidad del hábitat relacionado con la orografía podría ser un impulsor principal de la diversificación de las poblaciones a escala local, lo que podría mejorar el potencial de las especies para hacer frente a los cambios ambientales (Richardson et al., 2014; *Hipótesis A2; Fig. 3*). Según esta hipótesis, las poblaciones ligadas a las montañas del límite sur del Paleártico realizarían migraciones estacionales altitudinales, configurando morfologías alares adaptadas a estos movimientos.

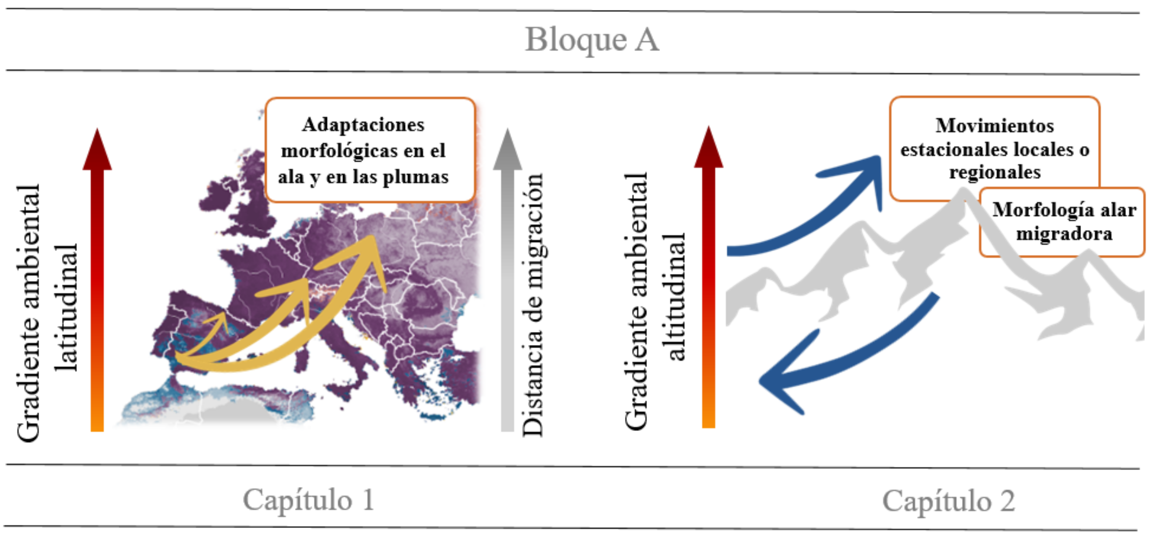

Figura 3. Hipótesis del primer bloque de la tesis.

Para concretar el primer objetivo, en el *capítulo 1* tratamos de arrojar luz sobre las adaptaciones morfológicas asociadas a la migración latitudinal del petirrojo europeo (*Erithacus rubecula*) con el fin de comprender la relación de la distancia de migración con las características estructurales y mecánicas de sus plumas (Lees, et al., 2017; Fig. 3). Este objetivo lo abordamos en las zonas de invernada simpátrica de las poblaciones sedentarias y migratorias de esta especie del sur de Iberia, donde utilizamos los valores de isótopos estables de hidrógeno de las plumas (δDf) como indicador del origen reproductivo. El área elegida es un antiguo refugio glacial que alberga poblaciones de petirrojos durante todo el año y a su vez recibe durante el invierno congéneres migratorios procedentes del resto de Europa (Bueno, 1998; Tellería & Pérez-Tris, 2004), por lo que nos permite comparar poblaciones con diferentes presiones selectivas asociadas a la migración.

Por otro lado, los movimientos altitudinales asociados a la heterogeneidad ambiental provocada por las montañas han sido estudiados en la región ibérica (Tellería & Carbonell, 1999; Tellería et al., 2001; Carrascal & Palomino, 2012; Tellería et al., 2020a) pero se sabe aún poco sobre sus particularidades en el Magreb, el límite meridional del Paleártico. Para aportar información sobre los movimientos de las aves en esta zona, en el *capítulo 2* exploramos si las poblaciones del pinzón vulgar africano (*Fringilla coelebs africana*)

rastrean los cambios espaciotemporales en la idoneidad del hábitat en los gradientes altitudinales del noroeste africano (Fig.3). Las evidencias obtenidas apoyarán el objetivo de analizar el efecto de los potenciales movimientos altitudinales sobre la muda y la estructura de las plumas, desarrollado en el apartado siguiente.

Bloque B. Muda y plumaje en aves de montaña.

La segunda parte de la tesis integra las ideas ilustradas en el bloque anterior con el fin de explorar el proceso de la muda y los rasgos de las plumas en las poblaciones periféricas que crían y mudan en las montañas del límite meridional del Paleártico, validando tales predicciones en una especie primero (*capítulo 3*) y en un conjunto mayor de especies después (*capítulo 4*). Para tratar de dilucidar los principales condicionantes de la variación en la muda de estas aves, este bloque plantea tres hipótesis, posiblemente complementarias, que se detallan a continuación:

Gradiente de calidad ambiental. El extremo meridional del Paleártico actualmente representa el límite de distribución de la mayoría de paseriformes forestales europeos que, en la mayor parte de los casos, tiende a concentrarse en los bosques de montaña (Thévenot et al. 2003). El bosque y sus aves se rarifican en este entorno en línea con los patrones de covariación de la marginalidad ecológica y geográfica observados en la zona (Tellería et al., 2021). Asimismo, al alejarse del óptimo forestal centro europeo, el deterioro ambiental y dificultades de recolonización de los sectores más meridionales, provocarían un patrón de deterioro de la condición corporal de las poblaciones marginales (Carbonell et al., 2003). De esta forma se genera un paisaje de distribución donde la disponibilidad espaciotemporal de recursos para las aves (por ejemplo, la productividad primaria durante la reproducción y muda) presenta una disposición calidoscópica que podría reflejarse en la muda y calidad de su plumaje (*Hipótesis B1*; Fig. 4). Esta hipótesis predice que la velocidad de la muda y consiguiente calidad del plumaje se asociaría positivamente con la productividad de las localidades estudiadas.

Estacionalidad altitudinal. Si los cambios ambientales asociados a la altitud favorecen movimientos estacionales de las aves a lo largo del gradiente de elevación (*Hipótesis A2*), podemos plantear la hipótesis de que las poblaciones de aves de montaña están sometidas a presiones selectivas en parte similares a las de las especies migratorias latitudinales que, en última instancia, darán lugar a una diferenciación con respecto a sus homólogas de las tierras bajas en el crecimiento y los rasgos del plumaje (García et al., 2021; *Hipótesis B2*; Fig. 4). Las mudas rápidas en las aves migratorias se han relacionado habitualmente con las estrechas ventanas temporales para criar y mudar en sus zonas de cría del norte (Hall & Fransson, 2000; De la Hera et al., 2012; Kiat et al., 2019). Según esta hipótesis, la velocidad de la muda, la consiguiente peor calidad del plumaje y ciertos rasgos que mejoran las propiedades mecánicas de las plumas (barbas cortas y densas y raquis anchos) se asociaría positivamente con la altitud si esta se vincula a un acortamiento del tiempo útil para la organización del ciclo anual de las aves.

Efecto barrera. El Estrecho de Gibraltar, originado hace más de 5 millones de años (Abril & Periáñez, 2016), parece condicionar la diferenciación poblacional de las aves forestales del gradiente ibero-magrebí (Clements et al., 2021). Es decir, si existe ruptura del flujo génico entre ambos lados de este accidente geográfico (Doña et al., 2015), la respuesta a la estacionalidad y gradientes planteados en las hipótesis anteriores puede presentar diferencias significativas según las poblaciones estudiadas se ubiquen en la Península Ibérica o el Magreb (*Hipótesis B3*; Fig. 4).

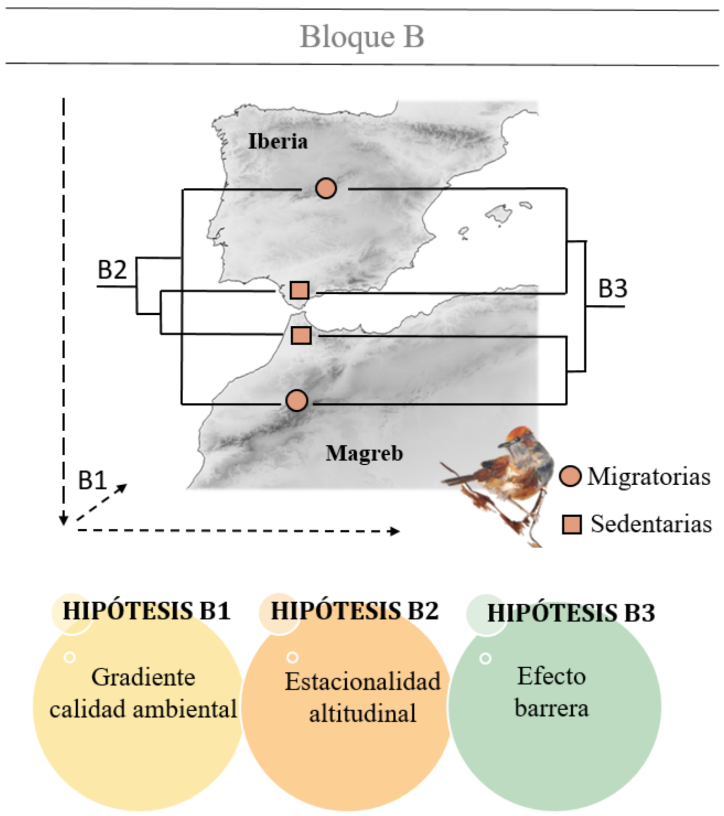

Figura 4. Hipótesis del segundo bloque de la tesis: Posibles escenarios de diferenciación poblacional con respecto a la muda de las aves de las montañas del suroeste del Paleártico.

Para poner a prueba las hipótesis planteadas, en el *capítulo 3*, evaluamos si los movimientos altitudinales explican la variación en algunos rasgos de las plumas de la cola (barras de crecimiento, masa, anchura del raquis y longitud de las barbas) entre cuatro poblaciones de la curruca capirotada (*Sylvia atricapilla*) que se reproducen a diferentes altitudes en el suroeste del Paleártico (*Hip. B2*, Fig. 4) o si las diferencias son una consecuencia directa la idoneidad inmediata del hábitat (p. ej. productividad primaria; *Hip. B1*, Fig. 4 Izq).

Sin embargo, los estudios monoespecíficos pueden dar a una visión demasiado idiosincrática de los procesos estudiados, por lo que en el *capítulo 4* exploramos si los patrones relacionados con el plumaje de la curruca capirotada, un ave conocida por su capacidad de rastrear recursos estacionales a diferentes escalas espaciales (Tellería & Pérez-Tris, 2002, 2003) son generalizables a otras especies de aves. Más explícitamente, exploramos la tasa de crecimiento del plumaje y la masa de las plumas de otros cinco paseriformes forestales (*Sylvia atricapilla, Erithacus rubecula, Turdus merula, Fringilla coelebs, Parus major* y *Cyanistes sp.*; O. Passeriformes) para validar los patrones observados en las currucas. En este caso, dado que las aves de montaña deben mudar dentro de estrechas ventanas temporales de condiciones óptimas, estudiamos la evolución estacional de la temperatura en las diferentes áreas de estudio. Y ponemos a prueba el efecto de la posible diferenciación genética sobre la muda (*Hip. B3*, Fig.4).

Estas evidencias nos acercarán a comprender cómo los compromisos entre migración y muda pueden haber influido en la organización del ciclo anual de las aves de montaña.

El estado de publicación y títulos de los capítulos se detallan a continuación:

- Capítulo 1 ***Publicado***

Adaptaciones mecánicas y estructurales a la migración en las plumas de vuelo de un paseriforme Paleártico.

De la Hera, I., **Hernández-Téllez, I.**, Pérez-Rigueiro, J., Pérez-Tris, J., Rojo, F. J., & Tellería, J. L. (2020). Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. **Journal of Evolutionary Biology**, 33(7), 979-989. https://doi.org/10.1111/jeb.13630

- Capítulo 2 ***Publicado***

La estacionalidad altitudinal como potencial impulsor de la diversificación morfológica en las poblaciones de aves de borde.

Tellería, J. L., **Hernández-Téllez, I.**, de la Hera, I., Aguirre, J. I., & Onrubia, A. (2022). Altitudinal seasonality as a potential driver of morphological diversification in rear-edge bird populations. **Avian Research**, 100039. https://doi.org/10.1016/j.avrs.2022.100039

- Capítulo 3 ***Publicado***

Rasgos del plumaje en cuatro poblaciones meridionales de curruca capirotada (*Sylvia atricapilla*): ¿explican los movimientos altitudinales las diferencias?

Hernández-Téllez, I., Aguirre, J. I., de la Hera, I., Onrubia, A., & Tellería, J. L. (2021). Feather traits in four southern populations of the Eurasian blackcap Sylvia atricapilla: do altitudinal movements explain the differences? **Journal of Avian Biology**, 52(12). https://doi.org/10.1111/jav.02832

- Capítulo 4 ***En revisión***

Las aves forestales de las tierras altas y de las tierras bajas difieren en sus tasas de crecimiento del plumaje: una prueba multiespecífica en el suroeste del Paleártico.

Hernández-Téllez, I., Aguirre, J. I., de la Hera, I., Onrubia, A., & Tellería, J. L. (2022). Highland and lowland forest birds differ in feather growth rates: a test in the south-western Palaearctic. **Ibis**.

METODOLOGÍA GENERAL

ÁREA DE ESTUDIO

Esta tesis se ha realizado con la información obtenida en cuatro sectores ubicados en el extremo suroccidental de la región Paleártica: *Guadarrama*, *Alcornocales*, *Rif* y *Atlas* (Fig. 5). Se trata de un territorio dominado por regiones montañosas de gran valor para la conservación (Myers et al., 2000), que engloba una gran diversidad de hábitats modulados por diferentes topoclimas vinculados a la altitud (Körner & Ohsawa, 2006). Así, el área de estudio se localiza en zonas de montaña y llanura de la Península Ibérica (en España): Sierra de Guadarrama (1090 m.s.n.m. de media) y Parque Natural de los Alcornocales (137 m.s.n.m.); y del Magreb (en Marruecos): Montañas del Rif (571 m.s.n.m.) y Cordillera del Atlas (1460 m.s.n.m.).

En estas montañas, las especies de estudio aparecen en los sectores forestales más húmedos (por ejemplo, parches de *Rubus sp.*), especialmente en los bosques frondosos de *Quercus pyrenaica*, *Q. canariensis* y *Q. suber* (Carbonell, 2003) pero también en bosques de coníferas (*Pinus sylvestris*, *Cedrus atlantica* y *Abies marocana*). Y en las zonas bajas, las aves estudiadas se asocian a bosques tolerantes a la sequía (*Q. ilex*, *Juniperus thurifera*, *Tetraclinis articulata*), y bosques de argán (*Argania spinosa*) y acacia (*Acacia spp.*) en los sectores más meridionales (Quézel, 1983). Por tanto, las áreas seleccionadas cubren un gradiente latitudinal y altitudinal dentro de las condiciones climáticas típicas del Mediterráneo con diferentes patrones de estacionalidad a lo largo del límite del área de distribución de las especies objetivo.

Con el fin de describir las condiciones ambientales y climáticas producidas por estos gradientes altitudinales, se ha caracterizado cada localidad a macroescala: cobertura de nieve para evaluar la dureza de las condiciones invernales (*capítulo 2*), variación de la productividad primaria y salud del bosque evaluada a través del Índice de Vegetación de Diferencia Normalizada (*capítulo 3*) y evolución de la temperatura a lo largo del año para explorar la duración de las ventanas temporales útiles para la cría y la muda, (*capítulo 4*); y a microescala: rasgos del hábitat para evaluar el efecto de la estructura de la vegetación en la morfología de las aves (*capítulo 4*).

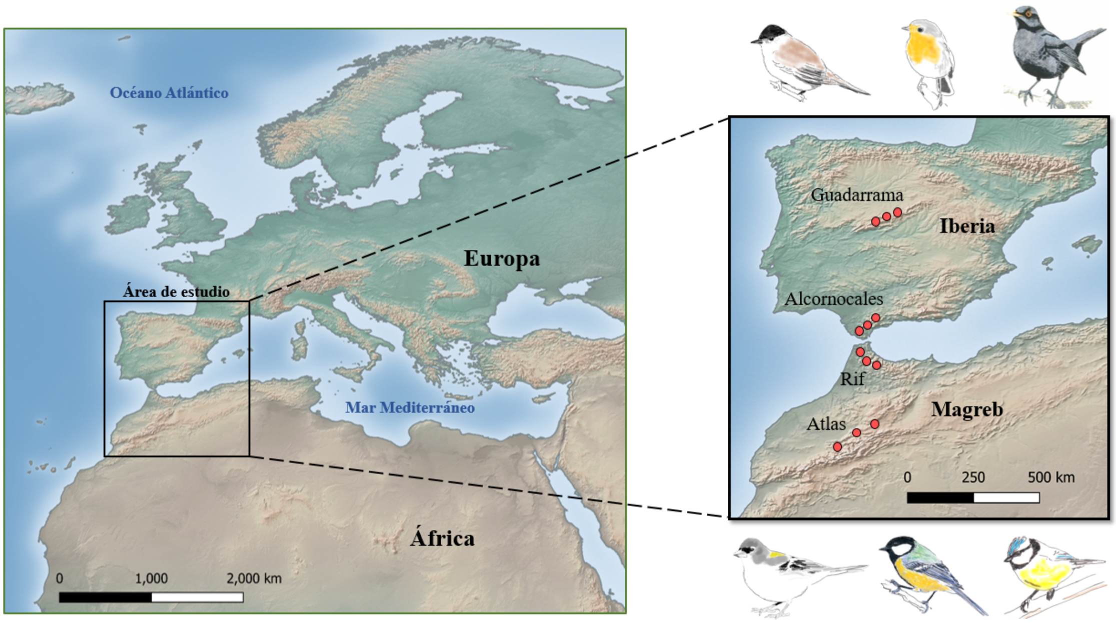

Figura 5. Localización del área de estudio con las diferentes especies modelo (en orden: *Sylvia atricapilla*, *Erithacus rubecula*, *Turdus merula*, *Fringilla coelebs*, *Parus major y Cyanistes sp.*) y localidades de muestreo (puntos rojos) dentro de los cuatro sectores de estudio en la Península Ibérica y el Magreb.

ESPECIES MODELO

La tesis se ha centrado en un conjunto de pequeños paseriformes forestales del extremo suroccidental del Paleártico (*Sylvia atricapilla*, *Erithacus rubecula*, *Turdus merula*, *Fringilla coelebs*, *Parus major y Cyanistes sp*; Fig. 5). Se trata de un grupo de aves generalistas de montaña, abundantes y de fácil observación y captura, compuesto por poblaciones con diferencias taxonómicas (subespecies monotípicas, politípicas y especies diferentes; Clements et al., 2021), distintos patrones migratorios (sedentarios, migrantes latitudinales y migrantes altitudinales; Tellería et al., 2001) y diferentes requerimientos tróficos (frugívoros, granívoros, insectívoros) y estilos de vida distintos (aves que se alimentan en las copas, en los arbustos o en el suelo; Cramp & Brooks, 1992). Sin embargo, presentan la misma estrategia de muda: los adultos reemplazan todas sus plumas (muda postnupcial completa) y los jóvenes sólo algunas de ellas (muda postjuvenil parcial) una vez al año antes del deterioro ambiental de finales de verano en sus áreas de reproducción (Jenni & Winkler, 1994). Esta variabilidad intraespecífica las convierte en buenos modelos para explorar los impulsores que determinan la diferenciación poblacional y la singularidad de los diferentes linajes de aves.

COMPORTAMIENTO MIGRATORIO

Para inferir el posible comportamiento migratorio de las poblaciones se llevaron a cabo diferentes aproximaciones:

Isótopos estables

El origen reproductor y, por tanto, la distancia de migración, puede estimarse a partir de las relaciones de isótopos estables de hidrógeno de las plumas (δDf; Catry et al., 2016; De la Hera et al., 2017), que varían geográficamente a lo largo del Paleártico (Hobson et al., 2004). Con este fin, en el *capítulo 1*, se analizaron los valores δDf de la pluma de la cola recolectada de cada individuo muestreado, cada una de las cuales habrá sido producida en las zonas de cría.

Abundancias

Los desplazamientos de las poblaciones de aves han sido inferidos históricamente por los cambios estacionales en su abundancia (Tellería et al., 2001). De esta manera, en los *capítulos 2 y 3* se estudió la distribución diferencial de poblaciones de aves en invierno y en primavera entre zonas altas y zonas bajas para explorar los movimientos altitudinales.

Morfología del ala

El análisis en mano de las aves nos permite obtener medidas morfométricas fiables con las que caracterizar el complejo funcional del vuelo. El comportamiento migratorio estará fuertemente asociado con alas más largas y puntiagudas (Hedenström, 2008). Por ello, en todos los capítulos de la tesis se han medido las distancias de las primarias a la punta del ala para esclarecer las posibles diferencias en el perfil alar de las diferentes poblaciones y predecir la eficiencia del vuelo (Weeks et al., 2022).

RASGOS DE LAS PLUMAS

El estudio de las plumas implicó la extracción y almacenaje de dos rectrices simétricas de cada individuo capturado en el campo. De esta manera, todos los datos utilizados se obtienen de aves de poblaciones naturales, un hecho trascendente si se tiene en cuenta que la mayoría de estudios sobre plumaje se han realizado sobre individuos en cautividad o ejemplares de museos (Terril, 2018). Con el fin de describir diferentes características de la infraestructura de las plumas que informan sobre el proceso de la muda y evaluar la posible variación de estos rasgos entre poblaciones, se llevaron a cabo diferentes procedimientos (Tabla 1, Fig. 6).

Tabla 1. Descripción y técnicas de análisis utilizadas para el estudio de los rasgos del plumaje.

PLUMAS	Rasgo	Significado biológico	Metodología	Capítulo
DESARROLLO	**Bandas de crecimiento**	Tasa de crecimiento de las plumas: aproximación a la velocidad de muda	Ptilocronología: medida de las 10 bandas de crecimiento centrales de plumas. Calibre digital (±0.01mm)	1, 3, 4
ESTRUCTURA	**Longitud de barbas**	Rasgos que facilitan el rendimiento mecánico de las plumas y la eficacia de vuelo	Longitud máxima de las barbas en el punto medio de la pluma. Papel milimetrado (±0,5 mm)	1, 3
	Densidad de barbas		Número de barbas en el centímetro central de la pluma. Lupa binocular (x10)	1, 3
	Raquis		Medida de la anchura dorsoventral y lateral del raquis en su base. Calibre digital (±0.01mm)	1, 3
	Ángulo de inserción barbas		Ángulo de inserción de la barba central en el raquis. Transportador de ángulos (resolución de 0,1°) sobre imágenes (LEICA DFC295 adaptada a un microscopio LEICA DM2500)	1
FUNCIONALIDAD	**Rigidez a la flexión**		Prueba de flexión dorsoventral en dos puntos (miliNewton/mm). Máquina Instron 4411 Tensile Strength Tester (TST) conectada a una balanza digital (Precisa XT220A; ±0,1 mg)	1
CALIDAD	**Masa**	Cantidad de materia depositada en las plumas	Báscula de precisión Mettler Toledo AG-245 (±0,01 mg)	1, 3, 4

En el *capítulo 1*, las medidas estructurales se tomaron sobre plumas primarias (primera primaria, la más interna); y en los *capítulos 3 y 4*, sobre plumas de la cola (quinta rectriz). Las medidas de ptilocronología se tomaron sobre la quinta rectriz a lo largo de toda la tesis.

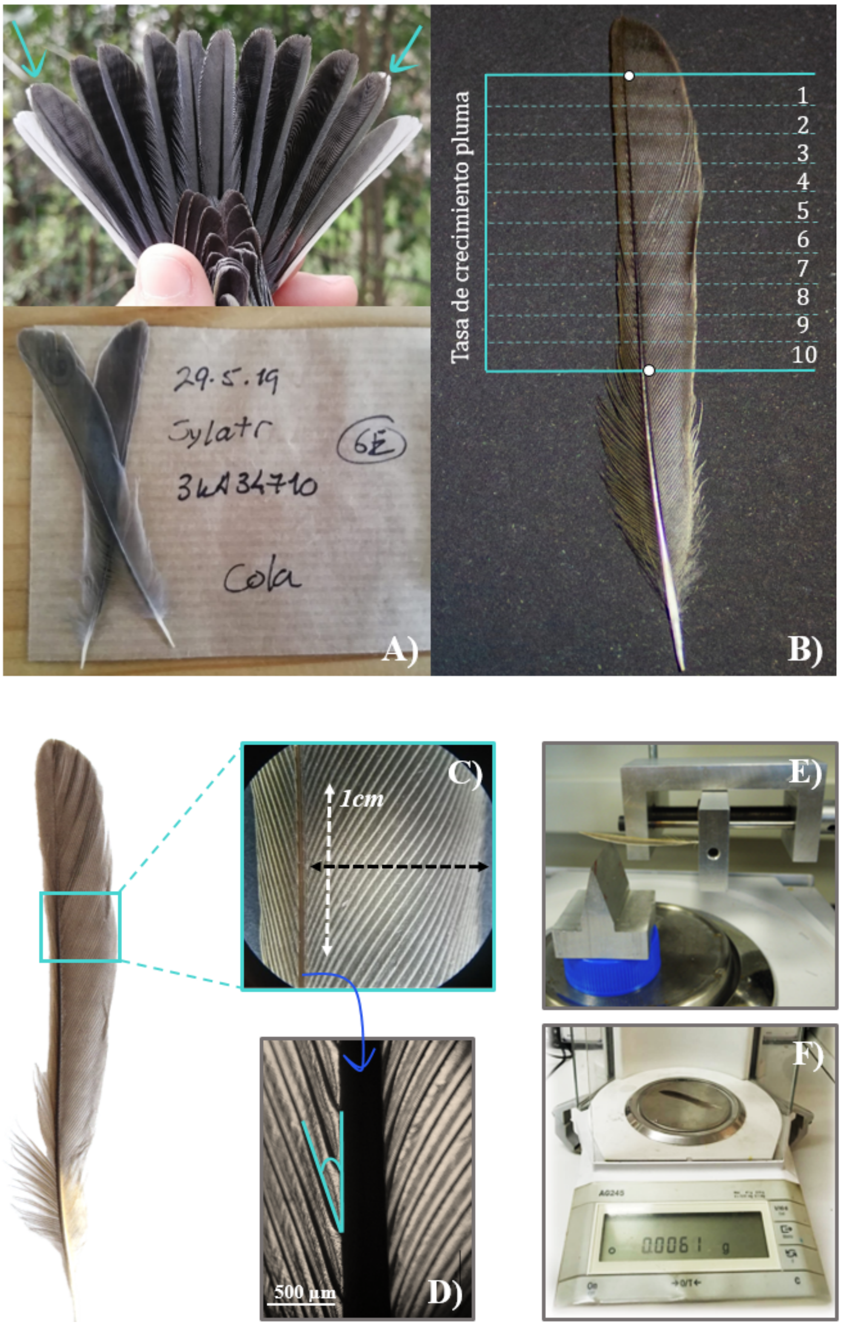

Figura 6. Ilustración de las técnicas de análisis de las plumas: A. Extracción y almacenaje de las plumas; B. Ptilocronología; C. Longitud, densidad de barbas y anchura del raquis; D. Ángulo de inserción de las barbas en el raquis; E. Rigidez a la flexión; F. Masa.

CONTRIBUCIONES METODOLÓGICAS DE LA AUTORA

La doctoranda coordinó la logística de muestreo de las dos temporadas de campo y realizó la captura, anillamiento, datado, sexado, condición física y medidas biométricas en campo de todos los ejemplares de estudio de los capítulos 2, 3 y 4 para los años 2018 y 2019 (933 individuos de las 6 especies diana). Asimismo, georreferenció cada punto de muestreo para posteriores análisis en sistemas de información geográfica y efectuó todas las plantillas de vegetación alrededor de cada red de niebla colocada (382 redes en total). Por otro lado, llevó a cabo el procesamiento de las medidas estructurales y de desarrollo de las plumas (ptilocronología, masa, longitud, número de barbas, longitud de barbas, anchura del raquis, ángulo de inserción de las barbas en el raquis) de todos los ejemplares de los capítulos 1, 3 y 4 (1227 plumas en total). Conjuntamente, analizó la morfología alar de todos los ejemplares de los capítulos 2, 3 y 4, colaboró en la elaboración de los modelos estadísticos de los capítulos 1 y 2, y fue la responsable de realizar todos los modelos estadísticos de los capítulos 3 y 4.

BLOQUE A

IMPLICACIONES DE LA MIGRACIÓN LATITUDINAL EN LAS PLUMAS Y EFECTOS DE LAS MONTAÑAS SOBRE EL COMPORTAMIENTO MIGRATORIO

CAPÍTULO 1

ADAPTACIONES MECÁNICAS Y ESTRUCTURALES A LA MIGRACIÓN EN LAS PLUMAS DE VUELO DE UN PASERIFORME PALEÁRTICO

Este capítulo está basado en el manuscrito: De la Hera, I., **Hernández-Téllez, I.**, Pérez-Rigueiro, J., Pérez-Tris, J., Rojo, F.J., & Tellería, J.L. (2020). Mechanical and structural adaptations to migration in the flight feathers of a Palaearctic passerine. **Journal of Evolutionary Biology**. 33(7): 979-989.

RESUMEN

Los actuales patrones migratorios de las aves en las regiones templadas se desarrollaron durante el retroceso de los glaciares y la posterior colonización de las zonas libres de hielo durante el Holoceno. Este proceso dio lugar a un gradiente geográfico de mayor estacionalidad a medida que aumentaba la latitud que favoreció las (co)adaptaciones morfológicas y fisiológicas relacionadas con la migración. La mayor parte de las evidencias de las adaptaciones morfológicas de las aves a la migración provienen del análisis de la variación de la longitud y la forma de las alas, pero la existencia de ajustes estructurales en las plumas ha sido muy ignorada a pesar de su potencial para estar bajo selección natural. Para arrojar algo de luz sobre esta cuestión, utilizamos datos de petirrojos europeos (*Erithacus rubecula*) que pasan el invierno en el Campo de Gibraltar (sur de Iberia), donde los petirrojos sedentarios coexisten durante el invierno con congéneres que muestran una amplia gama de orígenes reproductivos y, por tanto, de distancias de migración. Exploramos explícitamente cómo la longitud y la forma del ala, así como varias características funcionales (rigidez a la flexión), de desarrollo (tasa de crecimiento de las plumas) y estructurales (tamaño y complejidad de los componentes de las plumas) de las plumas de vuelo variaron en relación con la distancia de migración, que se estimó a partir de las relaciones de isótopos estables del hidrógeno de las plumas de la cola producidas en verano. Nuestros resultados revelaron que la distancia de migración no sólo favoreció unas alas más largas y cóncavas, sino que también promovió unas primarias con un raquis dorsoventral más grueso y unas longitudes de barbas más cortas, lo que a su vez confirió más rigidez de flexión a estas plumas. Sugerimos que estos ajustes estructurales intraplumas podrían ser una adaptación adicional, en gran medida inadvertida, dentro del síndrome migratorio aviar que podría tener el potencial de evolucionar con relativa rapidez para facilitar la ocupación de entornos estacionales.

ABSTRACT

Current avian migration patterns in temperate regions have been developed during the glacial retreat and subsequent colonization of the ice-free areas during the Holocene. This process resulted in a geographic gradient of greater seasonality as latitude increased that favoured migration-related morphological and physiological (co)adaptations. Most evidence of avian morphological adaptations to migration comes from the analysis of variation in the length and shape of the wings, but the existence of intra-feather structural adjustments has been greatly overlooked despite their potential to be under natural selection. To shed some light on this question, we used data from European robins (*Erithacus rubecula*) overwintering in Campo de Gibraltar (Southern Iberia), where sedentary robins coexist during winter with conspecifics showing a broad range of breeding origins and, hence, migration distances.

We explicitly explored how wing length and shape, as well as several functional (bending stiffness), developmental (feather growth rate) and structural (size and complexity of feather components) characteristics of flight feathers varied in relation to migration distance, which was estimated from the hydrogen stable isotope ratios of the summer-produced tail feathers. Our results revealed that migration distance not only favoured longer and more concave wings, but also promoted primaries with a thicker dorsoventral rachis and shorter barb lengths, which in turn conferred more bending stiffness to these feathers. We suggest that these intra-feather structural adjustments could be an additional, largely unnoticed, adaptation within the avian migratory syndrome that might have the potential to evolve relatively quickly to facilitate the occupation of seasonal environments.

INTRODUCTION

Current avian migration patterns in temperate regions have been shaped over the last 10 000-14 000 years, coinciding with the start of the Holocene glacial retreat (Newton, 2008). In the Western Palaearctic, glacier melting allowed the colonization of new lands by bird populations that had been confined within the Mediterranean refugia during millennia. As founder populations spread from low to high latitudes, the colonisation front gradually encountered more seasonal conditions. This shaped a latitudinal gradient of increased selection associated with longer migration distances towards the North, where individuals were able to take advantage of the summer surplus for breeding, but returned to southern latitudes annually to avoid the harsh winter conditions (Newton, 2008; Chapman et al., 2011). Subsequent changes in the environmental conditions at the Mediterranean Peninsulas could lead to the extinction of the ancestral sedentary populations that still remained in the refugia (Bell, 2000). However, there are still a few species in which the direct descendants of these ancestors persist and share their home ranges during winter with migratory conspecifics coming from different, more northern, breeding origins (Pérez-Tris & Tellería, 2002; Fandos & Tellería, 2019). These grounds of seasonal sympatry allow to simultaneously sample individuals with variable selection pressures associated with migration, whose analysis would contribute to strengthen our understanding of how avian life histories have evolved throughout this historical colonization process.

In order to effectively move between distant geographic locations, migratory birds have been selected for particular morphological, physiological and behavioural characteristics (Alerstam et al., 2003; Dingle, 2014). The overall length of the wing and its outline has captured most of the research focus in the study of the external avian morphological adaptations facilitating an energy-efficient migratory flight (Lockwood et al., 1998; Milá et al., 2008). Thus, many inter and intraspecific studies support the idea that wings become longer and more pointed as the distance between breeding and wintering grounds (i.e. migration distance) increases (Fiedler, 2005; Forschler & Bairlein, 2011; Vágási et al., 2016). However, although some structural elements of the feathers (e.g. rachis width) can determine their mechanical behaviour (i.e. bending stiffness) and potentially be under natural selection (De la Hera et al., 2010a; Szép et al., 2019), the existence of intra-feather structural adaptations to migration has been mostly overlooked, with only a few recent interspecific studies in the literature (Pap et al., 2015; 2019).

The complexity and size of feather structural components can be influenced by different, sometimes conflicting, factors. For example, migratory birds typically increase their wing span and obtain sharper wingtips by a differential elongation of the outer wing flight feathers (i.e. primaries; Lockwood et al., 1998). This feather lengthening is expected to be costly so that it might be associated with a simplification of feather structure (Aparicio et al., 2003), which could have antagonistic effects on flight performance and other plumage functions. Feather elongation could be particularly detrimental for feather structure if birds undergo time or energy constraints during feather production (Pap et al., 2008; De la Hera et al., 2009). Indeed, migratory birds tend to grow their feathers faster than their sedentary counterparts as a consequence of the temporal constraints that the former experience between breeding an autumn migration for moulting (Kiat et al., 2019). In this respect, several aviary experiments have shown that an accelerated moult affects feather structure and quality (Dawson et al., 2009; Vágási et al., 2010; Vágási et al., 2012). This could explain why the only study comparing feather characteristics between migratory and sedentary conspecific natural populations (i.e. the blackcap *Sylvia atricapilla*) found that migrants had flight feathers with a thinner rachis than sedentary counterparts (De la Hera et al., 2010a). Remarkably, however, the bending stiffness values were higher in the feathers of migratory blackcaps than in the sedentary fraction (De la Hera et al., 2010a), which suggests the existence of feather structural adjustments that allow migrants to favour some feather properties (i.e. bending stiffness), maybe at the expense of other functions (e.g. resistance to wear and mechanical fatigue; Weber et al., 2005; Weber et al., 2010).

This also highlights that our understanding of the relationship among migration (distance), feather structural characteristics and mechanical properties is still very limited (Lees et al., 2017).

In this study, we used data collected from European robins *Erithacus rubecula* seasonally sympatric during winter in *Campo de Gibraltar* (Southern Iberia), a region identified as a putative glacial refugia (Rodríguez-Sánchez et al., 2008; Médail & Diadema, 2009), to shed light into the morphological adaptations associated with migration that might have occurred in this species during the Holocene. Some mountains in this region sustain some relict submediterranean woodlands (De Dios et al., 2009) that host sedentary robin populations that also receive during winter a huge number of migratory conspecifics with a broad range of breeding origins (Bueno, 1998; Tellería & Pérez-Tris, 2004). The breeding origin and, hence, the migration distance of each wintering robin can be estimated from the hydrogen stable isotope ratios of their feathers (δD_f; Catry et al., 2016; De la Hera et al., 2017), which are produced in the previous summer at the breeding grounds. We then explored how wing length and shape, as well as several functional (i.e. bending stiffness), developmental (i.e. feather growth rate) and structural (i.e. size and complexity of feather rachis and vane) characteristics of flight feathers varied in relation to δD_f. We predicted that migration distance will be strongly associated with longer and more pointed wings, as described in other broadly distributed Palaearctic avian species and partially tested in robins (Pérez-Tris et al., 2000; Catry et al., 2016). Likewise, we expect higher values of bending stiffness in the feathers of robins migrating longer distances, as previously outlined in blackcaps (De la Hera et al., 2010a). We also tested whether ptilochronology-based measurements of tail feather growth rate, that are conservative proxies of moult speed (De la Hera et al., 2011), decrease with migration distance as expected from the existence of the abovementioned temporal constraints that might affect feather structure and quality. Finally, we explored the relationship between several feather structural characteristics and δD_f, predicting that those characteristics that might facilitate feather mechanical performance and, ultimately, long-sustained flight (e.g. longer feathers, wider rachis and more acute barb insertion angles) were favoured in birds migrating longer distances (Ennos et al., 1995; Pap et al., 2019).

METHODS

Study area and bird measurements

Birds were sampled using mist-nets and mesh-clap traps in four sites located in Campo de Gibraltar region, within the boundaries of *Los Alcornocales* and *Estrecho de Gibraltar* Natural Parks (Cádiz, Spain; Appendix 1, Fig. S1). There were less than 14 km in straight line between the farthest locations, so that these four sites could be effectively considered part of the same wintering region when inferring migration distances (see below). Two of these four localities represented woodlands, whereas the other two represented shrublands, the two main habitats that robins use for overwintering in this area (see De la Hera et al., 2018 for further details on the study sites). Given that the breeding origin of robins differs dramatically between woodlands and shrublands, obtaining samples from both habitats provided data from birds with a wide range of migration distances (De la Hera et al., 2018). Trapping sessions took place during two different winters (2006-07 and 2013-14) spanning the traditional winter season in this area (SEO/Birdlife, 2012). Thus, robins were sampled between mid-November and mid-February in winter 2006-07, and during January 2014 for winter 2013-14. Each captured Robin was aged as adult or juvenile using plumage features (Jenni & Winkler, 1994). We also measured tarsus length, maximum wing chord and wing shape considering the primary distances of the 9 longest primaries (excluding the vestigial outermost primary: P10). Primary distance was defined as the distance from the tip of each primary to the tip of the longest primary with the wing folded, assigning a value of zero to the primary (or primaries) constituting the wingtip. In winter 2006-07, all morphological variables were obtained by two experienced ringers who have their measurements standardized; while the robins captured in winter 2013-14 were measured by only one of them. Additionally, we used a syringe to extract a sample of blood from the jugular vein which was used for molecular sexing (Griffiths et al., 1998). We also collected two flight feathers. One innermost primary feather (primary 1) and one tail feather (the second outermost rectrix 5; Jenni & Winkler 1994) in order to obtain the feather traits and isotopic measurements detailed below. We could gather 146 individual robins with a complete set of data, plus one individual for which barb insertion angles could not be obtained for technical/logistical reasons. Maximum sample size was 147 (76 and 71 robins for winter 2006-07 and 2013-14, respectively).

δD_f as estimator of migration distance

The isotopic particularities of each geographic location are transferred to the feathers through the diet during plumage production. In robins, feather production typically occurs during summer at their breeding grounds. Since avian feathers are inert once they are fully-grown, these isotopic signatures are maintained on feathers until the next moulting process (Catry et al., 2016). Hydrogen stable isotopes vary geographically across the Palaearctic, where the heavy isotope (i.e. Deuterium) becomes progressively less common in rainfall from south-western Europe, where Campo de Gibraltar is located, towards the northeast (Hobson et al., 2004). Conveniently, this hydrogen isotopic pattern overlaps with one of the main migratory routes of robins (Korner-Nievergelt et al., 2014; Ambrosini et al., 2016), which probably follows the historical range expansion route of this species from the Iberian Peninsula during the Holocene (Newton, 2008). Consequently, it is reasonable to assume that the lower (the more negative) is the δD_f value of a robin wintering in Gibraltar, the more northern its breeding origin will be and, hence, a longer migration distance will have been travelled during autumn to arrive at Gibraltar (Hobson et al., 2004). Previous research strongly supports this assumption, although it also predicts the existence of some degree of variation in δD_f values between conspecifics growing their feathers in the same location (Catry et al., 2016; De la Hera et al., 2017; 2018). Although such circumstance might reduce the accuracy of the migration distance estimations made from δD_f values in our study, this would only lower the statistical power of our comparisons, making the study conservative.

In our study, migration distance was estimated from the δD_f values of the rectrix 5 feather, which were expressed in delta notation in units per mil (‰), and normalized according to the VSMOW-SLAP scale using the values obtained for three keratin standards (see De la Hera et al., 2018 for further details on the isotopic analyses). Isotopic analyses were performed in the Colorado Plateau Stable Isotope Laboratory (http://www.isotope.nau.edu/).

Wing shape estimations

We used transformed values of the primary distances described above to estimate the variation in the wing shape of robins wintering in Campo de Gibraltar region. For this

purpose, we opted for transforming primary distances into distances from the carpal joint (cP1-cP9) by subtracting, for each primary, its primary distance from the wing length. These transformed distances (cP1-cP9) were then standardized according to the method suggested by Senar and collaborators (1994), which provides more reliable measurements (cP1*-cP9*) that correct for the among-individual variation in wing size. These standardized values were included in a Principal Component Analysis (PCA) performed with the *prcomp* function in R, which gave rise to two principal components (wing concavity and wingtip pointedness) that reflected variation in wing shape among robins (see Results).

Bending stiffness of Robin feathers

Bending stiffness is a major mechanical property of flight feathers that transmits the aerodynamic forces to the musculoskeletal system during flight (Videler, 2005). According to this, it is expected that the feathers of birds performing longer flights show more resistance to be bent (i.e. greater values of bending stiffness; De la Hera et al, 2010a). Dorsoventral bending stiffness was estimated on the primary feather collected from each Robin using a two-point bending test. The system devised for this purpose consisted of a non-commercial feather testing equipment build specifically for this purpose mounted on an Instron 4411 Tensile Strength Tester (TST) machine that was connected to a high-resolution digital balance that measured the loads (Precisa XT220A; resolution of 0.1 mg). The feather testing equipment had two parts: (1) the clamping device, that was mounted in the mobile section of the TST machine and allowed clamping firmly the whole length of the calamus (inserted in the hole up to approximately the position of the superior umbilicus) using a small bolt; and (2) the loading platform, that was located on the digital balance and could be moved to the selected loading point of the feather. Each feather was tested during one minute, over which the TST machine was programmed to move the feather down at a speed of 4mm per minute, and the mass on the digital balance was automatically recorded every second. In all feathers the load was measured in the same position of the rachis (i.e. approximately 32mm from the superior umbilicus). This approach provided 60 (mass-time) points per feather. The slope of the relationship between mass (y) and time (x) for each feather was used to estimate bending stiffness (the steeper the slope, the higher the bending stiffness value). Bending stiffness was initially calculated in grams per second but it was

transformed into miliNewton/mm using the appropriate conversion factors (original value in g/s * 60s/4mm * 1kg/1000g * 9.81 m/s2 * 1000mN/1N). Each feather was measured twice and the average values used in subsequent analyses. Repeatability of the bending stiffness of primary feathers was very high and significant (intraclass correlation coefficient $r_i = 0.86$, $F_{145,146} = 13.5$, $P < 0.001$), supporting the reliability of this measurement.

Feather structural and developmental traits

Primary feathers were weighed in a high-resolution digital balance (Mettler Toledo AG-245; resolution 0.01 mg) and their full length measured (from inferior umbilicus to the distal tip) using a digital caliper (resolution 0.01 mm). For primary feathers, we also took a set of structural measurements that could show variation in relation to migration distance. Thus, we used a digital caliper to measure the dorsoventral and lateral width of the rachis at its base (at the position of superior umbilicus). We also used a binocular magnifier (x10) to count the number of barbs in the central centimetre of the feather, and the total length of the barbs located in the middle point of the feather, which were stretched using an entomological pin and its maximum length calculated using chart paper as background (resolution 0.5 mm). We also estimated the insertion angle of the central barb into the rachis by means of a Powerfix Prof angle conveyor (resolution of 0.1°). This was done on pictures taken using a LEICA DFC295 camera adapted to a LEICA DM2500 microscope. The density, length and angle of the barbs were measured in both the inner and the outer vane of each feather. Outer barbs insertion angles were measured in relation to the distal part of the rachis, considering a straight line from the insertion point of the barb to its position at 0.5 and 1.5 mm of rachis length towards its tip. We selected two different positions for estimating outer barb angles to explore the consistency of the measurement. Outer barb angles did not differ when they were measured at 0.5 or 1.5mm (paired $t_{145} = 0.11$, $P = 0.911$) and were also significantly correlated with each other ($r = 0.60$, $P < 0.001$). For simplifying subsequent analyses, we opted for using a combination of both measurements that was obtained from a PCA (eigenvalue = 1.60; explained variance = 0.80; factor loadings = 0.71). Only the 0.5 mm measurement could be obtained from the pictures for the inner barb insertion angle, given its larger angle compared to the outer barbs. Since outer insertion barb angles did not correlate with inner ones ($r = 0.06$, $P = 0.508$), inner and outer angles were analysed independently.

We followed a similar variable simplification procedure for outer and inner barb lengths (PCA: eigenvalue = 1.29; explained variance = 0.65; factor loadings = 0.71) and outer and inner barb densities (eigenvalue = 1.56; explained variance = 0.78; factor loadings = 0.71), which additionally provided a much better fit to a normal error distribution of these two variables (i.e. barb length and barb density) in the subsequent statistical analyses.

For tail feathers, we also measured their length and mass, following the same procedure described above, and obtained the width of 10 growth bars according to Grubb (2006). Juvenile birds (n = 72) were ruled out from this part of the study because growth bars are hardly visible in juvenile feathers and they might not follow a daily cycle (Elderbrock et al., 2012). Unlike juvenile feathers, growth bars are much more conspicuous in adult feathers (i.e. those feathers produced during a complete postbreeding moult; n = 75) and it has been shown that their (length-corrected) growth rate estimates are correlated with overall moult speed both within and between bird species (De la Hera et al., 2011).

Statistical analyses

We used linear models to test whether migration distance (δD_f) correlated with observed variation in wing length and shape (wing concavity and wingtip pointedness), primary feather characteristics (feather length, feather mass, dorsoventral and lateral rachis width independently, combined barb density, combined barb length, combined outer barb insertion angle, and inner barb insertion angle) and tail feather growth rate during the complete moult. All models included age (adult, juvenile), winter (2006-07, 2003-14), sex (male, female) and age-sex interaction as fixed effects factors. Winter-age and winter-sex interactions were excluded to avoid over-parameterization, but their inclusion in the models did not affect the results qualitatively. Tarsus length was included as a covariate representing bird body size in the wing length and primary feather length statistical models (see Table 2). Similarly, feather length was used as covariate in the remaining feather trait analyses (see Table 3). The only exception to this model structure was the analysis of tail feather growth rate, where only adults were considered, so that the age and the age-sex interaction terms were not computed. We finally explored the quantity of variance in bending stiffness that could be explained by length-corrected (where appropriate, see Results) feather structural characteristics (as size-independent measures of these traits) after accounting for feather length, age, winter, sex, age-sex interaction effects, and including or not migration distance (δD_f) in the model. The purpose of these last analyses was to explore whether observed variation in bending stiffness was better predicted by among-individual differences in these feather structural traits, by migration distance (δD_f) alone, or by a combination of both. The latter two options would suggest the existence of non-measured variation associated with δD_f in feather structure/configuration contributing to bending stiffness (De la Hera et al., 2010a). We did this by comparing the coefficients of determination (R^2) of each of the three models (see Results). All analyses were performed in R version 3.4.3 (R Core Team 2017) using the default *stats* package and considering a threshold for statistical significance of $\alpha = 0.05$.

RESULTS

The PCA on the standardized primary distances provided two principal components (PC). PC1 was interpreted as an index of wing concavity (eigenvalue = 4.09; explained variance = 0.45; factor loadings: cP9* = 0.17, cP8* = 0.19, cP7* = 0.17, cP6* = -0.12 , cP5* = -0.37, cP4* = -0.44, cP3* = -0.45, cP2* = -0.44, cP1* = -0.40,), where individuals with higher PC1 scores showed proportionally shorter inner primaries, i.e. more concave wings. On the other hand, PC2 reflected variation in wingtip pointedness (eigenvalue = 1.95; explained variance = 0.22; factor loadings: cP9* = 0.52, cP8* = 0.57, cP7* = 0.49, cP6* = -0.17, cP5* = 0.03, cP4* = 0.12, cP3* = 0.16, cP2* = 0.21, cP1* = 0.21), whereby higher PC2 scores were associated with longer outer primaries for a given degree of wing concavity, or more pointed wingtips. Wing length was not correlated with wing concavity (PC1; wing effect: estimate ± se = -0.04 ± 0.08, $t_{145} = -0.53$, P = 0.595) or wingtip pointedness (PC2 wing effect: estimate ± se = 0.05 ± 0.05, $t_{145} = 0.83$, P = 0.407) supporting the success of the standardization procedure.

After controlling for other confounding factors, robins with lower δD_f values exhibited longer (Fig. 7A) and more concave wings (PC1, Fig. 7B), but no significant association between δD_f and wingtip shape (PC2) was detected (Table 2). In parallel to the pattern observed for wing length, the innermost primary feathers also became longer with migration distance (Table 2, Fig. 7C).

Table 2. Results of the Linear Models that analysed the relationship between an isotopic proxy of migration distance (δD_f) and wing length, wing concavity (PC1), wingtip pointedness (PC2) and primary feather length, after accounting for other potential confounding effects. Significant effects were additionally highlighted in bold letter. Sample size was 147 for all the analyses. N.A. (not applicable) indicates effects that were not tested for some response variables according to the rationale raised in the Methods section.

Fixed effects		Wing length	Wing concavity (PC1)	Wingtip pointedness (PC2)	Primary length (P1)
Intercept (adult, female, 2006-07)					
Estimate ± se		56.08 ± 4.90	-2.39 ± 0.55	-0.84 ± 0.37	48.79 ± 3.95
δD_f					
	Estimate ± se	**-0.04 ± 0.01**	**-0.04 ± 0.01**	-0.01 ± 0.00	**-0.01 ± 0.00**
	t	**-6.67**	**-5.18**	-1.39	**-2.99**
	P	**<0.001**	**<0.001**	0.167	**0.003**
Tarsus length					
	Estimate ± se	**0.51 ± 0.20**	*N.A.*	*N.A.*	0.23 ± 0.16
	t	**2.62**			1.44
	P	**0.010**			0.153
Age (juv)					
	Estimate ± se	**-0.79 ± 0.34**	0.61 ± 0.39	**1.24 ± 0.26**	-0.33 ± 0.27
	t	**-2.34**	1.55	**4.74**	-1.20
	P	**0.021**	0.123	**<0.001**	0.231
Sex (male)					
	Estimate ± se	**2.24 ± 0.38**	0.32 ± 0.44	-0.17 ± 0.30	**1.33 ± 0.31**
	t	**5.85**	0.73	-0.83	**4.31**
	P	**<0.001**	0.467	0.559	**<0.001**
Winter (2013-14)					
	Estimate ± se	-0.15 ± 0.27	-0.10 ± 0.31	-0.17 ± 0.21	-0.36 ± 0.22
	t	-0.56	-0.33	-0.83	-1.65
	P	0.574	0.740	0.410	0.102
Age × sex					
	Estimate ± se	0.40 ± 0.54	-0.88 ± 0.63	-0.04 ± 0.42	0.47 ± 0.44
	t	0.74	-1.40	-0.10	1.07
	P	0.463	0.165	0.920	0.288
Model R-squared (R^2)		0.47	0.19	0.25	0.30

Note: Significant effects were additionally highlighted in bold letter. Sample size was 147 for all the analyses. N.A. (not applicable) indicates effects that were not tested for some response variables according to the rationale raised in the Methods section.

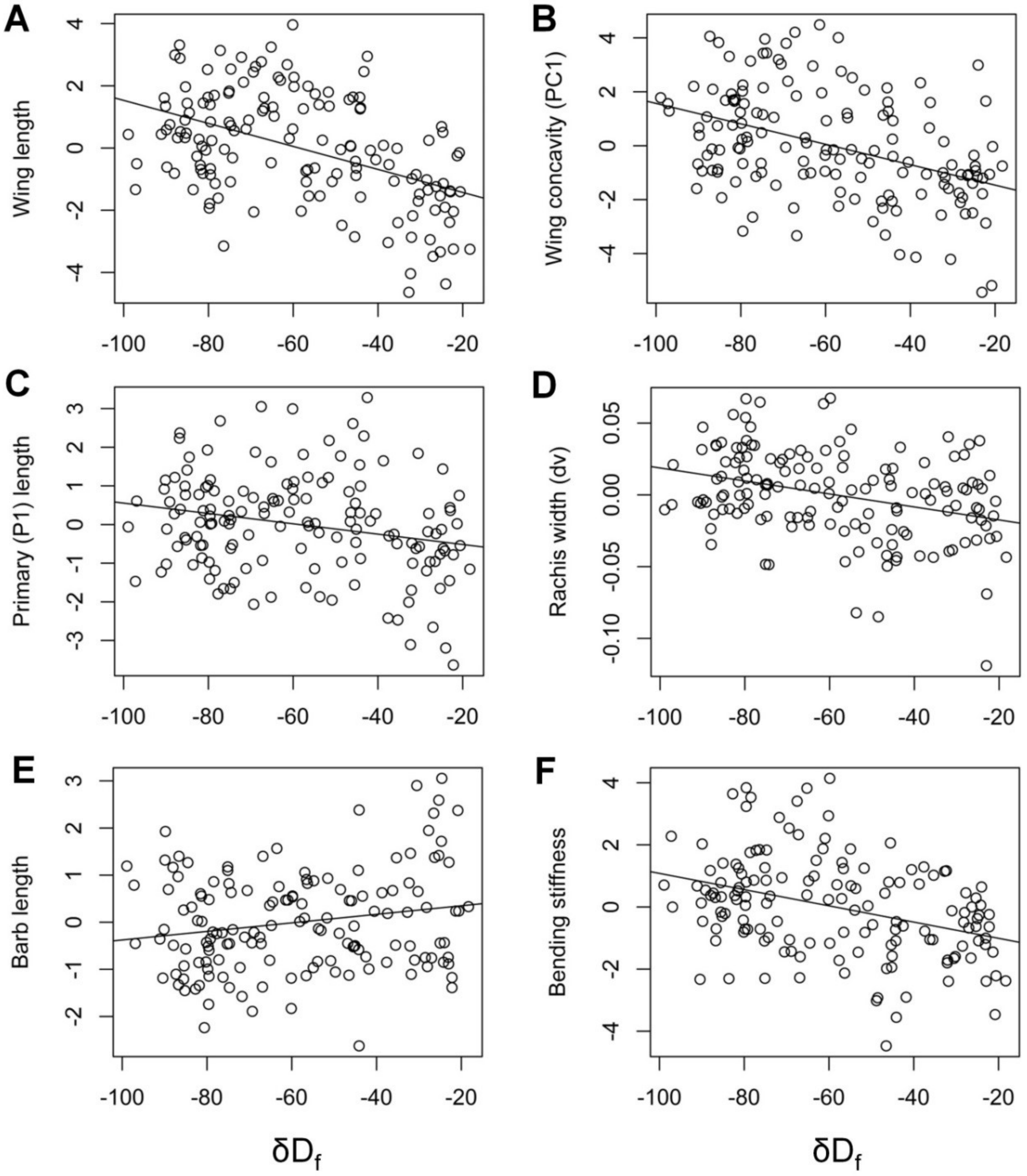

Figure 7. Relationship between an isotopic proxy of migration distance (δD_f) and a set of migration-related morphological and functional traits: (A) wing length, (B) wing concavity, (C) primary feather length, (D) dorsoventral rachis width, (E) barb length, and (F) bending stiffness. These traits were represented in the graphs as the residuals derived from the corresponding models shown in Table 2 and 3, but excluding δD_f effects, whose variation is represented in the Y axis.

Rachis dorsoventral width and bending stiffness increased significantly with migration distance (Fig. 7D and 7F), whereas the combined measure of outer and inner barb lengths decreased (Fig. 7E) after accounting for feather length and other factors affecting each trait variation (Table 3). No significant effects of δD_f were detected for primary feather mass, rachis lateral width or (inner or outer combined) barb insertion angles (Table 3). Neither was feather growth rate of adult feathers significantly correlated with migration distance

(δD_f effect: estimate ± se = -0.01 ± 0.01, t_{70} = -1.39, P = 0.169) after accounting for other fixed effects (feather length effect: estimate ± se = 0.38 ± 0.07, t_{70} = 5.34, P < 0.001; sex effects: estimate ± se =-0.80±0.32, t_{70} = -2.47, P = 0.016; winter effect: estimate ± se = 0.27± 0.28, t_{70} = 0.99, P = 0.325).

Table 3. Results of the Linear Models that analysed the relationship between an isotopic proxy of migration distance (δD_f) and some structural and functional feather characteristics (primary mass, dorsoventral (dv) and lateral (lat) rachis width, barb length, barb density, outer and inner barb insertion angles, and bending stiffness), after accounting for feather length and other effects. Sample size was 147 for all the analyses, except for the outer and inner barb angle analyses, whose samples sizes were 146.

Fixed effects		**Primary mass**	**Rachis width (dv)**	**Rachis width (lat)**	**Barb length (combined)**	**Barb density (combined)**	**Outer barb angle (combined)**	**Inner barb angle**	**Bending stiffness**
Intercept (adult, female, 2006-07)	Estimate±se	-2.55 ± 0.79	0.57 ± 0.10	0.37 ± 0.15	-7.39 ± 3.80	10.72 ± 4.21	-0.91 ± 4.55	29.3 ± 8.71	-33.1 ± 5.41
δD_f	Estimate ± se	-0.00 ± 0.00	**-0.00 ± 0.00**	-0.00 ± 0.00	**0.01 ± 0.00**	-0.00 ± 0.00	-0.00 ± 0.01	0.00 ± 0.01	**-0.03 ± 0.01**
	t	-1.73	**-4.56**	-0.04	**2.52**	-1.03	-0.14	0.14	**-5.09**
	P	0.086	**<0.001**	0.973	**0.013**	0.305	0.885	0.889	**<0.001**
Feather length	Estimate ± se	**0.14 ± 0.01**	**0.00 ± 0.00**	**0.01 ± 0.00**	**0.15 ± 0.07**	**-0.19 ± 0.08**	0.02 ± 0.08	-0.12 ± 0.16	**0.81 ± 0.10**
	t	**9.57**	**2.12**	**2.19**	**2.10**	**-2.49**	0.28	-0.77	**8.16**
	P	**<0.001**	**0.036**	**0.030**	**0.037**	**0.014**	0.783	0.444	**<0.001**
Age (juv)	Estimate ± se	**-0.18 ± 0.05**	-0.01 ± 0.01	**0.02 ± 0.01**	-0.29 ± 0.23	**-0.66 ± 0.25**	-0.30 ± 0.27	0.38 ± 0.52	-0.24 ± 0.32
	t	**-3.83**	-0.86	**2.23**	-1.29	**-2.63**	-1.12	0.72	-0.74
	P	**<0.001**	0.393	**0.027**	0.199	**0.009**	0.266	0.470	0.458
Sex (male)	Estimate ± se	**0.14 ± 0.06**	**0.03 ± 0.01**	**0.03 ± 0.01**	0.27 ± 0.27	-0.16 ± 0.30	-0.52 ± 0.32	-0.01 ± 0.62	**1.96 ± 0.39**
	t	**2.53**	**4.16**	**2.60**	0.99	-0.54	-1.59	-0.02	**5.06**
	P	**0.012**	**<0.001**	**0.011**	0.326	0.588	0.115	0.986	**<0.001**
Winter (2013-14)	Estimate ± se	0.02 ± 0.04	**0.01 ± 0.01**	0.01 ± 0.01	0.07 ± 0.18	0.13 ± 0.20	-0.25 ± 0.22	**1.61 ± 0.42**	-0.41 ± 0.26
	t	0.57	**2.27**	0.78	0.40	0.66	-1.14	**3.86**	-1.58
	P	0.572	**0.025**	0.438	0.690	0.510	0.255	**<0.001**	0.117
Age × sex	Estimate ± se	0.00 ± 0.08	-0.00 ± 0.01	**-0.03 ± 0.01**	-0.60 ± 0.36	-0.07 ± 0.40	0.36 ± 0.44	0.42 ± 0.0.83	-0.90 ± 0.52
	t	0.05	-0.33	**-2.39**	-1.65	-0.17	0.84	0.50	-1.74
	P	0.958	0.744	**0.018**	0.102	0.868	0.403	0.618	0.084
Model R-squared (R^2)		0.61	0.36	0.12	0.16	0.15	0.04	0.12	0.62

The model that included length-corrected feather structural characteristics explained 13% more variance in bending stiffness (Table 4; $R^2 = 0.75$) than the previous model that considered δD_f instead (Table 3; $R^2 = 0.62$). However, the residuals derived from the model shown in Table 4 were still significantly correlated with δD_f ($r = -0.20$, $P = 0.016$), although the addition of this term to the data structure shown in Table 4 only increased the coefficient of determination by 2% ($R^2 = 0.77$; see Appendix 1, Table S1).

Table 4. Relationship between feather structural characteristics and bending stiffness of primary feathers after accounting for age, sex, winter and age-sex interaction effects. The length-corrected residuals of feather mass, rachis width (dv and lat), barb length and barb density were included in the models to obtain size-independent measures of these traits as shown in Table 3. Sample size was 146 for this analysis.

Bending stiffness (Model R^2= 0.75)			
Fixed effects	Estimate ± se	*t*	*p*
Intercept (adult, female, 2006-07)	-44.92 ± 4.72		
Feather length	**1.07 ± 0.08**	**13.22**	**<0.001**
Age (juv)	0.38 ± 0.30	1.28	0.204
Sex (male)	**0.84 ± 0.33**	**2.52**	**0.013**
Winter (2013-14)	**-0.68 ± 0.23**	**-2.97**	**0.004**
Residuals feather mass	**3.38 ± 0.54**	**6.32**	**<0.001**
Residuals rachis width (dv)	**16.77 ± 3.67**	**4.57**	**<0.001**
Residuals rachis width (lat)	1.46 ± 2.68	0.55	0.586
Residuals barb length	**-0.36 ± 0.11**	**-3.21**	**0.002**
Residuals barb density	-0.11 ± 0.11	-1.07	0.285
Outer barb insertion angle	0.03 ± 0.09	0.33	0.741
Inner barb insertion angle	-0.03 ± 0.05	-0.61	0.543
Age × sex	**-0.99 ± 0.44**	**-2.24**	**0.027**

DISCUSSION

Our results revealed that migration distance not only favours a specific configuration of wing size and shape, but also predicts the variation of some intra-feather structural characteristics that could benefit long-sustained migratory flights.

By accounting in our statistical tests for the large variation between age and sex in wing size using molecular methods to discriminate between male and female robins (Griffiths et al., 1998) and standardization procedures (Senar et al., 1994), we could uncover the existence of longer and more concave wings, but not sharper wingtips, as migration distance increased in this passerine species. This widely acknowledged pattern across avian taxa had not been appropriately addressed in robins so far (Pérez-Tris et al., 2000; Catry et al., 2016), probably because of the difficulty of estimating the migration distance of specific robin individuals and populations (Korner-Nievergelt et al., 2014; Ambrosini et al., 2016), and because this pattern can be easily blurred by the large variation between sex and age in wing length (Ellrich et al., 2010; De la Hera et al., 2017). The use of δD_f values as indirect surrogates of breeding origin in Campo de Gibraltar, where robins with a wide range of geographic origins concur in sympatry during winter, has significantly facilitated this purpose.

Apart from these differences in the size and shape of the wings, the comparison of feather structural characteristics between conspecific individuals sharing the same wintering grounds but differing in migration distance allowed us to identify candidate feather traits that could have been favoured by the selective pressures of migration. Thus, we found that migration could have promoted a thicker dorsoventral rachis, shorter barb lengths and also longer inner primaries (P1). It could be argued that observed variation in these traits was not mediated by selection, but by geographic differences in food availability that might affect feather characteristics. However, we think this possibility is unlikely, since feather mass and feather growth rate (two potential body condition indexes; Grubb, 2006; De la Hera et al., 2009) did not vary significantly in relation to migration distance (see below).

An increased diameter of the rachis would be a straightforward adaptive solution to improve the bending stiffness of flight feathers (Tubaro, 2003; Weber et al., 2005). This possibility does not seem to be hampered in robins by the temporal and energetic constraints that migration could exert during moulting and the fledging period (De la Hera et al., 2010b). This is additionally supported by the fact that length-corrected feather growth rate, a surrogate of moult speed (De la Hera et al., 2011), and migration distance were not correlated in adult robins. Migration-constraints have been suggested to potentially limit the quantity of material available for feather production (Serra, 2001; Hall & Fransson, 2000), which would explain the narrower (dorsoventral) rachis in migratory blackcaps and the lighter mass of some of their feather tracts (i.e. tail feathers) in relation to sedentary conspecifics (De la Hera et al., 2010a; De la Hera et al., 2010b). Contrary to what was observed in blackcaps, migration was positively correlated with the dorsoventral width of the rachis in robins and, although non-significant, there was also a tendency in more migratory birds to show heavier primary (Table 3) and tail flight feathers (see Appendix 1, Table S2). These contrasting patterns between these two species may represent different ways in which (sedentary) populations of European passerines are adapted to living at the edge of their breeding range. Thus, body condition deteriorates in Campo de Gibraltar for robins (Pérez-Tris et al., 2000) but not for blackcaps (Carbonell et al., 2003), which not only could set limitations on feather production counterbalancing the benefits of a non-temporally constrained moult, but might also explain the recent population decline observed in local sedentary robins at this peripheral area (Tellería, 2015). However, in spite of these differences between robins and blackcaps in the relationship of migration with rachis width and feather mass, bending stiffness values were higher in the feathers of the migrants for both species. This suggests that the way whereby migration determines the configuration and distribution of feather structural resources to obtain feathers with better mechanical behaviour (i.e. increased bending stiffness) would vary among species (Lees et al., 2017).

We did not predict the existence of a significant association between barb length and migration distance. The few studies that compared feather structural characteristics across multiple avian taxa with variable flight types and life histories did not consider this trait (Pap et al., 2015; 2019), so it is difficult to elucidate at this point how shorter barbs could contribute to a more efficient migratory flight. Tentatively, barb length reduction might be explained as a counterbalance for obtaining thicker rachises and longer feathers that would impact on other feather functions not relevant for migration (Weber et al., 2005). Our results did not find evidence supporting that migration favoured the lateral width of the rachis, barb density or barb insertion angles, which suggests that the configuration of these traits could be more influenced by some life-history characteristics that would be more homogenous between robins differing in migration distance.

Our results additionally showed that observed variation in bending stiffness between robins was mostly explained by differences in the feather traits analyses (see Table 4 and

Appendix 1, Table S1), although there is still some room for additional, less perceptible (De la Hera et al., 2010a; Lees et al., 2017), structural adjustments at microscopic level that would require additional research with the appropriate technology (e.g. tomography of the feather shaft; Weber et al., 2010). Together with previous evidence in blackcaps (De la Hera et al., 2010a), this study provides additional support to the idea that the acquisition of flight feathers with better bending stiffness in migratory birds could have been a general pattern in birds during the Holocene to facilitate their migratory flights and the subsequent colonization of geographic grounds recently freed from ice. Thus, the adoption of migration in avian life histories not only has pervasive consequences on the physiology, behaviour and general morphology of birds, but its selective pressures would also have repercussions in the configuration of flight feather structure, a pattern that had been largely ignored so far. In a similar way to what has been reported for the size and shape of the flight apparatus, the structure and mechanical properties of flight feathers might also be affected in migratory birds by ongoing anthropogenic alterations, such as the widespread landscape changes (Desrochers, 2010) or global warming (Møller et al., 2010; Remacha et al., 2020), which would deserve further investigation. These intra-feather adjustments could have an adaptive nature and be part of the group of integrated adaptations that constitute the migratory syndrome in birds (Piersma et al, 2005). A coordinated evolution of all these traits might have occurred relatively quickly reducing the energetic costs of long-sustained flights, increasing fitness and, hence, allowing the colonization of seasonal environments.

CAPÍTULO 2

LA ESTACIONALIDAD ALTITUDINAL COMO POTENCIAL IMPULSOR DE LA DIVERSIFICACIÓN MORFOLÓGICA EN LAS POBLACIONES DE AVES DE BORDE

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RESUMEN

Las poblaciones situadas en los límites de baja latitud del área de distribución de una especie (poblaciones del borde posterior) suelen considerarse más vulnerables al cambio climático. Sin embargo, se ha pasado por alto su capacidad de rastrear diferentes entornos ambientales a escala regional, aunque esto puede ser relevante para evaluar con precisión su capacidad de adaptación para hacer frente a los cambios en curso. Aquí probamos si el pinzón africano endémico (*Fringilla coelebs africana*) sigue los cambios ambientales (por ejemplo, el aumento de las bajas temperaturas, la cubierta de nieve) reordenando sus números entre las estaciones (primavera vs. invierno) a lo largo de los gradientes de altitud de su área de distribución en el noroeste de África. Además, comprobamos si estos cambios estacionales en la abundancia iban acompañados de variaciones morfológicas, lo que sugiere un proceso de diversificación de la población. Se evaluó la abundancia del pinzón africano en tierras de cultivo cubiertas de árboles y en zonas boscosas distribuidas a lo largo de un gradiente de altitud en primavera e invierno. Además, capturamos y medimos a los pinzones dentro del gradiente de estudio para explorar los patrones de variación morfológica. Nuestros resultados mostraron que los pinzones se desplazaron a las tierras bajas desde las tierras altas cubiertas de nieve durante el invierno. Además, los individuos de las tierras altas mostraban alas más largas y cóncavas que sus homólogos de las tierras bajas. Estos rasgos morfológicos suelen estar relacionados con la eficiencia del vuelo en las aves migratorias, lo que sugiere la presencia de movimientos altitudinales destinados a seguir la estacionalidad ambiental causada por la orografía. Estos resultados sugieren un papel potencial de la estacionalidad altitudinal como impulsor de la diversificación regional dentro de las poblaciones del pinzón africano, que podría estar ocurriendo en otras especies de aves del norte de África dada su relativamente alta endemicidad. Las implicaciones evolutivas y de conservación de estos desplazamientos han sido a menudo pasadas por alto a pesar de que pueden conformar la capacidad de adaptación de las poblaciones de aves de borde para hacer frente a los cambios ambientales en curso en esta zona periférica del Paleártico.

ABSTRACT

Populations at the low latitude limits of a species range (rear-edge populations) are often considered more vulnerable to climate change. However, their ability to track different environmental settings at a regional scale has been widely overlooked, although this may be relevant to accurately assess their adaptive capacity to cope with ongoing changes. Here we tested whether the endemic African chaffinch (*Fringilla coelebs africana*) tracks environmental changes (e.g. increasing low temperatures, snow cover) by rearranging their numbers between seasons (spring vs. winter) along the altitude gradients of its northwestern

African range. We additionally tested whether these seasonal changes in abundance were paralleled by morphological variation, suggesting a process of population diversification. We assessed African chaffinch abundance in tree covered farmland and woodland sites distributed along an altitude gradient in spring and winter. In addition, we captured and measured chaffinches within the study gradient to explore the patterns of morphological variation. Our results showed that chaffinches shifted to lowlands from snow covered highlands during winter. In addition, highland individuals showed longer and more concave wings than their lowland counterparts. These morphological traits are usually related to flight efficiency in migratory birds, which suggest the presence of altitudinal movements aimed to track the environmental seasonality caused by orography. These results suggest a potential role of altitudinal seasonality as a driver of regional diversification within the African chaffinch populations, which could be occurring in other North African avian species given their relatively high endemicity in the region. The evolutionary and conservation implications of these displacements have been often overlooked despite they can shape the adaptive capacity of rear-edge bird populations to face the ongoing environmental changes in this peripheral area of the Palaearctic.

INTRODUCTION

In a context of global warming and poleward shift of species distributions, it has been suggested that populations living at the low latitude limits of a species range (rear-edge populations) would be more likely to become extinct (Hampe & Petit, 2005). In this context, the deterioration of environmental conditions due to climate change will particularly undermine the habitat quality in these peripheral locations, leading to the extinction of the populations they harbor. However, this assumption often overlooks some particularities affecting the sensitivity to changes of these peripheral populations (Vilà-Cabrera et al., 2019). For instance, many rear edge populations are taxonomically different from the core populations, suggesting reproductive isolation and putative adaptations to regional conditions (Pironon et al., 2017; Angert et al., 2020). Thus, some intrinsic characteristics of rear-edge populations can be useful to predict their responses to environmental change, which raises the interest of exploring the ecological drivers promoting their regional diversification within their restricted geographical setting (Williams et al., 2008). In this context, investigating trait variation along environmental gradients could reveal mechanisms critical for understanding the adaptive capacity of rear-edge populations.

The ability to track the current spatial-temporal changes in habitat suitability might be an advantageous trait to overcome future environmental challenges (Robinson et al., 2009; Travis et al., 2013). In this context, birds display a broad range of dispersion strategies (Sheard et al., 2020), including migratory movements which are evident between species, but can also occur among populations of the same species, or between individuals of the same population (e.g. partial-migratory species, Dingle & Drake, 2007; Chapman et al., 2011). In temperate regions of the northern hemisphere, a common pattern in widely distributed birds is the reduction of the migratory intensity and/or prevalence towards the lowest latitude of their range, which suggests a sedentary life style in the most southern populations (Newton & Dale, 1996). However, in the presence of environmental heterogeneity caused by mountain ranges, these southern populations could perform seasonal altitudinal displacements, whose biological and conservation implications have often been overlooked (Boyle et al., 2016; Boyle, 2017; Hsiung et al., 2018; Williamson & Witt, 2021). For instance, because of the similar environmental seasonality of latitudinal and altitudinal gradients, it can be hypothesized that individuals performing altitudinal movements would differ from their sedentary counterparts in some phenotypic traits associated with flight economy (Tellería et al., 2001; Lundblad & Conway, 2019). Thus, the spatial-temporal patterning of habitat suitability related to orography could be a main driver of population diversification at local scales, which could improve the potential of species to face environmental changes (Richardson et al., 2014).

Northwestern Africa is an area increasingly affected by drought as a consequence of raising temperatures (Bucchignani et al., 2018), which can jeopardize the long-term persistence of many species (Hampe & Petit, 2005). The region is covered by high plateaus and mountains (Fig. 8) occupied by rear-edge populations of Palaearctic forest birds (Merker & Chandler, 2020) whose taxonomic differentiation (Iseenman & Thévenot, 2018) could result from reproductive isolation and putative adaptations to regional conditions (García-Ramos & Kirkpatrick, 1997; Kawecki, 2008). Here we explore the altitudinal movements of the endemic African chaffinch (*Fringilla coelebs* subsp. *Africana* J.Levaillant 1850; Griswold & Baker, 2002; Perktas et al., 2017) in Morocco, which is distributed along a wide environmental gradient in northwestern Africa (Thévenot et al., 2003; Tellería et al., 2021). This population is reputed as sedentary since it is observed within its breeding range all year round (Thévenot et al., 2003). However, this distribution does not preclude the existence of seasonal movements of chaffinches from the most elevated areas that, together with a morphological differentiation to improve flight efficiency, could support independent dynamics of diversification shaped by orography (Tellería et al., 2001). In this study, we tested this hypothesis by exploring the putative link of altitude to seasonal changes in abundance and morphology according to the following predictions:

Seasonal changes in abundance. Birds can be compelled to leave highlands seasonally by the effect of some particular weather events, such as the direct or indirect effect of low temperatures. For instance, ground feeding birds will leave snow-covered areas when the access to ground food collapses (Carrascal et al., 1987, 2012a). Here we tested whether the abundance of the African chaffinch reduces along an altitude gradient and whether this decrease is especially sharp over an altitude threshold in which snowfalls might restrict the access to ground food on which this species relies (Cramp & Perrins, 1994).

Morphological variation. We tested whether the external flight apparatus of the African chaffinch varied with altitude. Since wing configuration can be related to flight efficiency, which affects migration and dispersal in birds (Winkler & Leisler, 1992; Hedenström, 2008; Vágási et al., 2016; Sheard et al., 2020; Claramunt, 2021), we predict that highland chaffinches will show longer and more concave, or pointed, wings than lowland counterparts, which would support the existence of altitudinal movements within their range.

METHODS

Study area

The study area covers the northwestern corner of Africa in Morocco (Fig. 8A), which is crossed by the Rif and Atlas mountains (Tubkal mountain, 4,164 m a.s.l., is the highest altitude). Since these mountains intercept the wet air masses arriving from the Atlantic Ocean, they strongly affect local rainfall, showing a more humid climate on the north-western than on the south-eastern slopes. Mountains also produce a sharp altitudinal gradient of environmental conditions, with lower temperatures and more frequent snowfalls at higher altitudes (Boudhar et al., 2011; Marchane et al., 2015). As a consequence of these climatic factors, the area is occupied by humid forests in the north (*Quercus suber*, *Q. pyrenaica*), fir (*Abies marocana*) and cedar forests (*Cedrus atlantica*) in some western slopes, drought-tolerant woodlands (*Q.ilex*, *Juniperus thurifera*, *Tetraclinis articulata*) in lowland areas, and argan (*Argania spinosa*) and acacia (*Acacia* spp.) woodlands in the southernmost sectors (Fig. 8B; Quézel, 1983).

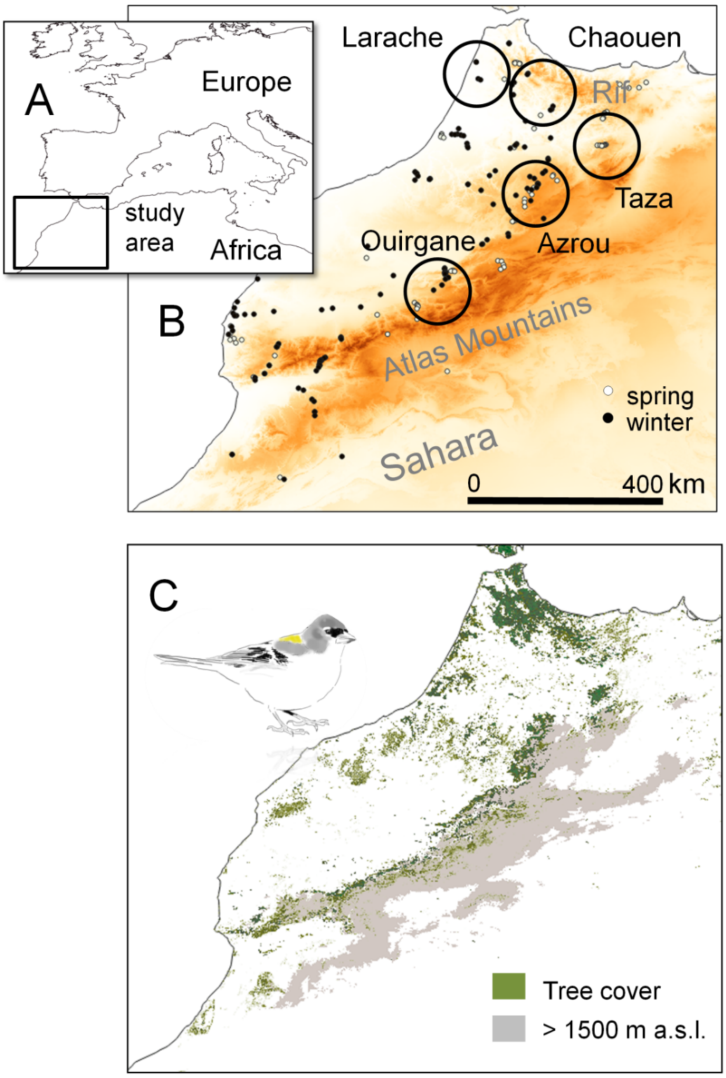

Figure 8. Situation of the study area within the Western Palaearctic (A) and location of line transects carried out in spring and winter (white and black small dots respectively) and the areas (circles) where birds have been captured to explore wing morphology (large circles) (B). Tree cover distribution, the main habitat of the African chaffinch, is represented in hues of green. The area over 1500 m a.s.l., where most snowfalls occur in winter, is represented in grey (C).

Altitudinal distribution of weather conditions.

We studied the winter distribution of temperature and snow cover of the sites where chaffinch abundance was estimated (see below) to assess the harshness of winter conditions. For this purpose, we used the minimum mean temperatures (ºC) of the coldest moth in CHELSA V 1.0 at a horizontal resolution of 30 arcsec (~1 km) for the period 1979-2013, which provides improved climatic estimates in landscapes with complex topography (http://chelsa-climate.org/; Karger et al. 2017). In addition, we recorded the monthly snow cover during the period November-March (2015-2017) provided by the Nasa Earth Observatory at a horizontal resolution of 0.1 degrees (https://earthobservatory.nasa.gov/global-maps/). This databank provides the monthly snowfall cover (s_i, in %) by using an index that ranges from 0 to 100. In this way we calculated the altitudinal distribution of the mean monthly snow cover ($[\Sigma s_i]/15$ months, $i=1-15$) during the study period. The altitude pattern of this mean monthly cover of snow was used to divide the altitude gradient in sectors above and below a threshold of potential strong snow cover effects on birds. All these cartographic data were managed with QGIS 3.4.15 (QGIS Asssociation 2021).

Abundance

We assessed African chaffinch abundance in 99 tree covered farmland and woodland sites distributed along an altitude gradient in spring (second half of April and May of 2015, 2016 and 2017) and in other 123 different sites in winter (January 2013; see Tellería et al., 2014, 2021). This sampling was aimed to work with independent samples covering the altitudinal distribution of wooded areas inhabited by African chaffinches (Cramp & Perrins, 1994). Within each study site, we recorded the individuals detected along a 500-m-long transect (Bibby et al., 2000). To account for the effects of habitat structure on species abundance, we assessed wood cover (vegetation >2 m height) in two 25-m-radius circles located at 150 and 350 m from the starting point of each transect.

Morphology

We mist-netted African chaffinches from the end of April to the end of June (2007, 2011, 2018 and 2019). This period encompasses the breeding time of the species minimizing the probability of capturing vagrant individuals. The sampling sites were located around the villages of Larache (35.1745ºN,-6.1475ºW; mean altitude of sampling sites 10 m a.s.l.), Chauen (35.1704ºN,-5.2690ºW; 450 m a.s.l.), Taza (34.1487ºN,-4.1265ºW; 1400 m a.s.l.), Azrou (33.4388ºN,-5.2222ºW; 1800 m a.s.l.) and Ouirgane (31.1757ºN,-8.080ºW; 970 m a.s.l.). Mist-netted birds were aged according to the EURING code classification (age 3: hatched during the year of capture; age 4: hatched before the year of capture- exact year unknown, age 5: hatched during the previous calendar year; age 6: hatched at least two calendar years before the year of capture) and sexed (males and females) following Svensson (1992) and Jenni & Winkler (1994). In subsequent morphological analyses, we only considered fully-grown individuals (n=97) of known plumage type, which restricted our dataset to birds coded as Euring 5 (juvenile plumage) and 6 (adult plumage). From these individuals, we obtained the length of several morphological variables using the appropriate rulers or a digital caliper: right wing (maximum wing chord method), primary 8th, bill (from skull base to bill tip), right tarsus (minimum tarsus) and tail (see Svensson, 1992 for more details). We also recorded body mass from each individual using a digital balance (resolution 0. 1g). These six morphological variables were used to carry out a principal component analyses (PCA) to detect some orthogonal variables to segregate individuals according to body size and flight related traits.

During 2018-2019, we studied the wing shape of 81 chaffinches in Chauen, Taza, Azrou and Ouirgane by measuring the primary distances of the nine longest primaries (excluding the vestigial outermost primary P10). Primary distance was defined as the distance from the tip of each primary to the tip of the longest primary with the wing folded, assigning a value of zero to the primary (or primaries) constituting the wingtip. For analyzing wing shape configuration, we opted for transforming primary distances into distances from the carpal joint (cP1–cP9) by subtracting, for each primary, its primary distance from the wing length. These transformed distances (cP1–cP9) were then standardized according to the method suggested by Senar et al. (1994), which provides more reliable measurements (cP1*–cP9*) that correct for the among-individual variation in wing size. These standardized values were included in a PCA performed with the prcomp function in R, which gave rise to two principal components (wing concavity and wingtip pointedness) that reflected variation in wing shape among chaffinches. Captures and measurements were carried out by IHT, AO and JIA, experts of the Spanish Ringing Scheme who had their measurement protocols standardized and highly repeatable, and worked under the permission of the Moroccan authorities.

Analyses

We performed a multivariate approach to test for the effects of altitude on the seasonal distribution of Chaffinch abundance. We specifically tested whether the relationship between bird abundance and altitude varied between seasons (breeding vs. winter) according to the prediction that bird numbers should decrease at high altitude during winter, and increase in lowland areas. In order to test this hypothesis, we included the "season x altitude" interaction term in our model. In the case of altitude and according to our proposal in the Introduction section, we carried out two alternative analyses: one of them using the altitude gradient as a covariate ("altitude gradient"), and another one using altitude as a 2-level factor, in which the study sites were classified as lowland or highland localities from a threshold of frequent snow covers ("altitude threshold"). After testing with ade-4 in R (Thioulouse et al., 2018) that abundance distribution of the African Chaffinch was not spatially autocorrelated (Mantel' test, r = 0.035, p=0.160, n=222), we dealt with the large number of zeros in transects (25% of sampling points, Fig. 9) by using the hurdle count model approach provided by pscl-R (Zeileis et al., 2008). This approach is composed of a hurdle component that models the zero counts and a truncated count model for positive counts. The hurdle model is a binomial logit regression and shows the features related to the occupancy (presence/absence) of the species. The count model is a truncated Poisson or negative binomial (with log link) model that explores the features affecting the abundance distribution.

We used linear models to explore the patterns of variation in bird morphological characteristics after testing with ade-4 in R the existence of spatial autocorrelation in all the study variables. These tests showed no evidence of spatial autocorrelation (all Mantel tests were non-significant). In this case, variation of morphological components resulting from principal component analysis (PCA; see Results) were analyzed in relation to altitude (independently for altitude gradient and threshold), sex (male vs. female) and age (Euring 5 and 6), that usually influence the observed patterns (e.g. de la Hera et al., 2014). We initially considered the two-way interactions between these three variables, but their effects were not included in the final models since they were non-significant. These morphological analyses were carried out with Rcmdr (Fox & Bouchet-Valat, 2020) and all of them fulfilled the assumptions of general linear modelling.

RESULTS

Environmental conditions and altitude

Tree cover increased progressively with altitude (Spearman correlation, rs: 0.30, $p<0.05$, $n=222$), particularly over 1000 m a.s.l. However, mean temperatures of the coldest month decreased monotonically along the altitude gradient (Spearman correlation, rs:-0.91, $p<0.001$, $n=222$), so that altitude can be considered a good surrogate of this environmental trait in the study area. Snow cover was positively correlated with altitude (rs: 0.69, $p<0.001$, $n=222$), but showed a sharp increase over the 1500 m a.s.l. (Fig. 9). Thus, this altitude was selected as a putative threshold over which many African chaffinches could be forced to leave the highlands during winter.

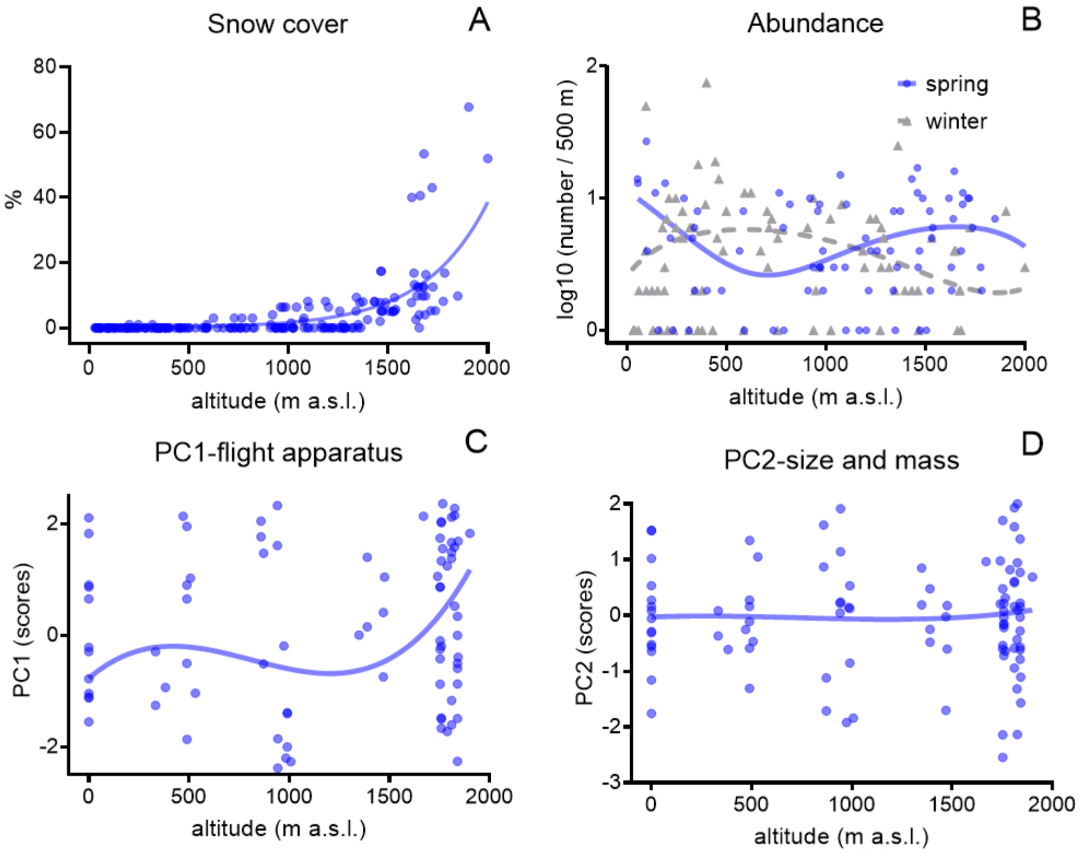

Figure 9. Altitudinal distribution of mean monthly snow cover (A) and spring and winter abundance distribution of the African chaffinch (B) within the study area. The size of the external flight apparatus (C) and body size (D) of this species along the altitude gradient are also showed. In all the figures, distance weighted least squares lines have been adjusted to better visualize how the patterns change with elevation.

Bird abundance

The raw data of African chaffinch abundance reflected a decrease in bird numbers during the winter in highlands over 1500 m (Table 5). After testing for the equi-dispersion assumption, the multivariate hurdle model suggested that both the occupancy and the abundance were strongly mediated by the distribution of tree cover and that the abundance was negatively related to altitude (Fig. 9, Table 6). We did not find an interaction between season and altitude when this effect was included in the model as a continuous variable (i.e. altitude gradient; Fig. 9, Table 6). However, this effect was stronger on bird abundance when the altitude was considered as a two-level factor (altitude threshold; Table 6). Further analyses in which the seasonal changes in abundance were compared reflected a significant decrease of bird numbers above 1500 m (season: -0.61 ± 0.72, p=0.010; tree cover: 0.18 ± 0.10, p=0.084, n:43)) and no significant changes under this altitudinal threshold (season: 0.23 ± 0.19, p=0.240; tree cover: 0.49 ± 0.12, p<0.001, n:177). This supports a numerical rearrangement between seasons, whereby African chaffinches experience a winter decrease in abundance over 1500 m (Table 5 and 6).

Table 5. Mean abundances and morphological traits of the African chaffinch in the study area. These scores are also arranged according to the distribution of individuals above or below the altitude threshold of 1500 m a.s.l.

	Total	**<1500 m a.s.l.**	**>1500 m a.s.l.**
ABUNDANCE	mean ± se (n)	mean ± se (n)	mean ± se (n)
Spring abundance (no /500 m)	4.90 ± 0.50 (98)	4.78 ± 0.86 (72)	5.23± 1.44 (26)
Winter abundance (no /500 m)	4.28 ± 0.80 (122)	4.62 ± 0.71 (105)	2.18 ± 1.78 (17)
MORPHOLOGICAL TRAITS			
Wing length (mm)	87.97 ± 0.36 (126)	86.61 ± 0.48 (67)	89.51 ± 0.45 (59)
8th primary length (mm)	68.21 ± 0.30 (117)	67,38 ± 0.41 (63)	69,19 ± 0.42 (54)
Bill length (mm)	15.04 ± 0.10 (104)	14.72 ± 0.16 (54)	15.40 ± 0.10 (50)
Tail length (mm)	69.52 ± 0.35 (114)	68.65 ± 0.51 (58)	70.43 ± 0.46 (56)
Tarsus length (mm)	19.01 ± 0.08 (122)	19.00 ± 0.11 (59)	19.02 ± 0.11 (63)
Body mass (g)	22.62 ± 0.12 (133)	22.33 ± 0.13 (67)	22.92 ± 0.19 (66)

Table 6. Results of a hurdle count model approach to explain African chaffinch abundance distribution in north-western Africa. Zero hurdle models show the features related to the occupancy of species and count models the features affecting abundance. The results show the coefficients (b ± se), the results (P) of the associated t-tests and the best spatial correlation structure. $^{+}$: under 1500.

ABUNDANCE	**Altitude gradient**	**Altitude threshold**
	estimate ± std. error (P)	estimate ± std. error (P)
Zero hurdle model (occupancy)		
Intercept	1.84 ± 0.338 (<0.001)	1.86 ± 0.38 (<0.001)
Altitude	0.02 ± 0.31 (0.960)	0.36 ± 0.75 (0.626)$^{+}$
Tree cover	1.63 ± 0.35 (<0.001)	1.84 ± 0.38 (<0.001)
Season (winter)	-0.24 ± 0.38 (0.535)	0.08 ± 0.41 (0.854)
Altitude x season	-0.08± 0.39 (0.830)	-2.263± 1.08 (0.037)
Count model (abundance)		
Intercept	1.66 ± 0.05 (<0.001)	1.62 ± 0.06 (<0.001)
Altitude	-0.23 ± 0.05 (<0.001)	-0.08 ± 0.10 (0.429)$^{+}$
Tree cover	0.30 ± 0.03 (<0.001)	0.28 ± 0.03 (<0.001)
Season (winter)	0.03 ± 0.07 (0.696)	0.28 ± 0.08 (<0.001)
Altitude x season	-0.08± 0.07 (0.250)	-0.97± 0.21 (<0.001)

Morphology

The raw data of morphological traits reflected longer wings, 8th primaries and tails in highlands over 1500 m (Table 5). The results of a first Principal Components Analysis (PCA) that included the five lineal morphological measurements described above (Table 5) produced two relevant principal components. The first component reflected the degree of development of the flight apparatus (PC1, eigenvalue = 3.10, variance = 0.62, factor loadings: wing= 0.55, p8= 0.54, bill length= 0.25, tarsus= 0.25, tail= 0.52), whereas the second component was related to tarsus length vs. bill length (PC2 eigenvalue = 0.86, variance = 0.17, factor loadings: wing: 0.03, p8: 0.03, bill length: -0.83, tarsus: 0.56, tail: 0.06). To test if those individuals with longer tarsus (a usual surrogate of body size; Senar and Pascual 1997) were also the heaviest ones and to explore their distribution along the altitudinal gradient, we included body mass in a new PCA. In this case, PC1 was positively correlated with the six variables included in the analysis but more strongly with those associated with flight-related morphology (eigenvalue = 3.31, variance = 0.55, factor loadings: wing: 0.52, p8: 0.51, bill length: 0.25, tarsus: 0.26, tail: 0.50, body mass: 0.29), so that we interpreted PC1 as an index of the development of the flight apparatus. Body mass and tarsus length were the variables more strongly associated with PC2 (eigenvalue = 1.02, variance = 0.17, factor loadings: wing: -0.23, p8: -0.30, bill length: 0.29, tarsus: 0.57, tail: -0,26, body mass: 0.62). This pattern suggests that chaffinches with higher scores in PC2 were the largest and heaviest ones within the study population, reflecting chaffinch body size. As individual component scores resulting from the two PCA approaches were highly correlated, we finally opted for using the PCA that included body mass to explore the changes in the flight apparatus (hereafter PC1-flight apparatus) and body size and mass (hereafter PC2-size and mass) along the altitude gradients.

The PCA on the standardized primary feather distances provided two principal components. PC1 was interpreted as an index of wing concavity (eigenvalue = 3.61; explained variance = 0.40; factor loadings: P9 = 0.21, P8 = 0.27, P7 = 0.24, P6 = -0.12, P5 = -0.29, P4 = -0.41, P3= -0.47, P2 = -0.40, P1 = -0.43), where individuals with higher PC1 scores showed proportionally shorter inner primaries, that is more concave wings. On the other hand, PC2 reflected variation in wingtip pointedness (eigenvalue = 1.63; explained variance = 0.18; factor loadings: P9 = 0.54, P8 = 0.48, P7 = 0.42, P6 = -0.33, P5 = 0.14, P4 = 0.18, P3= 0.22, P2 = 0.22, P1 = 0.17), whereby higher PC2 scores were associated with longer outer primaries for a given degree of wing concavity, or more pointed wingtips.

The models were carried out by considering all the 2-way potential interactions between altitude, sex and age, but all these interactions were non-significant. Thus we rerun the analyses without interactions to improve their ability to detect the effect of the involved variables. After accounting for the effects of sex (males larger than females) and age (individuals of age 6 were larger than those of age 5) in the models, PC1-flight apparatus clearly increased with altitude supporting a morphological differentiation of African chaffinches over such gradient (Fig. 9 and 10, Table 7). However, PC2-size and mass increased in males but did not vary along the altitude gradient and was not affected by age (Table 7). In the case of wing configuration, chaffinches in highlands reported more concave wings (PC1-wing concavity) than their lowland counterparts, but did not differ in wingtip pointedness (PC2-wingtip pointedness ; Fig. 10 and Table 7).

Table 7. Results of the General Lineal Models in which the components related to the development of the flight apparatus (PC1 of a PCA with the six morphological variables detailed in the Methods) and body size (PC2 of the same PCA that included with six morphological variables PCA), wing concavity and wingtip pointednesshave been analysed in relation to altitude (altitude gradient or altitude threshold) after controlling for the effect of sex and age. The results showestimates (± se), and significance values (P) according to the associated t-tests. $^{+}$: under 1500.

	Altitude gradient	**Altitude threshold**
	estimate ± error (P)	estimate ± error (P)
PC1flight apparatus		
Intercept	-1.98 ± 0.25 (<0.001)	-1.24 ± 0.29 (<0.001)
Altitude	0.62 ± 0.13 (<0.001)	-1.16 ± 0.26 (<0.001)$^{+}$
Sex (male)	2.19 ± 0.27 (<0.001)	2.16 ± 0.27 (<0.001)
Age (6)	1.02 ± 0.27 (<0.001)	0.84 ± 0.27 (0.002)
PC2-size and mass		
Intercept	-0.59 ± 0.19 (0.003)	-0.52 ± 0.22 (0.021)
Altitude	0.06 ± 0.10 (0.545)	-0.10 ± 0.20 (0.560)$^{+}$
Sex (male)	0.64 ± 0.20 (0.002)	0.63 ± 0.20 (0.002)
Age (6)	0.32 ± 0.20 (0.122)	0.30 ± 0.20 (0.145)
PC1-wing concavity		
Intercept	-0.34 ± 0.37 (0.367)	0.48 ± 0.39 (0.225)
Altitude	0.48 ± 0.21 (0.022)	-1.65 ± 0.39 (<0.001)$^{+}$
Sex (male)	-0.33 ± 0.43 (0.445)	-0. 32 ± 0.40 (0.425)
Age (6)	0.87 ± 0.43 (0.045)	0.60 ± 0.40 (0.141)
PC2-wingtip pointedness		
Intercept	0.19 ± 0.26 (0.479)	0.11 ± 0.30 (0.704)
Altitude	-0.13 ± 0.15 (0.383)	0.12 ± 0.30 (0.681)$^{+}$
Sex (male)	-0.04 ± 0.30 (0.882)	-0.03 ± 0.30 (0.919)
Age (6)	-0.27 ± 0.30 (0.378)	-0.23 ± 0.31 (0.440)

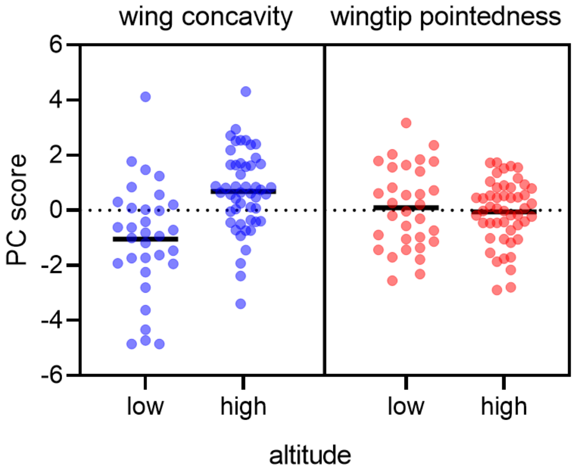

Figure 10. Distribution of wing concavity and wingtip pointedness of African chaffinches according to their distribution in lowlands and highlands (under and above 1500 m.a.s.l.) of the study area. Bars show mean scores.

DISCUSSION

Rear edge populations of birds occur in refuge areas in the south-western Palaearctic (Merker & Chandler, 2020) from where other populations of the same species progressively colonized more northern areas after the Quaternary ice retreat (Hewit, 1999; Husemann et al., 2014). In this historical context, migratory behaviour would have been a way to track the increasing availability of seasonal resources in the newly ice-free areas arising at higher latitudes (Bruderer & Salewki, 2008). It can be suggested that the evolution of latitudinal migrations in the Eurasian chaffinch populations were also accompanied by altitudinal displacements at a more local scale, and that both seasonal movements affected similarly several morphological and life history traits (Boyle et al., 2016). Results in this paper support this view and provide information on the way African chaffinches could track the spatial-temporal environmental patterning within the south-western edge of the Palaearctic.

Seasonal changes in abundance

Most rear-edge populations of forest birds inhabiting north-western Africa show a similar distribution, with their most suitable breeding habitats located in humid northern and western slopes of mountain ranges (Tellería et al., 2021). Results in this paper show that the distribution of the African chaffinch tracks tree covered habitats within a broad range of altitudes where they occur all around the year (Fig. 9B; Table 6). Despite this ubiquitous distribution along the altitude range, species abundance showed a significant decrease in winter over the 1500 m a.s.l., supporting the presumed link between the intensity of snowfalls and the winter abandonment of highlands by many African chaffinches (Table 5 and 6, Fig. 9). This reaction to seasonal changes supports the view that over a given altitude threshold, many chaffinches move to winter in lowlands, as reported in other areas of the south-western Palaearctic (Carrascal & Palomino, 2012b; Tellería et al., 2020). The true extent of these movements is far from being known, although most of them revolve within the breeding range of the species and may sometimes expand to nearby areas, such as the northern edge of the Sahara at the Atlas piedmont (Thévenot et al., 2003).

The presence of African chaffinches at the highest sectors during winter and the poor effect of these numerical rearrangements on the abundance in lowlands could be explained by some idiosyncratic traits of both the species and the study area. Many chaffinches (particularly males) are reluctant to leave their breeding grounds in winter (Cramp & Perrins, 1994). In this context, as snowfalls are uncommon in dry and sunny African high slopes in the shadow of oceanic rains (Fig. 8A; Marchane et al., 2011), many highland chaffinches could overwinter nearby the breeding grounds by moving along slopes in the search of suitable habitat patches as it has been reported in other mountain ranges (Carrascal et al., 2012a). The number of individuals involved in these altitudinal movements will probably be small if we have into account the limited area covered by woodlands (their breeding habitat) over the 1500 m threshold (Fig. 8C). This trait could dilute the effect of displaced individuals on the detected abundance patterns in lowland areas (Table 5). It also remains obscured the actual effect of the Eurasian chaffinches arrived to winter from Europe (Thévenot et al., 2003) on the observed seasonal patterns. As these birds are not easy to detect in field counts (e.g. immature and females are very similar to the African subspecies), they could distort the observed numerical arrangements of the African population. For instance, it could be speculated that an overall winter loss of individuals within the African range (e.g. mortality) could be compensated by the arrival of foreign individuals in lowlands areas, which are the best wintering grounds for birds in Morocco (Tellería et al., 2014). Thus, to cope with these potential difficulties, we used the spatial variation in bird morphology to interpret the extent to which African chaffinch movements might occur within the geographical setting of Morocco (Tellería et al., 2013).

Morphological variation

Morphological change is a widespread response to environmental change and can occur through phenotypic plasticity and/or natural selection (Gienapp et al., 2008). In this way, the presence of morphological clines can be used to detect the response of populations to environmental gradients at different spatial scales (Richardson et al., 2014).

The altitudinal variation in the external flight apparatus of the African chaffinch supports a different morphological configuration over and below 1500 m a.s.l. (Table 5 and 7, Fig. 9 and 10). More explicitly, our results show that birds above that threshold have more developed flight morphology (longer wing and tails) than their lowland counterparts (Table 5 and 6, Fig. 9). These results show an atypical pattern if we consider that a combination of longer wings and shorter tails have usually been related to flight efficiency in migratory flapping-flight birds, where long wings are designed to increase flight power and short tails to reduce drag (Leisler & Winkler, 2003, Hedenström, 2008). However, this pattern is not universal or can vary among species (De la Hera et al., 2012; Fudickar & Partecke, 2012; Huber et al., 2017). For instance, the pattern observed in the African chaffinch could be related to its bounding-flight, where longer wings would improve flapping in the powered phase and longer tails would increase lift and stability in the passive wing-folded phase (Sachs & Lenz, 2011). Thus, longer wings and tails could enhance flight efficiency in highland African chaffinches, an interpretation also supported by wing shape (Table 7, Fig. 10). In this case, more concave wings were detected in highland chaffinches, a trait usually related to flight efficiency of birds involved in migratory movements (Rayner, 1988; Lockwood et al., 1988; Leisler & Winkler, 2003).

Although we believe that seasonal migration is the most likely interpretation for the morphological differences observed between high and low altitude chaffinch populations, we acknowledge that these morphological changes could also be alternatively, or complementary, explained by other factors. For instance, it has been shown that changes in forest could drive intraspecific wing morphology of forest birds (Desrochers, 2001). In this context, it can be suggested that a more dense tree cover could affect flight morphology as birds show more rounded wings to improve manoeuvrability (Savile, 1957; Noreau & Desrochers, 2018). But tree cover, a trait related to the physiognomic complexity of woodlands in the study area (Tellería et al., 2021), increased with altitude making difficult to link this pattern with the increased wing concavity of the highland chaffinches. Decreasing air density could also affect these patterns, as it has been suggested before for flying birds (e.g. altering lift and drag balance, increasing wing beats; Pennycuick, 2001; Schmaljohann & Liechti, 2009). But the putative effect of air density on the intraspecific morphological variation of birds has not been proved to date. In addition, we presume that this putative change would affect wing morphology over the whole altitude gradient and not over a given altitude threshold as reported in this study. In any case, our study encourages further research on the potential influence of these and other environmental factors in shaping avian wing morphology.

Thus, it can be summarized that (i) the external flight apparatus of the African chaffinch varies along the altitudinal gradient, (ii) that the changes are detected between individuals breeding over and below an altitudinal threshold related to winter snow cover and (iii) that these changes could be related to an enhanced flight efficiency of the involved populations. In this context, it is interesting to highlight the lack of change in size and body mass of the African chaffinch along the altitude gradient (Table 5, Fig. 9D). This could be an idiosyncratic trait of this subspecies, reputed as one of the largest ones (Perktas et al. 2017), which is not compelled to increase body mass to cope with the colder conditions of highlands (Sander and Chamberlain 2020).

Conclusions

Results in this study support several main conclusions related to the way a rear-edge bird population face the environmental changes in the south-western edge of the Palaearctic. Far from being the sedentary counterpart of a partial-migratory species, the African chaffinch evolved independently within the seasonal environmental setting of its range. This process, which agrees with the morphological and genetic uniqueness of this population (Perktas et al., 2017), could be applied to many other birds and taxa of Northern Africa, given the high degree of endemicity in this region and the presumed adaptations to local conditions (Hampe & Jump, 2011; Husemann et al., 2014; Iseenman & Thévenot, 2018). This leads to several additional conclusions. First, these endemic populations cannot be viewed any more as the maladapted counterparts of the core populations (Angert et al., 2020 for discussion). Second, the morphological diversity associated with altitude within the African chaffinch range underlines its putative adaptive ability to track the existing spatial-temporal environmental dynamics (Richardson et al., 2014). This is an interesting trait in a context of climate change where the less drought tolerant woodlands preferred by the species (Tellería et al., 2021) will shift upwards along the altitude gradient (Ruiz-Labourdette et al., 2012). It has been suggested that, in this context, the adaptive capacity of populations will be linked to their ability to track the spatial-temporal patterning of habitat suitability (Hampe & Jump, 2011; Hannah et al., 2014), a process strongly linked to the idiosyncratic circumstance of the involved species (Angert et al., 2011; MacLean & Beissinger, 2017). Finally, the meso and microclimatic conditions created by mountains in the southern edge of the Palaearctic highlight not only their role as refuge areas for northern organisms during glacial periods (Husemann et al., 2014), but also suggest a role as drivers of population diversification in highly mobile organisms (e.g. birds). This makes the protection of habitats within these altitude gradients (e.g. tree covered areas for the African chaffinch) a main conservation strategy of rear-edge populations of birds (Tingley et al., 2014).

BLOQUE B

MUDA Y PLUMAJE EN AVES DE MONTAÑA

CAPÍTULO 3

RASGOS DEL PLUMAJE EN CUATRO POBLACIONES MERIDIONALES DE CURRUCA CAPIROTADA (*Sylvia atricapilla*): ¿LOS MOVIMIENTOS ALTITUDINALES EXPLICAN LAS DIFERENCIAS?

Este capítulo está basado en el manuscrito: **Hernández-Téllez, I.**, Aguirre, J. I., de la Hera, I., Onrubia, A., & Tellería, J. L. (2021). Feather traits in four southern populations of the Eurasian blackcap Sylvia atricapilla: do altitudinal movements explain the differences? **Journal of Avian Biology**. 52 (12).

RESUMEN

La muda de las aves está condicionada por factores ambientales y genéticos cuya contribución relativa a la estructura de las plumas puede diferir dentro de las poblaciones y entre ellas. En este estudio comparamos algunos rasgos de las plumas de la cola (barras de crecimiento, masa, anchura del raquis y longitud de las barbas) entre cuatro poblaciones de la curruca capirotada (*Sylvia atricapilla*) que se reproducen en diferentes elevaciones del suroeste del Paleártico. Se comprobó si estos rasgos estaban relacionados con la productividad primaria de los hábitats (un sustituto de la disponibilidad de alimento) o se explicaban mejor como una adaptación a los movimientos altitudinales. La distribución de la productividad primaria se relacionó positivamente con la abundancia de currucas, lo que sugiere que la especie rastreó las áreas más productivas para reproducirse. En este entorno ambiental, la morfología del ala (longitud del ala, concavidad y apuntamiento) sugirió que las currucas de las tierras bajas eran sedentarias mientras que las de las zonas altas realizaban movimientos altitudinales. Las plumas de las currucas que habitan en las tierras altas mostraban barras de crecimiento y raquis más anchos que las de las zonas más productivas de las tierras bajas, pero no diferían en la masa de las plumas ni en la longitud de las barbas. El rápido crecimiento de las plumas se ha relacionado con las limitaciones de tiempo para la muda y el raquis más ancho para mejorar la eficiencia del vuelo en las aves migratorias. Nuestros resultados sugieren, por tanto, que las diferencias en las características del plumaje entre las poblaciones meridionales de la curruca capirotada se interpretan mejor como una respuesta adaptativa a la migración altitudinal que como una consecuencia de la disponibilidad regional de alimento.

ABSTRACT

Moult of birds is shaped by environmental and genetic drivers whose relative contribution to the structure of feathers may differ within and between populations. In this study we compare some traits of tail feathers (growth bars, mass, rachis width and barb length) between four populations of the Eurasian blackcap (*Sylvia atricapilla*) breeding at different elevations within the southwestern Palaearctic. We tested if these traits were related to the primary productivity of habitats (a surrogate of food availability) or were better explained as an adaptation to altitudinal movements. The distribution of primary productivity was positively related to blackcap abundance suggesting that the species tracked the most productive areas to breed. In this environmental setting, wing morphology (wing length, concavity and pointedness) suggested that lowland blackcaps were sedentary while blackcaps from highland areas were involved in altitudinal movements. The feathers of blackcaps inhabiting the highlands showed wider growth bars and rachis than those of the most productive lowland areas, but did not differ in feather mass and barb length. Fast feather growth has been related to time constraints to moult and wider rachis to improve flight efficiency in migratory birds. Our results therefore suggest that differences in feather

characteristics between southern populations of the Eurasian blackcap are better interpreted as an adaptive response to altitudinal migration than as a consequence of regional food availability.

INTRODUCTION

Plumage is composed almost entirely of protein (keratin) and represents a significant part of the birds' lean body mass, which makes feather production a very demanding physiological challenge for birds (Jenni & Winkler, 2020). In addition, since feathers are metabolically inert structures once they are fully grown, the characteristics and quality achieved during their production can affect plumage performance with possible consequences for fitness (Harrison et al., 2011).

As some feather characteristics have been considered flexible traits whose expression is primarily determined by environmental constraints, they have been often used as indicators of body condition in birds (Grubb, 2006). However, increasing evidence suggest that genetic factors may contribute to phenotypic variation in feathers characteristics, raising the possibility that they have been partly shaped by selective pressures and subject to evolutionary change (Piersma et al., 2005; Gienapp & Merila, 2010; De la Hera et al., 2013; Saino et al., 2013). Thus, the expression of feather characteristics would be determined by both environmental and intrinsic factors, with the relative contribution of each factor differing within and between populations. When comparing populations, the intrinsic factors acting on plumage quality and production are diverse (body size and morphology, lifestyle or organization of the annual cycle, such as migratory requirements; Jenni & Winkler, 2020) and may indicate different evolutionary strategies or constraints (van Noordwijk & de Jong, 1986). In general terms, we know that there is a trade-off between feather growth rate and feather quality (Vágási, 2013), and that feather structural properties may indicate adaptation to flight requirements and environmental conditions (Pap et al., 2015; 2019), but some patterns remain unclear. For instance, variation between Iberian populations in the mass and growth rate of tail feathers in Eurasian blackcap fledglings (*Sylvia atricapilla*) was related to local changes in precipitation, an environmental factor linked to productivity in Mediterranean habitats (Carbonell & Tellería, 1999; Carbonell et al., 2003). However, a comparison between sedentary and North and central European migratory adults that winter in sympatry in southern Spain revealed lighter feathers and wider growth bars in migrants, including some differences in the mechanical properties of tail and wing feathers related to flight efficiency (De la Hera et al., 2009, 2010). It has been also shown that some traits (rachis width and barb length) seem to be related to flight efficiency in migrants (Pap et al., 2015; De la Hera et al., 2020). Thus, the question of whether the feather traits track the immediate environmental conditions or reflect an adaptation to migratory movements remains yet unresolved.

In this paper we study the feathers in four Eurasian blackcap populations distributed along an elevation gradient within the southwestern Palaearctic (Fig. 11 and Fig. 12A). Increasing evidence supports that the environmental heterogeneity caused by orography produces altitudinal displacements whose effects on bird biology have often been overlooked (Boyle et al., 2016; Boyle, 2017; Sander & Chamberlain, 2020). These movements could strongly affect the moult of the Eurasian blackcap populations, a partially migratory species in which migratory and sedentary individuals can coexist in a small geographical area (Chapman et al., 2011). In our case, blackcap populations of the Iberian highlands and lowlands (Guadarrama and Alcornocales; see Fig. 11) have been classified as migratory and sedentary, respectively (Tellería & Carbonell, 1999; Pérez-Tris & Tellería, 2002). Although the migratory behaviour of North African blackcaps remains yet unclear (Thévenot et al., 2003; Delmore et al., 2020), bird count data suggest that this species reduces its abundance at high elevation areas (Atlas mountains) during winter, suggesting the existence of seasonal altitudinal movements (Appendix 2; Fig. S2). Thus, the Eurasian blackcap and the heterogeneous configuration of the southwestern Palaearctic seems a suitable model to explore if the structure of feathers of different populations are shaped by immediate habitat suitability (e.g. food) or are better explained by adaptations to altitudinal movements. We will try to unravel this question by testing the following hypotheses:

Environmental effects. Primary productivity is a main driver of the abundance of primary consumers (Street & McNickle, 2019; Fernández-Tizon et al., 2020) and the amount of this food resource (e.g. invertebrates) will affect moulting since birds depends of animal food to produce feather keratin (Gregg & Rogers, 1986). Thus, if the study areas differ in primary productivity and blackcaps actively track the differences (e.g. through changes in abundance; Tellería & Pérez-Tris, 2003), we predict that birds in the most productive

areas will show faster growth rates and/or heavier feathers. Both traits have been positively related to food availability (Murphy, 1996; Grubb, 2006; Pap et al., 2008).

Migratory behaviour. Alternatively, we predict that changes in feather structure will result from evolutionary processes operating on populations, but not from immediate environmental effects. In this context, as the Eurasian blackcap populations inhabiting the southwestern Palaearctic may be divided into migratory and sedentary populations, we predict that feather structure will be shaped by their migratory behaviour. More explicitly, we will test if migratory populations show faster feather growth rates than sedentary conspecifics to cope with the putative effect of time constraints to moult described for migrants (Kiat et al. 2019), and/or show wider rachis and shorter barbs to improve flight efficiency (Tubaro, 2003; Weber et al., 2005; De la Hera et al., 2010, 2020).

METHODS

Study area

The four study areas are located in the Iberian Peninsula (Guadarrama Mountains and Los Alcornocales Natural Park) and the Maghreb (Rif and Atlas Mountains), covering different elevation ranges within the typical Mediterranean climatic conditions (Fig. 11). In these mountains, the Eurasian blackcap occurs in the moistest forest sectors (e.g. patches of *Rubus* sp.), particularly in broadleaved woodlands of *Quercus pyrenaica, Q. canariensis,* and *Q. suber* (Carbonell, 2003). The species is increasingly scarcer in the southern border of the study area (Fig. 12B), where it tends to be constrained to some suitable localities within mountain ranges (Thévenot et al., 2003; Appendix 2; Fig. S2). In this way, the mountain ranges selected in this study are located within a gradient of decreasing suitability that could strongly affect moult in the Eurasian blackcap.

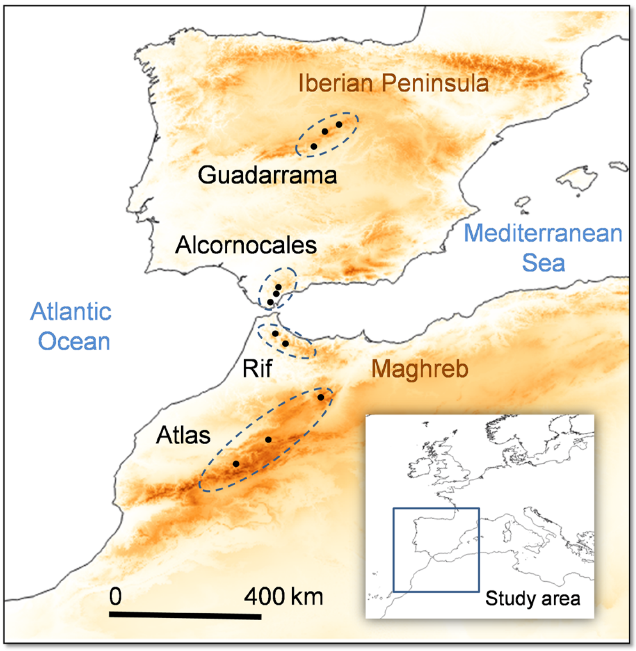

Figure 11. Location of the study areas where birds have been captured to study feather traits. The small spots show the sampling sites. The situation of the study area within the Western Palaearctic is also shown.

Capture and measurements of blackcaps

We mist-netted Eurasian blackcaps from the end of April to the end of June during two consecutive years (2018 and 2019). This period encompasses the breeding time of the species (Appendix 3; Table S3 and Fig. S3) and reduces the probability of capturing migratory individuals (the main passage period occurs between late March and late April; Gargallo et al., 2011). In Spain, the *Guadarrama* sampling sites were located around Rascafría (40.9050, -3.8795), whereas bird trapping in *Alcornocales* took place near Los Barrios (36.1851, -5.4926). In Morocco, the *Rif* samples were taken around Chauen (35.1704, -5.2690) and Moulay Abdeslam (35.3174, -5.5066), whereas the *Atlas* sampling occurred in areas of Taza (34.1487, -4.1265), Azrou (33.4388, -5.2222) and Ouirgane (31.1757, -8.080; Fig. 11). Mist-netted blackcaps were aged according to the EURING code system (age 3: hatched in the current spring; age 5: young individuals hatched during last spring, still with flight feathers that developed in the nest; age 6: adult individuals, with flight feathers that come from a complete moult), sexed (males and females) and measured (maximum wing chord, tail length, minimum tarsus length and bill length from skull front to bill tip) following Svensson (1992) and Jenni and Winkler (1994). Pectoral muscle was scored from 0 to 3 (by considering intermediate cases using 0.5 scores) following Bairlein (1995). We studied wing shape by considering the primary distances of the nine longest primaries (excluding the vestigial outermost primary: P10). Primary distance was defined as the distance from the tip of each primary to the tip of the longest primary with the wing folded, assigning a value of zero to the primary (or primaries) constituting the wingtip. All body and feather measurements were performed by official expert ringers of the Spanish Ringing Scheme (IHT, JAM and AO) who had their measuring procedures standardized. Finally, the second outermost tail feathers (rectrix number 5 from left and right side) were collected and stored in individual envelopes to be studied in the laboratory. We discarded those individuals of age 3 because they were not fully grown in some cases. Captures and collection of biological samples were performed under permission of the Moroccan and Spanish authorities.

Productivity and blackcap abundance

The suitability of the study areas for blackcaps was assessed from three complementary approaches. First, we used remotely sensed Normalized Difference Vegetation Index (NDVI) to assess primary productivity and forest health (Wang et al., 2004; Aubard et al., 2019). For this purpose, we downloaded the monthly distribution of NDVI scores from the NASA Earth Observations (NEO) program (https://neo.sci.gsfc.nasa.gov/about/). We selected the data from May to August for the years 2017 and 2018 to have a view of the productivity of the study areas during the breeding and moulting period of the captured blackcaps (2018 and 2019). These data were managed with QGIS 3.4.15 (QGIS Development Team 2020) and the productivity of those sites where each blackcap was mist netted (see below) was extracted by means of the Point Sampling Tool Plugin (https://plugins.qgis.org/plugins/pointsamplingtool/). Second, we explored whether blackcaps were more abundant in the most productive areas. To do this, we assessed the abundance of the Eurasian blackcap in the four study areas around the sampling points in May-June of 2019. This assessment was carried out by counting blackcaps in sampling points randomly distributed across different woodlands within each of the four areas (see Tellería et al., 2020 for further details on the sampling protocol). At each sampling point, the abundance of blackcaps was recorded during a 10-minute period within a 100-m-wide radius (Johnson, 2008). Finally, as density can be a misleading indicator of habitat quality by the effect of competition (Van Horne, 1983), we used the pectoral muscle score of the Eurasian blackcaps as an index of body condition (Cooper et al., 2015; see below). In this way, we tried to test if individuals of the most densely populated areas displayed a depleted condition during breeding. Although body mass controlled by bird size could also be a good indicator of body condition, we decided not to use it in this case due to the large allometry in body size-related morphological traits among the study populations (paper in preparation).

Wing morphology

We used wing morphology to infer the strength of seasonal movements of the Eurasian blackcap populations, since migratory populations are expected to have a more developed flight morphology (i.e. longer and more pointed wings) than sedentary ones (Tellería & Carbonell, 1999; Fiedler, 2005). We performed a principal component analysis (PCA) with the primary lengths to describe wing shape. For this purpose, we transformed primary distances into distances from the carpal joint by subtracting their primary distance from the wing length. These transformed distances (cP1–cP9) were then standardized according to the method suggested by Senar et al. (1994) that correct for the among-individual variation in wing size. The PCA provided two principal components. PC1 was interpreted as an index of wing concavity (eigenvalue = 4.47; explained variance =0.50; factor loadings: P9 = 0.37, P8 = 0.27, P7 = -0.07, P6 = -0.63, P5 = -0.83 P4 = -0.90, P3 = -0.93, P2 = -0.89, P1 = -0.84) and PC2 as an index of wingtip pointedness (eigenvalue = 1.59; explained variance = 0.18; factor loadings: P9 = 0.78, P8 =0.82, P7 = -0.29, P6 = -0.15, P5 = -0.09, P4 = 0.07, P3 = 0.18, P2 = 0.26, P1 = 0.29). Thus, higher scores in PC1 and PC2 were related to more concave wings and more pointed wingtips respectively, which are typical of the most migratory individuals.

Feather traits

Flight feathers have a natural pattern of light and dark bands perpendicular to the rachis that corresponds to different pulses of feather growth (Brodin, 1993). One light plus one dark band is called a growth bar and its width can be used to estimate feather growth rate (Grubb, 2006). We studied the growth rate of each tail feather (with traits correlated with wing feather traits in Blackcaps, Appendix 4; Tables S4-S6 and Fig. S4) by measuring the width occupied by ten growth bars centred at around two thirds of feather length from the base (Grubb, 2006). To do this, each feather was placed on a black cardboard and the width of the ten growth bars (hereafter, 'feather growth rate') was marked with two entomological pins on the edge of the internal vane. The distance between pins was measured with a Mitutoyo

500 digital calliper (resolution 0.01mm). This measurement showed a repeatability index (R) of 0.94 (SE=0.016; CI= [0.90, 0.97]), calculated through the rptR package (R=0.95 for age 5 and 0.92 for age 6). The feathers replaced after accidental losses or with growth bars difficult to see were discarded from analyses as well as those individuals born during the study year (age 3 according to EURING codes), because most of them had not a fully-grown plumage. In total, the feathers of 36 individuals were discarded (19 from Alcornocales, 2 from Rif, 10 from Guadarrama and 5 from Atlas). Feathers were weighed using a digital precision balance (Mettler Toledo ® AG-245 model; instrumental repeatability 0.01 ± 0.02 mg) in order to estimate the overall quantity of material invested in feathers. We used a binocular magnifier (×10) to measure the total length of the barbs located in the middle point of the feather, which were stretched using an entomological pin and its maximum length calculated using chart paper as background (resolution 0.5 mm) following De la Hera et al. (2020). We also measured the dorsoventral width of the rachis at the position of the superior umbilicus with a digital calliper (0.01 mm resolution). Finally, since all abovementioned feather metrics are expected to be larger in long feathers compared to short ones, we measured their overall length (resolution 0.01mm) to control for this potential variation. To avoid inter-personal bias, all feather traits were measured by the same person (IHT).

Analyses

We used general linear models (Zuur et al., 2007) to test for differences in productivity, bird abundance, wing morphology, body condition and feather traits between the four study Blackcap populations. All models met the assumptions of parametric tests except the analysis of pectoral muscle for which we alternatively used a set of Kruskal-Wallis tests. In the case of wing morphology and feather traits, all models included year (2018, 2019), sex (female, male) and age (age 5, age 6) as fixed effects, and in no case was there any correlation between the variables; whereas feather trait analyses additionally included feather length as a covariate). In addition, the parameter setting of “sum-to-zero contrast” was used for the 4 factors (i.e. year, age, sex and study area) in the models. For the case of habitat productivity, we assessed differences between years and areas by using repeated measures ANOVA. All analyses were carried out with Rcmdr 3.5.3 (Fox & Bouchet-Valat, 2020).

RESULTS

Productivity, abundance and body condition

The mean monthly distribution of NDVI at the sites where blackcaps were captured showed significant differences between areas and years (repeated measures ANOVA, study area: $F_{3,127}$=111.72, P<0.001; year: $F_{1,127}$=268.73, P<0.001; study area x year interaction: $F_{3,127}$=62.27, P<0.001. Fig. 12C), with 2018 being more productive than 2019 and lowland forests displaying a higher productivity than mountain forests. Within this environmental setting, Blackcap abundance displayed a significant decrease from lowlands to highlands (Fig. 12B; Appendix 5; Fig. S5). This pattern was not followed by the pectoral muscle scores. There are no significant differences between years, sex and age categories, but there is a significant difference between areas (Kruskal-Wallis $H_{3,132}$ =8.33 P =0040) with the highest scores in the most and less elevated areas (Atlas and Alcornocales; Appendix 5; Fig. S6).

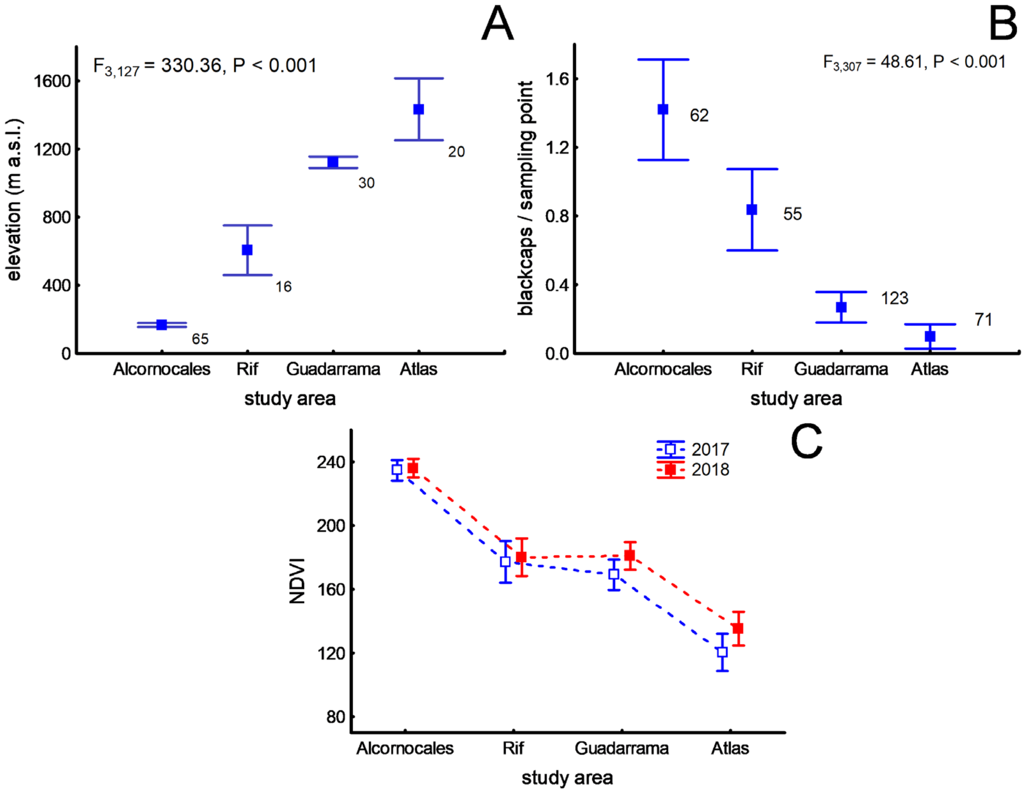

Figure 12. A) Distribution of elevations at which the Eurasian blackcaps were captured. Figures show the numbers of birds considered in this study (age >3). B) Distribution of the Eurasian blackcap abundance between the study areas as reported by sampling points. Figures show the number of sampling points. C) Between year distribution of primary productivity as reported by May to August NDVI scores. Figures A and B show the results of one-way ANOVA. In all cases the graphics show mean and standar error interval for the study areas.

Wing morphology

We studied 132 Eurasian blackcaps (age 5 and 6) distributed at different elevations in the four study areas (Fig. 12A). Wing length differed between areas but not between years, with highland blackcaps having the longest wings (Fig. 13A). There was also a significant effect of sex and age on the patterns, with males and older individuals (age 6) showing the longest wings (Table 8). Wing concavity differed between areas similarly to wing length, but did not show any effect of year, age, and sex (Table 8). Wing pointedness showed an effect of sex and showed opposite patterns between the lowland and highland Iberian localities (Fig. 13C, Table 8).

Table 8. Results of the linear models in which the differences between areas in wing length and shape have been analyzed after controlling for the effect of year, age and sex.

	Wing length (estimate ± SE)	Wing pointedness (estimate ± SE)	Wing concavity (estimate ± SE)
Intercept[1]	71.669 ± 0.174***	0.100 ± 0.104	0.023 ± 0.090
Year (2018)	-0.287 ± 0.152	-0.131 ± 0.091	0.135 ± 0.079
age (5)	-0.451 ± 0.161**	0.078 ± 0.097	-0.046 ± 0.083
Sex (male)	0.296 ± 0.145*	-0.178 ± 0.087*	-0.078 ± 0.075
Alcornocales	-0.746 ± 0.214***	-0.259 ± 0.128*	-0.250 ± 0.111*
Rif	-0.905 ±0.338**	-0.275 ±0.202	-0.653 ± 0.175***
Guadarrama	0.928 ± 0.267***	0.437 ± 0.160**	1.067 ± 0.139***
R^2 x 100	28.49	12.89	34.78
F6,125	8.301	3.083	11.11
P	<0.001	0.008	<0.001

[1] averaged intercept value according to sum to zero contrasts for study areas, sex categories, age classes and years. *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

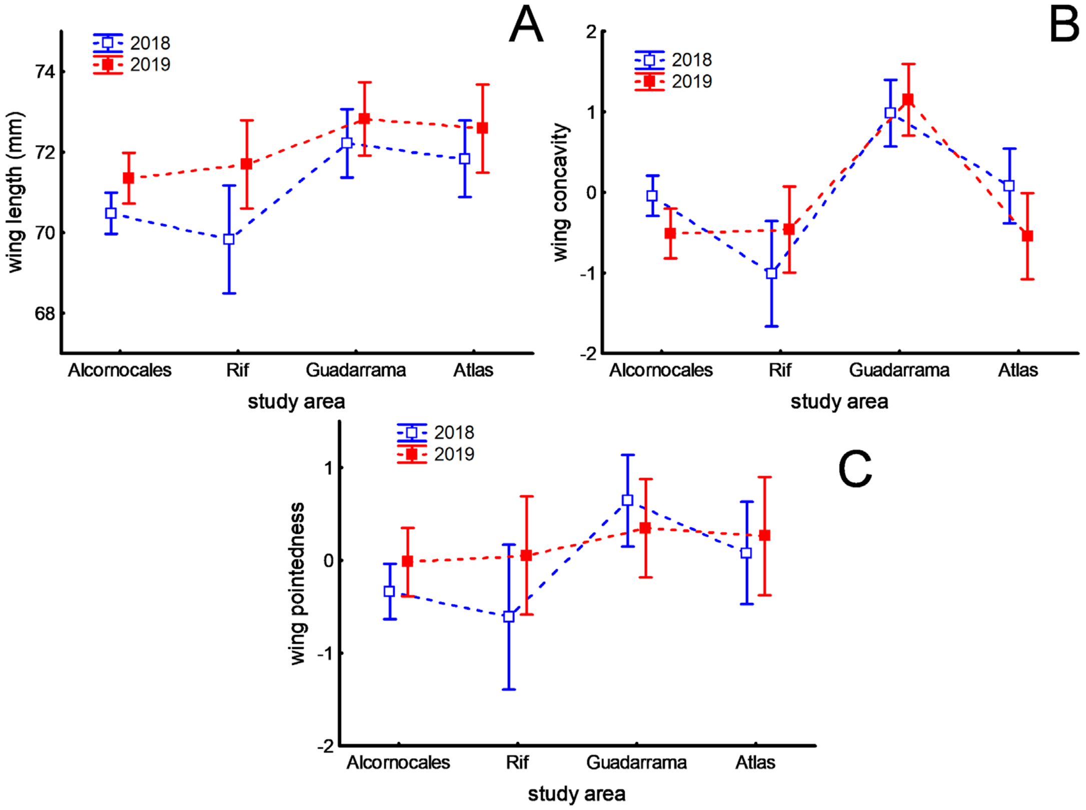

Figure 13. A) Distribution wing length between study areas. **B)** Distribution of wing concavity. C) Distribution of wing pointedness index. In all cases, the results show mean and standar error for the absolute values of the study areas.

Feather traits

After accounting for variation in feather length, blackcaps exhibited significant differences in feather growth rate in relation to year, age and sex. In addition, the results suggest a pattern between the study areas in which highland individuals showed the widest growth bars (Fig. 14A, Table 9). In contrast, feather mass did not vary in relation to year, age, sex, and neither showed any association with sites at different elevations (Fig. 14B, Table 9). Barb length was longer in adult and males, and displayed the lowest scores in Guadarrama Mountains. Finally, rachis width was not affected by year, age and sex, but was narrower in Alcornocales than in the highland populations (Fig. 14D, Table 9). These results do not support the prediction that blackcaps in the most productive areas would show wider feather bars and/or produce heavier feathers. More likely, they support the prediction that wider growth bars and rachis could be related to some adaptive traits related to migration.

Table 9. Results of the linear models in which the differences between areas in growth bars, feather mass, rachis width and barb length have been analyzed after controlling for the effect of year, age and sex.

	Growth bars (estimate ± SE)	Feather mass (estimate ± SE)	Barb length (estimate ± SE)	Rachis width (estimate ± SE)
Intercept[1]	15.085 ± 3.603***	2.750 ± 0.908**	8.135 ± 2.154***	0.562 ± 0.074***
Year (2018)	-0.372 ± 0.129**	-0.004 ± 0.003	0.079 ± 0.077	-0.004 ± 0.003
age (5)	0.369 ± 0.141**	-0.000 ± 0.005	-0.260 ± 0.04**	-0.001 ± 0.003
Sex (male)	-0.249 ± 0.124*	-0.000 ± 0.003	0.173 ± 0.074*	0.004 ± 0.003
Alcornocales	-0.981 ± 0.181***	0.010 ± 0.005*	0.022 ± 0.108	-0.020 ± 0.004***
Rif	-0.252 ±0.285	-0.016± 0.007*	0.183 ± 0.170	0.001 ± 0.006
Guadarrama	0.953 ± 0.237***	0.006 ± 0.006	-0.324 ± 0.142*	0.012 ± 0.005*
Feather length	0.271 ± 0.062***	0.0168 ± 0.016***	0.152 ± 0.037***	0.002 ± 0.001
R^2 x 100	39.17	58.24	31.90	27.68
F7,124	11.4	24.70	8.30	6.78
P	<0.001	<0.001	<0.001	<0.001

[1] averaged intercept value according to sum to zero contrasts for study areas, sex categories, age classes and years. *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

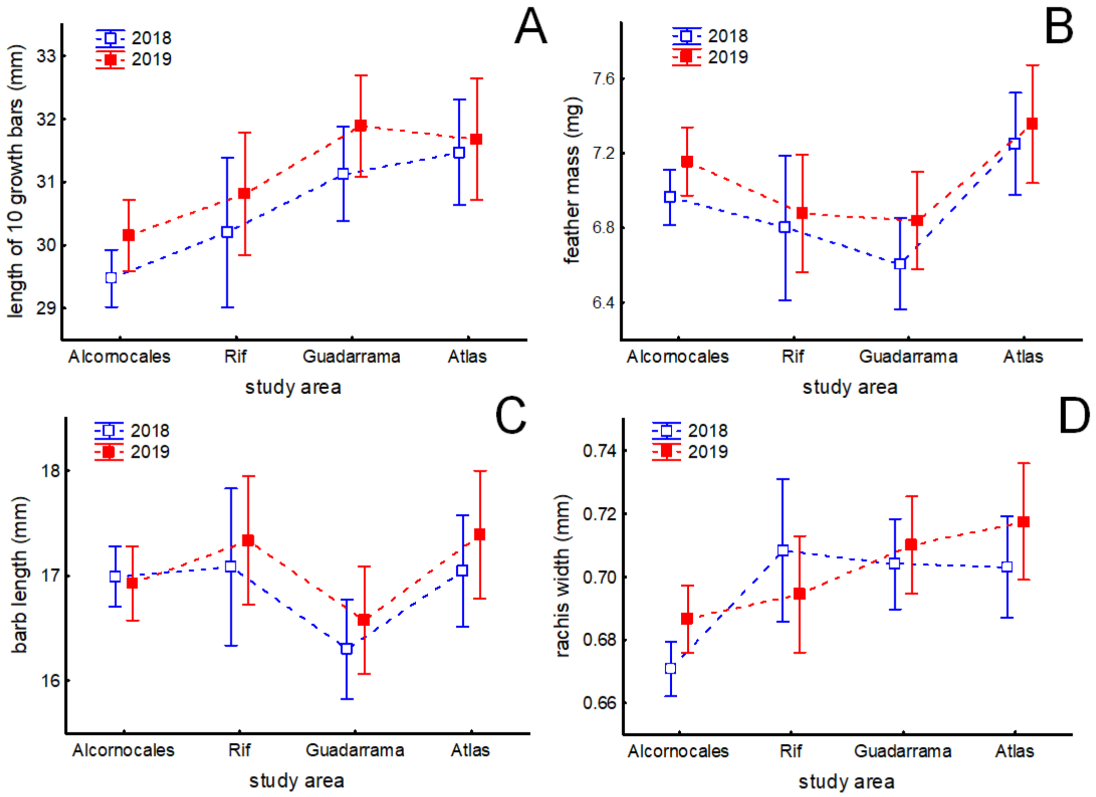

Figure 14. Variation between study areas in: A) the length of ten growth bars, B) feather mass, C) barb length, and D) rachis width. In all cases, the results show mean and standard error for the absolute values of the study areas.

DISCUSSION

General comments

Our results suggest that the strength of differences in the feather metrics of the Eurasian blackcap populations within the southwestern Palaearctic will vary according to the scale of approach (within vs. between population comparisons) and the idiosyncratic requirements of the studied traits. This means that the results in this paper are influenced by at least two experimental conditions to be considered when extending our conclusions to other experimental designs. First, potential links between feather traits and local environmental drivers are probably blurred by adaptations to migration that could not operate in sedentary or fully-migratory populations. Second, we have studied different feather traits (growth bars, mass, barbs and rachis) that are probably shaped by different environmental or evolutionary processes. This can explain why the study traits show idiosyncratic thresholds of change between blackcap populations and differences in flexibility to environmental changes. Having into account these particularities and constraints, our results support some predictions, but also suggest several uncertainties that we discuss below.

Environmental effects

The Eurasian blackcap is a forest passerine widely distributed across the Western Palearctic that, in the Mediterranean, tracks moist forest patches (Tellería & Pérez-Tris, 2003). This can be explained because summer drought, a main restriction of Mediterranean productivity, constrains tree growth and, hence, forest occurrence and its associated avifauna distribution (Tellería & Santos, 1993). Such habitat preferences fit well with the observed distribution of the Eurasian blackcap in our study area, where it reaches the highest abundances in the most productive woodlands of Southern Spain (Alcornocales; Fig. 12B), an outstanding southern forest refuge of this and other forest passerines (Pérez-Tris & Tellería, 2002). As body condition of the Eurasian blackcap did not deplete as its abundance increased, the observed pattern of primary productivity (Fig. 12C) seems a suitable surrogate of habitat suitability for the species. In this environmental setting, the altitudinal decrease in productivity and abundance underlines the increasing constraints that Eurasian blackcaps experience in mountain areas despite it is able to breed above 2000 m a.s.l. in the southernmost edge of this range (Thevénot et al., 2003). The low productivity of highlands has been often highlighted as a main constraint of species distribution in mountains (McCain, 2009) that does not prevent, however, the seasonal occupation of these high-altitude habitats by some birds for breeding (Boyle, 2017).

Despite the observed patterns of abundance and productivity, the growth rate and mass of feathers did not increase in the more productive lowlands. This pattern is particularly odd in the case of feather growth rate that displayed a significant change between the two years (the wider growth bars occurred in the most productive year; Fig. 14A, Table 9). Although this supports the flexibility of growth bars to this temporal change, they did not track at all the between-area differences in productivity (Fig. 12C). This suggests a causal link between productivity and growth bars within populations (Gienapp & Merilä, 2010), but not between them (Jenni & Winkler, 2020), which could be related to different constraints or evolutionary strategies of populations that end up affecting growth bars (e.g. the migratory behaviour, see below). However, this explanation is in trouble when comparing these patterns with the feather growth rate of blackcap fledglings (age 3) studied in summer 1997 in Guadarrama and Alcornocales (Carbonell et al., 2003). In both cases, the growth bars decreased as drought increased within areas, but did not show the between-area differences observed in this study. This was mainly related to a shortening of bars in the Guadarrama mountains (around 29 mm) if compared to the results in this study (Fig. 14A). These differences suggest the need for further research on the actual constraints of growing bars and the potential effect of some ongoing environmental changes in the resulting patterns (e.g. climate change and increasing tree cover etc.) in studies separated by 20 years. In fact, the Guadarrama mountains are under the strong effect of woodland encroachment that has enlarged the distribution of this species (Tellería, 2020). In any case, results in this paper do not support any causal link between the distribution of primary productivity between areas and the growth rate or mass of feathers.

Migratory behaviour

Longer and sharper wings, a set of traits related to flight efficiency in migratory birds (Leisler & Winkler, 2003), suggest that populations of the Eurasian blackcap inhabiting the highlands make seasonal movements along the elevation gradient (Fig. 13A-C). These morphological trends had been formerly detected in Iberian blackcaps and other passerines involved in seasonal movements between mountains and lowlands (Tellería & Carbonell, 1999; Tellería et al., 2001). Our study with African blackcaps enlarges the scope but also shows some idiosyncratic patterns of the Atlas mountain birds as they do not show a sharp increase of wing concavity (Fig. 13B). This suggests some differences in the way migration shapes wing morphological design in Iberian and African blackcaps inhabiting the highlands, perhaps because the distances that African populations have to travel are shorter as they are at the limit of their distribution area. Some preliminary analyses suggest that Atlas blackcaps disappear during winter from forests located over 1300 m a.s.l. (Appendix 2; Fig. S2), while the upper altitudinal limit of blackcap winter distribution in central Spain is located at around 600 m.a.s.l. (Pérez-Tris, 2012). Thus, the effect of latitude on winter severity could explain the differences in the extent of migratory movements and the concomitant changes in wing morphology. Despite these uncertainties, it can be concluded that changes in wing morphology support the existence of different migratory strategies in the Eurasian blackcap populations of the southwestern Palaearctic.

Results in this paper show a concordance between feather traits (measured in tail feathers) and some constraints usually related to continental migration in birds. For instance, time constraints to moult after breeding and before the onset of migratory movements have been usually linked to faster moult and the production of lighter feathers in populations involved in latitudinal movements (De la Hera et al., 2010; Terrill, 2018; Kiat et al., 2019). In our case, blackcap populations involved in altitudinal movements reported wider growth bars, which could suggest faster feather production in a context of time constraints. However, feather mass did not show the expected pattern as the two highland populations (Atlas and Guadarrama) had the heaviest and lightest feathers respectively (Fig. 14B). Feather mass showed an atypical pattern in the Atlas populations, with feathers that are both fast growing and heavier than the rest (Fig. 14B). This suggests that light feathers are not the by-product of faster moults (Dawson et al., 2000; Serra et al., 2007, 2010; Vagasi et al., 2012; Moller & Nielsen , 2018), but the putative result of other physiological and evolutionary processes (De la Hera et al., 2013; Jenni et al., 2020). Likewise, a recent study detected wider rachises and shorter barbs in migratory populations of the European robin (De la Hera et al., 2020), which is consistent with our results, although their functional role remains poorly understood. Tail evolution in birds is a balance between manoeuvrability and drag reduction, so that narrow tail feathers could be useful to reduce drag in migratory birds (e.g. Guadarrama, Fig. 14C). In any case, this trait seems linked to the effects of sex and age (Table 9; Tobalske, 2007) so that it remains unclear whether it is actually associated with flight efficiency in migratory birds. Finally, an increased diameter of the rachis would be a straightforward solution to improve bending stiffness in flight feathers (Tubaro, 2003; Weber et al., 2005), which would improve the transmission of the aerodynamic forces to the musculoskeletal system during flight (Videler, 2005). Consequently, rachis width is expected to increase in birds performing longer migratory journeys to obtain better mechanical properties (De la Hera et al., 2010). Our results support this view as rachis width, a trait unrelated to age or sex (Table 9), increased from lowland to highland populations (Fig. 14D). However, it is important to note that, while rachis width and bending stiffness are positively associated with migration distance in robins (De la Hera et al., 2020), the opposite pattern was detected in blackcaps, where migrants showed, on average, narrower rachis than the sedentary counterparts with which they wintered in sympatry in southern Spain (De la Hera et al. 2010). This contrasting patterns of rachis width variation between migratory and sedentary blackcaps could be influenced by the more northern origin of the migrant populations in the older study, where the allegedly Central European migrants could use other mechanisms, apart from enhancing rachis diameter, to increase bending stiffness (De la Hera et al., 2010). Still this raises a doubt on the actual role of rachis width in the flight mechanics of birds and if it can always be considered an adaptive trait related to migration in birds (Lees et al., 2017; Jenni et al., 2020). In view of the above, our results show that certain feather traits (such as accelerated growth rate or wide rachis) are maintained in both latitudinal and altitudinal migrants, but other traits (such as feather mass or barbs length) do not fit this scheme. It would be interesting to check whether the results obtained are really a pattern of the populations in this context or a specific condition of this species.

Concluding remarks

Moulting is an important landmark in bird life cycle that interacts with other processes (reproduction, migration) and provides feathers that can be useful for monitoring several aspects of bird biology. Unfortunately, the processes that modulate feather structure and production are far from being understood, probably because they result from some idiosyncratic traits of species (e.g. size, physiology, diet), individuals (e.g. sex, age), scales of approach (within vs. between population), particular adaptations (e.g. migration) or environmental settings (e.g. food availability, time constraints, competence, predation;

see chapter 3.2.7 Jenni & Winkler, 2020). This makes difficult to get plain links between different environmental or evolutionary settings and feather traits. Regardless, the results of this work demonstrate that there is variability in these traits among southwestern Palearctic populations of the Eurasian blackcap and suggest the inspiring idea that several of the study traits are better interpreted as adaptations to altitudinal movements of Eurasian blackcap populations.

CAPÍTULO 4

LAS AVES FORESTALES DE LAS TIERRAS ALTAS Y BAJAS DIFIEREN EN LAS TASAS DE CRECIMIENTO DE LAS PLUMAS: UNA PRUEBA MULTIESPECÍFICA EN EL SUROESTE DEL PALEÁRTICO

Este capítulo está basado en el manuscrito: **Hernández-Téllez, I.**, Aguirre, J. I., de la Hera, I., Onrubia, A., & Tellería, J. L. (2022). Highland and lowland forest birds differ in feather growth rates: a test in the south-western Palaearctic. **Ibis**. En revisión.

RESUMEN

Las aves de montaña se enfrentan a numerosos retos causados por la estacionalidad ambiental producida por la elevación, que puede afectar a su morfología, comportamiento y calendario de eventos estacionales, como la cría y la muda. Para inferir posibles diferencias en la duración de la muda y en la calidad del plumaje entre las poblaciones de aves de las tierras altas y las de las tierras bajas, comparamos la tasa de crecimiento y la masa de las plumas de la cola de seis especies de paseriformes forestales (O. Passeriformes) muestreadas a diferentes altitudes en la Península Ibérica (norte) y el Magreb (sur). Dado que el tiempo es crucial en los ambientes estacionales, también exploramos los cambios estacionales de temperatura en las diferentes áreas de estudio como una aproximación a las ventanas temporales adecuadas para la cría y la muda. Además, comprobamos las posibles diferencias en la configuración de las alas entre las poblaciones, que podrían sugerir diferencias en su comportamiento migratorio. Los resultados mostraron ventanas temporales óptimas más cortas para la cría y la muda, alas más largas y cóncavas y tasas de crecimiento del plumaje más rápidas en las poblaciones de las tierras altas en comparación con las de las tierras bajas, pero no encontramos patrones consistentes de variación en la masa del plumaje. Estos resultados sugieren que la selección podría haber favorecido una tasa de crecimiento del plumaje acelerada en las poblaciones con comportamiento migratorio altitudinal para hacer frente a la reducción de la ventana temporal óptima a medida que aumenta la elevación. Estos patrones son bastante similares a los observados en poblaciones migratorias que se desplazan a lo largo de gradientes latitudinales para criar en ambientes altamente estacionales del Norte, por lo que planteamos la hipótesis de que los gradientes de elevación en el límite sur del Paleártico son una fuerza motriz principal que promueve la variación de las características del plumaje y, probablemente, de otras características del ciclo vital de las aves.

ABSTRACT

Mountain birds face numerous challenges caused by the environmental seasonality produced by elevation, which may affect their morphology, behaviour and timing of seasonal events, such as breeding and moulting. To infer potential differences in moult duration and feather quality between highland and lowland bird populations, we compared the growth rate and mass of the tail feathers of six forest passerine species (O. Passeriformes) sampled at different altitudes in the Iberian Peninsula (North) and the Maghreb (South). As timing is crucial in seasonal environments, we also explored seasonal changes in temperature in the different study areas as a proxy of suitable temporal windows for breeding and moulting. In addition, we tested for potential differences in wing configuration between populations that could suggest differences in their migratory behaviour. Results showed shorter optimal temporal windows for breeding and moulting, longer and more concave wings and faster

feather growth rates in highland compared to lowland populations, but we found no consistent patterns of variation in feather mass. These results suggest that selection might have favoured an accelerated feather growth rate in populations with altitudinal migratory behaviour to cope with the reduction in the optimal temporal window as elevation increases. These patterns are quite similar to those observed in migratory populations moving along latitudinal gradients to breed in highly seasonal environments of the North, so that we hypothesize that elevation gradients in the southern limit of the Palearctic are a main driving force promoting variation in feather characteristics and, probably, other avian life history characteristics.

INTRODUCTION

Bird populations distributed along elevation gradients are seasonally challenged to cope with changing environmental conditions (Laiolo & Obeso, 2017; Quintero & Jetz, 2018; Spehn et al., 2019). This is the case of temperate mountains where hard winter conditions (low temperatures, snow cover, etc.) and unpredictability of food resources (Cortés & Wheeler, 2018) force breeding birds to move in the search of more suitable lowlands (Boyle, 2017; Ceresa et al., 2020; Barras et al., 2021). As a result, it can be conjectured that highland populations are under strong selective pressures that would ultimately result in behavioural, physiological and morphological differentiation from their lowland counterparts (Martin, 2004). However, whilst these environmental pressures can shape intraspecific variation along elevation gradients, the processes involved in these patterns are yet poorly understood (Boyle et al., 2016).

Plumage is a key trait in avian biology, as it is involved in thermoregulation, mechanical protection, flight and social and cryptic behaviour (Jenni & Winkler, 2020b). Feathers are progressively damaged over time, which impels most birds to moult their whole plumage once a year, typically after breeding (Barta et al., 2008). Moult is an energetically demanding process with strong consequences on individual fitness and survival (Dawson et al., 2000) as suggested by growing evidence of strong selection pressures acting on feather traits (Takaki et al., 2001; Gienapp & Merila, 2010).

It is commonly acknowledged that feather traits are driven by some environmental conditions that may shape feather growth and quality (Pap et al., 2015). However, whilst feather growth could be conditioned by the sharp environmental changes caused by elevation, there is not conclusive evidence on the way feather production differs between highland and lowland bird populations (Hernández-Téllez et al., 2021). A previous study showed that mountain populations of the Eurasian Blackcap (*Sylvia atricapilla*) showed wider growth bars (an index of feather growth rates; Grubb, 2006) than populations in lowland areas, but did not differ in feather mass (an index of moult investment in feathers by birds) despite highland populations occurring in less productive areas (De la Hera et al., 2009, Hernández-Téllez et al., 2021). An alternative explanation to this pattern is to consider that blackcaps in highlands were impelled to fast moult by a shortening of the temporal window to breed before displacing to lowland areas for overwintering. Interestingly, highland blackcaps had longer and more concave wings typical of migratory birds so that it was hypothesized that the observed feather traits were mediated by these altitudinal movements. Fast moults in migratory birds have been usually related to the narrow temporal windows to breed and moult in their northern breeding grounds (Hall & Fransson, 2000; De la Hera et al., 2012; Kiat et al., 2019). In this context, recent studies highlight the importance of latitude in shaping some aspects of plumage development, finding faster feather growth rates as latitude increases (Dietz et al., 2015; Terrill, 2018; Horák et al., 2022). Thus, we conjectured that elevation effects in the southern populations of the Eurasian blackcap could resemble the effects of latitude at larger geographic scales (Hernández-Téllez et al., 2021), which might allow us to predict the expression of plumage traits if elevational gradients modify the organisation of the annual cycle of birds (Lundblad & Conway, 2020).

In this study, we explore whether the above patterns were linked to the idiosyncratic traits of the Eurasian blackcap, a bird reputed by its ability to track seasonal resources at different spatial scales (Tellería & Pérez-Tris, 2003) or, alternatively, are also applicable to other bird species. For this purpose, we explored the growth rate and mass of tail feathers in six forest bird species (O. Passeriformes) captured at highlands and lowlands of the Iberian Peninsula and the Maghreb (Table 10). Interestingly, since highland areas are located in the southern part of the Maghreb, this gives us the opportunity to partially dissociate the effects of latitude and altitude, which may be confounded in the Iberian Peninsula where both gradients are positively correlated (more northern populations live in higher sectors). More explicitly, we explored the following aspects:

Feather traits. First, we tested whether highland populations of all the study species show higher feather growth rates than their lowland counterparts. We predict that if highland birds face shorter optimal temporal windows than lowland counterparts, they will be more prone to migrate and will show shorter moulting periods and faster moults (Dawson, 2004). In addition, as a fast feather growth has been linked to a low investment in feather mass (Dawson et al., 2000; Vágási et al., 2012; but see De la Hera et al., 2022), it can be suggested that lighter feathers will be produced in highland birds, although not always a rapid moult is associated with lower feather mass.

Morphological variation. Secondly, we explored if wing length and shape of highland populations suggest a process of population differentiation similar to the one observed in birds migrating along latitudinal gradients (Hedenström, 2008). We expect longer and more pointed wings in highland populations compared to lowland counterparts, two traits usually selected to reduce the energetic costs of avian migration (Leisler & Winkler, 2003; Piersma et al., 2005), regardless of the potential differences between Iberia (more northern and, predictably, more migratory) and the Maghreb (potentially less migratory based on latitudinal patterns). However, we acknowledge that differences in wing length and shape could also result from local adaptations to habitat structure since more rounded and shorter wings improve manoeuvrability in cluttered vegetation (Noreau & Desrochers, 2018) so that we accounted for the effects of vegetation structure as a potential confounding factor of variation in wing morphology between highland and lowland birds.

METHODS

Study species

We have selected a set of partial migratory forest species (*Sylvia atricapilla*, *Erithacus rubecula*, *Turdus merula*, *Fringilla coelebs*, *Parus major and Cyanistes sp*; Table 10), which means that they can show from fully migratory (e.g. when they breed in strongly seasonal environments) to fully sedentary populations (in the most stable areas) over their distributional range (Chapman et al., 2011). This pattern of variation has been also observed within the Iberian Peninsula, where the abundance of some species during breeding is higher in the highlands than in lowlands, while the opposite occurs during the

winter period, i.e. lowlands show higher bird numbers than highlands. Interestingly, these populations differ morphologically as highlands birds show longer and more pointed wings than lowland counterparts, which could be suitable for traveling between breeding and wintering areas (Tellería & Carbonell, 1999; Tellería et al., 2001). Less is known, however, about the North-African populations, although seasonal changes in the distribution of some species suggest similar, but weaker, seasonal patterns in the numerical rearrangement of populations (Thevenot et al., 2003; Dingle, 2008; Hernández-Tellez et al., 2021; Tellería et al. 2022). In addition, some bird species show processes of population differentiation in the Maghreb (Clements et al., 2021; Table 10), which suggests that the Iberian and African populations have different evolutionary histories. For this reason, our analyses will differentiate Iberian and North African individuals when comparing the growth and mass of feathers, as well as morphology between highland and lowland populations.

Table 10. Taxonomic differences (subspecies or species) between the Iberian Peninsula and the Maghreb of the forest passerines (O. Passeriformes) considered in this study according to Clements et al. (2021). Some traits of their biology (main food, feeding substrata and spatial distribution; Cramp & Brooks, 1992) and the distribution of the total individuals sampled are resumed. Sample sizes for the four areas (Guadarrama; Alcornocales; Rif; Atlas) in brackets.

	Family	**Distribution**		**Winter ecology**	**Total samples**
		Iberia	**Maghreb**		
Monotypic subspecies					
Sylvia atricapilla (Blackcap)	Sylvidae	*S. a. atricapilla* and *S. a. heineken*	*S. a. atricapilla*	Frugivorous, shrub, vagrant	141 (31;70;16;24)
Erithacus rubecula (Robin)	Muscicapidae	*E.r. rubecula*	*E. r. rubecula*	Insectivorous, ground, territorial	112 (25;29;23;35)
Polytypic subspecies					
Turdus merula (Blackbird)	Turdidae	*T. m. merula*	*T. m. mauritanicus*	Omnivorous, ground, territorial	80 (24;26;10;20)
Fringilla coelebs (Chaffinch)	Fringillidae	*F. c. balearica*	*F. c. africana*	Granivorous, ground, vagrant	114 (26;22;17;49)
Parus major (Great Tit)	Paridae	*P. m. major* and *P. m. corsu*	*P.m. excelsus*	Insectivorous, canopy, vagrant	104 (23;20;18;43)
Different species					
G. Cyanistes (Blue Tit)	Paridae	*C. caeruleus caeruleus* and *C. c. ogliastrae*	*C. teneriffae ultramarinus*	Insectivorous, canopy, vagrant	96 (18;20;28;30)

Study areas and temporal windows for breeding and moulting

The study area is located in highland and lowland areas in the Iberian Peninsula: Guadarrama Mountains (mean 1090 m.a.s.l) and Los Alcornocales Natural Park (137 m.a.s.l); and in the Maghreb: Atlas Mountains (1460 m.a.s.l) and Rif Mountains (571 m.a.s.l; Fig. 15A), where woodlands range from broad-leaved (*Quercus pyrenaica*, *Quercus suber*) to conifer (*Pinus sylvestris, Cedrus atlantica*) woodlands. The selected areas cover a latitudinal and altitudinal gradient (see details in Hernández-Téllez et al., 2021) with different patterns of seasonality along the range limit of the target species.

To explore the length of the temporal windows useful for breeding and moulting, we recorded the variation of temperature throughout the year. This variable triggers the productive activity of plants (Huang et al., 2019) and is therefore related to increased primary (Anav et al 2015) and invertebrate productivity (Thomas et al., 2001). The lengthening of warm periods will favour a greater availability of food for birds for a longer period of time, which is essential for relaxed reproduction and feather renewal (Martin, 1987). Environmental temperature is also related to the birds' climatic conditions (thermoregulatory requirements or reproductive phenology; Shutt et al., 2019). To observe the seasonal variation of this parameter among the four study areas, we downloaded mean temperatures (in °C) for each month from the Climate Research Unit (CRU) (<https://www.uea.ac.uk>) for the period 2011-2016 as a reliable source with the appropriate scale (0.1° resolution; 10 x 10 km2 grid) and available time frame of climatological conditions in the study area. Using the point sampling tool in QGIS 3.4.15 (QGIS Development Team 2020), temperatures were averaged for each sampling site (mist nets where birds were captured).

The observed patterns suggest a complex environmental heterogeneity between the different sectors, where lowlands are warmer than highland sectors throughout the year (Fig. 15B). Temperatures showed a hump-shaped distribution in all cases but with a shorter warm period in the highlands. Highlands displayed a drastic drop in temperatures from August onwards lasting until the following spring (May-June). This also included winter frosts until March that do not occur in the lowlands (García-Martín et al., 2021). Therefore, it can be inferred that highlands exhibit optimal windows of resource availability for breeding and moulting that are narrower than those of lowlands.

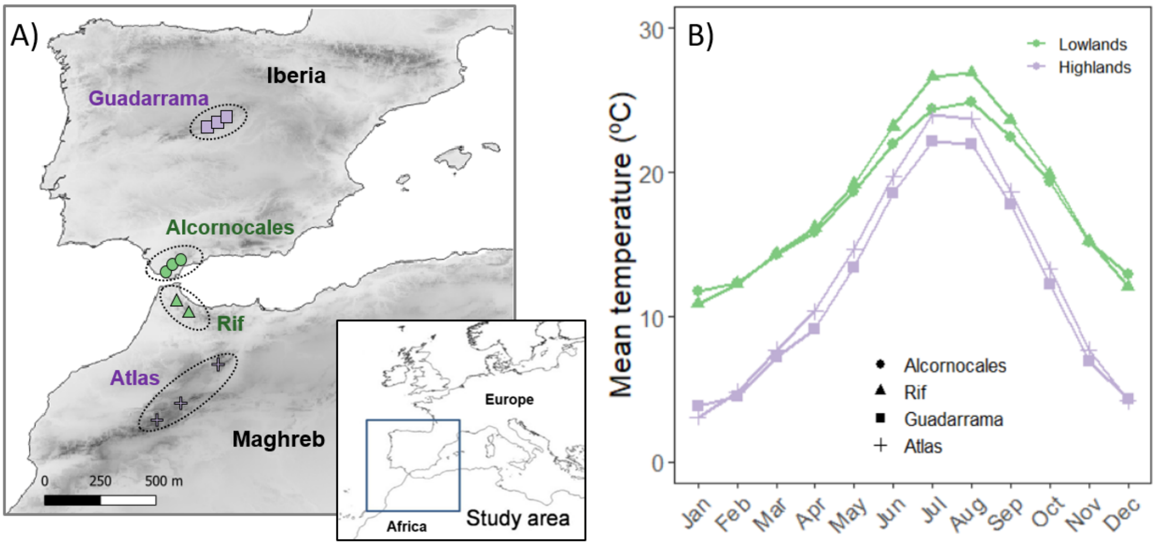

Figure 15. A) Location and geographical distribution of the study areas in the Iberian Peninsula and Maghreb where birds were captured to study morphological and plumage traits. B) Evolution of temperatures throughout the year.

Vegetation structure

To control for the effects of vegetation structure on bird morphology when comparing highland and lowland birds, we sampled habitat traits in 25 m radius buffer from the midpoint of each mist net in which each bird was captured (see below). At each sampling point, we obtained the following measurements: (1) grass cover, (2) vegetation cover up to 0.5 meters, (3) vegetation cover between 0.5 to 2 meters, (4) vegetation cover over 2 meters, (5) average tree height, (6) number of woody plant species less than 2 meters high and (7) number of woody plant species over 2 meters high. All these data were used to perform a principal component analysis (PCA) to detect any latent variable able to describe vegetation gradients. The PCA provided two main components, one that reflects the variation in the undergrowth development (PC1, eigenvalue = 1.95 ; explained variance = 0.28 ; factor loadings: grass = -0.42, low vegetation = 0.48, medium vegetation = 0.55, high vegetation = -0.17, tree height= -0.10, low species = 0.50, high species = 0.02) and a second component related to the development of the tree canopy (PC2, eigenvalue = 1.52; explained variance = 0.22 ; factor loadings: grass = -0.08, low vegetation = 0.03, medium vegetation = 0.02, high vegetation = 0.53, tree height = 0.65, low species = 0.17, high species = 0.51). Only PC2 was selected in order to avoid interactions that would blur the results. Thus, a single variable is included in the models to account for habitat structural complexity as a possible factor driving variation in avian wing morphology (Desrochers, 2010). Factor scores of each individual along the gradients were used to test for the effect of habitat structure on morphology.

Capture and measurements of birds

We mist-netted the six study passerine species along an elevation gradient from late April to late June for two consecutive years (2018 and 2019). This period spans the breeding season of the study species, which moult in the same area where they hatch or breed (Jenni & Winkler, 2020a). The location of the different sampling sites is detailed in Hernández-Téllez et al. (2021), where selected species with different genetic backgrounds coexist (Clements et al., 2021). Mist-netted birds were ringed, aged based on plumage data according to the EURING code system (age 3: hatched in the current spring; age 5: young individuals hatched during last spring, still with flight feathers that developed in the nest; age 6: adult individuals, with flight feathers that come from a complete moult), sexed (males and females) according to available literature (Jenni & Winkler, 2020a) and measured (maximum wing chord, minimum tarsus length) following Svensson (1992). We also studied wing formula by considering the primary distances of the nine longest primaries (excluding the vestigial outermost primary: P10). Primary distance was defined as the distance from the tip of each primary to the tip of the longest primary with the wing folded, assigning a value of zero to the primary (or primaries) constituting the wingtip. Wing chord measurements were recorded to the nearest 0.5 mm (Svensson, 1992) and tarsus and primary distances measurements were taken with a digital calliper with a resolution of 0.01 mm. All measurements were made by official expert ringers of the Spanish Ringing Scheme (IHT, JIA and AO) who had their measuring procedures standardized, after testing the interpersonal repeatability. Finally, the second outermost tail feathers (rectrix number 5 from left and right side) were collected from each individual and stored in individual envelopes until further analyses. We discarded immature individuals (age 3) because they were not fully grown in some cases. Captures, ringing and collection of biological samples were performed under permission of the Moroccan and Spanish authorities.

Feather traits

We obtained measurements of feather growth rate and feather mass in a total of 622 birds (Table 10). Each tail feather was studied by the same person (IHT) to avoid interpersonal bias. The total feather length (from the inferior umbilicus to the distal tip) was measured with a digital calliper (resolution 0.01 mm) as a potential confounding factor influencing the growth rate and mass of feathers. The study of growth rate was carried out using ptilochronology, a technique that consists in measuring the width of 10 growth bars, which was obtained following a similar approach to Grubb (1989, 2006). We assumed that each growth bar (one light band plus one dark band perpendicular to the rachis) occurs over a 24-hour period, therefore the width of these growth bars indicates daily increases in feather length (Brodin, 1993). Ptilochronology-based estimates of feather growth rate have been shown to correlate with overall moult speed both within and between bird species (De la Hera et al., 2011). The length of feather occupied by ten growth bars (located at about two-thirds of the feather length from its base) was marked with two entomological pins on the edge of the internal vane and this distance measured with a digital calliper (resolution 0.01 mm). In addition, the feather mass was obtained using a high-resolution digital balance (Mettler Toledo ® model AG-245; instrumental repeatability 0.01 ± 0.02 mg) to estimate the amount of deposited material in each feather.

Wing morphology

We used wing morphology to predict the potential ability of populations of different species to perform seasonal movements. Since wing configuration is related to flight efficiency, it is expected that, as the elevation of breeding areas increases, populations will require longer and more pointed wings that are more favourable for these seasonal movements (Tellería & Carbonell, 1999; Fiedler, 2005). To describe wing shape we performed a principal component analysis (PCA) with the lengths of the primaries. To do so, we transformed primary distances into carpal joint distances by subtracting their primary distance from the wing length. These transformed distances (cP1-cP9) were then standardized, for each species independently, according to the method suggested by Senar et al. (1994) that corrects for between-individual variation in wing length. In order to perform the calculations correctly, those individuals that did not have all the measurements of the primary distances were eliminated. The PCA provided two principal components that reflected variation in wing concavity (PC1) and wingtip pointedness (PC2) among the individuals of each species (Appendix 6; Table S7 and S8). Thus, higher scores for these components were associated, respectively, with more concave wings and more pointed wingtips, which are typical of

more migratory individuals.

Statistical analyses

We used general linear (Gaussian) models (Zuur et al., 2007) to compare feather growth rate and mass between highland and lowland areas in Maghreb and Iberia accounting for the effect of sex (female, male), age (5 age, 6 age) and feather length (covariate). General linear models were also run to test whether variation in wing length and shape were related to the altitudinal category (highland vs. lowland) of study areas accounting for the effect of sex (female, male), age (5 age, 6 age) and habitat structure (PC2) as covariate. In the case of wing length we also included tarsus length (a skeletal measurement of body size) as covariate. Note that our standardized measurements of wing concavity and wingtip pointedness are independent from wing length (Appendix 6; Table S9). All models met the assumptions of parametric tests (Appendix 6; Table S10) and in no case was there any correlation between explanatory variables (Appendix 6; Table S11). All analyses were performed with the *stats* package and statistical graphics with the *ggplot2* package in R version 4.0.2 (<www.r-project.org>).

RESULTS

Feather traits

Highland populations showed broader growth bars than lowland counterparts, although this difference was not significant for the Great tit (P-value= 0.108; Table 11). This supports the view that the observed trends in the Eurasian Blackcaps also occur in other forest passerines (Table 11, Fig. 16A). The strength of the effect of altitudinal category on feather growth rate varied between regions for blackcaps and blackbirds. Thus, although highland populations of these two species had a faster growth rate than lowland birds in both regions, this difference was more marked in Iberia than in the Maghreb (Table 11).

Feather mass did not vary between highland and lowland populations, except for the Blue Tit, where lowland blue tits had relatively lighter feathers (Fig. 16B). We found that Maghreb birds had significantly heavier feathers than Iberian counterparts in four out of six species (Table 12). In addition, feather mass also showed a significant interaction between

Table 11. Results of linear models analysing the variation in the width of 10 growth bars in relation to altitude (2-level factor) and sampling region, after controlling for the effects of age, sex and feather length. (*p < 0.05, **p < 0.01, ***p < 0.001)

	Sylvia atricapilla (estimate ± SE)	***Erithacus rubecula*** (estimate ± SE)	***Turdus merula*** (estimate ± SE)	***Fringilla coelebs*** (estimate ± SE)	***Parus major*** (estimate ± SE)	***G. Cyanistes*** (estimate ± SE)
Intercept	0.59 ± 0.18**	0.35 ± 0.22	0.34 ± 0.21	0.20 ± 0.20	0.18 ± 0.20	-0.05 ± 0.30
Year (2019)	**0.43 ± 0.15****	0.34 ± 0.17	0.18 ± 0.17	**0.37 ± 0.17***	**-0.28 ± 0.14***	**0.63 ± 0.17*****
Age (Adult)	**-0.46 ± 0.17****	-0.23 ± 0.20	0.23 ± 0.18	0.00 ± 0.18	0.10 ± 0.15	0.06 ± 0.23
Sex (Female)	0.28 ± 0.14	0.22 ± 0.22	0.11 ± 0.21	0.32 ± 0.24	**0.42 ± 0.17***	-0.16 ± 0.21
Feather length	**0.36 ± 0.08*****	**0.26 ± 0.12***	**0.43 ± 0.13****	0.29 ± 0.15	**0.90 ± 0.13*****	0.08 ± 0.12
Altitude category (Lowland)	**-1.15 ± 0.18*****	**-0.88 ± 0.26****	**-1.25 ± 0.22*****	**-1.25 ± 0.25*****	-0.34 ± 0.21	**-1.04 ± 0.32****
Region (Maghreb)	-0.43 ± 0.24	-0.44 ± 0.25	-0.44 ± 0.29	-0.21 ± 0.27	-0.32 ± 0.22	0.34 ± 0.26
Altitude*Region	**0.89 ± 0.33****	0.66 ± 0.35	**0.94 ± 0.39***	0.21 ± 0.34	0.37 ± 0.27	0.31 ± 0.37
R^2 x 100	34.55	20.12	44.39	33.77	60.26	32.41
F	$F_{7,133}$= 11.56	$F_{7,104}$= 4.99	$F_{7,72}$= 10.01	$F_{7,106}$= 9.23	$F_{7,96}$= 22.66	$F_{7,88}$= 7.30
p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 12. Results of linear models analysing the variation of feather mass as a function of altitudinal gradient according to sampling region, after controlling for the effect of age, sex and feather length. (*p < 0.05, **p < 0.01, ***p < 0.001).

	Sylvia atricapilla (estimate ± SE)	***Erithacus rubecula*** (estimate ± SE)	***Turdus merula*** (estimate ± SE)	***Fringilla coelebs*** (estimate ± SE)	***Parus major*** (estimate ± SE)	***G. Cyanistes*** (estimate ± SE)
Intercept	-0.28 ± 0.15	0.09 ± 0.14	-0.57 ± 0.14***	-0.39 ± 0.09***	-0.21 ± 0.09*	-0.31 ± 0.19
Year (2019)	0.19 ± 0.13	-0.08 ± 0.12	0.12 ± 0.12	0.15 ± 0.08	0.05 ± 0.06	**0.33 ± 0.11****
Age (Adult)	0.02 ± 0.14	**0.32 ± 0.13***	**0.64 ± 0.12*****	**0.18 ± 0.08***	0.13 ± 0.07	**0.27 ± 0.14***
Sex (Female)	0.11 ± 0.12	**-0.50 ± 0.15*****	**-0.37 ± 0.14***	**-0.25 ± 0.10***	**-0.45 ± 0.07*****	**-0.35 ± 0.13****
Feather length	**0.69 ± 0.06*****	**0.63 ± 0.08*****	**0.47 ± 0.09*****	**0.69 ± 0.07*****	**0.59 ± 0.06*****	**0.54 ± 0.07*****
Altitude category (Lowland)	0.27 ± 0.15	0.28 ± 0.17	0.14 ± 0.15	-0.02 ± 0.11	-0.05 ± 0.09	**-0.44 ± 0.20***
Region (Maghreb)	0.31 ± 0.20	-0.06 ± 0.16	**0.73 ± 0.19*****	**0.56 ± 0.12*****	**0.62 ± 0.1*****	**0.53 ± 0.16****
Altitude*Region	**-0.86 ± 0.27****	**-0.46 ± 0.23***	**-0.85 ± 0.27****	-0.07 ± 0.15	-0.20 ± 0.12	-0.03 ± 0.23
R^2 x 100	54.55	65.32	74.49	87.49	91.64	72.8
F	$F_{7,133}$= 25.00	$F_{7,104}$= 30.87	$F_{7,72}$= 33.96	$F_{7,106}$= 113.9	$F_{7,96}$= 162.2	$F_{7,88}$= 37.33
p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

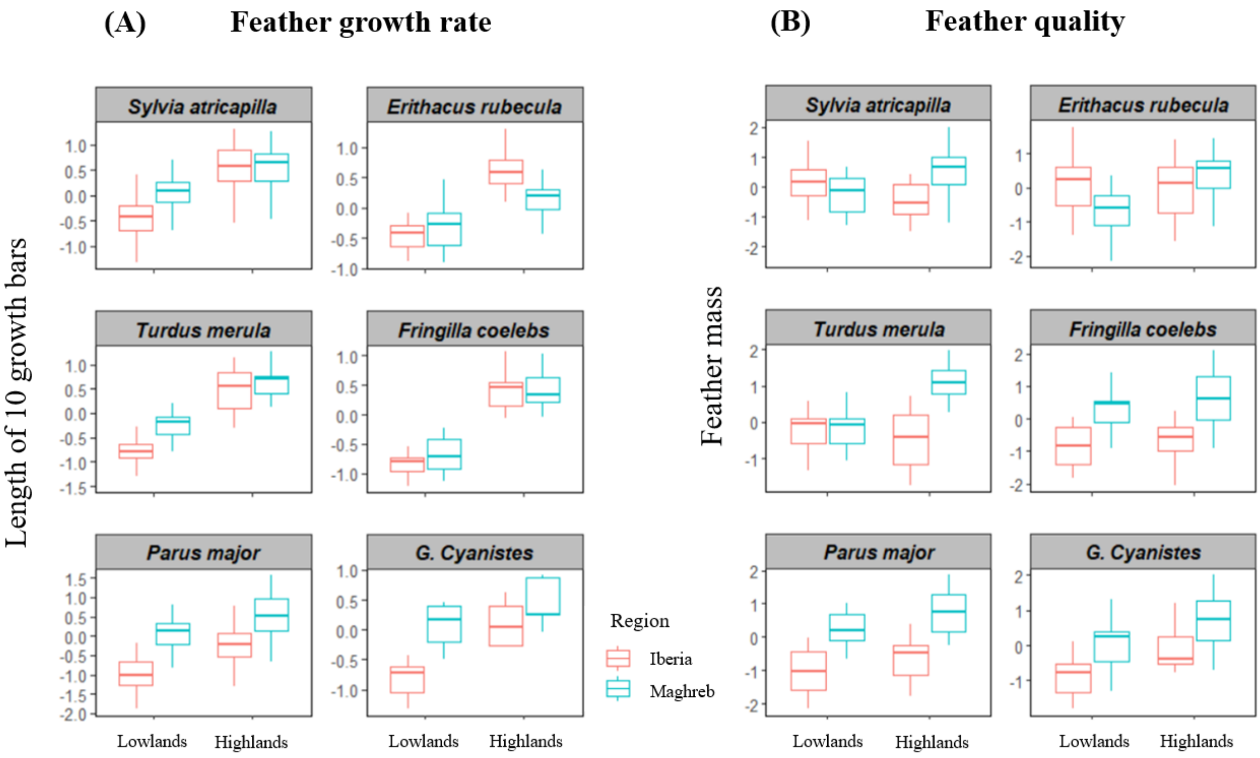

Figure 16. Variation in (A) the feather growth rate and (B) feather quality for the different species between the high and low areas of the study regions. In all cases, the horizontal line inside the boxes shows the median (with correction of the values for significant variables in the model) and the length of the whiskers expresses the variability of the distribution (excluding outliers, if any).

Morphological differentiation

Wing length was longer in highland populations of all the species, but variation in wing length was not consistent between regions across species (blackbirds, chaffinches and great tits had longer wings in the Maghreb, whereas blue tits had longer wings in Iberia; Table 13, Fig. 17A). In addition, the effect of altitude on wing length differed between regions in some cases. Thus, robin and blackbird highland populations had longer wings, but in the Maghreb the difference was more marked than in Iberia. On the other hand, highland blue tits had longer wings, but in Iberia the difference was more marked than in the Maghreb (Table 13). In the case of wing shape and as predicted according to the general patterns of latitudinal variation, all species showed more concave wings in the Iberian Peninsula than in the Maghreb, with four species (blackcaps, blackbirds, chaffinches and great tits) showing significant differences (Table 14, Fig. 17B). Wing concavity showed significantly higher

values in highland birds than in lowland counterparts in most cases, except for the Robin. Furthermore, the effect of altitude on wing concavity in blackcaps, great tits and blue tits was stronger in Iberia than in the Maghreb (Table 14). For the case of wingtip pointedness, the trend differed between species, and only highland blackcaps showed significantly more pointed wingtips than lowland conspecifics (Table 15). In addition, wing length and wing shape of the different species were generally not related to vegetation structure, so the potential confounding effects of habitat structure on wing morphology in this context could be ruled out. The only exception was the Chaffinch that showed more pointed wings in open areas.

Table 13. Results of linear models analysing the variation in wing length as a function of altitudinal gradient according to sampling region and vegetation structure at the point where individuals were captured, after controlling for sex, age and tarsus. (*p < 0.05, **p < 0.01, ***p < 0.001).

	Sylvia atricapilla (estimate ± SE)	***Erithacus rubecula*** (estimate ± SE)	***Turdus merula*** (estimate ± SE)	***Fringilla coelebs*** (estimate ± SE)	***Parus major*** (estimate ± SE)	***G. Cyanistes*** (estimate ± SE)
Intercept	0.42 ± 0.18*	0.37 ± 0.18*	-0.13 ± 0.16	-0.00 ± 0.16	-0.47 ± 0.17**	0.68 ± 0.27*
Year (2019)	**0.36 ± 0.16***	**0.39 ± 0.14****	**0.35 ± 0.13****	**0.31 ± 0.12***	**0.48 ± 0.11*****	**0.37 ± 0.16***
Age (Adult)	**0.49 ± 0.17****	0.27 ± 0.16	0.27 ± 0.14	**0.45 ± 0.12*****	**0.48 ± 0.11*****	**0.65 ± 0.17*****
Sex (Female)	**-0.33 ± 0.15***	**-1.06 ± 0.16*****	**-0.92 ± 0.14*****	**-1.21 ± 0.11*****	**-0.66 ± 0.11*****	**-0.88 ± 0.16*****
Tarsus	**0.24 ± 0.07****	0.01 ± 0.07	-0.05 ± 0.07	**0.25 ± 0.07*****	0.02 ± 0.05	0.09 ± 0.09
Vegetation structure (PC2)	-0.11 ± 0.06	0.02 ± 0.05	-0.04 ± 0.05	-0.02 ± 0.04	-0.04 ± 0.04	0.02 ± 0.08
Altitude category (Lowland)	**-0.87 ± 0.20*****	**-0.62 ± 0.22****	**-0.58 ± 0.16*****	**-0.53 ± 0.17****	**-0.68 ± 0.16*****	**-1.90 ± 0.28*****
Region (Maghreb)	-0.13 ± 0.24	0.13 ± 0.21	**1.14 ± 0.18*****	**0.55 ± 0.19****	**0.99 ± 0.15*****	**-0.72 ± 0.25****
Altitude*Region	-0.10 ± 0.36	**-0.69 ± 0.32***	**-0.75 ± 0.29***	-0.39 ± 0.24	-0.42 ± 0.23	**1.43 ± 0.35*****
R^2 x 100	30.88	52.66	74.78	72.17	77.48	56.06
F	$F_{8,124}$=8.37	$F_{8,92}$=14.91	$F_{8,58}$=25.46	$F_{8,92}$=33.42	$F_{8,78}$=37.98	$F_{8,74}$=14.08
p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 14. Results of linear models analysing the variation in wing concavity as a function of altitudinal gradient according to sampling region and vegetation structure at the point where individuals were captured, after controlling for sex and age. (*p < 0.05, **p < 0.01, ***p < 0.001).

	Sylvia atricapilla (estimate ± SE)	***Erithacus rubecula*** (estimate ± SE)	***Turdus merula*** (estimate ± SE)	***Fringilla coelebs*** (estimate ± SE)	***Parus major*** (estimate ± SE)	***G. Cyanistes*** (estimate ± SE)
Intercept	2.44 ± 0.37***	0.68 ± 0.48	1.04 ± 0.51*	1.55 ± 0.46**	1.19 ± 0.58*	1.41 ± 0.63*
Year (2019)	-0.65 ± 0.33	-0.06 ± 0.38	0.13 ± 0.43	0.18 ± 0.38	0.54 ± 0.39	-0.31 ± 0.37
Age (Adult)	0.08 ± 0.34	-0.48 ± 0.44	0.87 ± 0.46	**0.81 ± 0.36***	0.34 ± 0.39	0.50 ± 0.40
Sex (Female)	0.51 ± 0.31	-0.98 ± 0.43*	-0.37 ± 0.46	-0.36 ± 0.34	-0.02 ± 0.38	-0.69 ± 0.38
Vegetation structure (PC2)	0.03 ± 0.13	-0.02 ± 0.14	-0.07 ± 0.18	0.04 ± 0.13	**-0.38 ± 0.15***	**0.73 ± 0.20*****
Altitude category (Lowland)	**-2.90 ± 0.40*****	0.24 ± 0.58	**-1.90 ± 0.54*****	**-1.61 ± 0.52****	**-1.43 ± 0.57***	**-1.77 ± 0.67***
Region (Maghreb)	**-2.92 ± 0.49*****	-0.44 ± 0.56	**-2.03 ± 0.60****	**-2.35 ± 0.48*****	**-2.22 ± 0.53*****	**-1.69 ± 0.57****
Altitude*Region	**1.97 ± 0.75****	-0.52 ± 0.84	0.41 ± 0.93	0.12 ± 0.71	**1.64 ± 0.80***	**1.92 ± 0.82***
R^2 x 100	36.65	5.52	25.16	34.54	23.15	21.16

Table 15. Results of linear models analysing the variation in wingtip pointedness as a function of altitudinal gradient according to sampling region and vegetation structure at the point where individuals were captured, after controlling for sex and age. (*p < 0.05, **p < 0.01, ***p < 0.001).

	Sylvia atricapilla (estimate ± SE)	***Erithacus rubecula*** (estimate ± SE)	***Turdus merula*** (estimate ± SE)	***Fringilla coelebs*** (estimate ± SE)	***Parus major*** (estimate ± SE)	***G. Cyanistes*** (estimate ± SE)
Intercept	0.44 ± 0.26	0.47 ± 0.36	0.35 ± 0.36	0.18 ± 0.39	-0.28 ± 0.45	0.90 ± 0.54
Year (2019)	0.24 ± 0.24	0.51 ± 0.28	0.36 ± 0.30	0.24 ± 0.32	**0.97 ± 0.30****	**0.88 ± 0.32****
Age (Adult)	-0.28 ± 0.24	**-0.79 ± 0.33***	**-1.26 ± 0.32*****	-0.31 ± 0.30	-0.59 ± 0.30	-0.53 ± 0.34
Sex (Female)	**0.56 ± 0.22***	-0.09 ± 0.32	0.29 ± 0.32	-0.08 ± 0.29	0.11 ± 0.29	-0.27 ± 0.33
Vegetation structure (PC2)	-0.03 ± 0.09	0.07 ± 0.10	0.01 ± 0.13	**-0.24 ± 0.11***	0.04 ± 0.12	0.12 ± 0.17
Altitude category (Lowland)	**-0.96 ± 0.28*****	-0.73 ± 0.43	0.17 ± 0.38	-0.28 ± 0.43	0.36 ± 0.44	**-1.26 ± 0.57***
Region (Maghreb)	-0.37 ± 0.35	-0.21 ± 0.41	0.13 ± 0.42	-0.09 ± 0.40	-0.22 ± 0.41	-0.69 ± 0.48
Altitude*Region	0.54 ± 0.53	-0.02 ± 0.62	0.61 ± 0.66	-0.03 ± 0.59	-0.31 ± 0.62	0.53 ± 0.70
R^2 x 100	11.31	11.14	18.84	0.46	14.82	10.7
F	$F_{7,125}=3.35$	$F_{7,93}=2.70$	$F_{7,59}=3.19$	$F_{7,93}=1.06$	$F_{7,79}=3.14$	$F_{7,75}=2.35$
p	0.003	0.014	< 0.01	0.39	< 0.01	0.03

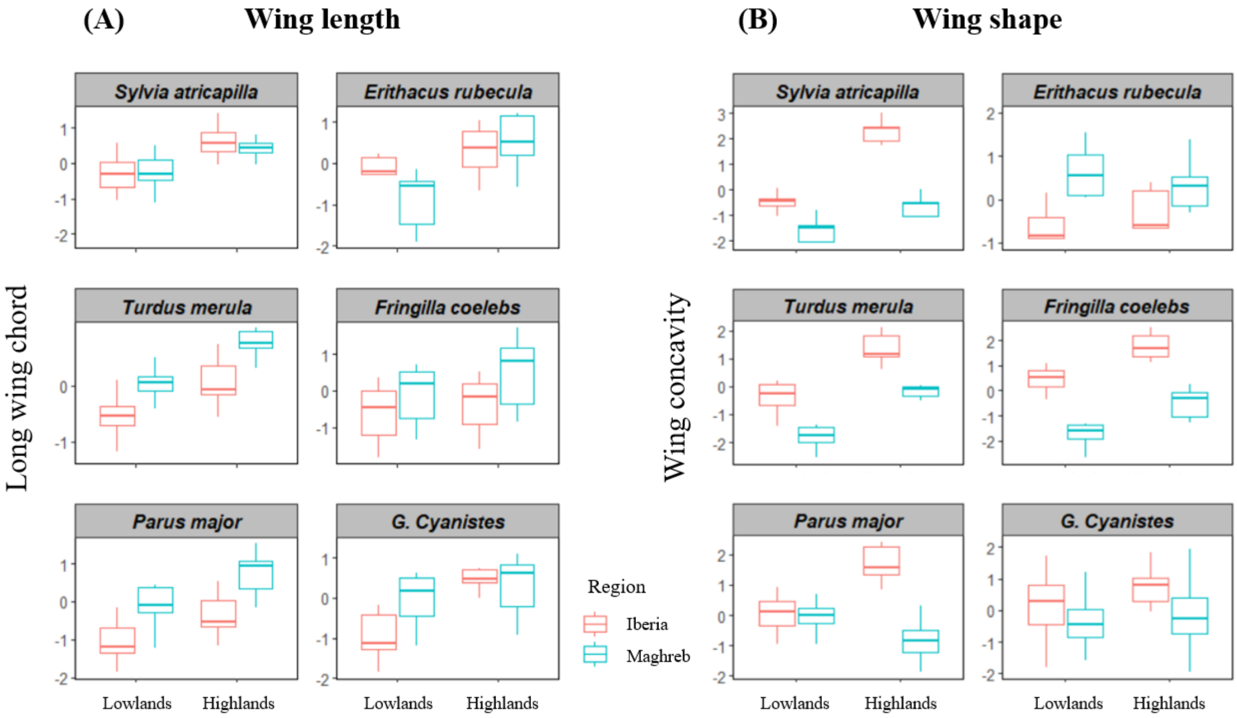

Figure 17. Variation in (A) wing length and (B) wing shape for the different species between the high and low areas of the study regions. In all cases, the horizontal line inside the boxes shows the median (with correction of the values for variables in the model) and the length of the whiskers expresses the variability of the distribution (excluding outliers, if any).

DISCUSSION

Morphological clines are often used to detect the response of populations to environmental gradients, particularly if they can detect the ecological and historical drivers involved in these processes (Richardson et al., 2014). However, the actual input of these studies is usually flawed by a number of methodological shortcomings that must be evaluated. For instance, conclusions on the actual contribution of the potential drivers involved in population differentiation may vary under different geographical settings, methodological approaches, or model species, which makes it difficult to generalize mono-specific approaches obtained in each geographical setting. Interestingly, results in this paper suggest that the distribution of feather traits and wing morphology we had previously observed for the Eurasian Blackcap is widely replicated in other forest passerines within the environmental setting of the southwestern Palaearctic.

Results in this paper also show that, despite the biological differences among the species (Table 10), feather growth rate and wing morphology of most bird species responded similarly to variation in elevation in the south-western Palaearctic. Little is known about the mechanisms underlying the adaptation of populations to the seasonal high-altitude environments and, in particular, the potential feather structural characteristics that could have been selected in these altitudinal contexts (e.g. Gienapp & Merilä, 2010; Pap et al., 2015, 2019). To our knowledge this is the most comprehensive study that, by using a multi-species approach, revealed intraspecific variation in feather growth rate with altitude that cannot be alternatively explained by latitudinal effects.

Feather traits

Results in this study support the idea that some altitude-mediated environmental changes promote migratory movements that could indirectly cause the accelerated growth of tail feathers in highland compared to lowland birds for most of the study passerine species, and this effect was independent from feather length (Table 11). Interestingly, our results did not detect any significant effect of age or sex, two main intrinsic factors that often affect moult and feather traits (Szép et al., 2019; Kiat & Sapir, 2021). Nor did we detect significant differences along the Iberian-Maghreb latitudinal gradient, which is remarkable since latitude had been described until now as a good predictor of variation in feather growth rate (Terrill, 2018; Horák et al., 2022).

The main effect of elevation on feather growth rates could be explained by the temporal shortening of suitable conditions for breeding and moulting in seasonal highlands (Fig. 15B) which in turn seems to promote the migration of highland populations, a parallelism of what happens in birds along latitudinal gradients (Dietz et al., 2015; Terril, 2018; Kiat et al., 2019). Populations at higher latitudes typically show a faster rate of feather growth but, in the geographical scope of this study, this effect is blurred by the effects of altitude, although in some of the species (Blackcaps and blackbirds) the difference between high and low latitudes was more pronounced in Iberia, probably due to the additional effect of latitude. In this context, interspecific variation could be explained by differences in substrate use when foraging. For instance, we suggest that the smaller difference in feather growth rate between highland and lowland populations of the great tit and the blue tit compared to the rest of species (Fig. 16) could be related to a more stable feeding substrate such as canopy. In contrast, ground feeders, such as finches, robins and blackbirds, are more exposed to the harsh and dry conditions of the Mediterranean drought on ground resources mediated by ground moisture (Smithies et al., 2022).

Variation in the onset of the breeding season is probably the reason for differential timing of moult among different areas, particularly in seasonal breeders, which after renewing their plumage, must embark on their migratory journey (Strinella et al., 2015). It has been shown that birds with time constraints due to late moulting can decrease the time needed to renew their plumage by increasing the growth rate of individual feathers (Rohwer & Rohwer, 2013). Several studies show that the breeding season is later and shorter as altitude increases (Mansouri et al., 2020; Lundblad & Conway, 2020), which is consistent with the results of our research. In our case, we found that the complex climatic characteristics of mountainous regions differ fundamentally from those of lowland regions in a differential window of resource availability. Highland populations face lower temperature conditions and for a longer period than lowland populations, so that favourable conditions and, thus, resource availability are restricted to a more narrow temporal window in the mountains (Fig. 15B). Physiologically, low temperatures have also been shown to delay the onset of moult (Wingfield et al., 2003; Dawson, 2015), which is associated with faster moults to get the plumage ready before favourable environmental conditions are exhausted (Dawson, 2004).

These factors independently or in combination could explain the faster feather growth rates in the highlands compare to lowlands (Fig. 16A). In the case of the study lowlands, the temperature dramatically increases from April and remains high until October, as it is usual in temperate zones, while in the highlands it does not exceed 20 °C (Martin & Wiebe, 2004) until June and drops drastically from August on. This means that the optimal conditions tracked by birds to breed will be limited to a short period of time in the highlands, in which they will have to organize the moulting period before leaving their breeding areas. In addition, this marked altitudinal seasonality is maintained among the mountain ranges studied, without observing the influence of the latitudinal difference. Thus, the variation over the year in the mean temperature of Guadarrama, the northernmost study site, shows similar shape and values (only 1 or 2º lower) than the Atlas, which highlights the thermal homogeneity between different mountain areas on the edge of the Palearctic region. Note that our two highland sites are much more set apart than the two lowland sites. In contrast, lowland populations are not constrained by this seasonal variation or low temperatures, as they find better and more stable conditions all year round, which could allow them to maintain a sedentary lifestyle. The limitations of optimal temporal windows in highlands require further research in order to better understand the differences in feather growth rates between highlands and lowlands populations. For instance, the study of spatio-temporal availability of food resources in altitudinal gradients (Barras et al., 2021) and their effects on moult processes should be addressed in the future for a better mechanistic understanding of observed patterns.

The increase in the speed of feather growth related to elevation does not seem to affect feather masses, as they showed similar values in highland and lowland populations. This suggests that faster growth rates were not related to a decrease in feather investment by highland migratory populations, as might be expected (e.g. Vágási et al., 2012). Interestingly, differences in feather mass in some species were related to the distribution of populations at the two sides of the Strait of Gibraltar since African birds tended to exhibit a higher feather mass than the Iberian counterparts. This pattern is difficult to explain by differences in temperature regimes and its potential effect on the invertebrate abundance that constitutes a suitable food resource for birds (Grubb, 2006), since the less productive Atlas Mountains (see details in Hernández-Téllez et al., 2021) reported the heaviest feathers (Fig. 16B). As most of the species showing significantly heavier feathers in northern Africa also show taxonomic differentiation in relation to their Iberian counterparts, it can be conjectured that this variation could be related to some idiosyncratic traits of these isolated, southern populations, which would make sense since a genetic component in bird feather mass has been demonstrated (De la Hera et al., 2013, 2022). It seems that the structural complexity or massiveness of feathers (mass per length) is directly related to follicle size (Jenni et al., 2020), so we could speculate that these populations at the edge of their distribution, far from being maladapted, have the capacity to produce better quality feathers and that this could even be a trait inherited from the original populations with a common ancestor in southern latitudes (Chapman et al., 2011).

Morphological differentiation

The highland populations of the study forest passerines showed a set of morphological adaptations that, as wing length and shape (concavity), are usually related to flight efficiency in migratory birds (Leisler & Winkler, 2003; Claramunt, 2021). It seems that, in this context, highland populations might have the capacity to make altitudinal movements. This can be related to the seasonal climatic changes occurring in the mountains (Fig. 15B). This suggests that highland and lowland populations of forest passerines could represent different ecotypes adapted to exploit habitats of different seasonality within the environmental setting of the south-western Palaearctic. This has been supported by previous studies in the Iberian Peninsula and the Maghreb, where highland and lowland populations of forest passerines show different migratory behaviour and wing morphology related to flight efficiency (Tellería & Carbonell, 1999; Pérez-Tris & Tellería, 2002; García et al., 2021; Tellería et al. 2022). It is also true that Iberian birds tend to show a more migratory-like morphology than Maghreb counterparts, possibly due to the combined effects of altitude and latitude on wing morphology (Balasubramaniam & Rotenberry, 2016). However, latitude and altitude are negatively correlated between Rif and Atlas (Fig. 15A), which allows to decouple their effects in the populations of the Maghreb.

Although we believe that adaptation to seasonal movements is a straightforward interpretation of the morphological differences in wing length and shape of high and low altitude populations (García-Peiró, 2003; Saino et al., 2010; Förschler & Bairlein, 2011), we acknowledge that these morphological changes could also be alternatively or complementary explained by other drivers. For instance, it has been shown that changes in forest structure could drive intra-specific wing morphology of forest birds as those populations inhabiting cluttered habitats tend to show shorter and more rounded wings to improve manoeuvrability (Savile, 1957; Noreau & Desrochers, 2018). However, our results do not support such a link between canopy development and flight morphology so that the observed differences do not seem to be related to vegetation structure. Other factors that could explain observed differences between highland and lowland birds in their feather characteristics are predation risk that could be higher at highlands favouring faster growth rates to reduce vulnerability (Badyaev & Ghalambor, 2001), parasites (Coon et al., 2016) or environmentally mediated pace of life (Horák et al., 2022). However, the effects of all these factors on feather production are largely unexplored and further investigation is required to clarify their contribution in an altitudinal context.

Conclusions

The results of this work suggest that mountains within the Southwest Palaearctic are drivers of population differentiation in forest passerines. The altitudinal variation in wing morphology for all species studied supports the idea that populations respond to environmental gradients created by elevation, so we could propose that the populations of these mountains are to some extent nomadic (Ceresa et al., 2020), or at least they have the capacity to move seasonally (Tellería et al. 2001, 2022). That is, the seasonal occupation of elevated areas seems associated with changes in wing morphology compatible with an improvement of bird ability to move between highlands and lowlands. Interestingly, this seasonal occupation of mountains seems related to changes in the rate of feather production in all the study species, which suggests a temporal shortage of resources for feather production in the highlands. In addition, the Maghreb populations located in low-latitude, but high-altitude areas (Atlas mountain range) allow us to dissociate the effects of altitude and latitude, an important fact when it comes to understanding the mechanisms that underlie the growth, size and shape of feathers. In this context, the effects of altitude at a regional scale are equivalent to those of latitude at large geographical scales. We could therefore be detecting an altitudinal syndrome on feather characteristics that deserves further investigation. Considering that the bird populations studied are restricted in this peripheral area of the Palearctic, the results support the existence of a regional dynamic of population differentiation in some key aspects of avian biology (moult, movements). This highlights the great heterogeneity of these rear-edge populations, and their putative ability to adapt to local conditions in response to altitude-mediated seasonality (Tellería et al., 2022).

DISCUSIÓN GENERAL

A lo largo de la tesis aportamos información y análisis que nos ayudan a entender la biología y ecología de la muda de las aves de montaña, pero también advertimos de la dificultad para obtener vínculos claros entre los diferentes entornos ambientales o evolutivos y los rasgos de las plumas, ya que muchos factores intrínsecos y extrínsecos de las poblaciones interactúan entre sí. Con esto sugerimos que el estudio de los procesos que modulan la estructura y producción del plumaje es un tema abierto en el que merece la pena seguir investigando y ponemos de manifiesto la importancia de detectar rasgos fenotípicos, fisiológicos y comportamentales que podrían favorecer la capacidad de adaptación de las poblaciones ante posibles cambios. En el contexto del Paleártico suroccidental, parece que la estacionalidad altitudinal determina comportamientos migratorios de las poblaciones periféricas que a su vez conducen a una aceleración de la velocidad de muda y probablemente modulan la propia estructura de las plumas.

Bloque A. Implicaciones de la migración latitudinal en las plumas y efectos de las montañas sobre el comportamiento migratorio.

La primera parte de este bloque confirma que la distancia de migración favorece adaptaciones en el complejo de vuelo (alas más largas y cóncavas) y apunta patrones nuevos relacionados con el diseño estructural de las plumas que favorecen la eficacia de vuelo en las aves migradoras (plumas con raquis más grueso y barbas más cortas, lo que a su vez les confiere más rigidez de flexión). De esta manera corroboramos algunas de las predicciones de la *hipótesis A1* (Fig. 3) y sugerimos que estos ajustes en el plumaje podrían ser una adaptación inadvertida dentro del síndrome migratorio aviar para facilitar la ocupación de entornos estacionales (Piersma et al., 2005). Un hecho interesante es que la masa y la tasa de crecimiento de las plumas no variaron significativamente en relación con la distancia de migración, lo cual podría apuntar a que ciertas adaptaciones en el plumaje no tengan tanto que ver con la distancia recorrida sino con la diferenciación de la estrategia migradora vs. sedentaria (De la Hera et al., 2009b).

Así, los resultados del *capítulo 2* tienen una gran relevancia en el contexto de esta tesis. Las poblaciones periféricas de pinzón africano (y seguramente de otras especies de aves del norte de África) reducen su abundancia durante el invierno en las partes más altas de las montañas y estos movimientos se relacionan con una variación de la morfología alar vinculada a una mejora de su capacidad de vuelo. Por ello, confirmamos la *hipótesis A2* (Fig. 3) en este entorno geográfico y sugerimos que la estacionalidad vinculada al gradiente altitudinal actúa como impulsor de la diversificación morfológica y comportamental en estas poblaciones de aves del extremo sur del Paleártico. Parece que la evolución de las migraciones latitudinales en las poblaciones periféricas estuvo acompañada de desplazamientos altitudinales a una escala más local, y que ambos movimientos estacionales afectaron de manera similar a varios rasgos morfológicos y de historia vital (Boyle et al., 2016).

Bloque B. Muda y plumaje en aves de montaña.

Una adaptación coordinada de varios rasgos morfológicos podría haber ocurrido con relativa rapidez permitiendo la colonización de entornos estacionales, tanto a nivel latitudinal como altitudinal. En general, los resultados de este bloque apoyan la idea de que la adopción de la migración altitudinal en las historias vitales de las aves no sólo tiene consecuencias en su comportamiento y morfología general, sino que sus presiones selectivas también repercutirían en el desarrollo y configuración de la estructura de las plumas.

Los resultados del *capítulo 3*, mostraron que la distribución de la productividad primaria se relacionó positivamente con la abundancia de currucas (sin afectar a su condición corporal), que alcanzó mayores densidades en los bosques bajos más productivos. La morfología del ala y los cambios en la abundancia sugirieron que las currucas de las tierras bajas eran sedentarias mientras que las de las zonas altas realizaban movimientos altitudinales (con alas más largas y cóncavas). A su vez, las plumas de las aves de montaña, aun con alimento limitado, mostraron tasas de crecimiento de las plumas más rápidas, posiblemente para hacer frente a las limitaciones temporales impuestas por los movimientos estacionales, y raquis más anchos, lo cual les confiere mejor comportamiento mecánico. Estas evidencias apoyan la *Hipótesis B2* (Fig. 4) y rechazan la predicción basada en el gradiente de calidad ambiental (*Hip. A*, Fig. 4). De esta manera, sugerimos que las presiones selectivas asociadas a los movimientos altitudinales en este contexto ambiental repercuten en la configuración de la estructura de las plumas de vuelo, independientemente de la disponibilidad regional de alimento.

La distribución de los rasgos de las plumas y la morfología de las alas se repite ampliamente en otros paseriformes forestales dentro del entorno medioambiental del suroeste del Paleártico (*capítulo 4*). Las zonas de montaña muestran ventanas temporales óptimas más cortas para la cría y la muda y están ocupadas por poblaciones con alas más largas y cóncavas y tasas de crecimiento del plumaje más rápidas (que no afectó a las masas de plumas). Esto corrobora la relevancia de la *Hipótesis B2* (Fig. 4) en este contexto ambiental. Por tanto, la selección podría haber favorecido una muda acelerada en poblaciones de montaña para hacer frente a la reducción de la ventana temporal óptima al igual que ocurre con las migradoras latitudinales.

Esta tesis avanza en el conocimiento de cómo las aves integran la muda dentro de su ciclo anual. Hasta donde sabemos, se trata del único estudio que revela una variación intraespecífica de la tasa de crecimiento del plumaje con la altitud en un grupo de paseriformes, que no puede explicarse alternativamente por efectos latitudinales ni por diferencias genéticas. A su vez, exponemos que el compromiso sobre la calidad de las plumas para hacer frente a la aceleración en su tasa de crecimiento no siempre se produce. En este entorno ambiental, demostramos que las plumas ligeras no son el subproducto de mudas más rápidas (Dawson et al., 2000; Serra et al., 2007, 2010; Vagasi et al., 2012; Moller & Nielsen, 2018), sino el resultado putativo de otros procesos fisiológicos y evolutivos (De la Hera et al., 2013; Jenni et al., 2020), y conjeturamos que la variación en la calidad de las plumas podría estar relacionada con algunos rasgos idiosincrásicos de estas poblaciones periféricas aisladas (*Hipótesis B3*; Fig.4).

Creemos que comprender los mecanismos naturales involucrados en el origen de la diversidad biológica de las poblaciones es particularmente desafiante para las aves de montaña y un punto clave en investigación y conservación. Sin embargo, las implicaciones evolutivas y de conservación de los desplazamientos altitudinales han sido a menudo pasadas por alto en las regiones templadas, seguramente por el hecho de que se convierten en migraciones crípticas en estos entornos estacionales al solaparse con las migraciones latitudinales. Por tanto, los resultados de esta tesis son particularmente valiosos en un contexto de cambio climático en el que los bosques seleccionados por las especies de estudio (Tellería et al., 2021) se desplazarán hacia arriba a lo largo del gradiente de altitud (Ruiz-Labourdette et al., 2012; Tellería, 2020) por el efecto del aumento de la sequía y la temperatura. En este entorno en el que el cambio global amenaza significativamente a las aves migratorias, esta tesis destaca el papel de ciertos rasgos fenotípicos para estudiar la forma en que las poblaciones podrían seguir el patrón ambiental espacio-temporal dentro del borde suroccidental del Paleártico (Richardson et al., 2014, Hampe & Jump, 2011; Hannah et al., 2014). Muchas de las poblaciones presentes en esta frontera paleártica pueden verse amenazadas en un escenario de cambio climático por lo que es interesante discriminar sus linajes y predecir su futuro encaje en un ambiente previsiblemente inadecuado (Hampe & Petit, 2005; Keppel et al., 2012; Pérez-Tris et al., 2015).

Por último, las poblaciones sedentarias del sur de Iberia y norte del Magreb ponen de manifiesto el papel de los bosques de tierras bajas más productivos como destacados refugios para las poblaciones periféricas de paseriformes forestales (Pérez-Tris & Tellería, 2002). A su vez esta tesis señala el potencial de las especies compuestas por poblaciones con diferentes comportamientos migratorios para explorar las adaptaciones de las aves a los cambios ambientales (PérezTris et al., 2004, 2015; Hampe & Petit, 2005) y comprender los procesos que afectan a las especies migratorias a diferentes escalas (Runge et al., 2015a).

LIMITACIONES Y PERSPECTIVAS

Uno de los objetivos clave de cualquier proceso de investigación, además de aportar nuevos conocimientos, es confrontar supuestos y explorar lo que nos falta por conocer. Por ello, a continuación exponemos algunas limitaciones de nuestro estudio y hacemos sugerencias de futuras investigaciones.

Comprender las trayectorias evolutivas sigue siendo una tarea difícil. Los procesos que modulan la estructura y producción del plumaje están lejos de ser comprendidos, probablemente debido a la dificultad de separar los factores que actúan sobre los rasgos de las plumas (Jenni & Winkler, 2020b) y por la falta de consideración de algunos de estos rasgos en investigación. En este sentido, una importante limitación metodológica de la tesis es la falta de estudios previos similares. La dificultad de la logística de muestreo en zonas de montaña hace que los esfuerzos científicos se vean reducidos y muy pocos estudios han adoptado un enfoque integrado para comprender cómo los distintos requerimientos determinan las propiedades del plumaje en zonas montañosas. Por ello, se precisa más investigación para dilucidar cómo algunos rasgos de las plumas podrían contribuir a un vuelo migratorio más eficiente en otros contextos altitudinales.

A su vez, el enfoque metodológico desarrollado en esta tesis basado en la comparación entre sectores de zonas altas y bajas será útil para mejorar nuestro conocimiento de las aves migratorias pero no contamos con un gradiente altitudinal en cada sector de estudio. Se sabe poco sobre los mecanismos que subyacen a la adaptación de las poblaciones a los entornos estacionales de gran altitud y, en particular, sobre las posibles características estructurales de las plumas que podrían haber sido seleccionadas en estos contextos altitudinales (por ejemplo, Gienapp & Merilä, 2010; Pap et al., 2015; Pap et al., 2019). Por lo que las conclusiones sobre la contribución real de los posibles impulsores implicados en la diferenciación de las poblaciones pueden variar en función del entorno geográfico. Se necesitan futuros estudios integrados para evaluar el alcance de la flexibilidad en estas compensaciones entre migración y muda a lo largo de otros gradientes altitudinales.

Aunque creemos que la migración altitudinal es la interpretación más probable para las diferencias morfológicas observadas en los diferentes capítulos de la tesis, el verdadero alcance de estos movimientos está lejos de conocerse y las evidencias indirectas de migración basadas en la morfología alar podrían no tratarse de un patrón universal (De la Hera et al., 2012; Fudickar & Partecke 2012; Huber et al., 2017). La disminución de la densidad del aire con la altitud también podría afectar a estos patrones, como se ha sugerido anteriormente para las aves voladoras (por ejemplo, alterando el equilibrio de la sustentación y la resistencia, aumentando los batidos de las alas; Pennycuick, 2001; Schmaljohann & Liechti, 2009). Pero el supuesto efecto de la densidad del aire en la variación morfológica intraespecífica de las aves no se ha demostrado hasta la fecha. Además, suponemos que este cambio putativo afectaría a la morfología de las alas a lo largo de todo el gradiente de altitud y no a partir de un umbral de altitud determinado, como se argumenta en el *capítulo 2*. En cualquier caso, nuestro trabajo anima a seguir investigando la posible influencia de estos y otros factores ambientales en la conformación de la morfología del ala de las aves.

Además, sugerimos que la fuerza de las diferencias en las métricas del plumaje de las poblaciones de aves en el suroeste del Paleártico variará en función de la escala de aproximación y de los requisitos idiosincrásicos de los rasgos estudiados. Esto significa que los resultados de esta tesis están influenciados por al menos dos condiciones experimentales que deben tenerse en cuenta al extender nuestras conclusiones a otros diseños experimentales. En primer lugar, los posibles vínculos entre los rasgos del plumaje y los factores ambientales locales probablemente se vean desdibujados por adaptaciones a la migración que no podrían operar en poblaciones sedentarias o totalmente migratorias. En segundo lugar, hemos estudiado diferentes rasgos de las plumas (barras de crecimiento, masa, barbas, raquis y resistencia a la flexión) que probablemente estén moldeados por diferentes procesos ambientales o evolutivos. Incluso podrían existir ajustes estructurales adicionales a nivel microscópico, menos perceptibles (De la Hera et al., 2010a; Lees et al., 2017) que requerirían investigaciones adicionales con la tecnología adecuada (por ejemplo, tomografía del eje de las plumas; Weber et al., 2010).

Ciertos rasgos morfológicos, como la longitud de la cola, se han asociado históricamente con la capacidad migratoria de las poblaciones, sin embargo, no fue un patrón consistente en las especies de estudio. En muchas de las especies, las poblaciones de zonas altas presentaron colas más largas lo cual podría tratarse de otro trade-off entre la eficiencia del vuelo y la reproducción, ya que se ha comprobado que individuos con colas más largas presentan mayor éxito reproductivo (Fargallo & López-Rull, 2022). La capacidad de una población para establecerse en zonas montañosas podría ocurrir señalando un fenotipo más competitivo. Esta cuestión podría reafirmarse estudiando otros rasgos de señalización sexual como la coloración del plumaje. Disponemos de plumas de todos los individuos muestreados por lo que pondremos en marcha este estudio a corto plazo.

Por otro lado, una explicación complementaria que está tomando fuerza es la influencia sobre la calidad del plumaje mediada por la infección de parásitos sanguíneos (Pap et al., 2013). De tal manera, se podría proponer que las poblaciones menos infectadas tendrían la capacidad de producir plumas de mayor calidad, independientemente de su velocidad de muda. Por ello, y debido a que se extrajo una muestra de sangre de cada individuo capturado durante el trabajo de campo, hemos iniciado una investigación en esta línea, con el fin de aclarar la posible contribución de los parásitos sanguíneos en la producción de las plumas en un contexto altitudinal.

Por último, los rasgos de las plumas parecen estar determinados en parte por características genéticas de los individuos. Recientemente se encontró una correlación entre las tasas de crecimiento y el tamaño del alelo del gen Creb 1 (Bazzi et al., 2017), por lo que estudiar el grado de divergencia genética nos permitiría profundizar en los procesos responsables de la aparición de nuevos linajes y ayuda a discriminar las unidades de gestión conservacionista (Crandall et al., 2000; Funk et al., 2012; Orsini et al., 2013). Para solucionar esta cuestión, otra potente línea que tenemos en marcha es el análisis de la estructura genética a nivel genómico de las poblaciones de estudio. Aunque somos conscientes de que el comportamiento migratorio no tiene por qué requerir cambios genéticos drásticos entre poblaciones de aves, podremos interpretar desde una perspectiva evolutiva robusta las diferencias observadas en los rasgos de las plumas y contrastar nuestras hipótesis sobre los procesos implicados.

CONCLUSIONES

I. La selección mitiga los costos de la migración latitudinal favoreciendo morfologías alares particulares y ajustes estructurales, funcionales y de desarrollo en las plumas.

II. La heterogeneidad ambiental creada a lo largo de los gradientes de elevación de las montañas promueve desplazamientos altitudinales que conformarían en última instancia la capacidad de adaptación de las poblaciones periféricas de aves para hacer frente a los cambios ambientales en curso en el sur del Paleártico.

III. Los movimientos estacionales (latitudinales y altitudinales) afectaron de manera similar a varios rasgos morfológicos y de historia vital de las poblaciones de aves. Los efectos de la altitud a escala regional son equivalentes a los de la latitud a grandes escalas geográficas en este contexto y podríamos estar detectando un síndrome altitudinal sobre el desarrollo y diseño estructural de las plumas.

IV. Las poblaciones de paseriformes forestales de tierras altas y tierras bajas representan diferentes eco tipos adaptados a explotar hábitats de diferente estacionalidad dentro del entorno medioambiental del suroeste del Paleártico.

V. El patrón de aceleración en la producción del plumaje, sin comprometer la calidad de las plumas, en las zonas montañosas es coincidente en un conjunto de paseriformes forestales indistintamente de sus requerimientos ecológicos. Esto constituye mecanismos similares de adaptación de las poblaciones periféricas a las condiciones locales para conseguir maximizar su aptitud en el límite de su distribución, por lo que estas poblaciones no pueden considerarse más como las contrapartes mal adaptadas de las poblaciones centrales.

VI. Las montañas del suroeste del Paleártico parecen ser una de las principales fuerzas motrices que promueven la diferenciación poblacional en las aves forestales de borde, que presentan una dinámica regional propia en algunos aspectos clave de su biología (muda, características del plumaje y movimientos).

VII. Todo esto hace que la protección de los hábitats dentro de estos gradientes de altitud sea una estrategia principal de conservación de las poblaciones de aves de montaña del límite occidental del Paleártico.

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MATERIAL SUPLEMENTARIO

CAPÍTULO 1:

APPENDIX 1. RELATIONSHIP BETWEEN FEATHER STRUCTURE AND MIGRATION DISTANCE WITH BENDING STIFFNESS AND RELATIONSHIP BETWEEN TAIL FEATHER MASS AND MIGRATION DISTANCE IN ROBINS.

Figure S1. Location of the study area in Campo de Gibraltar region, within the boundaries of Los Alcornocales and Estrecho de Gibraltar Natural Parks (Cádiz, Spain)

Table S1. Results of the analysis of bending stiffness of primary feathers in relation to feather structural characteristics and an isotopic proxy of migration distance (δD_f) after accounting for age, sex, winter and age-sex interaction effects. The length-corrected residuals of feather mass, rachis width (dv and lat), barb length and barb density were included in the models to obtain size-independent measures of these traits as shown in Table 3 and 4. The overall sample size was 146.

	Bending stiffness (Model R^2= 0.77)		
Fixed effects	Estimate ± se	t	P
Intercept (adult, female, 2006-07)	-41.76 ± 4.73		
δD_f	**-0.02 ± 0.01**	**-2.85**	**0.005**
Feather length	**0.99 ± 0.08**	**11.94**	**<0.001**
Age (juv)	0.30 ± 0.29	1.02	0.309
Sex (male)	**1.13 ± 0.34**	**3.33**	**0.001**
Winter (2013-14)	**-0.58 ± 0.23**	**-2.56**	**0.012**
Residuals feather mass	**3.25 ± 0.52**	**6.20**	**<0.001**
Residuals rachis width (dv)	**13.32 ± 3.78**	**3.53**	**<0.001**
Residuals rachis width (lat)	1.98 ± 2.62	0.76	0.450
Residuals barb length	**-0.28 ± 0.11**	**-2.50**	**0.014**
Residuals barb density	-0.10 ± 0.10	-0.97	0.335
Outer barb insertion angle	0.04 ± 0.08	0.50	0.620
Inner barb insertion angle	-0.03 ± 0.05	-0.58	0.564
Age:sex	**-1.03 ± 0.43**	**-2.37**	**0.019**

Table S2. Results of the analysis of tail (rectrix) feather mass in relation to an isotopic proxy of migration distance (δD_f) for all robins (n=147) and restricted to adults (n=75), after accounting for other appropriate fixed effects. N.A. (not applicable) indicates effects that were not tested for some response variables according to the rationale raised in the Methods section.

Fixed effects		Feather mass (All robins)	Feather mass (only adults)
Intercept (adult, female, 2006-07)	Estimate ± se	-1.97 ± 0.66	-3.30 ± 0.92
δD_f	Estimate ± se	-0.00 ± 0.00	-0.00 ± 0.00
	t	-1.18	-1.87
	P	0.242	0.065
Feather length	Estimate ± se	**0.12 ± 0.01**	**0.13 ± 0.02**
	t	**10.55**	**8.93**
	P	**<0.001**	**<0.001**
Age (juv)	Estimate ± se	-0.07 ± 0.05	*N.A.*
	t	-1.30	
	P	0.198	
Sex (male)	Estimate ± se	**0.23 ± 0.07**	**0.20 ± 0.07**
	t	**3.50**	**2.84**
	P	**<0.001**	**0.006**
Winter (2013-14)	Estimate ± se	0.01 ± 0.04	0.05 ± 0.06
	t	0.27	0.77
	P	0.787	0.444
Age:sex	Estimate ± se	0.07 ± 0.09	*NA*
	t	0.86	*NA*
	P	0.392	*NA*
Model R-squared (R^2)		0.67	0.71

CAPÍTULO 3:

APPENDIX 2. ALTITUDINAL MOVEMENTS OF SOUTHERN POPULATIONS OF THE EURASIAN BLACKCAP (*Sylvia atricapilla*)

The altitudinal movements of the southern populations of the Eurasian Blackcap (*Sylvia atricapilla*) have been illustrated in the Iberian Peninsula by seasonal shifts in abundance and concomitant variations in the external flight apparatus (Tellería et al., 2001; Pérez-Tris, 2014). However, the altitudinal displacements of this scarce resident bird in northwestern Africa has been poorly documented to date. Some wintering individuals have been reported at 1700 m in high valleys of the Atlas Mountains (Thevénot et al., 2003) suggesting a putative sedentary population, but these records do not exclude a shift downwards of most mountain blackcaps to overwinter in the most productive lowlands (Tellería et al., 2014). The main problem is that the altitudinal distribution of the number of Moroccan breeding Blackcaps from summer to winter is strongly distorted by the huge numbers of migratory conspecifics arriving from North and Central Europe to overwinter in this same region.

Here we used the data from two previous papers on winter (Tellería et al., 2014) and spring (Tellería et al. 2021) bird distribution in Morocco to explore the altitudinal movements of blackcaps. In both studies, we recorded all the blackcaps detected along a 500m-long transect (Bibby et al., 2000) carried out in different tree and shrub covered sampling points. Results showed the presence of Blackcaps in 12 out of 98 transects in spring (12%) and in 39 out of 122 transects in winter (32%). This result supports the view that the species has a restricted distribution in spring if compared to winter time (Thevénot et al., 2003), a pattern similar to the one detected in the Iberian Peninsula (Carbonell, 2003; Tellería & Pérez-Tris, 2003; Pérez-Tris, 2014).

Sampling effort in winter was greater in the lower elevations than in spring. To avoid this bias affecting the average altitude at which blackcaps occurred each season, we selected 76 spring and 76 winter transects that were distributed homogeneously in altitude (between 50 to 2100 m a.s.l.; Fig. S2). We then compared for these 152 transects whether the mean elevations at which blackcaps were detected differed between spring and winter. Breeding blackcaps were mainly constrained to moist mountain woodlands, but were also detected in some suitable river banks in lowlands. During winter, blackcaps occurred at lower elevations than in spring (Fig. S2), which would be caused by Moroccan breeders moving downhill or (and) by the arrival of European migratory conspecifics to overwinter in the same lowlands. Therefore, despite the scarcity of breeding blackcaps and the difficulties in discriminating the breeding origin of the overwintering birds, the results suggest an altitudinal displacement of the Moroccan Blackcaps to lowlands during winter.

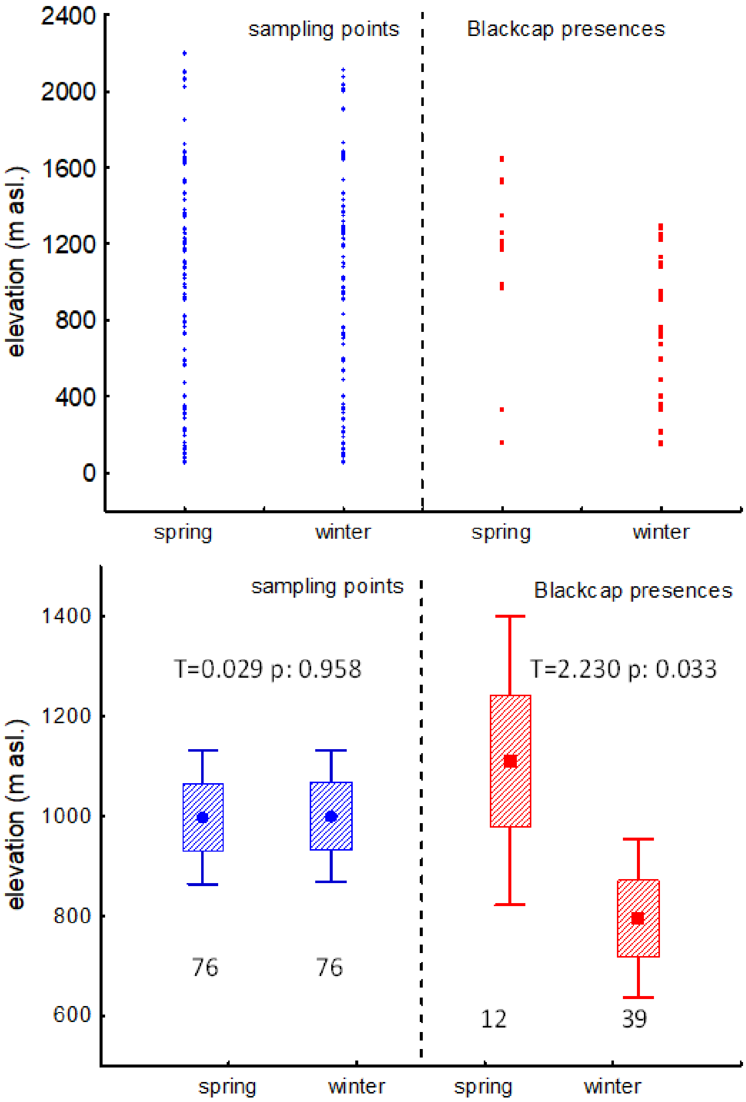

Figure S2. Altitudinal range of the Eurasian blackcap in north-western Africa. Upper panel. Altitudinal distribution of transects (blue dots) and elevations (=altitude) of the transects where the Blackcap was detected (red dots) in spring vs. winter. Lower panel. Variation in elevation between the transects conducted in spring and winter (blue boxplot), and differences between seasons in elevation for the transects where Blackcaps were detected (red boxplot). Whiskers show mean elevation (dot), standard error (whisker) and 95% confidence interval (box). Sample sizes and the results of a Student t test between samples are also shown.

APPENDIX 3. BREEDING AND MOULTING PERIODS OF SOUTHERN POPULATIONS OF THE EURASIAN BLACKCAP (*Sylvia atricapilla*)

According to data provided by Alejandro Onrubia (one of the authors of this manuscript) from blackcaps breeding in southern Spain and northern Morocco, their breeding period ranges from April to July (females with active incubation patches; Fig. S3A). Just after breeding, between July and September, moult begins (partial moult in juveniles and complete moult in adults; Fig. S3B). These results (they include Alcornocales and a peripheral range of our Rif sampling area) show how moult occurs just at the end of the breeding period within these southern breeding grounds. These results confirm what was already known about breeding and moulting periods of the blackcaps (e.g. Heim de Balsac & Mayaud, 1962; Cramp & Brooks, 1992; Shirihai, et al., 2001).

To test if our four study populations agreed with this breeding phenology, we assessed breeding activity of captured individuals by the presence of active incubation patches in females and extended cloacal protuberances in males (both are morphological evidences of active breeding; Demongin, 2016). Results show that many females had incubation patches and some males had elongated cloacal protuberances (Table S3). Therefore we can conclude that our four study populations were breeding within the usual period for the Eurasian blackcap in the Palaearctic.

These results also show that the moult phenology, which extends from July to September, fit the usual moult phenology of the species (Cramp & Brooks, 1992). In October, when overwintering individuals arrive to lowlands they mix with locals in breeding areas (Pérez-Tris &Tellería, 2002; Tellería & Pérez-Tris, 2003). By that time blackcaps had already accomplished a full moult. Our sampling period was very early to detect active moulting birds, but we can presume that the highlands populations behaved as in Figure S3 (note data in this figure refer to Alcornocales and some peripheral areas of Rif study areas). More explicitly, if all blackcap populations in our study breed according to the typical species' phenology, we can assume that highlands populations will also moult immediately after breeding as usual. This syllogism can be reinforced by taking into account that blackcaps remain in breeding areas of the Iberian highlands until the end of September. In this period, just after autumn rains eliminate the pervasive effects of the Mediterranean summer drought in lowlands, the region is invaded by large numbers of

European blackcaps (Cantos, 1995). This spatial-temporal pattern of blackcaps within the Iberian Peninsula has previously been reported (see Tellería et al., 1999, Figure 104, p. 117: Monthly distribution of blackcap abundance recorded in sixteen localities distributed across different bioclimatic levels and habitats of the Iberian Peninsula).

We agree that we have not many data on the seasonal changes in the altitudinal distribution of the Blackcap population in north-western Africa, but it seems very similar to the pattern observed in the Iberian Peninsula (see Appendix 2). African blackcaps are constrained to breed in moist oak and cedar woodlands and some river banks within an extremely dry environmental setting of the Mediterranean drought (Tellería et al., 2021). Under these conditions, it would be too daring to suggest an altitudinal migration to moult outside the breeding areas. Of course, we cannot rule out this possibility, but it should be an exceptional behavior that is not supported by the evidence recorded to date. Thus, despite we can assume local tracking of the most suitable habitat patches, we have no reason to speculate on moult outside breeding areas.

Table S3. Distribution of active incubation patches* and male cloacal protuberances (in parenthesis) between the four study populations.

Study	dates	sex	sample	active reproduction	%
Alcornocales	17-23 April	males	55	55(7)	100 (13)
		females	34	18	53
Rif	9-21 May	males	12	12 (0)	100(0)
		females	6	6	100
Guadarrama	29 May-6 June	males	26	19 (4)	73(15)
		females	15	15	100
Atlas	15-26 May	males	22	22(4)	100(18)
		females	7	7	100

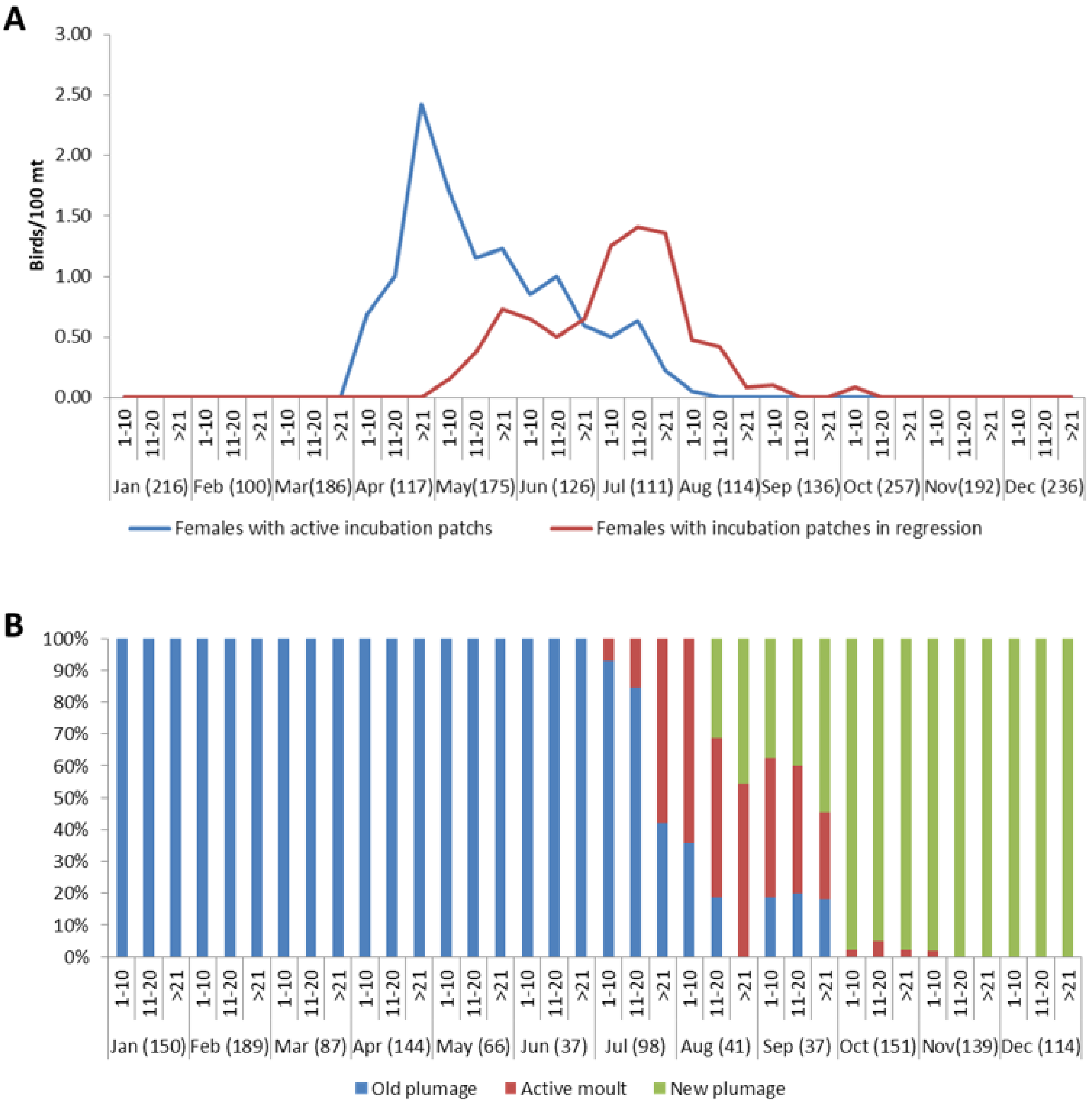

Figure S3. Annual dynamics of blackcaps ringed in Cádiz and Morocco. A) Relative abundance (birds trapped by 100 m of nets) of females with active or in regression incubation patches (n= 1 966). B) Proportion of blackcaps with old plumage, active moult and new plumage (n= 1 253). Sample sizes per month are shown in parentheses.

APPENDIX 4. CORRELATION OF TAIL FEATHER MORPHOLOGY WITH WING FEATHER MORPHOLOGY IN EURASIAN BLACKCAP (*Sylvia atricapilla*).

There is evidence supporting the idea that variation between Blackcaps in tail feather characteristics are positively associated with the existing variation in wing primary feathers (see De la Hera et al., 2010a, 2010b). According to this, we can confidently use rectrices to characterize Blackcap feather traits that can provide us information about the migratory activity of the birds. From an animal welfare point of view, sampling tail feathers would be less detrimental for the bird than primary feather collection.

To reinforce this idea, we showed below data from 120 Blackcaps obtained from De la Hera et al. (2010b) to better illustrate statistically and graphically this reality for three relevant feather characteristics: feather mass (Table S4), bending stiffness (related to the mechanical characteristics of the feathers, Table S5) and rachis width (Table S6). For each analysis and for the graphs, feather trait values for each feather type were standardized by feather length using the method suggested by Lleonart et al. (2000). In all the cases, we detected a significant positive association between the trait values of tail and primary feathers (Table S4-S6, and Fig. S4), after accounting for other potential confounding factors (bird size estimated from tarsus length, sex, age and migratory behavior).

Table S4. Analysis of standardized primary feather mass in relation to standardized tail feather mass and other factors.

	Estimate	Std. Error	t value	P
Intercept	0.62	0.54	1.15	0.253
Standardized tail feather mass	0.53	0.04	11.81	<0.001
Age (5)	0.00	0.03	0.04	0.969
Sex (male)	0.03	0.03	1.08	0.282
Migratory behavior	-0.03	0.03	-0.90	0.372
Tarsus length	0.07	0.02	3.26	0.001

Table S5. Analysis of standardized primary bending stiffness in relation to standardized tail bending stiffness and other factors.

	Estimate	Std. Error	t value	P
Intercept	0.0014	0.0008	1.51	0.134
Standardized tail bending stiffness	0.58	0.11	5.06	<0.001
Age (5)	-0.00003	0.00006	-0.42	0.678
Sex (male)	0.00006	0.00006	0.99	0.324
Migratory behavior	-0.00005	0.00006	-0.801	0.425
Tarsus length	0.00005	0.00004	1.330	0.186

Table S6. Analysis of standardized primary rachis width in relation to standardized tail rachis width and other factors

	Estimate	Std. Error	t value	P
Intercept	0.52	0.08	6.79	<0.001
Standardized tail rachis width	0.35	0.06	5.53	<0.001
Age (5)	-0.002	0.005	-0.46	0.644
Sex (male)	-0.0003	0.004	-0.08	0.939
Migratory behavior	0.01	0.004	1.24	0.217
Tarsus length	-0.0002	0.003	-0.06	0.954

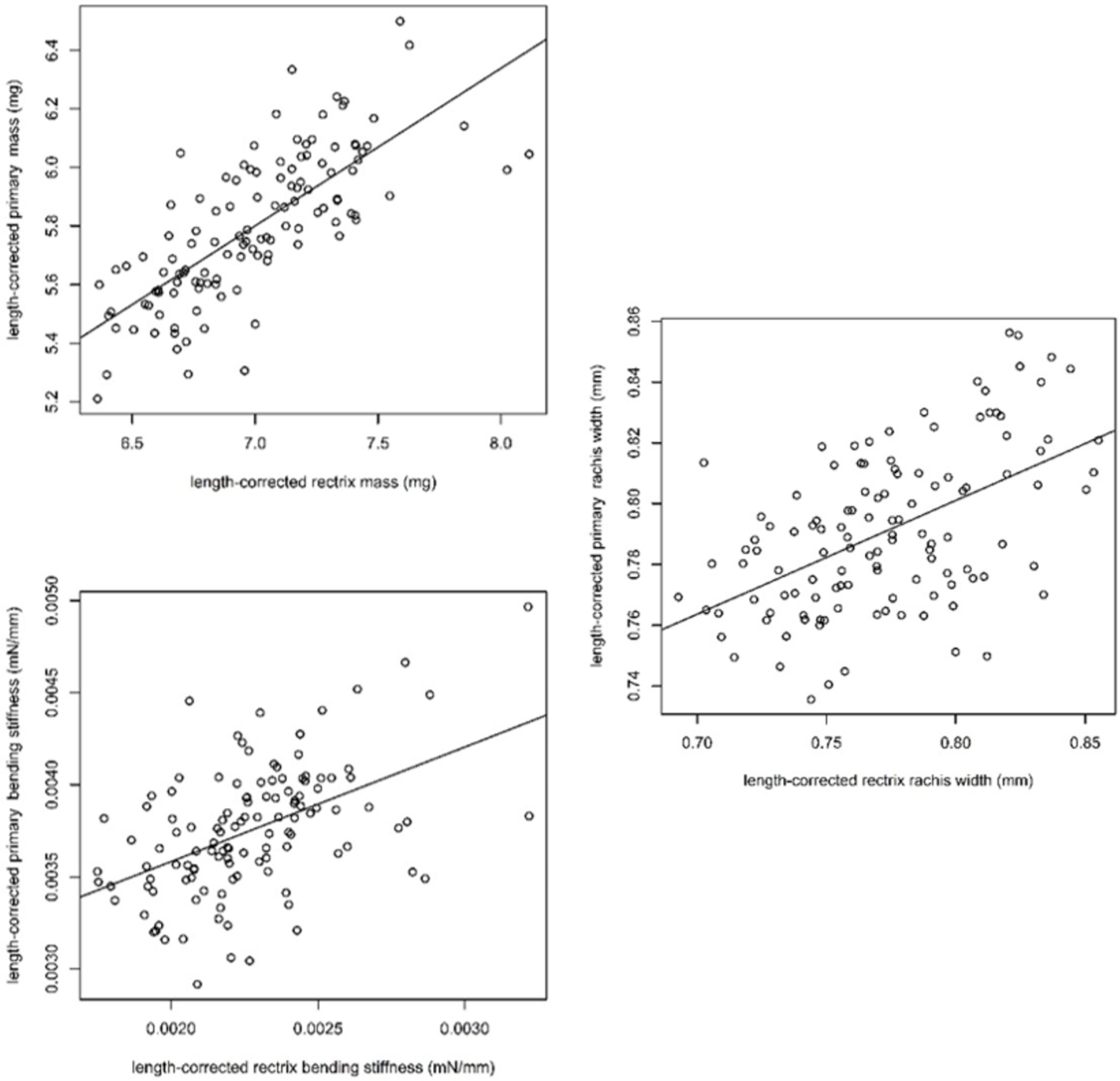

Figure S4. Association between rectrix and primary feather characteristics in Blackcaps.

APPENDIX 5. ABUNDANCE DISTRIBUTION, BODY CONDITION AND COMPLEMENTARY ANALYSES

Abundance distribution

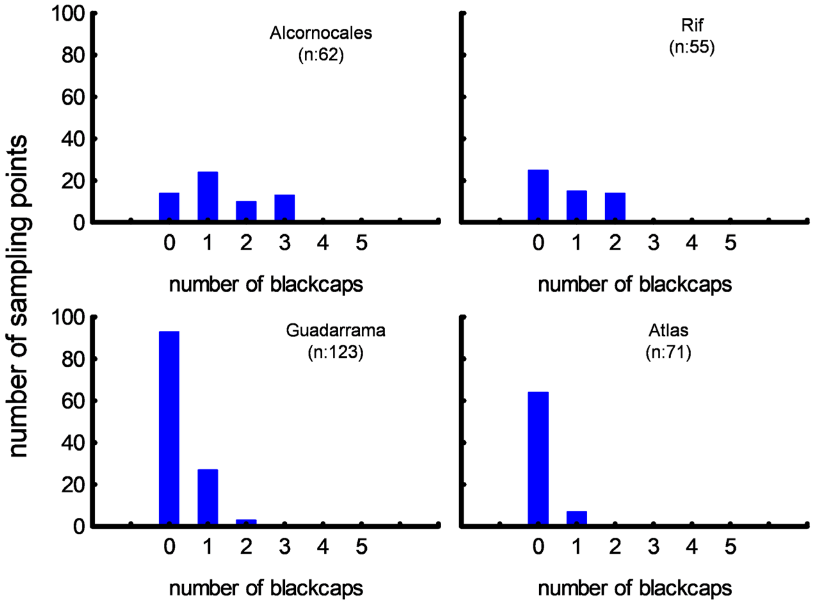

Figure S5. Distribution of the number of Eurasian blackcaps detected per sampling point in the four study areas.

Body condition

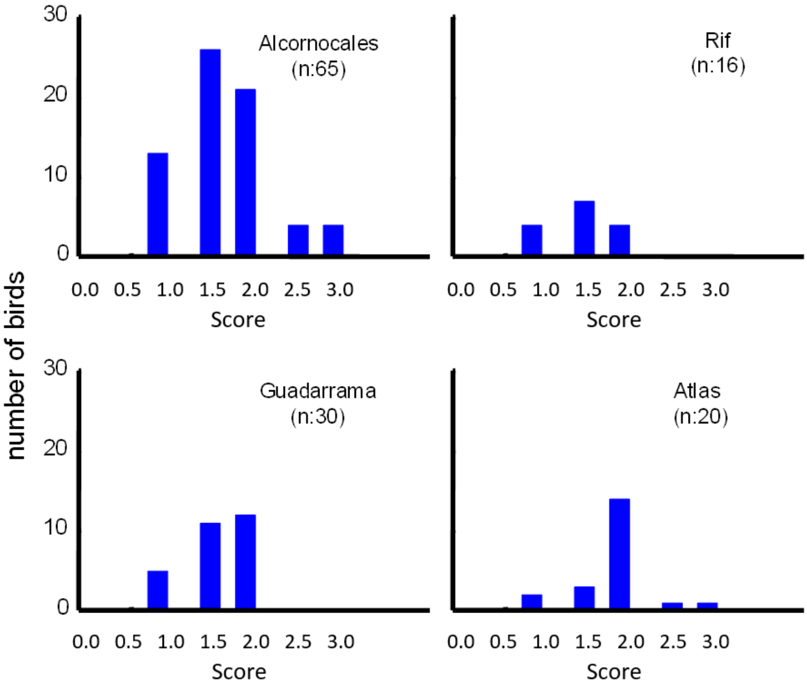

Figure S6. Distribution of the pectoral muscle scores between the four studies populations of the Eurasian blackcap.

Complementary analyses

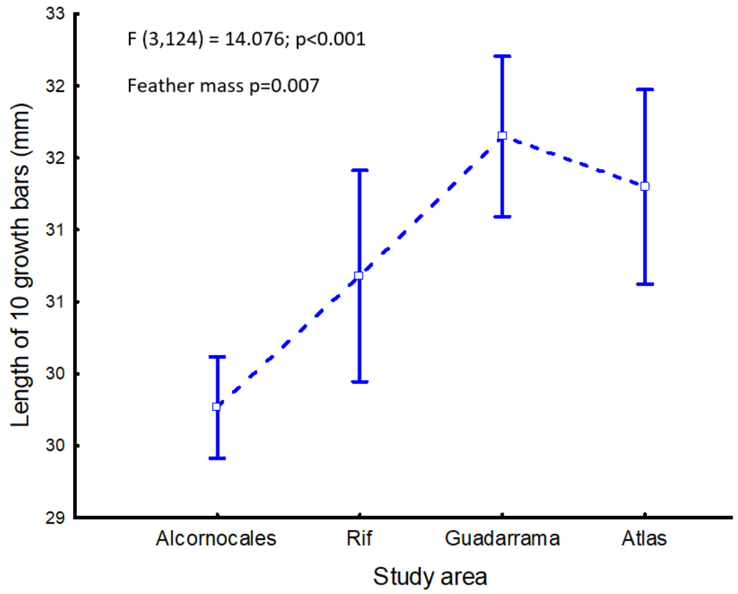

Figure S7. Feather growth rate pattern according to growth by mass. Distribution of the length of ten growth bars between study areas.

CAPÍTULO 4:

APPENDIX 6. SUPPLEMENTARY RESULTS

Table S7. Results of PC1 principal component analyses to describe wing concavity with standardized primary lengths according to Senar et al. (1994).

		Sylvia atricapilla	*Erithacus rubecula*	*Turdus merula*	*Fringilla coelebs*	*Parus major*	*G. Cyanistes*
Eigenvalue		4.41	3.30	3.73	3.80	3.61	3.04
Variance explained		0.49	0.37	0.41	0.42	0.40	0.34
Component loadings	**P9**	0.16096952	-0.09041444	0.2132966	0.05076026	0.06549794	-0.23882392
	P8	0.09924066	0.16479011	0.3476037	0.14657956	0.20468640	-0.04985928
	P7	-0.03726397	0.09340776	0.2773969	0.05065285	0.16288597	0.04449688
	P6	-0.28694947	-0.06221969	-0.2034127	-0.15010592	0.09004087	-0.21965277
	P5	-0.40702704	-0.25029073	-0.2969560	-0.38601371	-0.39316698	-0.36835491
	P4	-0.42800352	-0.45757514	-0.3771691	-0.44258700	-0.38164859	-0.45758022
	P3	-0.44376928	-0.49931000	-0.4126273	-0.47976565	-0.47375831	-0.41119335
	P2	-0.42098515	-0.48618834	-0.4327296	-0.42928371	-0.46204226	-0.44618204
	P1	-0.39685490	-0.44086632	-0.3569243	-0.43759675	-0.42545082	-0.42074516

Table S8. Results of PC2 principal component analyses to describe wingtip pointedness with standardized primary lengths according to Senar et al. (1994).

		Sylvia atricapilla	***Erithacus rubecula***	***Turdus merula***	***Fringilla coelebs***	***Parus major***	***G. Cyanistes***
Eigenvalue		1.60	1.92	1.71	1.74	1.94	1.94
Variance explained		0.18	0.21	0.19	0.19	0.22	0.22
Component loadings	**P9**	0.62757321	0.56490860	0.46873542	0.64142003	0.36709709	0.49854260
	P8	0.65791840	0.57181602	0.39101841	0.61394310	0.55735767	0.61519080
	P7	-0.23844248	0.49605517	0.27658722	0.27179216	0.52948547	0.58082242
	P6	-0.12335136	0.05719941	-0.36477341	0.10619429	0.41707250	-0.01141135
	P5	-0.05709362	-0.25742896	-0.20070731	0.24595684	0.14065099	-0.05159804
	P4	0.03368656	-0.01219645	0.07185492	0.20613791	0.22671479	0.01740797
	P3	0.12124053	0.14760498	0.35977718	0.04835063	0.15272845	-0.09782669
	P2	0.19880234	0.11000564	0.30963921	-0.09442341	0.05652429	-0.01491243
	P1	0.20641892	0.06523287	0.38349572	-0.11074672	0.05083848	-0.15084037

Table S9. Exploration of the independence of wing shape standardisations from wing size. Results of the ANOVA test, p-values greater than 0.05 mean that the variables are independent.

	Sylvia atricapilla (p-value)	***Erithacus rubecula*** (p-value)	***Turdus merula*** (p-value)	***Fringilla coelebs*** (p-value)	***Parus major*** (p-value)	***G. Cyanistes*** (p-value)
Wing pointedness	0.747	0.641	0.572	0.803	0.564	0.749
Wing concavity	0.977	0.193	0.138	0.694	0.818	0.287

Table S10. Exploration of the residuals of the models, through the assumptions of normality (Shapiro-Wilk test) and homoscedasticity (Breusch-Pagan test). P-values were non-significnat or only marginally significant.

	Models	Normality (p-value)	Homocedasticity (p-value)
Sylvia atricapilla	LM1. Feather growth	0.92	0.3397
	LM2. Feather mass	0.05	0.2614
	LM3. Wing length	0.24	0.05374
	LM4. Wing Concavity	0.51	0.7662
Erithacus rubecula	LM5. Feather growth	0.44	0.0817
	LM6. Feather mass	0.74	0.8987
	LM7. Wing length	0.98	0.111
	LM8. Wing Concavity	0.83	0.2999
Turdus merula	LM9. Feather growth	0.04	0.8186
	LM10. Feather mass	0.05	0.3387
	LM11. Wing length	0.85	0.9147
	LM12. Wing Concavity	0.98	0.1683
Fringilla coelebs	LM13. Feather growth	0.05	0.2864
	LM14. Feather mass	0.06	0.5555
	LM15. Wing length	0.08	0.3246
	LM16. Wing Concavity	0.26	0.6639
Parus major	LM17. Feather growth	0.47	0.2648
	LM18. Feather mass	0.35	0.5028
	LM19. Wing length	0.32	0.3449
	LM20. Wing Concavity	0.21	0.8304
G. Cyanistes	LM21. Feather growth	0.81	0.0036
	LM22. Feather mass	0.77	0.7974
	LM23. Wing length	0.44	0.1632
	LM24. Wing Concavity	0.07	0.6231

Table S11. Exploration of collinearity between exploratory variables, through VIF (Variance Inflation Factor) tests. Values lower than 4 mean that there is no correlation between these variables.

	Models	Year	Age	Sex	Feather length	Tarsus length	Canopy	Altitude	Region
Sylvia atricapilla	LM1. Feather growth	1.199815	1.336510	1.025646	1.240996	-	-	1.640616	2.520247
	LM2. Feather mass	1.199815	1.336510	1.025646	1.240996	-	-	1.640616	2.520247
	LM3. Wing length	1.262531	1.241456	1.011979	-	1.027204	1.213524	1.749627	2.226580
	LM4. Wing Concavity	1.254342	1.223290	1.012774	-	-	1.230692	1.699008	2.142657
Erithacus rubecula	LM5. Feather growth	1.049282	1.208367	1.475464	1.872131	-	-	2.342443	2.149229
	LM6. Feather mass	1.049282	1.208367	1.475464	1.872131	-	-	2.342443	2.149229
	LM7. Wing length	1.097602	1.249585	1.105010	-	1.088180	1.397267	2.533534	2.258300
	LM8. Wing Concavity	1.092613	1.262882	1.093495	-	-	1.374866	2.522231	2.352745
Turdus merula	LM9. Feather growth	1.037535	1.116539	1.408669	2.360491			1.639023	2.737238
	LM10. Feather mass	1.037535	1.116539	1.408669	2.360491			1.639023	2.737238
	LM11. Wing length	1.086315	1.125104	1.124996	-	1.195185	1.126972	1.723201	1.928006
	LM12. Wing Concavity	1.080828	1.118991	1.077017	-	-	1.124466	1.723095	1.927682
Fringilla coelebs	LM13. Feather growth	1.306387	1.412237	2.233408	3.772509	-	-	2.457091	3.113177
	LM14. Feather mass	1.306387	1.412237	2.233408	3.772509	-	-	2.457091	3.113177
	LM15. Wing length	1.376126	1.249539	1.078697	-	1.706681	1.040783	2.505323	3.018609
	LM16. Wing Concavity	1.254342	1.223290	1.012774	-	-	1.230692	1.699008	2.142657
Parus major	LM17. Feather growth	1.208570	1.393685	1.749134	3.846233	-	-	2.507074	3.018202
	LM18. Feather mass	1.188670	1.390496	1.701194	3.846233	-	-	2.490061	2.848301
	LM19. Wing length	1.159533	1.197886	1.118470	-	1.118095	1.194996	2.423461	2.190412
	LM20. Wing Concavity	1.153158	1.191451	1.108787	-	-	1.193814	2.420841	2.087178
G. Cyanistes	LM21. Feather growth	1.052611	1.272567	1.415653	1.842679	-	-	3.603527	2.267233
	LM22. Feather mass	1.052611	1.272567	1.415653	1.842679	-	-	3.603527	2.267233
	LM23. Wing length	1.136217	1.055431	1.185964	-	1.410785	1.378336	3.779252	2.633429
	LM24. Wing Concavity	1.109763	1.052105	1.164871	-	-	1.355406	3.692109	2.457742

GLOSARIO DE TABLAS Y FIGURAS

INTRODUCCIÓN GENERAL

METODOLOGÍA GENERAL

CAPÍTULO 1

CAPÍTULO 2

CAPÍTULO 3

CAPÍTULO 4

MATERIAL SUPLEMENTARIO

CAPÍTULO 1

CAPÍTULO 3

CAPÍTULO 4