


Estrategias de migración del género *Acrocephalus* en la Península Ibérica

MIREN ANDUEZA OSÉS

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Directores: **Dr. Juan Arizaga Martínez**
Dr. Emilio Barba Campos

Universitat de València

Unidad de Vertebrados Terrestres
Instituto Cavanilles de Biodiversidad y Biología Evolutiva

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Memoria presentada por Miren Andueza Osés para optar al grado de Doctor en Biología

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Fdo. Miren Andueza Osés

Tesis dirigida por los Doctores en Biología de la Universidad de Valencia, D. EMILIO BARBA CAMPOS, y de la Sociedad de Ciencias Aranzadi, D. JUAN ARIZAGA MARTÍNEZ

Fdo. Dr. Emilio Barba Campo	Fdo. Dr. Juan Arizaga Martínez
Profesor Titular de Ecología	Director Departamento de Ornitología
Universidad de Valencia	Sociedad de Ciencias Aranzadi

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“The Road goes ever on and on
down from the door where it began.
Now far ahead the Road has gone,
and I must follow, if I can,
pursuing it with weary feet,
until it joins some larger way,
where many paths and errands meet.
And whither then? I cannot say”

(The Lord of the Rings, J. R. R. Tolkien**)**

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Índice

CAPÍTULO 1

Introducción general

1.1. El fenómeno migratorio en las aves

El fenómeno migratorio ha evolucionado independientemente entre numerosos taxones animales como una adaptación a los cambios estacionales que se producen en los hábitats que ocupan (Alerstam et al. 2003). Así, la migración permite a los organismos explotar la abundancia temporal de recursos y escapar de la escasez estacional hacia otras áreas donde los periodos cíclicos de abundancia/escasez siguen un patrón opuesto. Ejemplos de organismos migradores se pueden encontrar en casi todos los grupos animales, desde los invertebrados (e.g. mariposa monarca *Danaus plexippus*, Altizer & Davis 2010), hasta los mamíferos (e.g. ballena jorobada *Megaptera novaeangliae*, Barendese et al. 2010; caribú *Rangifer tarandus*, Fancy et al. 1989). Sin embargo, es quizá en la Clase Aves, gracias a su adaptación al vuelo, donde este fenómeno ha alcanzado un mayor desarrollo y complejidad, tanto por su prevalencia como por la magnitud de los desplazamientos implicados. Tan sólo en la región Paleártica, 215 especies de aves migran al sur del desierto del Sáhara (migradores trans-saharianos) cada año, lo que supone el desplazamiento anual de unos 5.000 millones de individuos (Moreau 1972; Newton 2008). Asimismo, es en las aves donde se encuentran las mayores distancias migratorias. Por ejemplo, el charrán ártico *Sterna paradisaea*, recorre 20.000 km entre sus áreas de cría en las regiones árticas y sus áreas de invernada en la Antártida (Alerstam et al. 2003). La curiosidad por cómo estos pequeños animales, frágiles en apariencia, son capaces de llevar a cabo cada año un viaje de ida y de vuelta de miles de kilómetros, cruzando desiertos y mares, ha llevado a muchos ecólogos a interesarse por el estudio de este fenómeno y, en este caso particular, a la realización de la presente Tesis Doctoral.

La migración es un proceso complejo, que requiere de unos mecanismos de regulación internos, incluidos en el genoma, para su coordinación con los otros procesos clave del ciclo anual de un ave (reproducción y muda) (Coppack & Bairlein 2011). Esta coordinación ha evolucionado a través del establecimiento de un equilibrio entre la maximización del éxito reproductor y la supervivencia individual entre los periodos reproductivos (Lack 1968; Newton 2004; Newton 2011). En particular, debe regularse: (1) el momento oportuno y la duración dentro del ciclo anual del ave; (2) las adaptaciones fisiológicas y metabólicas para la acumulación y consumo de reservas energéticas; (3) el comportamiento adaptativo ante factores externos variables (e.g. meteorología); y (4) la orientación y navegación (Berthold 2001). A pesar de que las aves migratorias presentan unas adaptaciones comunes, denominadas en su conjunto como “síndrome migratorio” (Berthold 2001; Piersma et al. 2005), el comportamiento migratorio se caracteriza por una gran flexibilidad a nivel inter- (Calmaestra & Moreno 2001; Newton 2011) e intra-específico (Copete et al. 1999; Pérez-Tris & Tellería 2001). Por tanto, las soluciones óptimas a los diferentes retos que las aves deben superar durante el viaje migratorio y que, en conjunto, configuran las estrategias de migración, pueden variar entre especies y entre poblaciones de una misma especie. Desde la publicación del trabajo de Alerstam & Lindström (1990) sobre estrategias óptimas de migración, muchos han sido los estudios que han abordado este tema para tratar de entender en base a qué factores se organiza la migración, analizando las limitaciones, costes y beneficios que conlleva (Alerstam 2011). En general, la organización de la migración está altamente condicionada por los procesos (dónde, cuándo y cómo) de acumulación de las reservas energéticas necesarias para los vuelos migratorios (Alerstam 2011), que a su vez están condicionados por las características geográficas y ecológicas de las zonas que las aves han de cruzar durante la migración. Parece ser que la minimización de la duración de la migración y, por tanto, la maximización de la velocidad de ésta, es la estrategia más común adoptada por las especies trans-saharianas (Alerstam & Lindström 1990; Hedenström 2008), aunque es una cuestión todavía en debate.

1.2. Organización espacial de la migración

Entender qué factores determinan el patrón espacio-temporal de las aves durante la migración entre sus áreas de cría y sus cuarteles de invierno es una cuestión básica en el estudio de las estrategias migratorias. La existencia a lo largo del recorrido de barreras geográficas, como mares, desiertos o cadenas montañosas, que actúan como barreras ecológicas, tiene una gran influencia en el modelado de las estrategias migratorias (Moreau 1972; Newton 2008; Alerstam 2011). La presencia de estas áreas inhóspitas puede repercutir de tres formas diferentes sobre la organización de la migración (Alerstam et al. 2003): (1) constituir el límite final del viaje migratorio; (2) promover la evolución de rodeos para minimizar la distancia de cruce sobre las barreras, o evitarlas; y (3) generar adaptaciones en lo que respecta a la acumulación extra de reservas energéticas para permitir franquearlas.

En el sistema de migración Paleártico-Africano, las principales barreras geográficas a las que se enfrentan las aves trans-saharianas son el mar Mediterráneo y el desierto del Sáhara. Las rutas migratorias han evolucionado para atravesar el Mediterráneo por los puntos que suponen una menor distancia de vuelo sobre mar abierto. Así, la mayor parte de las poblaciones europeas cruzan dicho mar por sus extremos occidental, desde la Península Ibérica, en cuyo caso las aves atraviesan la franja marítima formada por el Mediterráneo y el Atlántico, donde se localiza el estrecho de Gibraltar, y oriental (estrecho del Bósforo). Adicionalmente, una fracción de las poblaciones de las distintas especies migradoras europeas lo atraviesan por su parte central, vía Italia (Rubolini et al. 2002). Esto se traduce en la presencia de divisorias migratorias, que marcan el límite entre poblaciones con diferentes direcciones de migración genéticamente determinadas (e.g. Helbig 1996; Bairlein 2003; Bensch et al. 2009; Reichlin et al. 2009).

1.2.1. Conectividad entre áreas de cría y de descanso

Normalmente, las aves tienden a seguir las rutas más cortas entre sus áreas de cría y de invernada, lo que les permite minimizar el tiempo y la energía consumidos (Newton 2011). La descripción de las principales rutas migratorias ha sido un pilar básico en el estudio de la migración de las aves (Bairlein 2001). Sin embargo, otras cuestiones importantes, como la conectividad migratoria, aún no han sido ampliamente abordadas. La conectividad puede definirse como la relación que existe entre la distribución geográfica de las áreas reproductivas y las áreas que ocupan las aves durante el periodo no reproductor (Webster et al. 2002; Zwarts et al. 2009). Así, un elevado grado de conectividad implica que las aves del mismo origen utilizan áreas de descanso y de invernada similares, sin solapamiento con poblaciones de distinto origen, cuya distribución geográfica es similar a la de las áreas de origen (las aves de origen más oriental ocuparán áreas de descanso e invernada más orientales que las provenientes de áreas más occidentales y viceversa). El estudio de la conectividad permite ahondar en la comprensión de la evolución de la migración y explicar la distribución espacio-temporal de las aves durante el periodo no reproductor. Asimismo, tiene importantes implicaciones para la conservación (Webster et al. 2002), especialmente en especies que muestran una elevada conectividad, de forma que las distintas poblaciones usan áreas geográficas distintas, donde pueden ocupar hábitats vulnerables, como los humedales (Atienza et al. 2001; Pain et al. 2004). A nivel europeo, la conectividad se ha estudiado principalmente entre las áreas de cría y las áreas de invernada (Pain et al. 2004; Procházka et al. 2008), por lo que se desconoce hasta qué punto la distribución geográfica de poblaciones con distinto origen durante la migración está relacionada también con la distribución de las áreas de cría. Si la conectividad se mantiene entre las áreas de cría y de descanso durante la migración, las aves provenientes de áreas más occidentales migrarán por regiones situadas más al oeste que las que tienen un origen más oriental, con un bajo grado de solapamiento entre poblaciones de distinto origen.

1.2.2. Variación geográfica en las cargas de grasa

La migración es un proceso energéticamente costoso, y normalmente se divide en fases alternativas de vuelo, en las cuales se consume gran cantidad de energía, y etapas de acumulación de ésta, fundamentalmente en forma de depósitos de grasa (Jenni & Jenni-Eiermann 1998; Salewski et al. 2009; Chernetsov 2012). La presencia de barreras geográficas importantes, como el Mediterráneo y el desierto del Sáhara, donde virtualmente no existe posibilidad de reponer la energía consumida, hace necesario que las aves acumulen con anterioridad suficientes reservas de energía que permitan su cruce, a la vez que se optimizan los costes de transporte y tiempo (Alerstam & Lindström 1990; Schaub & Jenni 2000a; Rubolini et al. 2002; Delingat et al. 2008; Fransson et al. 2008; Yohannes et al. 2009). Dependiendo del tipo de alimentación y de la distribución espacial de hábitats apropiados, se han descrito cuatro estrategias generales de acumulación de grasa antes de una barrera geográfica, en particular del desierto del Sáhara (Schaub & Jenni 2000a): (1) acumulación progresiva conforme las aves se aproximan a la barrera (e.g. curruca mosquitera *Sylvia borin*); (2) acumulación a cierta distancia de la barrera (e.g. carricerín común *Acrocephalus schoenobaenus*); (3) acumulación justo en el borde de la barrera (e.g. carricero común *Acrocephalus scirpaceus*); (4) no acumulación de grandes reservas previas, sino realización de paradas regulares para alimentarse al atravesar la barrera (e.g. papamoscas gris *Muscicapa striata*). Aparte de esta variación latitudinal, la acumulación de grasa puede variar temporalmente, de forma que las aves que migran más tarde tienden a llevar mayores reservas que las más tempranas. Las razones de esta variabilidad temporal no están claras, y se ha postulado que puede deberse bien a una estrategia para aumentar la velocidad migratoria (Bayly 2006), o a un paso diferencial de poblaciones de distinto origen (Maggini et al. 2013).

Estas estrategias se han descrito desde un contexto continental (a gran escala) a partir de una serie de puntos de muestreo a lo largo de las rutas migratorias (Schaub & Jenni 2000a, b, 2001a; Yohannes et al. 2009). Sin embargo, a nivel más local (regional) se desconoce hasta qué punto otros factores, más allá de la distancia hasta la barrera geográfica, pueden modificar el patrón esperado para una especie, dado el escaso número de localidades empleadas para inferir las estrategias generales, especialmente en puntos clave, como por ejemplo las zonas próximas a una barrera importante (Schaub & Jenni 2000a). La distribución y calidad de las áreas de descanso pueden tener un papel fundamental en el patrón de acumulación de grasa observado a nivel regional (Ktitorov et al. 2008; Chernetsov 2013).

1.3. Comportamiento en áreas de descanso

La mayor parte del tiempo que un ave emplea en completar el viaje migratorio transcurre en las denominadas áreas de descanso, en las cuales las aves reposan y/o recargan las reservas energéticas consumidas (Hedenström & Alerstam 1997). Por tanto, el comportamiento en estos lugares determina en gran medida la velocidad y duración global de la migración, por sus implicaciones en la acumulación y gestión de las reservas energéticas necesarias para las fases de vuelo (Alerstam & Hedenström 1998). Conocer cuáles son los factores más importantes en que las aves basan sus decisiones de cuándo parar y abandonar un área de descanso, así como cuáles son los mecanismos que determinan su distribución espacial y la selección de hábitats en ellas, es esencial para entender las estrategias de migración.

1.3.1. Factores que influyen en las decisiones de parar y abandonar un área de descanso

La mayoría de paseriformes trans-saharianos son migradores nocturnos, de forma que vuelan durante las horas de oscuridad y paran durante el día, bien para descansar antes de proseguir con la migración en la siguiente noche, o para reponer reservas, en cuyo caso pueden permanecer en el lugar durante varias jornadas consecutivas (Delingat et al. 2006; Schmaljohann et al.

2007; Jenni-Eiermann et al. 2011; Chernetsov 2012). Además, otros factores pueden forzar la interrupción nocturna de la migración. En particular, la meteorología adversa, como lluvia y vientos de cara, puede provocar que las aves paren, incluso en lugares considerados sub-óptimos, para evitar volar bajo condiciones que incrementarían los costes de vuelo y la mortalidad (Pyle et al. 1993; Newton 2007; Saino et al. 2010; Arizaga et al. 2011a). Sin embargo, cómo las aves deciden dónde y cuándo parar es un aspecto de la ecología migratoria que ha sido objeto de escasos estudios (Barriocanal et al. 2002; Yaukey & Powel 2008; Saino et al. 2010; Arizaga et al. 2011a).

Por el contrario, el efecto de diferentes factores sobre las decisiones de partir de un área de descanso ha sido más ampliamente estudiado (e.g. Dänhart & Lindström 2001; Dierschke & Delingat 2001; Schaub et al. 2004; Tsvey et al. 2007; Schaub et al. 2008; Arizaga et al. 2011b). Entre los factores exógenos, las condiciones meteorológicas se cuentan entre los más importantes a la hora de decidir si iniciar los vuelos migratorios o no. Los vientos de cola son ventajosos desde el punto de vista de la optimización de la migración, dado que aumentan el rango de vuelo para una carga de grasa determinada, por lo que las aves, en general, buscan su asistencia (Weber et al. 1998a; Åkesson & Hedenström 2000; Dänhardt & Lindström 2001; Åkesson at al. 2002; Erni et al. 2005; Morganti et al. 2011). Por el contrario, las aves tienden a evitar volar bajo la lluvia, ya que ésta moja el plumaje, incrementando los costes de vuelo, además de aumentar la probabilidad de desorientarse (Schaub et al. 2004). Asimismo, la densidad de individuos de la misma especie en la zona de descanso pude ser un factor importante en determinar las decisiones de partida. Una alta densidad de individuos puede generar competencia intra-específica por los recursos (Moore & Yong 1991), repercutiendo negativamente en las tasas de engorde de los individuos socialmente más débiles (Lindström et al. 1990) y, por tanto, aumentando su probabilidad de partida (Åkesson et al. 1996a) (Tabla 1.1).

Entre los factores endógenos, la fecha (como indicador del ciclo anual interno del ave) y la carga de grasa son factores clave que determinan la estancia en un área de descanso. Conforme avanza la estación migratoria, las aves tienden a aumentar la velocidad de migración, entre otros modos reduciendo la duración de la estancia en estas áreas (Bayly 2006). Por otra parte, hay evidencias de que la carga de grasa puede influir a la hora de decidir si continuar con la migración, de forma que las aves con mayores reservas tienen una mayor probabilidad de abandonar las áreas de descanso (Tsvey et al. 2007; Goymann et al. 2010), aunque no siempre es así (Salewski & Schaub 2007; Schaub et al. 2008) (Tabla 1.1).

Diversos aspectos de la ecología y comportamiento en las áreas de descanso pueden variar según la experiencia de los individuos, en general asociada a la edad (Woodrey 2000). Los adultos (en este contexto, aves que ya han realizado al menos un viaje migratorio de ida y vuelta) pueden organizar su migración de acuerdo a la distribución de lugares de parada óptimos, realizando un menor número de paradas y utilizando las áreas subóptimas para descansos diurnos, pero no para la reposición de reservas de energía. Además, los adultos son más eficientes a la hora de acumular los depósitos de grasa (Ellegren 1991; Heise & Moore 2003; Neto et al. 2008) y, por tanto, realizan paradas de menor duración que los juveniles (Grandío 1998, 1999; Rguibi-Idrissi et al. 2003) (Tabla 1.1).

Adicionalmente, el comportamiento en lo relativo a las decisiones de abandonar un área de descanso puede modificarse en función de las condiciones ecológicas esperables en el siguiente tramo de vuelo. En particular, antes de una barrera geográfica, las aves deben prepararse para cruzarla con éxito, acumulando mayores cargas de grasa que si dicha barrera no existiese (Dierschke & Delingat 2001; Fransson et al. 2008; Yohannes et al. 2009). En aves que acumulan las reservas energéticas necesarias justo antes de una barrera (e.g. carricero común), es esperable que la carga de grasa juegue un papel crucial en las decisiones de partir en sus proximidades (las aves no cruzarán una barrera sin alcanzar unas mínimas reservas), pero que no sea tan relevante en sitios mas alejados de ésta (Klaassen & Linström 1996). Asimismo, es esperable que las condiciones de viento sean más importantes antes de cruzar una barrera, especialmente el mar, para minimizar los riegos de una deriva hacia el océano abierto causada por vientos desfavorables (Liechti 2006) (Tabla 1.1). Para las especies que minimizan el tiempo en migración, no sólo es importante la cantidad de grasa acumulada antes de partir, sino también el tiempo invertido en ello (Biebach et al. 1986; Alerstam & Lindström 1990; Delingat et al. 2008; Schaub et al. 2008). Las tasas de engorde experimentadas por las aves en un lugar dependen en gran medida de la disponibilidad de alimento (Schaub & Jenni 2000b; Fransson 1998a; Smith & McWilliams 2010). Sin embargo, éstas pueden verse limitadas a niveles sub-óptimos, independientemente de la disponibilidad trófica, para mantener una mayor vigilancia que permita reducir el riesgo de depredación asociado a la intensidad de alimentación (Schmaljohann & Dierschke 2005; Bayly 2006, 2007; Newton 2011).

Tabla 1.1. Efecto esperable de diversos factores exógenos y endógenos sobre las probabilidades de abandonar un área de descanso de paseriformes trans-saharianos. +: efecto positivo (incremento de la probabilidad de partir); -: efecto negativo (disminución de la probabilidad de partir); 0: efecto nulo (no modifica la probabilidad de partir).

Factor	Efecto sobre la probabilidad de partir
Exógenos	
Viento de cola	cerca de barrera: + lejos de barrera: +/0
Lluvia	-
Abundancia	+
Endógenos	
Fecha	+
Carga de grasa	cerca de barrera: + lejos de barrera: +/0
Edad	+

1.3.2. Distribución espacial y selección de hábitat en un área de descanso

El uso espacial que el ave hace de un área de descanso, incluyendo la distribución espacial y selección de hábitats, repercute directamente sobre la tasa de acumulación de grasa y, como consecuencia, condiciona la velocidad y probabilidad de éxito de la migración (Chernetsov 2006; Chernetsov 2012). Por otra parte, entender cómo las aves se distribuyen espacialmente y explotan los hábitats disponibles, es de utilidad para la correcta gestión de los espacios que éstas usan durante la migración (Petit 2000).

Cuando un ave para en un área de descanso, ésta se encuentra en un entorno desconocido que tiene que explotar para reponer sus reservas energéticas y proseguir con la migración lo más rápidamente posible. Además, debe compartir ese espacio con otros individuos en migración, o, incluso, con individuos locales que no han abandonado su área de cría. Por ello, a pesar de que las aves tienden a seleccionar hábitats similares a los de sus áreas de cría (Davis & Stamp 2004), durante la migración pueden ser más generalistas (Chernetsov 2006). Además, el comportamiento espacial puede adaptarse según la disponibilidad y distribución espacial del alimento (Chernetsov & Bolshakov 2006).

Fretwell y Lucas (1969) describieron dos modelos para explicar la distribución espacial de organismos en hábitats de calidad heterogénea, considerando el éxito reproductor como un indicador de rendimiento: (1) distribución ideal-libre (los individuos se distribuyen dependiendo de la calidad de hábitats y densidad de individuos; no hay diferencias de rendimiento);

(2) ideal-despótica (los individuos dominantes relegan a los subordinados a las zonas de peor calidad, de forma que éstos experimentan un rendimiento más bajo). Estos modelos pueden resultar de utilidad para explicar el comportamiento espacial de las aves durante la migración, considerando la tasa de engorde como el indicador de rendimiento o éxito de la estancia en un lugar (Chernetsov 2006).

1.4. Planteamiento de la tesis

El objetivo general de esta tesis es profundizar en el conocimiento de la ecología migratoria de aves trans-saharianas durante la migración postnupcial. Con este propósito se han abordado aquellos aspectos que tienen una mayor relevancia en el modelado de las estrategias de migración, empleando el carricero común (*Acrocephalus scirpaceus*, Hermann 1804) y el carricerín común (*Acrocephalus schoenobaenus,* Linnaeus 1758) como modelos.

Aparte de los capítulos que contienen la Introducción (Capítulo 1), Metodología (Capítulo 2) y Discusión General (Capítulo 9), así como las principales conclusiones obtenidas (Capítulo 10), la tesis recoge un compendio de artículos científicos sobre la organización espacial de la migración (Capítulos 3-4) y el comportamiento en las áreas de descanso (Capítulos 5-8). Estos capítulos están escritos en inglés y tienen la estructura típica de un artículo científico. Cada uno de ellos consta de un resumen en inglés y castellano, introducción, metodología, resultados y discusión. Los objetivos específicos de cada capítulo son:

Capítulo 3: estudiar si las especies que tienen un clara divisoria migratoria en Europa y una elevada conectividad entre sus áreas de cría e invernada, como el carricero común, mantienen ese grado de conectividad durante la migración, de forma que las poblaciones de distinto origen empleen rutas paralelas a su paso por la Península Ibérica. Así, las aves provenientes de Europa Occidental atravesarían la Península Ibérica por áreas más occidentales (zona atlántica), las originarias de Europa Oriental lo harían preferentemente por la vertiente mediterránea, mientras que aquellas con orígenes intermedios cruzarían la Península por su parte central.

Capítulo 4: comprobar si el patrón geográfico de carga de grasa observado en la Península Ibérica para el carricero común (individuos juveniles) se adecua a la estrategia general esperable que se ha descrito a nivel europeo para esta especie (acumulación de las reservas justo antes de una barrera geográfica), y determinar si la variación geográfica a nivel regional está modelada por otros factores adicionales, más allá de la distancia a una barrera geográfica (franja de mar Atlántico/Mediterráneo).

Capítulo 5: determinar la influencia de las condiciones meteorológicas y la edad en las decisiones del carricerín común de parar en un área de descanso, empleando modelos de captura-recaptura (Cormack-Jolly-Seber). Adicionalmente, se busca probar la utilidad de esta metodología para este propósito, dada la escasez de precedentes.

Capítulo 6: abordar el análisis simultáneo, mediante modelos de captura-recaptura, de diversos factores, tanto endógenos (edad, carga de grasa, fecha, ésta última como indicador del ciclo circanual interno del ave) como exógenos (meteorología, abundancia de congéneres), para cuantificar la importancia relativa de éstos en las decisiones de abandonar un área de descanso para el carricerín común.

Capítulo 7: comparar si la influencia de la condición corporal y condiciones de viento en las decisiones de abandonar un área de descanso varía según la proximidad a una barrera geográfica (franja de mar entre la Península Ibérica y África) para el carricero común (individuos juveniles), particularmente entre áreas de descanso del norte y sur peninsular. Adicionalmente, se estudia el impacto de las tasas de engorde en dichas decisiones y su relación con la disponibilidad de alimento.

Capítulo 8: analizar el comportamiento espacial y uso de hábitats del carricero común en un área de descanso, comparando individuos locales y foráneos, tanto adultos como juveniles, y determinar si se ajusta a una distribución ideal despótica o libre.

CAPÍTULO 2

Metodología general

2.1. Especies de estudio

Esta tesis se centra en el estudio de las estrategias migratorias de dos especies del género *Acrocephalus,* el carricero común, *A. scirpaceus*, y el carricerín común, *A. schoenobaenus*. El interés de ambas especies radica además en que, a pesar de ser especies cercanas y similares en apariencia, sus estrategias migratorias difieren notablemente. Las aves del género *Acrocephalus* pertenecen a la familia Sylviidae, dentro del orden Passeriformes. De las siete especies de este género que crían en Europa, cinco son migradoras trans-saharianas, siendo las especies más abundantes el carricero común y el carricerín común. Dada su abundancia, ambas especies han sido ampliamente empleadas como modelos para estudiar diversos aspectos sobre las estrategias de migración. A modo ilustrativo, hay alrededor de 150 artículos indexados en la Web of Knowledge sobre esta temática y estas especies (Abril 2014). Sin embargo, muchas cuestiones siguen necesitando de un estudio más profundo y detallado.

El carricero común (también denominado a lo largo del texto como carricero) es un ave de tamaño pequeño (13 cm de longitud y 17-21 de envergadura alar) y color marrón uniforme, sin dimorfismo sexual en cuanto a tamaño y coloración (Cramp 1992). Realiza una muda postjuvenil/postnupcial parcial, de las plumas del cuerpo, que puede solaparse con la migración (Herremans 1990). Tanto jóvenes como adultos realizan una muda completa en sus cuarteles de invierno (Svensson 1998). Se distribuye ampliamente por la región Paleártica, incluyendo el sur de Europa, durante el periodo reproductor (Figura 2.1), y su población se estima entre 2,7 y 5 millones de parejas reproductoras, aunque desde hace unas décadas está en moderado declive (BirdLife 2013). *A. baeticus,* residente en el sur de África, puede considerarse conspecífico con *A. scirpaceus*, pero se suelen separar debido a su diferente comportamiento migratorio. Cría asociado a carrizales, pero durante la migración puede encontrarse en otros hábitats, y se alimenta de forma oportunista de una amplia variedad de invertebrados (Cramp 1992). Inverna al sur del Sáhara (Figura 2.1) Su estrategia de migración general consiste en dividir la migración en tramos cortos, que no requieran una acumulación importante de reservas de grasa, y acumular los depósitos necesarios para cruzar el Sáhara inmediatamente antes de esta barrera, en el norte de África (Schaub & Jenni 2000a). El comportamiento espacial en las áreas de descanso que ocupa durante la migración es variable, pudiendo establecer territorios no defendidos (Bibby & Green 1981), o abarcar todo el área de descanso (Chernetsov & Titov 2001).

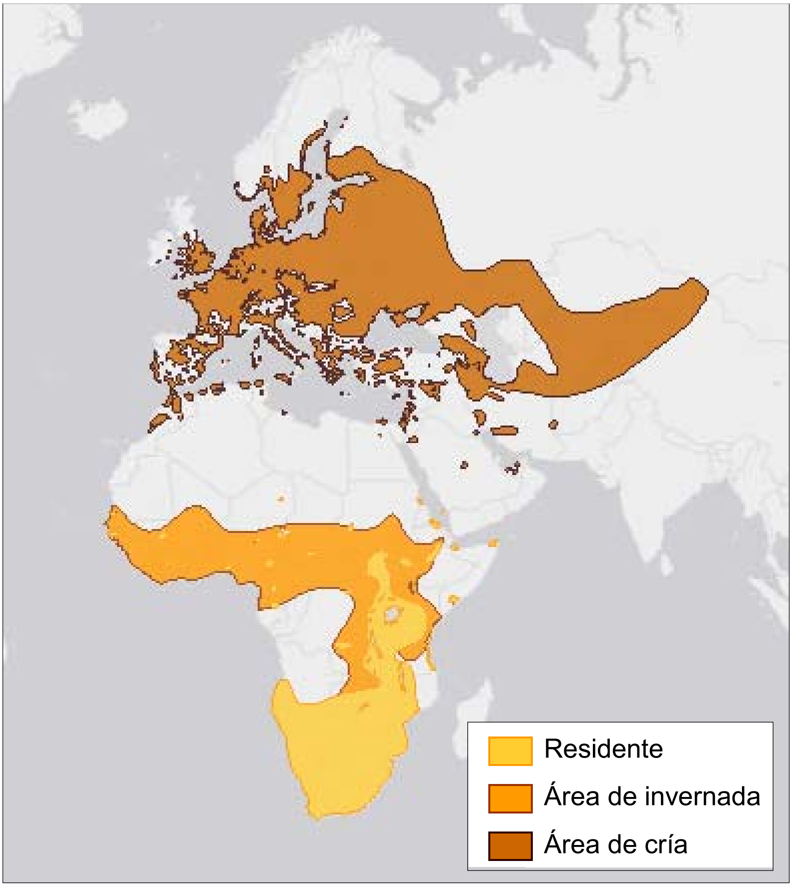

Figura 2.1. Mapa de distribución del carricero común *A. scirpaceus* (Fuente: The UICN red list of threatened species).

El carricerín común (también denominado a lo largo del texto como carricerín) tiene un tamaño similar al carricero común. Su plumaje es listado, de tonos marrones y negros, y se caracteriza por tener una banda superciliar de color crema (Cramp 1992). No hay diferencias de plumaje entre sexos. Al igual que el carricero, realiza una muda parcial antes de iniciar la migración de otoño y una muda completa en las áreas de invernada (Svensson 1998). Su distribución paleártica en época de cría abarca desde regiones árticas hasta latitudes medias, encontrándose ausente de la región mediterránea en Europa occidental (Cramp 1992) (Figura 2.2). La población reproductora en Europa de estima entre 4.4 y 7.4 millones de parejas (BirdLife 2013). Ocupa preferentemente carrizales y zonas de marisma, y se alimenta fundamentalmente de áfidos, aunque puede capturar otro tipo de invertebrados (Cramp 1992). Dado que los áfidos se caracterizan por presentar picos de superabundancia, éstos son aprovechados por los carricerines para acumular grandes reservas de grasa, principalmente en el noroeste de Europa, con las que alcanzar el sur del Sáhara sin necesidad de recargarlas (Bibby & Green 1981; Schaub & Jenni 2000a). No establecen territorios definidos durante su estancia en las áreas de descanso (Chernetsov & Titov 2001; Chernetsov 2005).

Figura 2.2. Mapa de distribución del carricerín común *A. schoenobaenus* (Fuente: The UICN red list of threatened species).

2.2. Área de estudio

La presente tesis abarca dos ámbitos de estudio: (1) la Península Ibérica y (2) un área de descanso situada en el norte de España (marismas de Jaizubia, en Guipúzcoa).

La Península Ibérica es una región de gran interés para el estudio de la migración, dado que constituye un lugar de paso obligado para gran cantidad de aves en su camino hacia África (Tellería et al. 1999). Además, es una de las últimas regiones donde las aves pueden acumular las reservas energéticas que necesitan para cruzar las barreras geográficas que suponen el Mar Mediterráneo/Atlántico y el Desierto del Sáhara.

Para el estudio de la migración a nivel peninsular se emplearon datos de 17 estaciones distintas de anillamiento. Doce de ellas se emplearon para estudiar la organización espacial de la migración, cubriendo las principales rutas de paso a través de este territorio: ruta este (vertiente mediterránea), centro (región central), oeste (vertiente atlántica, principalmente a través de Portugal) (Galarza & Tellería 2003; Navedo et al. 2010), y zona suroriental (cuadrante SO de la Península; zona de convergencia de las distintas rutas peninsulares debido a la dirección preferente de migración de las aves) (Hilgerloh 1989; Cantos 1998) (Figura 2.3). Las cinco restantes, más una (Jaizubia) que se utilizó para ambos objetivos, se emplearon para comparar la importancia relativa de distintos factores en las decisiones de abandonar un área de descanso en el norte y sur peninsular (Figura 2.4). En cada zona, norte y sur, se eligieron 3 localidades distintas a modo de réplica para controlar la heterogeneidad dependiente de cada sitio. El carrizal

(*Phragmites australis*) era la formación vegetal dominante en casi todas las de estaciones de muestreo, con excepción de Manecorro (en el área de Doñana) donde predominaba la vegetación arbustiva mediterránea (principalmente *Pistacea lentiscus*) junto con praderas inundadas.

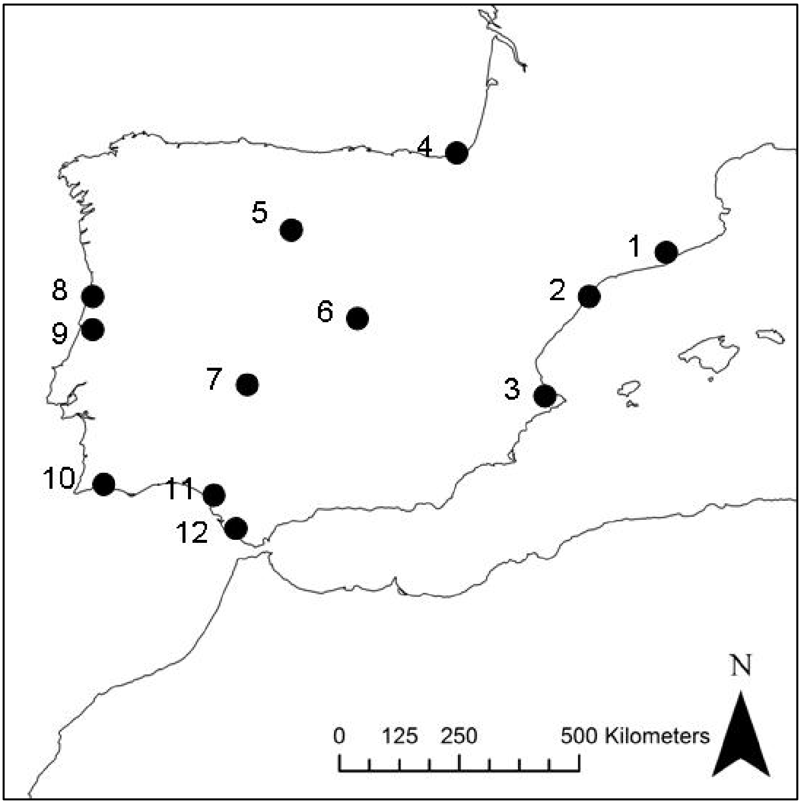

Figura 2.3. Estaciones de muestreo en la Península Ibérica empleadas en los Capítulos 3 y 4. 1, Viladecans; 2, Canal Vell; 3, Pego; 4, Jaizubia; 5, El Cruce; 6, Las Minas; 7, Arroyo Budión; 8, Salreu; 9, Taipal; 10, Sítio das Fontes-Charito; 11, Manecorro; 12, Vejer.

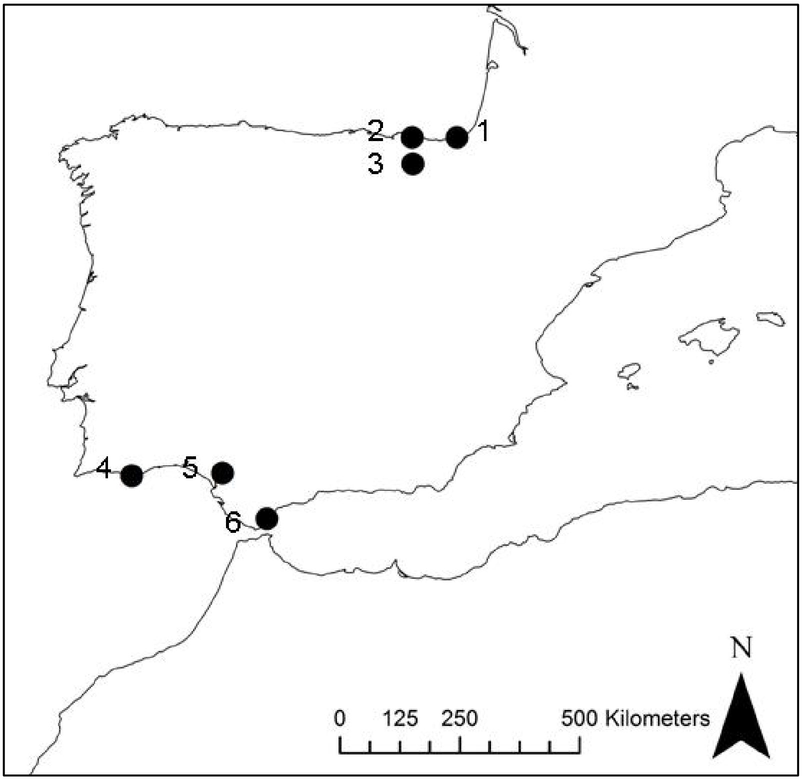

Figura 2.4. Estaciones de muestreo del norte y sur peninsular empleadas en el Capítulo 7. 1, Jaizubia; 2, Urdaibai; 3, Salburua; 4, Faro; 5, San Ramón; 6, Guadiaro.

Para el desarrollo de los capítulos sobre comportamiento en un área de descanso se eligió la marisma de Jaizubia, en Guipúzcoa (43º21´N 01º49´W; 2 m s.n.m.). Este espacio, que forma parte del sistema estuarino Txingudi-Bidasoa incluido en la Lista RAMSAR, ocupa un área de 70.4 ha. De esta superficie, 38.1 ha se encuentran sujetas a protección especial mientras que el resto está sujeta a protección agrícola. La marisma abarca la llanura de inundación de la regata de Jaizubia, y fue restaurada en 2003. Climatológicamente, esta área de estudio se sitúa en la región Eurosiberiana, en la provincia Cántabro-Atlántica, en el piso climático colino/termoclino, con ombrotipo hiperhúmedo. Así, el clima se caracteriza por una abundante precipitación (media anual de 1728.5 mm/m^2) que se distribuye de forma homogénea a lo largo del año, con ausencia de periodos de estiaje. Los máximos de precipitación se registran en otoño-invierno. Las temperaturas son suaves, con una media anual de 13.9 ºC, sin cambios bruscos debido a la influencia del Mar Cantábrico.

La vega de la regata de Jaizubia está sometida a la influencia mareal, de forma que sufre periodos de inundación con agua salina conforme a los ciclos mareales (Figura 2.5). Este hecho condiciona los hábitats que conforman la marisma. Aparte de las manchas de carrizo (*Phragmites australis*) que constituyen la vegetación dominante, cabe destacar la presencia, en las zonas más expuestas a la influencia mareal, de formaciones herbáceas de especies halófitas, compuestas principalmente por *Salicornia ramossisima*, *Spartina alterniflora, Aster trifolium* y *Suaeda maritima*. En las zonas más altas se sitúan matorrales de *Halimione portulacoides,* que están siendo desplazados por la especie invasora *Baccharis halimifolia*, y *Tamarix gallica.* Por último, se pueden encontrar llanuras fangosas y/o arenosas que quedan al descubierto durante la bajamar. Toda la zona está rodeada de campiña atlántica, compuesta por prados de siega con arbolado disperso, principalmente alisos (*Alnus glutinosa*).

Figura 2.5. Imágenes de la marisma de Jaizubia en bajamar y en pleamar. Se observa como, con la marea baja, zonas con limos y vegetación halófita quedan al descubierto.

La marisma de Jaizubia se sitúa a los pies de los macizos montañosos de Jaizkibel (al O) y Peñas de Aia (al SE) con el Mar Cantábrico al N. Debido a su localización geográfica, en las estribaciones occidentales de la cordillera pirenaica y al borde del mar Cantábrico, es un lugar de paso obligado para numerosas poblaciones de aves migradoras de Europa, que evitan sobrevolar los Pirineos (Mendiburu et al. 2009; Tellería et al. 2009). Esto convierte a Jaizubia en un lugar idóneo como área de descanso, y por tanto muy adecuada para el estudio del comportamiento de aves migradoras.

2.3. Metodología general

2.3.1. Captura de aves y obtención de datos biométricos y carga de grasa

Las rutas migratorias han sido tradicionalmente estudiadas usando recapturas de individuos marcados (e.g. anillados) a lo largo de la ruta migratoria (Bairlein 2001), información que actualmente puede obtenerse de la base de datos de EURING. Asimismo, dada la baja probabilidad de recapturar un ave anillada y el desigual esfuerzo de anillamiento a lo largo de las rutas migratorias, esta información presenta a menudo sesgos en su distribución espacial y temporal. En consecuencia, el análisis de recapturas de aves anilladas se revela insuficiente para responder a algunas cuestiones sobre las rutas migratorias de las diferentes poblaciones (Arizaga & Tamayo 2013).

Por otro lado, la morfología alar ha evolucionado junto con el comportamiento migratorio, de forma que en especies o poblaciones que recorren mayores distancias el ala es más larga y ha adoptado una forma más apuntada, debido a que esta morfología minimiza el coste de transporte y por tanto aumenta la eficiencia energética del vuelo (Lockwood et al. 1998). Por tanto, las diferencias biométricas del ala pueden ser empleadas en estudios de conectividad, como método complementario al uso de recapturas, para distinguir poblaciones de distinto origen de una especie determinada (e.g. Chandler & Mulvihill 1990; García-Peiró 2003; Fiedler 2005; Arizaga et al. 2006).

Para obtener datos biométricos, así como de carga de grasa, se capturaron las aves mediante redes de niebla que permanecieron abiertas durante un número de horas determinado desde el amanecer (normalmente 4 h), de acuerdo a un protocolo estandarizado de captura y toma de datos para todas las estaciones de muestreo. En primer lugar, las aves capturadas se marcaron con una anilla metálica numerada que permite la identificación individual de las aves en caso de recaptura, y se determinó su edad. En el caso de aves del género *Acrocephalus* se pueden identificar dos clases de edad: juveniles nacidos en el año, que presentan un plumaje nuevo; o adultos, de más de un año de vida, que ya han realizado, como mínimo, un ciclo migratorio completo (ida a los cuarteles de invierno y vuelta a las áreas de cría) y que muestran un elevado desgaste en las plumas (Svensson 1998). Posteriormente, se tomaron medidas de longitud alar (± 0.5 mm, de acuerdo al método III de Svensson 1998), grasa subcutánea (siguiendo la escala Kaiser 1993) y peso (± 0.1 g). En algunas estaciones de muestreo se obtuvieron además la longitud de todas las primarias así como el estado de la muda (muda sí o no).

2.3.2. Modelos captura-marcaje-recaptura (CMR)

Los modelos basados en datos de captura-marcaje-recaptura (CMR), como los modelos de Cormack-Jolly-Seber (CJS) permiten estimar por separado la supervivencia (ϕ) y probabilidad de captura (p) de los individuos, considerando poblaciones abiertas (descripción detallada del método en Schaub et al. 2001). En el caso de aves en migración presentes en un área de descanso determinada, se puede asumir que la supervivencia real de los individuos de un día para otro en un área de descanso es 1, de forma que ϕ se puede definir como la probabilidad de permanecer en ese lugar, y su complementario, ε ($\varepsilon = 1-\phi$), como la probabilidad de abandonar el área de descanso. Por ello, los modelos CJS han sido ampliamente empleados para abordar el estudio del efecto de diversos factores en las decisiones de partir de áreas de descanso y establecer la importancia relativa de éstos (e.g. Schaub et al. 2004; Tsvey et al. 2007; Schaub et al. 2008; Arizaga et al. 2011b). Por tanto, ha sido la metodología elegida para estudiar las decisiones de partir en esta Tesis Doctoral.

Otro ejemplo de modelos CMR son los modelos inversos (Pradel 1996), que permiten estudiar el reclutamiento poblacional. En este caso el parámetro estimado es la denominada *seniority* (γ), que puede definirse como la probabilidad de que un individuo en la ocasión t ya estuviera presente en la población en t-1. En el caso de aves en migración, γ puede considerarse como la probabilidad de que un individuo ya estuviese en un área de descanso en la ocasión de captura (muestreo) previa a un evento de captura, y 1-γ como la probabilidad de que ese individuo haya llegado entre ambas ocasiones de captura. A pesar de que este parámetro es empleado para estimar la duración de la estancia en las áreas de descanso (Schaub et al 2001), esta metodología estadística no ha sido prácticamente aplicada para estudiar las probabilidades de parar, con la excepción de Schaub et al. (1999) para probar el efecto de reclamos. En la presente Tesis Doctoral, se ha empleado para estudiar las condiciones (e.g. meteorológicas) bajo las cuales llegan los individuos presentes en un área de descanso y probar su utilidad en el estudio de este aspecto de la ecología migratoria.

Para aplicar cualquier modelo CMR es necesario obtener el historial de captura de cada individuo, que incluye las ocasiones de captura (muestreos) en los que un individuo dado fue visto (recapturado) o no. El procedimiento de captura y marcaje de las aves fue el explicado en el apartado "Captura de aves y obtención de datos biométricos y carga de grasa". En este caso, el protocolo de muestreo fue diario en todas las estaciones de muestreo empleadas para estudiar las decisiones de parar y partir para maximizar el número de recapturas.

La aplicación de modelos CMR requiere que los datos cumplan los siguientes requisitos:

- Todos los individuos presentes en la población en tiempo t_i tienen la misma probabilidad de captura.
- Cada animal marcado en la población inmediatamente después de t_i tiene la misma probabilidad de sobrevivir a t_{i+1}.
- Las marcas no se pierden.
- Todas las capturas son instantáneas en relación al periodo entre t_i y t_{i+1} y la liberación es inmediata.

Por tanto, antes de proceder a la aplicación de dichos modelos es necesario comprobar si los datos se ajustan a estos requerimientos. Algunos de estos requisitos se comprueban mediante tests (e.g. para detectar transeúntes o un efecto de la trampa en la probabilidad de captura), mientras que otros se cumplen debido al método de muestreo empleado (las anillas metálicas no se pierden una vez colocadas y la liberación de las aves es inmediata).

2.3.3. Estimación de la disponibilidad trófica

A pesar de su importancia para entender aspectos de la ecología migratoria, la estimación de la disponibilidad trófica para aves insectívoras en carrizales está muy poco representada en estudios de migración (e.g. Grandío 1999) En esta Tesis se calculó la biomasa de invertebrados (peso seco con una precisión de 0.01 g) muestreados durante el periodo de migración postnupcial en distintas áreas de descanso. La técnica de muestreo elegida consistió en realizar un número predeterminado de barridos de vegetación con una manga entomológica a lo largo de transectos predefinidos (método descrito por Poulin et al. 2002). Se eligió esta metodología frente a otras como el uso de trampas de intercepción (Bibby & Thomas 1985) debido a que es la técnica que permite capturar la mayoría de taxones del nicho principal de alimentación de las aves de carrizo y en un periodo corto de tiempo (Poulin & Lefebvre 1997).

2.3.4. Radioseguimiento

El radioseguimiento es una técnica apropiada para estudiar el uso del espacio (distribución y selección de hábitats) por parte de las aves en un área de descanso, puesto que permite localizar a los individuos equipados con radioemisor a distancia, sin necesidad de verlos ni capturarlos. En este caso particular, se emplearon emisores PIP41 de Biotrack, de tamaño adecuado para la especie de estudio, el carricero común (Caccamise & Hedin 1985). Los emisores fueron colocados en la zona dorsal de las aves mediante arneses Rappole (Rappole & Tipton 1991) (Figura 2.6) cuyo tamaño adecuado para no interferir con las actividades del ave fue estimado siguiendo lo indicado por Naef-Daenzer (2007). Las localizaciones se realizaron mediante receptores Sika (30MHz) con antenas Yagi, de Biotrack, mediante la técnica de biangulación. El equipo empleado permite obtener información direccional de la posición de los individuos, por lo que las localizaciones exactas de cada individuo se obtuvieron por la intersección de las direcciones obtenidas, en el menor espacio de tiempo posible, desde dos puntos distintos. La precisión de esta metodología fue de 30 m (SE: 7 m) y se calculó tras comparar la localización exacta de 6 puntos obtenida por GPS con la resultante de la biangulación.

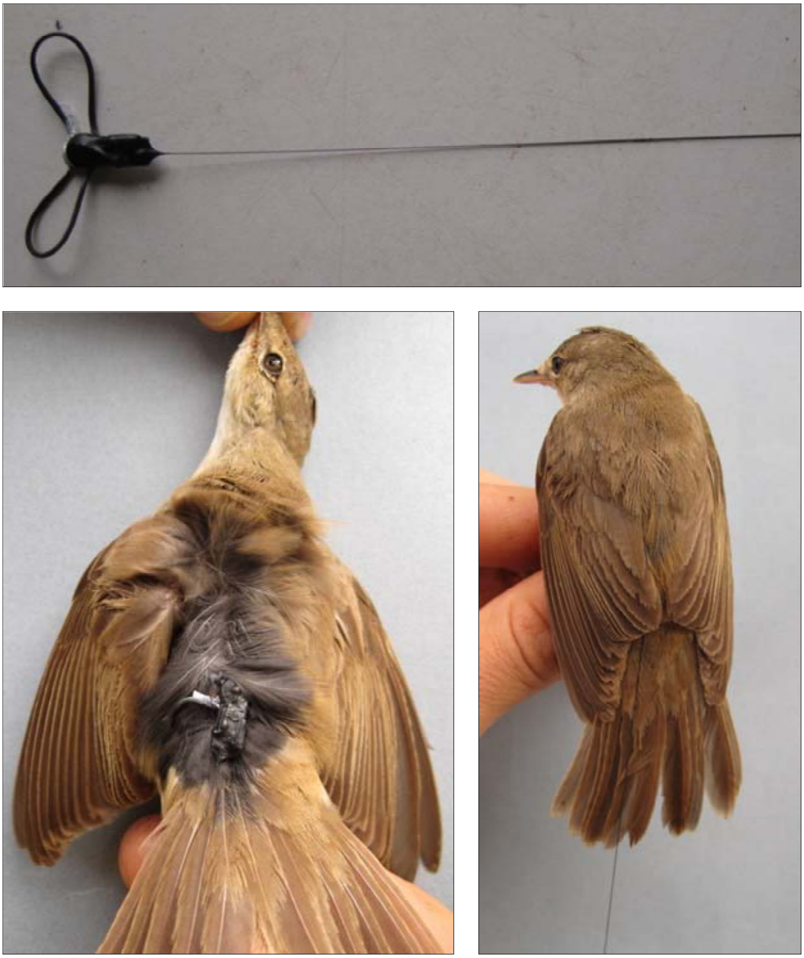

Figura 2.6. Modelo de radioemisor con arnés colocado en carriceros.

CAPÍTULO 3

Connectivity in Reed Warblers *Acrocephalus scirpaceus* between breeding grounds in Europe and autumn stopover sites in Iberia

Este capítulo es una reproducción del artículo: Andueza, M., Barba, E., Arroyo, J.L., Feliu, J., Greño, J.L., Jubete, F., Lozano, L., Monrós, J.S., Moreno-Opo, R., Neto, J.M., Onrubia, A., Tenreiro, P., Valkenburg, T., Zumalacárregui, C., González, C., Herrero, A. & Arizaga, J. 2013. Connectivity in Reed Warblers *Acrocephalus scirpaceus* between breeding grounds in Europe and autumn stopover sites in Iberia. *Ardea* 101: 133-140.

3.1. Abstract and keywords/Resumen y palabras clave

Abstract: We determined the degree of connectivity in the Eurasian Reed Warbler *Acrocephalus scirpaceus* between breeding regions in central and northern Europe and stopover sites in Iberia, during the autumn migration. We used both recovery data and wing length analyses to achieve this. Biometric data were obtained during 2009 at 11 sampling localities in Iberia, which we amalgamated into four major migratory areas within the region (Central, Western, Eastern and

Southwestern Iberia, hereafter CI, WI, EI, SW). From the EURING database, we selected birds captured at their breeding sites in Europe and recaptured in Iberia during the autumn migration. Reed Warblers passing through WI had shorter wings than those in CI, EI and SW, suggesting that birds in WI migrated shorter distances, a fact also supported by recovery data. Although Reed Warblers showed some population overlap when passing through Iberia, we found that birds passing through EI and CI came from areas further to the east (continental Europe) than those passing through WI (mainly British Isles), thus supporting parallel migration. Reed Warblers tended to converge in southwestern Iberia, suggesting an effect of nearby geographical barriers.

Keywords: Iberia, migration routes, parallel migration, recoveries, wing length.

Resumen: En este trabajo determinamos el grado de conectividad en el carricero común *Acrocephalus scirpaceus* entre sus regiones de cría en el centro y norte de Europa y sus áreas de descanso en Iberia durante la migración postnupcial. Para ello, empelamos datos de recapturas y longitud alar. Los datos biométricos se obtuvieron en 2009 en 11 estaciones de muestreo de la Península Ibérica, que fueron asignadas a 4 áreas migratorias principales (Centro, Oeste, Este y Suroeste, abreviadas como CI, WI, WI, SW). De la base de datos de

EURING, seleccionamos aquellos individuos capturados en sus lugares de cría en Europa y recapturados en Iberia durante la migración otoñal. Los carriceros que pasaron por WI presentaron alas más cortas que en CI, EI y SW, sugiriendo que las aves en WI migran distancias más cortas, lo que es apoyado por los datos de recapturas. Aunque los carriceros presentaron cierto soleamiento poblacional a su paso por la Península Ibérica, encontramos que aquellos que pasan por EI y CI vinieron de lugares más orientales (Europa continental) que aquellos que pasan por WI (principalmente Islas Británicas), apoyando la existencia de una migración paralela según origen dentro de la Península Ibérica. Los carriceros mostraron una tendencia a converger en la región suroccidental de la Península, sugiriendo la existencia de una influencia de las barreras geográficas cercanas.

Palabras clave: Iberia, longitud alar, migración paralela, recuperaciones, rutas de migración.

3.2. Introduction

The migratory connectivity of a population can be defined as the link between breeding and non-breeding areas and/or as the extent to which different breeding populations mix at the winter quarters (Webster et al. 2002; Norris et al. 2006). Connectivity patterns affect the degree of adaptation of birds to their nonbreeding areas, and their study can provide clues about the evolution of migration and the actual spatio-temporal distribution of birds during the non-breeding period. The study of connectivity has direct conservation implications (Pain et al. 2004). This is particularly true in species showing strong connectivity (i.e. when individuals from a population overwinter together in the same area without mixing with others from different populations) as well as in those species which depend on very specific habitats, or have very restricted ecological requirements, such as many wetland species (Atienza et al. 2001; Pain et al. 2004). Such birds are often particularly vulnerable, as wetlands are especially threatened by human pressure and global climate change (Hartig et al. 1997; Airoldi & Beck 2007).

The connectivity patterns of European passerines have been the target of several studies that have chiefly focused on the location of wintering grounds (Pain et al. 2004; Procházka et al. 2008). It remains largely unknown, however, whether connectivity is maintained between breeding and stopover sites during migration. Population-specific travel (migratory) directions and the use of population-specific key stopover places are likely to be among the chief factors that determine connectivity during the migration period.

The existence of migratory divides between western and eastern Europe (e.g. Helbig 1996; Pulido 2007) results in European populations of several bird species having different migratory directions. Thus, western populations migrate following a southwest axis in autumn, whereas eastern populations migrate following a southeast axis (e.g. Schlenker 1988; Bensch et al. 2006; Procházka et al. 2008; Reichlin et al. 2009). In this context, high connectivity between breeding and stopover grounds is expected if the divide is strongly marked and hence there is no overlap between western and eastern populations.

On a smaller scale, in populations using a main migratory direction a positive relationship between the geographic location of breeding and stopover areas can be expected. This connectivity could evolve when migrants follow the most direct routes during migration, saving time and reducing the energy cost (Alerstam 1990a; Newton 2008). In other words, if connectivity is strong, migrants breeding in regions further east should pass through regions which are further east than those used by migrants breeding in regions further west.

Iberia is a region of passage for several European Afro-tropical migrants (Tellería et al. 1999), therefore it is a suitable area for the investigation of the existence of population-specific stopover or passage regions. The particular geographic position of Iberia allows us to consider, for analytical purposes, three major regions of passage: (1) Central Iberia (CI), entering through the western edge of the Pyrenees (Galarza & Tellería 2003) and heading south following a south-west axis of migration; (2) Western Iberia (WI), entering Iberia through the north coast and flying parallel to the Atlantic coast until reaching southern Portugal, following a southern axis of migration; (3) Eastern Iberia (EI), entering Iberia through the eastern edge of the Pyrenees and continuing south following a south-west axis along the Mediterranean coast. Migrants passing through CI and WI and, to a lesser extent, EI, should be expected, owing to their main migration axes, to converge in southwestern Iberia (SW), as reported by Cantos (1998).

Due to aerodynamics (Norberg 1990), flight morphology is co-adapted with migratory behaviour: wings are more pointed and longer and the tail shorter with increasing distances of migration (Pérez-Tris et al. 1999; Calmaestra & Moreno 2001). These adaptations are observed at both inter- (Mönkkönen 1995; Calmaestra & Moreno 2001) and intra-specific level (Copete et al. 1999; Pérez-Tris et al. 1999; García-Peiró 2003; Chernetsov 2004; Förschler & Bairlein 2010). As a result, these biometric differences can be used to assess the origin of migrants, or at least, to distinguish different populations (i.e. Chandler & Mulvihill 1990; García-Peiró 2003; Fiedler 2005; Arizaga et al. 2006).

In this study, we investigate whether species with a marked migratory divide in Europe also show connectivity on a smaller scale, testing whether migrants use parallel routes between their breeding and stopover areas. With this goal, we used both recovery and morphology data of Reed Warbler *Acrocephalus scirpaceus,* captured in Iberia during the autumn migration period. Our hypothesis is that if this species, which presents a high connectivity between breeding and wintering areas (Procházka et al. 2008), also maintains a strong connectivity during migration, on a smaller scale, a positive relationship should be expected between its longitude of origin and capture in Iberia, resulting in parallel migration of different populations within the region. Also, biometric differences are expected within Iberia, with birds originating from further away, which therefore cover longer distances, presenting longer and more pointed wings.

3.3. Methods

3.3.1. Study species

Reed Warblers have a wide geographic distribution, breeding in much of Europe and overwintering in tropical Africa (Cramp 1992). This species is a suitable model to study the degree of connectivity between breeding and stopover regions in Iberia since Reed Warblers are common migrants passing through the area en route to their wintering areas (Tellería et al. 1999). In this study we considered birds likely to be true stopping-over migrants (i.e. accumulating fuel) and also birds which merely land and resume their migration the next day. Aiming to identify the origin of migrants passing through specific regions, rather than detecting the potential use of Iberia, we did not make a distinction by passage time.

3.3.2. Sampling sites and field data

Reed Warblers were captured with mist nets at 11 localities in Iberia during the autumn migration period of 2009 (Fig. 3.1). Each locality was assigned to one of the migratory regions in Iberia (CI, WI, EI, SW) (Fig. 3.1). Data were collected from 15 July to 15 October and mist nets were open with a variable frequency, ranging between daily and fortnightly, during a period of 4-6 h starting at dawn. The vegetation in all localities was composed mainly of reed beds (*Phragmites australis*).

Each bird was individually ringed and its age determined as either first-year (birds with fresh juvenile feathers in their wings, hatched in 2009) or adult (with worn feathers in their wings, hatched in 2008 or before) following Svensson (1998). Wing length (± 0.5 mm, according to method III in Svensson 1998) was recorded at all sampling localities. Additionally, primary feathers length (± 0.5 mm; P1 to P9, numbered from innermost to outermost) were measured at 4 of 11 sites (Taipal, Jaizubia, Canal Vell, Pego).

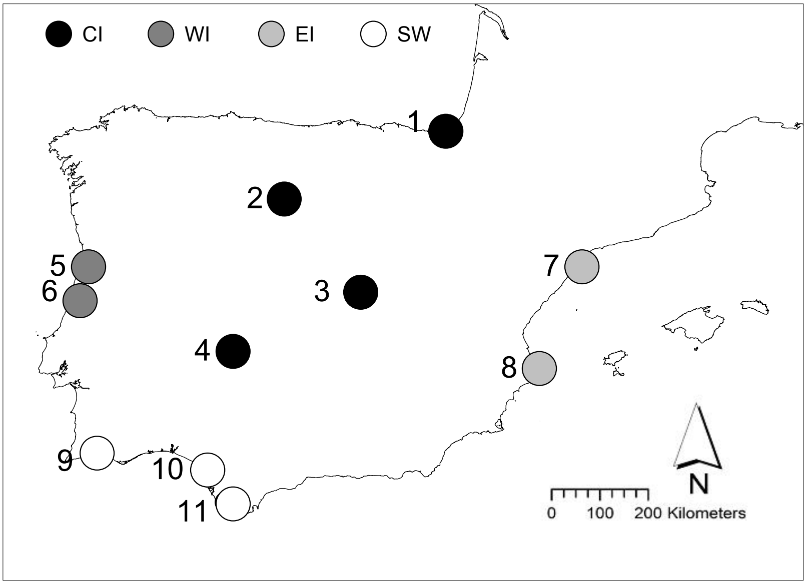

Figure 3.1. Sampling localities in the Iberian Peninsula. Central Iberia (CI): 1, Jaizubia; 2, El Cruce; 3, Las Minas; 4, Arroyo Budión. Western Iberia (WI): 5, Salreu; 6, Taipal. Eastern Iberia (EI): 7, Canal Vell; 8, Pego. Southwestern Iberia (SW): 9, Sítio das Fontes-Charito; 10, Manecorro; 11, Vejer.

3.3.3. Biometric analyses

Wing morphology is known to have evolved with migratory behaviour, wing pointedness being a good indicator of migratory distances (Lockwood et al. 1998). The C_2 index, as defined by Lockwood et al. (1998) is a commonly used wingtip shape index

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to describe wing pointedness. Negative values represent more pointed wings, whilst positive values indicate a more rounded shape. In our data set, only wing length was available at all sampling sites, so we used this measure as an indicator of wing pointedness, since wing length was negatively correlated with the C_2 index value at all the sites where primary feather length was recorded (total of birds: r = -0.238, P < 0.001, n =1319; first-year birds: r = -0.356, P< 0.001, n = 890; adults: r = -0.159, P < 0.001, n = 429).

To check whether there were morphology variations between migratory regions, we conducted a GLM on wing length with age (first-year birds, adults) and region (CI, WI, EI, SW) as factors. Localities were nested into regions, as indicated in Figure 1, and they were included in the models as a random factor. Apparently, we would not be able to separate migrants and local birds using the wing length (as suggested in Bibby & Green 1981), due to the high overlap observed (M. Andueza, pers. obs.). Therefore, in order to minimize local birds' effect, we selected Reed Warbler data collected during the peak of migration (presumably with a higher proportion of migrants in relation to local birds). The migration peak differed between age classes (Bibby & Green 1981; Cramp 1992). To identify it for each age category, we used data from sites with daily trapping sessions and a sufficiently high number of captures, selecting the date frame with higher number of daily captures for each age. Thus, we determined that the main period of passage lasted from 10 August to 30 September for first-year Reed Warblers, and from 1 August to 30 September for adults.

As a complement, we also compared the proportion of age classes in the four migratory regions using the χ^2 test (applying Yate´s correction) on contingency tables, to see if there was a differential use of regions depending on age, and hence whether connectivity patterns differed between juveniles and adults.

3.3.4. Recovery data analyses

Data on Reed Warblers captured at their breeding areas outside Iberia (from May to the end of June; Cramp 1992) and in Iberia during the autumn migration period (from July to October) were obtained from the EURING data bank ($n = 210$).

To test the prediction that parallel migration of the European populations between their breeding grounds and Iberian stopover areas occurs depending on their origin, we conducted a stepwise linear regression on location in Iberia (longitude) with origin in Europe (latitude and longitude) as predictor variables, using the EURING recovery data set.

To check whether possible biometric (wing length) differences between migratory regions in Iberia (CI, WI, EI, SW) could be explained by differences in both the origin of migrants passing through them, and the distance covered from their breeding sites in Europe, we selected those birds recaptured in each migratory region (CI, WI, EI, SW) from the EURING data set. Particularly, we considered those birds captured within a 100 km-radius area of each of the sampling localities belonging to each migratory region. We ran two analyses: 1) ANOVAs to see if birds' origin (latitude and longitude) differed between the four sampling areas; 2) an ANCOVA to compare the distance covered from breeding areas amongst regions, including birds' capture locations in Iberia (longitude and latitude) as covariates so as to remove the effect (heterogeneity) of capture location in Iberia on distance from origin.

For all the analyses, each bird was considered only once at each site in order to avoid pseudoreplication. The software SPSS v. 15.0 was used for statistics. We give mean values ± SE.

3.4. Results

A total of 3073 different Reed Warblers were captured, of which 2103 (68.4%) were first-year birds and the rest adults. Age ratios varied between regions ($\chi^2 = 19.11$, $P < 0.001$), with the lowest proportion of first-year birds being found in SW (61.2%), followed by CI (67.5%), WI (71.5%) and EI (72.1%) (Table 3.1).

Table 3.1. Comparison of percentages of first-year Reed Warblers at each region (CI: Central Iberia; WI: Western Iberia; EI: Eastern Iberia, SW: Southwestern Iberia), and Yates-χ^2 test results derived from pairwise comparisons.

	EI (72.1%)	CI (67.5%)	WI (71.5%)
CI (67.5%)	$\chi^2 = 5.05$ $P = 0.025$		
WI (71.5%)	$\chi^2 = 0.029$ $P = 0.866$	$\chi^2 = 2.073$ $P = 0.150$	
SW (61.2%)	$\chi^2 = 16.346$ $P < 0.001$	$\chi^2 = 5.807$ $P = 0.016$	$\chi^2 = 9.972$ $P = 0.002$

Table 3.2. GLM to test the effect of region (Central, Western, Eastern, Southwestern) and age (adults, first-year birds) on the wing length of Reed Warblers during the autumn migration period in Iberia. Localities were nested within regions.

Factor	SS	*df*	*F*	*P*
Region	406.21	3	0.84	0.514
Age	6500129.7	1	59859.39	<0.001
Locality(Region)	785.88	7	19.19	<0.001
Region×Age	66.67	3	3.60	0.013

Wing length varied between routes and ages, with the interaction between both factors being significant (Table 3.2).

For first-year birds, Reed Warblers passing through WI had significantly shorter wings than those passing through other regions, whilst those in SW had significantly longer wings (Fig. 3.2). For adults, birds in WI also showed shorter wings but there was no difference between the other three regions (Fig. 3.2). For all regions, first-year birds had shorter wings than adults (Fig. 3.2).

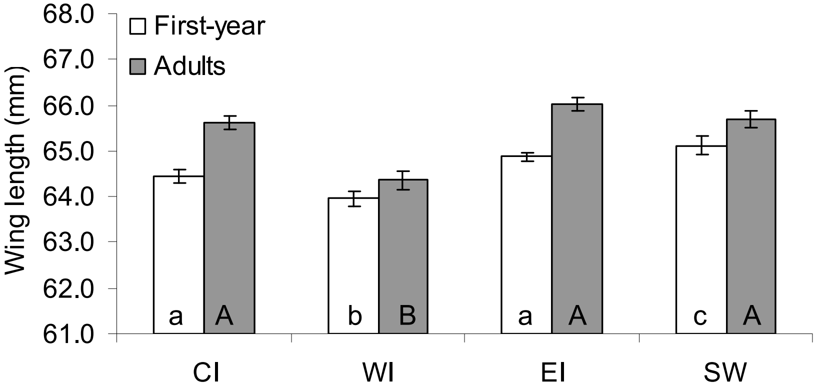

Figure 3.2. Wing length (mean ± SE) of Reed Warblers for each age class and region. Different letters between regions indicate significant differences.

The longitude of capture in Iberia was interrelated with coordinates of origin (GLM, *B*-parameters: latitude: $B = -0.35$, $P < 0.001$; longitude: $B = 0.20$, $P < 0.001$; $n = 105$). Hence, the European breeding sites of Reed Warblers recaptured in more eastern locations in Iberia were located further east and south than those of birds recaptured further west. Particularly, Reed Warblers from the British Isles migrated through western Iberia, with no recoveries found in the Mediterranean façade, whereas birds from the continent migrated through more eastern regions, although they covered most of the area (Fig. 3.3).

When comparing the average longitude of origin of recaptures at each Iberian migrating region, we found that birds passing through EI and CI had more eastern origins than those from WI and SW ($F_{4,77} = 11.35$, $P < 0.001$) (Fig. 3.4). Significant differences between regions were also found in latitude of origin ($F_{4,77} = 6158.08$, $P < 0.001$). Although *a posteriori* tests did not detect significant differences, birds from EI tended to have a more southern origin (Fig. 3.4). Also, the distance to the breeding areas (once the effect of covariates, latitude and longitude of capture in Iberia, was removed from the variable distance to origin) differed between regions ($F_{4,77} = 1.22$, $P < 0.001$). Although *a posteriori* tests did not show significant differences, birds passing through EI and CI tended to come from more distant origins than those in WI and SW (Fig. 3.4).

Finally, recovery data showed a high concentration of Reed Warblers in some areas, especially in southwest Iberia, but also on the western edge of the Pyrenees and some zones in eastern and central Iberia (Fig. 3.5).

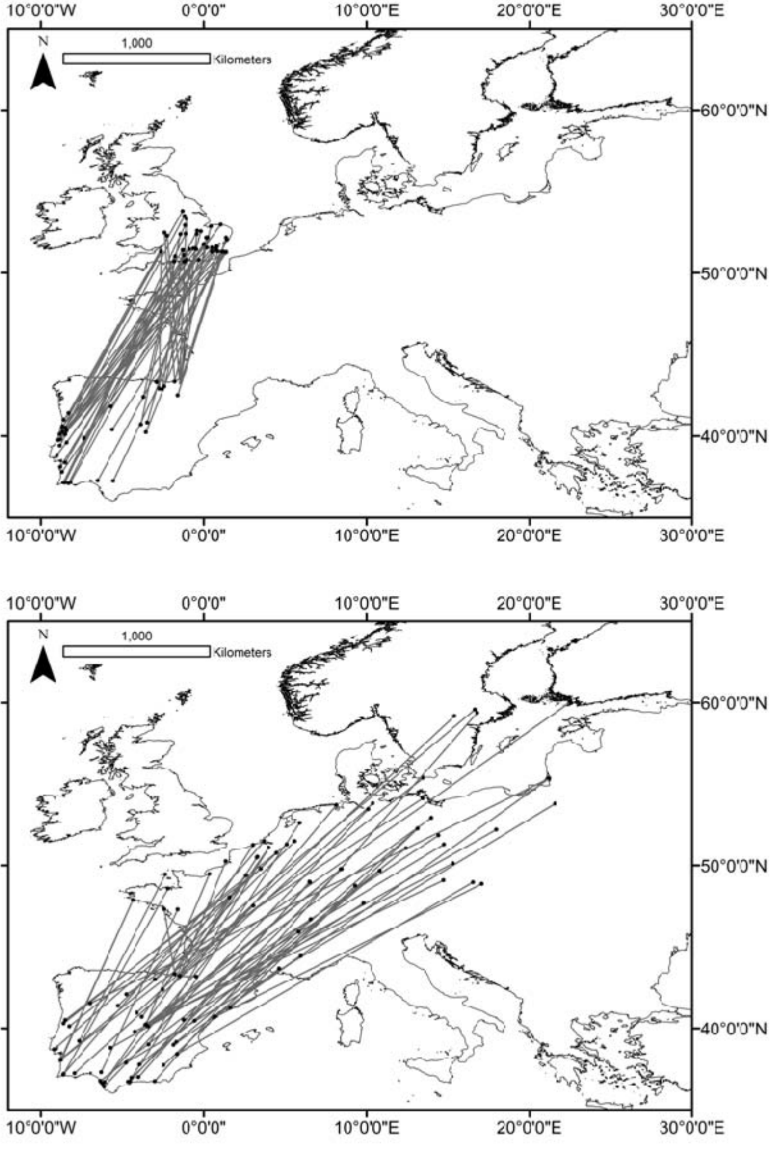

Figure 3.3. Recoveries of Reed Warblers captured/recaptured in Europe during the breeding period (upper panel = Britain and lower panel = continental Europe) and recaptured/captured in Iberia during the autumn migration.

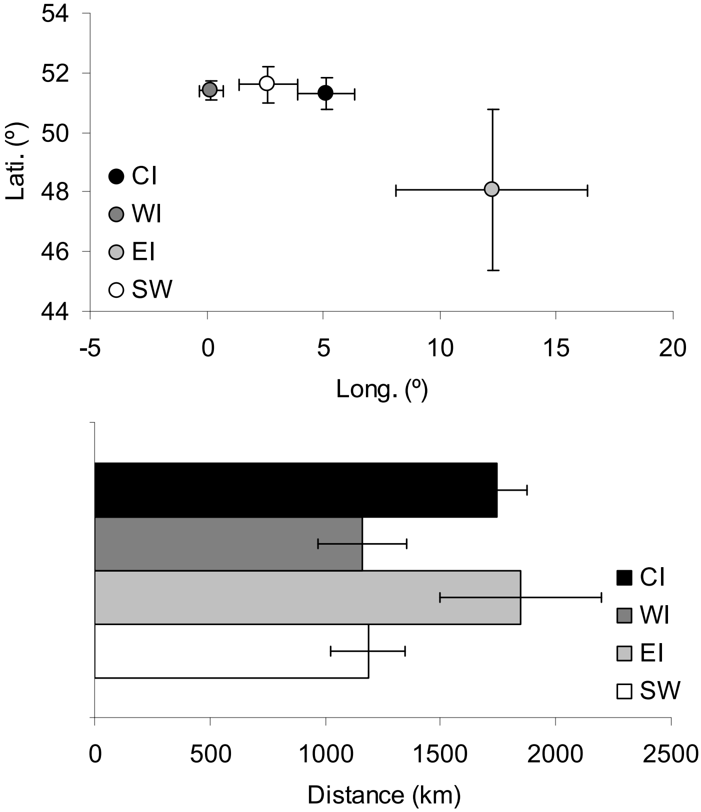

Figure 3.4. Mean ± SE geographic origin and distance from breeding sites (free of the effect of capture location in Iberia) of Reed Warblers captured at each migratory region in Iberia (CI: *n* = 34; WI: *n* = 17, EI: *n* = 4, SW: *n* = 22). For each region, the recoveries of Reed Warblers lying inside a 100 km radius area around each sampling site were considered.

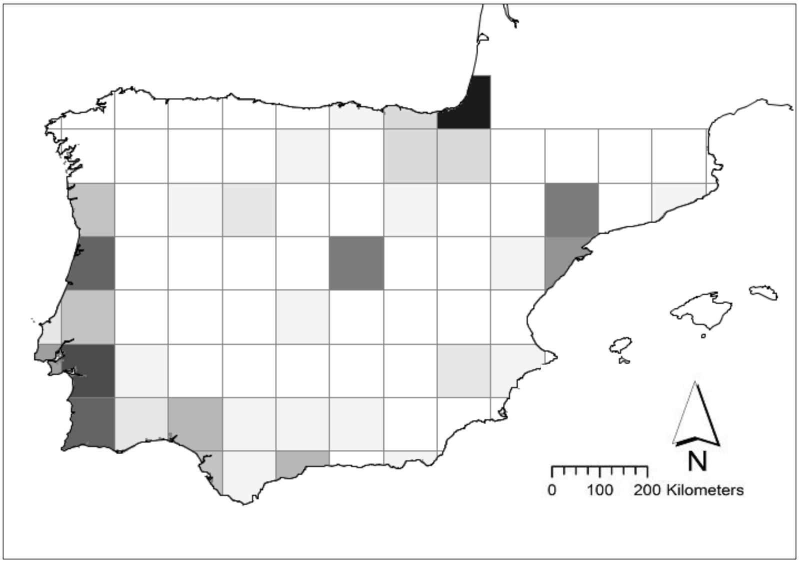

Figure 3.5. Density of Reed Warblers (number of recoveries/square). Darker squares are related to higher densities, ranging from 0 to 90 captures/square.

3.5. Discussion

The need for fuelling before the Mediterranean Sea and the Sahara desert may lead migrants to stop over in key sites and, accordingly, show a higher philopatry in Iberia than elsewhere (Cantos & Tellería 1994). In this context, studying the connectivity between breeding and stopover sites is of great importance in understanding the spatio-temporal distribution patterns of European bird populations during migration, as well as in identifying target stopover sites, which is crucial from a conservation standpoint.

The Reed Warblers passing through more eastern regions in Iberia during autumn came from breeding sites further to the east and south, whilst those passing through more western Iberian zones came from breeding areas further west and north. For example, birds breeding in the United Kingdom or Ireland passed mainly through WI and no recoveries were found in EI, [see Wernham et al. (2002) for further details]. This result agrees with the prediction that the different European populations of Reed Warblers tend to migrate in parallel flyways between their breeding and stopover areas according to their origin, following the shortest routes. Procházka et al. (2008) concluded that Reed Warblers breeding in Europe show high connectivity in their wintering areas south of the Sahara Desert. Hence, their geographic distribution in Africa during the winter is a mirror image of their distribution in Europe during the breeding period.

Although connectivity between breeding regions in Europe and passage regions in Iberia exists, the degree of this was found to be relatively low. Less than 20% (r^2 = 0.177) of the variance was associated with the geographic distribution of Reed Warblers in Iberia. In part this apparently weak connectivity may be due to the particular geographic conditions of southern Europe. The fact that the sea crossing is longer through the central Mediterranean than via its western edge probably forces many migrants to displace to the latter area. This gives rise to a funnel effect in Iberia (i.e., population overlapping), larger than that which would be expected if such a geographic obstacle did not exist (Galarza & Tellería 2003). This is supported by the high concentrations of Reed Warblers detected in southwest Iberia, probably due to the effect of nearby geographic barriers (Newton 2008), namely the Atlantic Ocean and the Sahara Desert. Our results support the idea that Reed Warblers tend to cross this desert along the Atlantic coast, where conditions are more favourable than in central Saharan zones (Hilgerloh 1990; Cramp 1992). Hence, in order to facilitate this, the different populations within Iberia converge towards southwest. Moreover, first-year birds show more variation in migratory direction (Fransson & Stolt 2005), so adults should theoretically show stronger connectivity. However, our sample size was too small to run detailed analyses considering both age categories separately.

Although Reed Warblers from East Europe have been reported to migrate towards Africa following a southeast route of migration (Cramp 1992; Berthold 2001; Procházka et al. 2008), we observed that a fraction of this population migrates through a southwest axis, thus flying to Africa *via* Iberia. This suggests the presence in East Europe of a fraction of Reed Warblers with a genetically determined southwest direction of migration (c.f. Helbig 1996; Pulido 2007).

Reed Warblers from western Europe fly over a shorter distance to arrive in Iberia, *en route* to Africa in autumn, than those from eastern Europe. As a consequence of this they were predicted to have a less marked long-distance-like morphology. Our analyses on wing length between regions agreed with this hypothesis, with birds in WI (coming from closer regions, mainly Britain) showing significantly shorter wings than those captured in the other three regions (coming from more distant origins, mainly continental Europe). However, the lack of difference in wing length between CI and EI suggests that biometric differences exist between British birds and the other European populations, but not between the latter. Moreover, we also observed that, in first-year birds, the longest wings were found in SW. These results would support an influx of Reed Warblers of eastern origin, which may converge in southwestern Iberia before crossing the sea to Africa (Cantos 1998), without stopping at northern Iberian sites. In adults, however, we did not find this pattern and the wing length of SW birds did not differ from that of birds from CI and EI. We are unable to give an explanation for this difference between age classes.

In SW a lower proportion of first-year birds in relation to adults was observed. First-year birds show more scattered migratory directions than adults (Alerstam 1990b; Fransson & Stolt 2005) and due to their inexperience do not always follow the optimal migratory direction, which in our study case would be through a southwestern axis in Iberia. So, in this scenario, a fraction of juveniles would cross the sea to Africa by eastern southern sites. Additionally, the proportion of adults could be increased by migrants that do not stopover in Iberia until reaching its southwestern corner, where they prepare for barrier crossing (Cantos 1998; Schaub & Jenni 2000b).

In conclusion, we showed that Reed Warblers have a population distribution during autumn migration within Iberia consistent with the hypothesis that migrants maintain a moderate degree of connectivity between their breeding and stopover sites in this region. However, although population segregation occurs (i.e. British and continental Reed Warblers), a certain degree of overlapping exists, probably due to a barrier crossing effect.

3.6. Acknowledgements

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Appendix 3.1. Characteristics of the sampling localities in Iberia (WI, Western Iberia; CI, Central Iberia; EI, Eastern Iberia; SW, Southwestern Iberia). Sampling freq. indicates the minimum sampling frequency; sampling effort, metres of mist nets; and sampling duration, the number of hours since dawn. RW (Reed Warbler) shows the number of captures of first-year birds/adults during the period considered for analyses. Locality abbreviations: TAIP, Taipal; SALR, Salreu; JAIZ, Jaizubia; CRUC, El Cruce; MINA, Las Minas; ARRO, Arroyo Budión; CANA, Canal Vell; PEGO, Pego; MANE, Manecorro; VEJE, Vejer; FONT, Charito-Sítio das Fontes.

Region	Locality	Coord.	Sampling period	Sampling freq.	Sampling duration (h)	Sampling effort (m)	RW
WI	TAIP	40° 11’N 08° 41’W	04 Aug/ 12 Sep	Weekly	5	240	70/71
WI	SALR	40° 44’N 08° 33’W	03 Jul/ 30 Sep	Weekly	5	108-120	223/46
CI	JAIZ	43º 21’N 01º 49’W	15 Jul/ 15 Oct	Daily	4	240	445/286
CI	CRUC	42° 01’N 04º 49´W	15 Jul/ 15 Oct	Daily	4	162	349/59
CI	MINA	40º 13´N 03º 35´W	04 Jul/ 30 Oct	Weekly	4	138	48/53
CI	ARRO	39º 03´N 48º 00´W	12 Jul/ 25 Oct	Fortnightly	4	36	35/24
EI	CANA	40º 43’N 00º 44’E	4 Aug/ 30 Nov	Daily	4	240-210	302/114
EI	PEGO	38° 50’N	1 Aug/	Daily	6	90	349/138

		00 07’W	1 Oct				
SW	MANE	36º 56´N 06º 21´W	1 Sep/ 31 Oct	Daily	4	252	28/23
SW	VEJE	36º 15´N 05º 58´W	10 Jul/ 27 Oct	Weekly	4	210	59/76
SW	FONT	37º 10´N 08º 27´W	09 Aug/ 30 Sep	Weekly	2-14.5	40-164	195/80

Appendix 3.2. Mean (SE) number of daily captures during the study period standardised for 4 h and 100 m of nets for Reed Warblers (RW) at each site and region (see abbreviations as in Appendix 3.1).

	RW	
Site	First-year	Adults
TAIP	10.0 (3.4)	13.5 (3.0)
SALR	21.0 (1.9)	5.8 (1.3)
Total WI	17.46 (2.0)	5.7 (1.2)
JAIZ	9.1 (1.4)	7.8 (2.0)
CRUC	10.6 (1.1)	2.4 (0.5)
MINA	5.0 (0.8)	4.7 (1.5)
ARRO	19.4 (4.7)	11.1 (3.7)
Total CI	4.4 (0.4)	1.7 (0.3)
CANA	6.5 (1.1)	3.3 (7.2)
PEGO	12.7 (1.5)	6.7 (1.1)
Total EI	7.9 (0.9)	4.7 (0.8)
MANE	0.4 (0.1)	0.3 (0.1)
VEJE	2.6 (0.7)	3.0 (0.7)
FONT	3.9 (1.1)	2.2 (0.7)
Total SW	2.1 (0.5)	1.5 (0.3)

CAPÍTULO 4

Geographic variation in body mass of first-year Reed Warblers *Acrocephalus scirpaceus* in Iberia

Este capítulo es una reproducción del artículo: Andueza, M., Barba, E., Arroyo, J.L., Feliu, J., Gómez, J., Jubete, F., Monrós, J.S., Moreno-Opo, R., Neto, J.M., Onrubia, A., Valkenburg, T. & Arizaga, J. En prensa. Geographic variation in body mass of first-year Reed Warblers *Acrocephalus scirpaceus* in Iberia. *Ornis Fennica*.

4.1. Abstract and keywords/Resumen y palabras clave

Abstract: On their route to tropical Africa, European trans-Saharan migrants must cross two major geographical barriers, the Mediterranean Sea and the Sahara Desert, which necessitates the accumulation of large fuel loads. While northern Africa is the chief region where most migrants gain fuel for the Sahara crossing, Iberia is a target area to gain fuel before the sea crossing existing between Europe and Africa. Despite the large body of studies approaching the question of fuel accumulation before geographic barriers, it is still poorly known which factors apart from distance to a certain barrier shape the geographical pattern of fuel reserves. To investigate this question in detail we used data of first-year Reed Warblers from 12 localities within Iberia during the autumn migration period of 2009. We run linear models to analyze the effects of location in Iberia, date, and body size on body mass variation at each migratory flyway (eastern, central and western Iberia). Flight ranges from each site were also calculated. Our results showed that Reed Warblers in Iberia had the necessary fuel needed to arrive in northern Africa but not to tropical Africa. However, body mass patterns varied depending on the geographical region (eastern, central or western Iberia). Date did not affect body mass in central and western Iberia, but it did in eastern Iberia, where heavier birds tended to pass later. Thus, the factors shaping body mass of Reed Warblers in Iberia before the sea crossing to Africa seemed to be more complex than just the distance to this geographical barrier, with underlying stopover quality-associated factors possibly playing a relevant role.

Keywords: Autumn migration, desert crossing, flight range, fuelling strategy, sea crossing, stopover.

Resumen: En su camino hacia África, las aves trans-sharianas deben cruzar dos barreras geográficas, el mar Mediterráneo y el desierto del Sahara, para lo cual deben acumular importantes cargas de grasa. Mientras que el norte de África es la región principal donde la mayoría de migradores acumulan las reservas

necesarias para cruzar el Sáhara, la Península Ibérica es un área clave para preparar el cruce del mar. A pesar de los numerosos trabajos que han abordado la cuestión de la cómo las aves acumulan las reservas necesarias para cruzar barreras geográficas, aún se desconoce en gran medida que factores adicionales, a parte de la distancia a la barrera, modelan los patrones geográficos de las cargas de grasa. Para estudiar en detalle esta cuestión empleamos datos de carriceros juveniles obtenidos en 12 localidades ibéricas durante la migración postnupcial de 2009. Mediante modelos lineales estudiamos el efecto de la posición en la Península Ibérica, la fecha y tamaño corporal en las cargas de grasa dentro de cada ruta migratoria (este, centro y oeste peninsular). Adicionalmente, se obtuvieron los rangos de vuelo desde cada lugar de muestreo. Los resultados mostraron que los carriceros en la Península Ibérica tuvieron las reservas necesarias para alcanzar el norte de África, pero no África tropical. Sin embargo, el patrón en las cargas de grasa varió según la ruta migratoria. La fecha no afectó a la carga de grasa en la ruta central y occidental, pero sí en la oriental, en la que las aves más pesadas pasaron más tarde. El patrón de acumulación de grasa en la Península Ibérica antes de cruzar el mar parece estar modelado por otros factores más allá de la distancia a la barrera, en particular factores asociados a la calidad y distribución de las áreas de descanso.

Palabras clave: Área de descanso, cruce del desierto, cruce del mar, estrategia de acumulación de fuel, migración postnupcial, rango de vuelo.

4.2. Introduction

Geographic and ecological barriers, such as deserts, oceans or high mountain ranges are important factors in the shaping of bird migration strategies (Moreau 1972), since crossing them implies flying over inhospitable areas, where fuelling is either impossible or almost so. Accordingly, migrants have developed fuelling strategies which allow them to make a successful barrier crossing (Rubolini et al. 2002; Delingat et al. 2008) whilst optimizing fuel accumulation, time and/or the energy expenditure (Alerstam & Lindström 1990; Hedenström & Alerstam 1997; Alerstam et al. 2003).

Afro-tropical European migrants (i.e. European birds that spend the winter in tropical Africa in areas south of the Sahara) must cross two major geographical barriers on their route to Africa from Europe: the Mediterranean Sea crossing between Europe and Africa and the Sahara Desert. Although a fraction of migrants may cross the sea by the Strait of Gibraltar (14 km), most migrants are supposed to cross it from a wider area covering the southern coast of Iberia (Moreau 1953; Casement 1966; Bernis 1980; Tellería 1981; Finlayson 1992). Fuelling at sea is impossible and in the Sahara it is only possible if birds find oases en route (Bairlein 1985). Therefore, with the perspective of not finding sufficient feeding possibilities in these zones most small, flapping flight migrants, such as passerines, must accumulate large fuel loads before crossing the barriers (Bairlein 1991; Schaub & Jenni 2000a; Fransson et al. 2005; Yosef & Chernetsov 2005; Fransson et al. 2006; Yohannes et al. 2009).

Depending on species-specific feeding requirements and the availability of suitable habitats expected to be found *en route*, four general strategies of body mass gain for crossing the Sahara Desert have been reported for European passerines migrating to tropical Africa during the autumn migration period (Schaub & Jenni 2000a): 1) a steady increase in body mass along the route until reaching the northern border of the desert (e.g. Garden Warblers *Sylvia borin*); 2) fuel accumulation well before the Sahara (e.g. Sedge Warblers *Acrocephalus schoenobaenus*); 3) fuel accumulation just in front of the Sahara (e.g. Reed Warblers *Acrocephalus scirpaceus*); and 4) fuelling whilst crossing the Sahara (e.g. Spotted Flycatchers *Muscicapa striata*). In defining these strategies the importance of the sea band (Atlantic/Mediterranean Sea) between Iberia and Africa was not considered. However, sea crossing has been reported to be relevant to the fuel management of migrants (Rubolini et al. 2002).

How body mass of some European long-distance migrant passerines increases before barriers is known on a broad scale, mainly from a continental perspective (Schaub & Jenni 2000a, b, 2001; Rubolini et al. 2002; Yohannes et al. 2009). However, such studies fail to show whether local (i.e., countrywide) variations from the general continental pattern occur, in particular near the edge of geographical barriers. Understanding these small-scale variations is not a trivial matter because the use of a few stopover sites to infer general fuelling strategies might cause bias if these sites are not optimal or if they are not used as true stopover sites (i.e., to gain energy reserves and not only for resting) (Arizaga et al. 2011c).

Situated in south western Europe, Iberia is a converging area for many European passerines moving to or from their wintering areas in western-tropical Africa (Tellería et al. 1999). As a result, Iberia can be considered as a key area for preparation before the sea and the Sahara Desert crossing. Thus, it is an excellent location for the study of fuelling strategies prior to barrier crossing.

The Reed Warbler *Acrocephalus scirpaceus* is a widespread Palaearctic songbird breeding across most of Europe and overwintering in tropical Africa (Cramp 1992). The species is closely linked with reed beds (*Phragmites australis*) where it feeds on small invertebrates. During the autumn migration, Reed Warblers have been reported to gain the fuel needed to cross the Sahara Desert mainly in northern Africa (Schaub & Jenni 2000a, b, 2001, but see Hilgerloh & Wiltschko 2000). However, crossing the sea band between southern Iberia and Africa may be relevant to the fuel management of Reed Warblers, as has been found for other species in similar circumstances (Rubolini et al. 2002). In this context, if the main factor determining fuel loads is the distance to the barrier's edge, we can expect a north-south increase in fuel load in Iberia. However, if another factors, such as the distribution of suitable habitats (Ktitorov et al. 2008; Chernetsov 2013), play a relevant role in the fuel accumulation strategy the accumulation of the reserves needed to cross the sea could occur at sites further north. Previous studies with Reed Warblers used a very low number of sampling sites, mainly in southern Iberia (see Hilgerloh & Wiltschko 2000 and Schaub & Jenni 2000a for further details), so where migrants actually prepare for barrier crossing remains unknown.

Additionally, body mass patterns are also likely to be affected by date (Schaub & Jenni 2000a, b; Maggini et al. 2013). In particular, late migrants have been reported to be more fuel loaded than earlier individuals (Schaub & Jenni 2000a, b). The causes underlying this phenomenon still remain unclear. Late migrants experience higher time-pressure to arrive at their wintering areas, hence they would tend to accumulate more fuel in order to increase their migration speed (Schaub & Jenni 2000a; Bayly 2006). Therefore, we should expect an increase in fuel load with date. Additionally, body mass can change across the season due to population-associated differential passage (Maggini et al. 2013).

The aim of the study was to investigate whether the pattern of Reed Warblers' body mass variation during autumn migration period in Iberia is shaped just by distance to geographic barriers or by additional parameters.

4.3. Methods

4.3.1. Sampling localities

Reed Warblers were captured with mist nets at 12 localities within Iberia during the autumn migration period of 2009 (Table 4.1, Fig. 4.1). The sampling frequency ranged from daily to fortnightly at different sites (see Table 4.1 for details). The vegetation in all localities was composed mainly of reed beds, except in Manecorro, where Mediterranean bushy vegetation (mainly *Pistacea lentiscus*) was abundant, together with a flooded prairie rich in halophytes with scattered tamarisks *Tamarix* spp., willows *Salix* spp. and ash trees *Fraxinus* spp.. Each sampling locality was assigned to one of these three flyways defined in Iberia (Table 4.1, Fig. 4.1) (Galarza &

Tellería 2003; Navedo et al. 2010; Andueza et al. 2013a): Eastern, Central and Western (hereafter, EI, CI, WI).

Each bird was individually ringed and its age determined according to Svensson (1992). Two age categories were identified: first-year birds (birds with fresh juvenile feathers in their wings, hatched in 2009) and adults (with worn feathers in their wings, hatched in 2008 or before). Wing length (± 0.5 mm, according to method III in Svensson 1992) and body mass (± 0.1 g accuracy) were recorded at all the sampling localities.

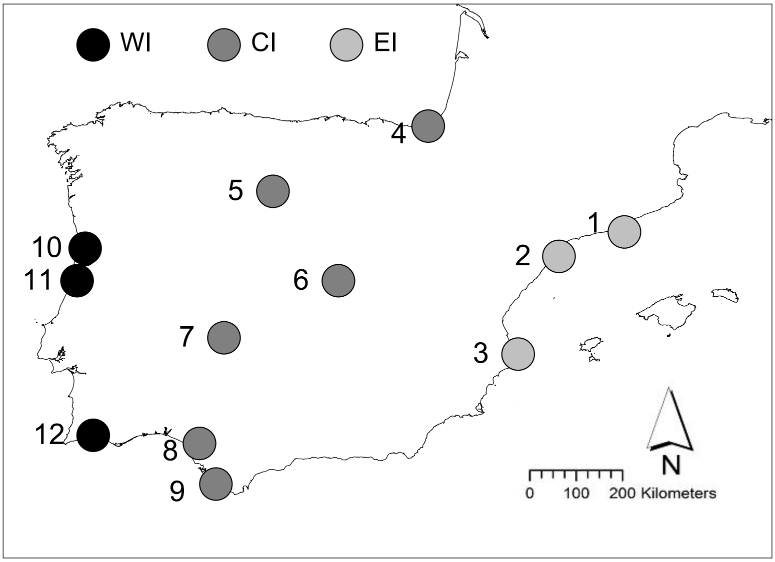

Figure 4.1. Sampling localities in Iberia. EI (eastern Iberia): 1 Viladecans, 2 Canal Vell, 3 Pego. CI (central Iberia): 4 Jaizubia, 5 El Cruce, 6 Las Minas, 7 Arroyo Budión, 8 Manecorro, 9 Vejer; WI (western Iberia): 10 Salreu, 11 Taipal, 12 Fontes.

Table 4.1. Characteristics of the sampling localities in Iberia. Captures refer to the number of first-year birds used in analyses (captured on the days considered, with all the necessary data recorded). Each bird has been considered only once (i.e. recaptures have been omitted).

Route	Locality (Code)	Coord.	Mist nets (m)	Sampling period	Sampling freq.	Captures
E	Viladecans (VILA)	42º 18´N 02º 07´E	207	18 Sep–30 Sep	Daily	26
E	Canal Vell (CANA)	40º 43´N 00º 44´E	240-210	10 Ago–30 Sep	Daily	304
E	Pego (PEGO)	38° 50´N 00º 07´W	90	10 Ago–30 Sep	Daily	319
C	Jaizubia (JAIZ)	43º 21´N 01º 49´W	240	10 Ago–30 Sep	Daily	437
C	El Cruce (CRUC)	42º 01´N 04º 49´W	162	10 Ago–30 Sep	Daily	344
C	Las Minas (MINA)	40º 13´N 03º 35´W	138	10 Ago–30 Sep	Weekly	45
C	Arroyo Budión (ARRO)	39º 03´N 48º 00´W	36	10 Ago–30 Sep	Fortnightly	33
C	Manecorro (MANE)	36º 56´N 06º 21´W	252	01 Sep–30 Sep	Daily	28
C	Vejer (VEJE)	36º 15´N 05º 58´W	210	10 Ago–30 Sep	Weekly	58
W	Salreu (SALR)	40° 44´N 08° 33´W	108-120	10 Ago–30 Sep	Weekly	200
W	Taipal (TAIP)	40° 11´N 08° 41´W	240	10 Ago–14 Sep	Weekly	66
W	Sitio das Fontes-Charito (FONT)	37º 10´N 08º 27´W	40-164	10 Ago–30 Sep	Weekly	27

4.3.2. Data selection

Reed Warblers are abundant breeders in Iberia (Martí & Moral 2003) and both local and non-local birds occur in sympatry at stopover sites during the migration period. Since we were interested in studying true migrants (thus avoiding local birds still moulting or still at their breeding sites and non-migrating), we selected a sampling period (from 10 August to 30 September) coinciding with the main period of migration (Grandío & Belzunce 1987; Cantos & Tellería 1992), when the proportion of local birds could be expected to be very marginal (negligible) in relation to the bulk of true migrants, and therefore the potential bias caused by including some locals would be small (Schaub & Jenni 2000a). For the analyses, we considered only first-year birds captured during the first 4 h from dawn at each site (except in Fontes, where the birds were captured over a 5 h period). Ideally, our analyses should have considered body mass at departure, but in the case of migrants captured more than once, we just considered the first capture event to make their data comparable with those birds trapped just once. Furthermore, birds first captured at a ringing station are not always caught the day of arrival (Schaub et al. 2001). Therefore, our sample had a mixture ranging from birds just arrived to birds just about to depart. We assume that a higher mean body mass at a site compared to others is ultimately due to the fact that migrants at that site are more fuel loaded, so likely depart with more fuel that those which would be captured at a site with lower mean fuel loads.

4.3.3. Statistical analyses

Firstly we conducted a Hierarchical Analysis of Clusters (HAC) in order to quantify the similarity between localities in relation to a size-corrected body mass index consisting in the residuals from a regression of the log-transformed body mass against log-transformed wing length (body size was assessed with wing length; Gosler et al. 1998) of Reed Warblers. For the HAC we used the UPGMA method with a similarity index based on the Euclidean distance between sampling sites. We repeated this HAC for the geographic distance between sampling sites. We conducted a Mantel test between the body mass index and geographic distances between sites, to check whether body mass depended on the geographic location.

Secondly, we ran Generalized Linear Models (with a linear-link function) to determine the relevance of several factors on Reed Warblers' body mass pattern in Iberia. In particular we considered as dependent variable the size-corrected body mass index (as described above) and route (EI, CI, WI) as a factor. Date and "location" of capture in Iberia were included as covariates. The covariate "location" was the first principal component (PC1) of a Principal Component Analysis (PCA) on latitude of capture in Iberia, shortest distance to south Iberian coast, northern Africa and tropical Africa (i.e., distance to geographical barriers edges). The PC1 was the only component from the PCA with an eigenvalue > 1, and it explained > 95% of the total variance (Table 4.2). Higher positive values of PC1 were related to locations situated in more northern latitudes and further from the southern coast of Iberia, the north African coast and tropical Africa. In the construction of linear models we considered both additive and interaction models, including double interactions between the factor "route" and the covariates. We used the small sample sizes' corrected Akaike Information Criterion (AICc) to select the models that best fitted to data (Burnham & Anderson 1998). Models with a difference of AICc < 2 were considered to fit similarly to data. Complementary, we run a liner model on daily number of captures as dependent variable, with route as factor and both date and latitude as covariates so as to see if the duration of the migratory peak was homogeneous within Iberia.

Finally, we estimated the potential flight ranges for both the entire sample and the 25% heaviest birds fraction from each site, since these birds would be those likely about to depart (Ellegren & Fransson 1992; Arizaga et al. 2011d). We considered for the calculations an intermittent strategy (Schmaljohann et al. 2007). In particular, we considered that migrants fly for a period of 10 h from 20.00 to 06.00 (night) and rest during the day for 14 h

(Salewski et al. 2010). For each bird, we calculated the number of flying and resting hours before they would have consumed their fuel store (i.e., until reaching their lean body mass), assuming a body mass loss of 1%/h during the flight (Hussell & Lambert 1980; Kvist et al. 1998) and 0.5%/h during the diurnal resting (Meijer et al. 1994). The duration of the resting period on the day of capture was considered to be 8 h, starting at 12.00, when sampling ended. Knowing the flying period of each individual assuming this intermittent strategy, the potential flight ranges were then calculated multiplying the flying hours by the flight speed of passerines under still air as in Delingat et al. (2008). We calculated the minimum potential flight ranges considering a flight speed of 40 km/h (Bruderer & Boldt 2001).

To estimate lean body mass we selected Reed Warblers without any visible fat content and ran a linear regression on body mass with wing length as an independent variable. There is evidence from analyses of recovery data and wing length within Iberia (Andueza et al. 2013a) that during migration different European populations converge in Iberia and segregate in different regions according to their origin, resulting in a geographical morphology variation. Hence the relationship between body mass and wing length is expected to vary between sites. Consequently, we obtained a different equation at each site for estimating m_0. For sites without fatless birds (Fontes and Viladecans), the equation of the nearest site was used. Manecorro and Vejer had less than

10 individuals each, so, owing to their proximity, we pooled both sites into a single equation.

Table 4.2. Factor loadings of the two Principal Components from a Principal Component Analysis on the latitude of capture in Iberia and the shortest distances to the geographical barrier´s edges: distance to south Iberian coast [Dist(SI)], to north African coast [Dist(NA)] and to the south of the Sahara [Dist(SS)]. All the variables were correlated with the factor loadings of the PC1.

Variable	PC 1	PC 2
Latitude	+0.51	+0.19
Dist(SI)	+0.49	+0.74
Dist(NA)	+0.50	-0.46
Dist(SS)	+0.50	-0.46
Eigenvalue	3.86	0.14
% Variance	96.47	3.45

All analyses were carried out using SPSS 15.0, except the Hierarchical Analysis of Clusters, which was done with PAST.

4.4. Results

Overall, we captured 1887 first-year Reed Warblers (each bird considered only once) with their body mass and wing length recorded. The number of first-year Reed Warblers captured per site ranged from 26 (Viladecans) to 437 (Jaizubia). Mean body mass ± SE for the complete data set was 10.9 ± 0.03 g (*n* = 1887), and ranged from 10.0 ± 0.1 g (Salreu, *n* = 200) to 11.8 ± 0.3 g (Fontes, *n* = 27) (Fig. 4.2). The 25% heaviest fraction of birds, the most likely to be ready to depart, had a mean body mass of 12.7 g ± 0.1 g (*n* = 462), ranging from 11.3 ± 0.1 g (Salreu, *n* = 50) to 14.2 ± 0.5 (Fontes, *n* = 6) (Fig. 4.2).

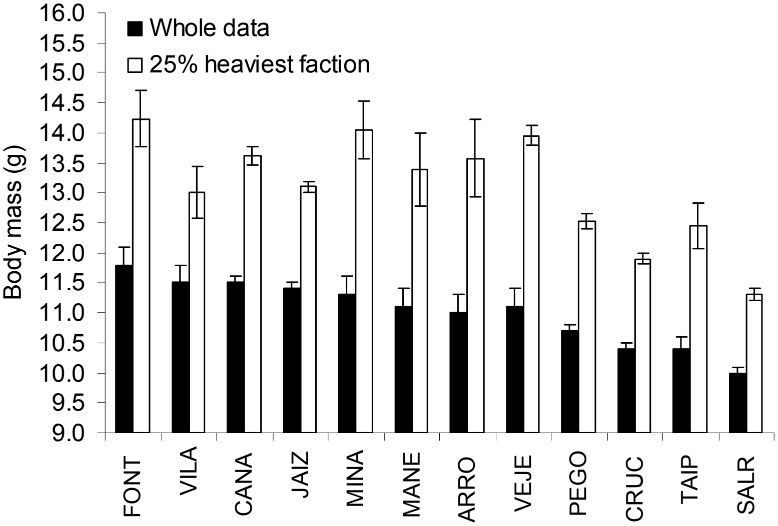

Figure 4.2. Mean body mass (weight) ± SE of Reed Warblers for the entire sample, and the 25% heaviest birds fraction at each locality.

The HAC revealed two clusters of localities in relation to Reed Warblers' size-corrected body mass index (Fig. 4.3). Such clusters, however, were not correlated with the geographic distance between localities (Mantel test: *r* = -0.04, *P* = 0.592), suggesting that body mass was independent of geographic location in Iberia and the distance between sampling sites.

Table 4.3. The 7 linear models run to test the effect of route, date and latitude on the body mass index of Reed Warblers captured in Iberia during the autumn migration period, ranked according their AICc values (small sample sizes' corrected Akaike Information Criterion). Abbreviations: ROU, route; DAT, date; LOC, location; ΔAICc, difference of AICc values in relation to Model 1.

Models	Parameters included	AICc	ΔAICc
1	ROU, LOC, DAT, ROU x LOC, ROU x DAT	-6083.126	0.000
2	ROU, LOC, ROU x LOC	-6036.925	46.201
3	ROU, DAT, ROU x DAT	-6001.139	81.987
4	ROU, LOC, DAT	-5997.134	85.992
5	ROU, DAT	-5994.924	88.202
6	ROU	-5965.679	117.447
7	ROU, LOC	-5965.596	117.530

We tested 7 linear models overall. Only one model was observed to fit the data better than the rest: the one including the interactions between route and date and route and location of capture in Iberia (Table 4.3). Both interaction terms were significant although the principal effect of date was not (Table 4.4). Body mass tended to increase in WI towards the south but to decrease in EI (Fig. 4.4), whilst remaining unchanged in CI.

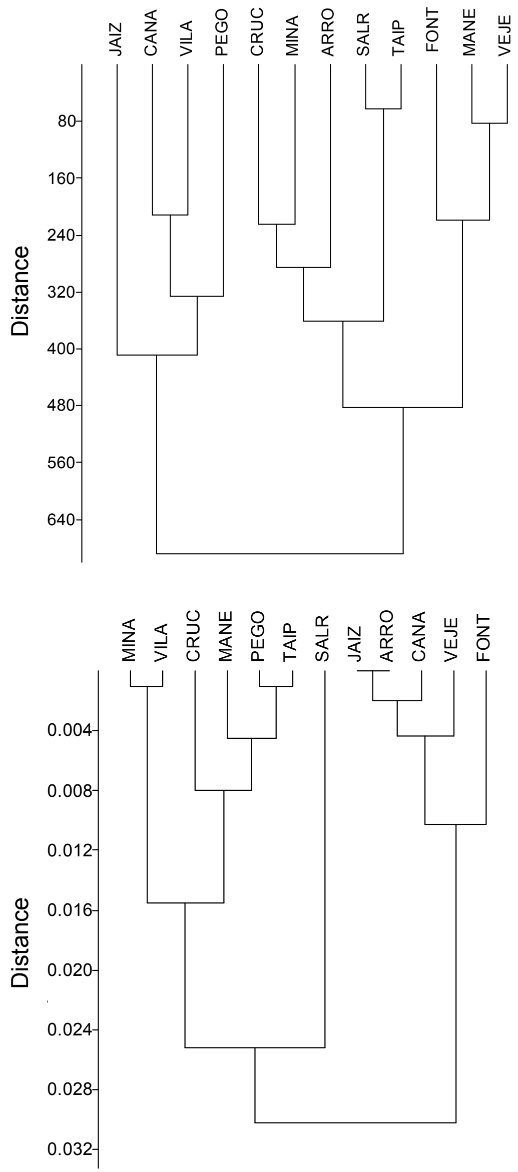

Figure 4.3. Cluster showing the distance (km) between sites (above) and diagram obtained from a Hierarchical Analysis of Clusters showing the Euclidean distance between localities in relation to size-corrected body mass of Reed Warblers (below).

Table 4.4. Wald χ^2 values for each effect of the best model (Model 1 in Table 4.2) explaining body mass variation of Reed Warblers stopping over in Iberia during the autumn migration period. Abbreviations: ROU, route; LOC, location in Iberia; DAT, date.

Effect	Wald χ^2	df	*P*
ROU	22.733	3	< 0.001
LOC	1.051	1	0.305
DAT	25.939	1	< 0.001
ROU x LOC	84.692	2	< 0.001
ROU x DAT	8.256	2	0.016

Moreover, body mass tended to increase with date in EI, whereas in CI and WI remained constant as season progressed (Fig. 4.4). The daily number of captures varied between routes (Wald $\chi^2 = 18.44$, $P < 0.001$) and the interaction of latitude with date was significant (Wald $\chi^2 = 6.42$, $P = 0.011$). Later in the season captures tended to decrease in northern latitudes and increased towards the south ($B_{\text{latitude x date}} = -0.03$).

Potential flight ranges from each site revealed that, on average, Reed Warblers stopping over at southern Iberian sites (Vejer, Manecorro and Fontes) could reach the north African coast without further refuelling (Table 4.5). The south of the Sahara Desert could not be reached from any site in Iberia on average (Table 4.5), and none of the Reed Warblers had enough fuel to do so. The 25% fraction of heaviest birds could reach north

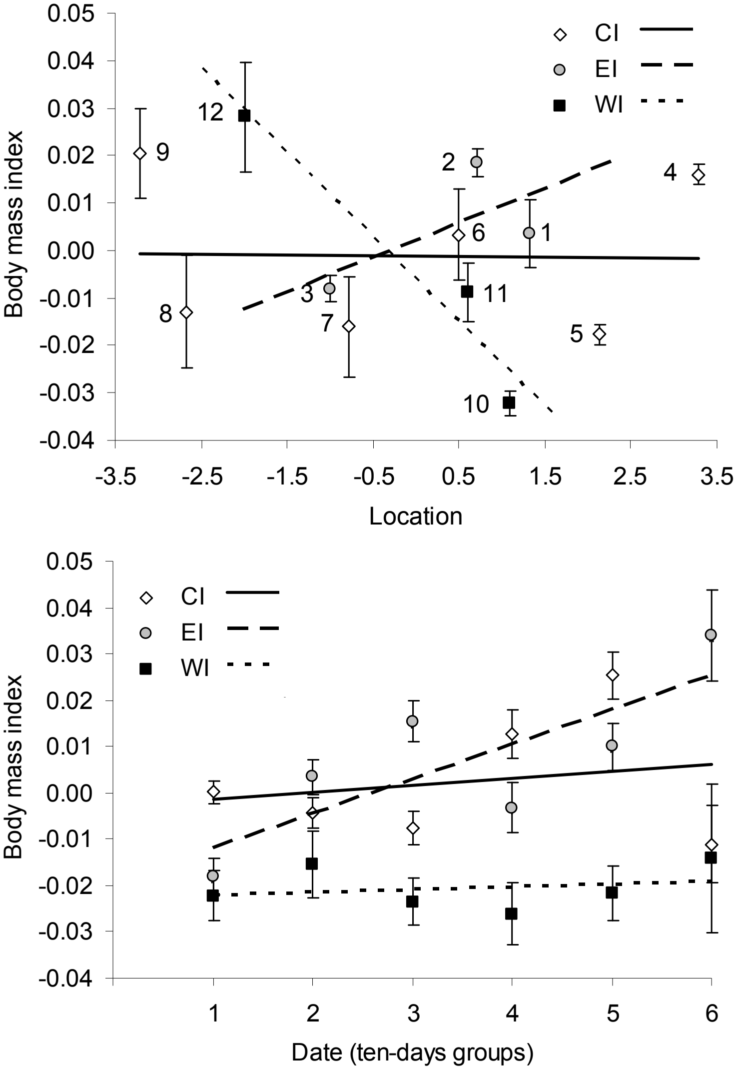

Figure 4.4. Variation in Reed Warblers size-corrected body mass index (Mean ± SE) depending on the location (above) and date (below) in eastern (EI: 1 Viladecans, 2 Canal Vell, 3 Pego), central (CI: 4 Jaizubia, 5 El Cruce, 6 Las Minas, 7 Arroyo Budión, 8 Manecorro, 9 Vejer) and western Iberia (WI: 10 Salreu, 11 Taipal, 12 Fontes). The variable date is shown as groups of ten sampling days.

Table 4.5. Mean potential flight ranges (SE; km) of Reed Warblers from each sampling site in Iberia assuming an intermittent flying strategy, for the entire sample (100%) and the 25% heaviest fraction of birds (25%). Additionally, we indicate the shortest distance (in km) from each site to the south Iberian coast (S Iberia), north African coast (N Africa), and southern border of the Sahara (S Sahara).

Site		Flight ranges	Dist. S Iberia	Dist. N Africa	Dist. S Sahara
FONT	100%	431 ± 62	7	275	1775
	25%	811 ± 91			
VEJE	100%	420 ± 47	8	52	1552
	25%	875 ± 52			
CANA	100%	332 ± 16	509	469	1968
	25%	701 ± 26			
VILA	100%	302 ± 44	626	521	2021
	25%	533 ± 84			
TAIP	100%	252 ± 33	339	545	2045
	25%	579 ± 66			
MANE	100%	223 ± 61	11	136	1636
	25%	669 ± 125			
MINA	100%	275 ± 46	385	501	2001
	25%	688 ± 78			
JAIZ	100%	224 ± 11	725	802	2303
	25%	520 ± 16			
ARRO	100%	206 ± 53	225	348	1848
	25%	590 ± 120			
PEGO	100%	187 ± 13	292	282	1782
	25%	508 ± 24			
CRUC	100%	152 ± 10	590	678	2178
	25%	393 ± 17			
SALR	100%	152 ± 13	401	596	2095
	25%	390 ± 23			

Africa from sites further north, such as Canal Vell, Pego, Arroyo Budión and Las Minas (Table 4.5).

4.5. Discussion

Average body masses of first-year Reed Warblers captured in Iberia during the autumn migration period were low, especially when compared to values obtained in other works in southern Iberia (Peiro 1995; Schaub & Jenni 2000a; Hilgerloh & Wiltschko 2000) or in northern Europe (Chernetsov 1999; Schaub & Jenni 2000a). Reed Warblers have been reported to show high year to year variations in body condition even near the edge of geographical barriers (Yosef & Chernetsov 2005). Although this may explain the discrepancy between our results, which included a single season, and other previous works, it is also possible that heavy birds were underrepresented in our data, given their lower mobility (Bairlein 1987; Titov 1999a; Chernetsov 2006) and thus their lower capture probability.

We found that the north-south body mass variation in Iberia was not homogeneous, as it varied between migratory flyways, suggesting that, when descending to a more regional scale, Reed Warblers' fuelling strategy is flexible and can be shaped by other factors apart from just distance to the barrier's edge. Thus, Reed Warblers passing through EI tended to be more fuel loaded at sites located further north and further from the barrier's edge, whereas the opposite was observed in WI. In CI, some southern sites were found to record higher mean body masses, but some northern sites showed similar values (i.e. Jaizubia and Vejer). Furthermore, in southern Iberia birds at sites which were very close together were observed to have very different values (i.e. Manecorro and Vejer). Such differences may be due to differences in habitat quality (Ktitorov et al. 2008; Chernetsov 2013). Thus, at a site where reed beds were not the dominant vegetation (Manecorro), body masses were lower than at nearby stations with abundant reed beds. Therefore, at a relatively local scale, the distribution of suitable habitats probably shapes body mass patterns across different routes of migration (Moore & Aborn 2000; Fransson et al. 2008; Chernetsov 2013). Consequently (or alternatively), our findings may be related to a different sea crossing preparation of the Reed Warblers passing through each migratory flyway in Iberia. In WI, Reed Warblers seem to accumulate an amount of fuel required to just reach a close (one-day flight) next stopover site, except in the south, where they would increase their energy stores to reach the north of Africa (Weber et al. 1998b). In EI, however, Reed Warblers seem to preferably gain fuel at reed beds located further from south Iberian coast, in northern latitudes (maybe given the lack of suitable reed beds in southeastern Iberia). Southern sites would act more as resting sites instead of true fuelling ones and as a result body mass decreases from north to south along this route, since the distance to northern Africa (with target stopover sites that would be used to gain fuel before the Sahara crossing) is shortened. Also, a fraction of Reed Warblers could cross the Mediterranean directly from reed beds further north without needing to reach the southern Iberia coast before “jumping” to Africa. We have no data to determine departure direction from these two sites to support this hypothesis.

In EI, body mass increased with date, as expected according to other works (Schaub & Jenni 2000a; Bayly 2006). However, in the rest of Iberia, body masses remained constant as season progressed. Differences in body mass change with date between flyways can be associated to a differential passage of European populations in Iberia (Maggini et al. 2013; Andueza et al. 2013a). Thus, in CI and WI populations with similar body masses would pass during the whole migration period, whereas populations in EI would present different fuel loads. Moreover, the use of the sites within routes was not homogeneous during all the study period, as Reed Warblers were more abundant in southern sites than in northern ones later in the season.

The estimation of flight ranges showed that birds could reach the north-African coast only from southern Iberia. If we consider the 25% heaviest birds, hence focusing on those birds more likely to be about to depart, then those from EI could also reach the north of Africa. Thus, fuel accumulation before the Sahara Desert may happen in northern Africa, as concluded by

Schaub & Jenni (2000a). A number of authors have pointed out the importance of this region as a key fuelling area between tropical Africa and Europe (e.g., Maggini & Bairlein 2011). Moreover, the sea crossing between Iberia and Africa could demand extra fuel accumulation (a safety strategy) as the flight ranges observed, especially in southern Iberia, exceeded the north of Africa. However, our findings seem to contradict previous estimations where Reed Warblers were described as being able to make a non-refuelling flight from northern Iberia to northern Africa (Arizaga et al. 2011d), and from southern Iberia to tropical Africa (Hilgerloh & Wiltschko 2000). In these cases flight ranges were calculated assuming a faster airspeed (60 km/h) and a non-stop flying strategy, without regarding the important energetic costs of diurnal stopovers (Wikelski et al. 2003). Our results are similar to what was found for first-year Savi's Warblers (*Locustella luscinioides*) in Portugal (Neto et al. 2008). However, real flight ranges could be higher because we used here fuel loads of first captures at ringing stations, which would be lower than departure fuel loads. Estimations were made considering still air conditions, but migrants usually select the best (or the least worse) wind conditions to perform their migratory flights (e.g. Weber & Hedenström 2000; Dänhardt & Lindström 2001; Tsvey et al. 2007; Morganti et al. 2011). Hence, depending on the frequency of favourable wind conditions during the migratory period (tailwinds vs. headwinds), real flight ranges could be increased or decreased.

Moreover, adult birds would probably have longer flight ranges (Woodrey & Moore 1997), because fuel loads in adult birds are commonly higher than in first-year birds (Merom et al. 1999; Heise & Moore 2003; Arizaga & Barba 2009).

Although fuel load of migrants before barriers crossing has been the target goal of several studies (e.g. Fransson et al. 2006, 2008; Delingat et al. 2008; Yohannes et al. 2009), its geographical variation at a more local scale in the proximities of a geographical barrier has not been studied in detail. We have highlighted that the fuelling strategy of Reed Warblers in Iberia before the sea and the Sahara Desert crossing is consistent with that described by Schaub & Jenni (2000a), as Iberia is not used to gain the large fuel loads that would be required to reach tropical Africa without further refuelling. Additionally, we have reported how sea crossing constitutes an energetically demanding challenge for Reed Warblers, which must accumulate relatively important fuel reserves to overfly it. However, the factors shaping fuel storage are more than just the distance to the geographical barrier, in this particular case distance to the Atlantic or the Mediterranean Sea, and there may be underlying geographical or stopover quality-associated factors, revealing that a higher degree of landscape complexity in the fuelling strategy of Reed Warblers in relation to barrier crossing exists (Ktitorov et al. 2008).

4.6. Acknowledgements

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CAPÍTULO 5

Using capture-mark-recapture models to asses the effect of age and weather on landing decisions of Sedge Warblers *Acrocephalus schoenobaenus* during migration

Este capítulo es una reproducción del artículo: Andueza, M., Barba, E. & Arizaga, J. En prensa. Using capture-mark-recapture models to assess the effect of age and weather on landing decisions of Sedge Warblers *Acrocephalus schoenobaenus* during migration. *Ardeola*.

5.1. Abstract and keywords/ Resumen y palabras clave

Abstract: Bird migration is usually performed in several consecutive flights, interrupted by stopovers when birds rest or replenish their fuel loads. As a result, migrants must take decisions on when and where to land during migration. Here, we have studied the effects of meteorological conditions (wind and rain) and age (used here as a surrogate of bird experience) on the landing probabilities of Sedge Warblers *Acrocephalus schoenobaenus* at a stopover site in northern Iberia. Data used here were collected over a period of three consecutive years at a ringing station during the autumn migration period. We used reverse-time capture-mark-recapture models to estimate seniority, γ (i.e., probability that an individual at time *t* was already present in the population at time *t*-1), a methodological approach rbarely used previously to analyse landing decisions in passerine migrants. We ran 14 models, of which just 4 were better supported by the data than the other ones. Only rain showed a significant effect. As expected, rain showed a positive effect on γ, indicating that birds avoid flying during rainfall and prefer to interrupt their migration. These results were are similar to those obtainedbased on from an analysis of day-to-day variations in first captures, that was used to validate the usefulness of capture-mark-recapture models, and suggest that in some specific cases CMR models can serve to study bird landing decisions during migration.

Keywords: Cormack-Jolly-Seber models, northern Iberia, rain, seniority, stopover, Txingudi, wind.

Resumen: Las aves realizan su migración en etapas alternativas de vuelos, interrumpidas por periodos de parada en áreas de descanso. Como consecuencias, las aves deben tomar decisiones sobre cuando y donde parar a lo largo de la migración. Hemos estudiado lo efectos de las condiciones meteorológicas (lluvia y viento) y edad (como indicador de la experiencia de las aves) en las probabilidades de parar en el carricerín común *Acrocephalus* *schoenobaenus* en un área de descanso del norte de la Península Ibérica. Los datos empleados fueron obtenidos en tres años consecutivos durante la migración postnupcial. Se aplicaron modelos de captura-recaptura para estimar el parámetro *seniority*, γ (probabilidad de que un individuo en la ocasión *t* estuviese presente en la población en la ocasión *t*-1), metodología nunca antes aplicada para analizar las decisiones de parar de aves migradoras. Se construyeron 14 modelos, 4 de los cuales se adecuaron a nuestros datos. Sólo la lluvia mostró un efecto significativo. De acuerdo a lo esperado, la lluvia mostró un efecto positivo sobre γ, indicando que las aves tienden a interrumpir la migración bajo la lluvia. Estos resultados fueron similares a los obtenidos en un análisis de la variación en el número de primeras capturas, empleado para validar la metodología basada en modelos de captura-recaptura. Adicionalmente, se señalan los casos específicos en los que los modelos CMR pueden ser útiles para estudiar las decisiones de para en áreas de descanso durante la migración.

Palabras clave: Lluvia, modelos Cormack-Jolly-Seber, norte de Iberia, parada, seniority, Txingudi, viento.

5.2. Introduction

Migration is a highly energy-demanding process for birds, as it often involves flying over long distances, in some cases across inhospitable areas where fuelling is impossible or nearly impossible (Newton 2008). Migration is usually performed in several consecutive flights, interrupted by stopover periods when migrant birds replenish their fuel reserves, mainly stored as fat (Berthold 2001). Birds have developed different migration strategies in order to optimize fuel and journey time during the migration period (Alerstam & Lindström 1990). This involves continuous tactical decisions to land at particular stopover sites or to leave them (Chernetsov 2012). In this scenario, knowing which factors determine both landing and departure decisions at stopover sites is key to understanding the migration strategies of birds. The effect of factors such as meteorological conditions, fuel load, and date on departure decisions has been the object of numerous studies (e.g. Dänhart & Lindström 2001; Dierschke & Delingat 2001; Schaub et al. 2004; Tsvey et al. 2007; Schaub et al. 2008; Arizaga et al. 2011b), whereas less attention has been paid to factors affecting landing decisions (but see Barriocanal et al. 2002; Yaukey & Powel 2008; Saino et al. 2010; Arizaga et al. 2011a).

Nocturnal migrants normally fly during the hours of darkness and remain on the ground during the day, either just to rest and pass the time until night falls, before continuing their migration, or to refuel (Delingat et al. 2006; Schmaljohann et al. 2007; Jenni-Eiermann et al. 2011; Chernetsov 2012). However, adverse meteorological conditions, in particular headwind and rain has been reported to force birds to interrupt their migration, obliging them to land even at places considered to be suboptimal (Pyle et al. 1993; Barriocanal et al. 2002; Shamoun-Baranes et al. 2010; Arizaga et al. 2011a). By doing so, birds may avoid flying under bad conditions, thus saving energy and increasing their en route survival prospect. By contrast, both tailwind and the lack of rain drive migrant birds to continue their migration at night and even permit them to look for optimal sites to land (Chernetsov 2012). Therefore, it can be expected that a headwind and/or rain at night will force birds to land, increasing the number of migrant birds settled at a particular site in comparison to nights with a tailwind and/or no rain (e.g. Saino et al. 2010).

Bird experience, determined by age, has also been reported to affect stopover decisions during migration (Moore & Yong 1991; Woodrey 2000; Jakubas & Wojczulanis-Jakubas 2010; Morganti et al. 2011), so it would be reasonable to expect an effect of age on landing decisions. Adults should be able to organise their stopover strategy in relation to the distribution of known favourable sites. By contrast, juveniles, i.e. first-year birds, may not be able to identify these favourable sites as efficiently as adults, and, therefore, they may be more likely to stop at sub-optimal stopover sites, irrespective of other potential variables such as meteorological conditions.

In small passerine birds, landing decisions in relation to e.g., meteorological conditions have traditionally been studied using daily changes in the number of captures (Saino et al. 2010; Arizaga et al. 2011a) or, more rarely, using high mist nets to catch the birds as they land (Bolshakov et al. 2003a, b). Both approaches work at the individual level, allowing more accurate analyses than would be obtained using a population approach. However, the first method involves an inherent bias associated with the fact that the first capture event of a bird at a stopover site does not always occur on the first day of its stay (Schaub et al. 2001). High mist nets solve this problem but require a huge, even disproportionate, sampling effort (Bolshakov et al. 2003a, b). Cormack-Jolly-Seber (CJS) models (or, in a broader context, capture-mark-recapture models, CMR) work at a population level, hence they estimate stopover duration rather than calculating a mean from individual stopover durations. CMR models have been commonly used for the study of departure decisions in migrants and stopover duration (e.g. Schaub et al. 2001; Schaub et al. 2004; Arizaga et al. 2011b), but not to analyse which factors influence landing decisions (but see Schaub et al. 1999).

The aim of this work is to determine the influence of meteorological conditions and age on landing decisions at a stopover site of a long-distance, nocturnally migrating passerine, using CMR models, a methodological approach which has been barely used before to study this question. Rain and headwinds are expected to increase landing probabilities for both adults and juveniles. Additionally, juveniles are expected to show higher landing probabilities than adults under good weather conditions at our study site.

5.3. Methods

5.3.1. Study species

The Sedge Warbler *Acrocephalus schoenobaenus* is a long-distance migratory songbird that breeds in most of Europe, excluding the circum-Mediterranean region and the northernmost boreal region (Cramp 1992). It overwinters in tropical Africa (Cramp 1992). Many Sedge Warblers breeding in central-western Europe cross Iberia during the autumn migration period. As is the case with many other insect-eating passerines in Europe, the Sedge Warbler is a nocturnal migrant (Åkesson et al. 2002). During migration, West European populations of this species have been reported to depend on the superabundance of Plum Aphids (*Hyalopterus pruni*) and to gain the necessary fuel to arrive to tropical Africa mainly in northwestern France and Britain, using southern sites (i.e. Iberia) more as resting places than refuelling ones (Bibby & Green 1981; Grandío 1998; Schaub & Jenni 2000a, b; Wernham et al. 2002).

5.3.2. Sampling site and data collection

Sedge Warblers were captured with mist nets during the autumn migration period of 2009-2011 at the Jaizubia stream (Txingudi marshlands), in Gipuzkoa, northern Spain (43º21´N 01º49´W). The sampling site is a ca. 25 ha tidal marsh with abundant reed beds composed by *Phragmites australis*, where migrant birds (especially wetland-associated species) are common during migration periods (Mendiburu et al. 2009). On average (mean ± SE), 50.3 ± 11.0 different species and 2921.3 ± 968.6 migrating individuals were captured during the autumn migration periods of 2009-2011. The Sedge Warbler do not breed in the study area (Aierbe et al. 2001) so all captured individuals were in migration.

The sampling period each year lasted from 15 July to 30 October, although here we used only the data obtained in August, the month where the peak of migration for the species at this sampling site occurs, according to our own ringing results. Sampling was carried out daily during a period of 4 h starting at dawn. Overall, we used 204 linear meters of mist nets, placed at fixed sites across the reed bed. Once captured, each bird was individually ringed (or the ring was read, if one was already present) and its age determined according to Svensson (1992) (first-year birds or adults). Birds were not retained for a period longer than 1.5 h (usually < 1 h).

5.3.3. Meteorological data

Sedge Warblers depart from their stopover sites around sunset, as do most nocturnal migrants (Moore 1987; Zehnder et al. 2001; Åkesson et al. 2002). We considered meteorological data (wind and rain, see below for further details) during a period of 8 h starting at dusk (i.e. ranging along the season between 22:00 to 06:00 and 21:00 to 05:00). Meteorological data were obtained from the nearest meteorological station, situated at the top of the Jaizkibel mountain (525 m above sea level), 3.5 km from the ringing station where the birds were caught. Wind velocity and direction measurements, available every 10 min, were averaged for the period of 8 h and the tailwind component, *b*, was calculated according to Åkesson and Hedenström (2000):

$$b = V \times \cos\left[\alpha_T - (180 + \alpha_W)\right]$$

where V is wind velocity (m/s), α_T is the expected departure/migration direction from Jaizubia for the studied species (225º; Arizaga et al. 2011a; Andueza et al. 2013a), and α_W is the wind direction (0º is wind of northern origin). High positive values of *b* indicate a strong tailwind, whilst high negative values correspond to a strong headwind. Precipitation values were transformed into a binary variable ("rain", "no rain"), considering rainy nights as those with accumulated precipitation values ≥ 2mm over the 8 h-period (Schaub et al. 2004).

5.3.4. CMR models

Capture-mark-recapture (CMR) data were analysed with reverse-time capture-recapture models (Pradel 1996), using MARK software (White & Burnham 1999). CMR models have been largely used in survival analyses as they allow estimating survival (ϕ) and recapture (p) probabilities separately, and specifically reverse-time models can be used to study population recruitment (Pradel 1996). In this approach the parameter estimated is seniority (γ), which can be defined as the probability that an individual at time t was already present in the population at time t-1. In our study it can be considered as the probability of being at the site during the previous capture event, hence 1-γ can be seen as the probability of a bird landing at our sampling stopover site after the previous capture event.

Before starting modelling landing probabilities, we explored the fit of our data to the assumptions of CJS models (no transients, no trap dependence) with a goodness-of-fit (GOF) test performed with program U-CARE (Choquet et al. 2001). Our data met the CJS assumptions (global GOF test: $\chi^2 = 185.9$, $P = 0.999$; test 3SR to detect transients: $z = 0.74$, $P = 0.459$; test 2CT to detect trap dependence: $z = 1.12$, $P = 0.261$).

We created a matrix with the individual capture histories of Sedge Warblers, containing 889 rows (individuals) and 90 columns (trapping sessions). We pooled the data from 1st to 31st August 2009-2011 longitudinally in the matrix (columns), removing days with no captures and indicating the time elapsed between capture days. The values of γ and p from the last day of one year to the first day of the next year were fixed at zero. Before modelling seniority in relation to different variables, we ran basic models on γ and p assuming either constant or time-dependent parameters. p were observed to fit to the data better when constant (Table 5.1), so it was fixed to be constant when we ran most γ complex models which included these variables: age (as a binary variable: first-year birds/adults), rain (transformed into a binary variable: rain or no rain, associated with the date) and tailwind assistance, b (as a linear variable, associated with the date). The meteorological conditions (wind and rain) considered refer to those existing during the night previous to the capture day (morning). We considered a constant p in all these models since the model with a constant p fitted the data better than the models considering a time-dependent p. Due to sample size constraints we tested the effect of these variables using additive models of up to 3 variables, as well as interaction models of up to 2 variables. The logit-link function was used in all the models.

Table 5.1. CMR models used to study landing probabilities in relation to rain, wind and age. Basic models, assuming either constant or time-dependent γ and *p*, were ran before modeling γ in relation to different variables (Alternative models). Abbreviations: γ: seniority; *p*: recapture probability; AICc: corrected Akaike's Information Criterion; ΔAICc: difference in AIC values of each model with the first one; +: additive models; ×: models considering interaction between variables.

Model	AICc	ΔAICc	AICc Weight	No. Parameters
Starting Models				
1. γ(.), *p*(.)	3300.813	0.00	0.783	2
2. γ(t), *p*(.)	3303.383	2.570	0.217	88
3. γ(.), *p*(t)	3315.552	14.739	< 0.001	88
4. γ(t), *p*(t)	3389.411	88.598	< 0.001	166
Alternative Models (with constant *p*)				
1. γ(rain×wind), *p*(.)	3250.613	0.000	0.302	5
2. γ(age+rain), *p*(.)	3251.029	0.417	0.245	4
3. γ(rain), *p*(.)	3252.194	1.582	0.137	3
4. γ(age+rain+wind), *p*(.)	3252.216	1.603	0.136	5
5. γ(age×rain)	3252.756	2.143	0.103	5
6. γ(rain+wind)	3253.353	2.740	0.077	4
7. γ(age×wind)	3268.364	17.752	< 0.001	5
8. γ(age+wind)	3268.860	18.247	< 0.001	4
9. γ(wind), *p*(.)	3270.540	19.927	< 0.001	3
10. γ(age), *p*(.)	3298.662	48.050	< 0.001	3

We used the small sample sizes corrected Akaike's Information Criterion (AICc) to rank the models and identify the one (or ones) that best fitted to data (Burnham & Anderson 1998). Models were considered to be significantly different if they showed an AICc difference < 2 (Burnham & Anderson 1998). In a given model, the effect of a variable was considered to be significant if the 95% confidence interval of the corresponding model parameter (B parameter) did not include "zero".

5.3.5. Analyses on changes of birds abundance

To support the utility of CMR models, we compared the results obtained from CMR models with those obtained after studying the day-to-day variations in the number of first captures. For that, we compared the change in number of first captures of each day (t) in relation to the previous sampling day ($N_t - N_{t-1}$) (as in Saino et al. 2010), for (1) days (nights) with and with no rain, and (2) with tail- and head-winds (tailwind, $b > 0$; headwind, $b < 0$). For such comparisons we ran non-parametric U tests since this variable and its residual values did not follow a normal distribution. By using daily changes instead of absolute number of captures the possible effect of the date was omitted, because the number of captured birds tends to change as migration progresses depending on timing of passage of different waves of migrants (Saino at al. 2010).

Table 5.2. Number of sampling days (sampling days with no captures in brackets), number of captures (first-year birds/adults in brackets; only one capture per bird is considered here, so within-season recaptures are not included), number of nights with rain (≥ 2mm for a period of 8 h starting at dusk), and number of nights with a tailwind/headwind from 1st to 31st August 2009-2011.

	Sampling days	Captures	Nights with rain	Nights with tail-/headwind
2009	31 (2)	382 (270/112)	6	23/8
2010	31 (0)	350 (225/125)	4	21/10
2011	30 (1)	157 (96/61)	4	17/13
Total	92 (3)	889 (591/298)	14	61/31

5.4. Results

Overall, 889 different Sedge Warblers were captured during the sampling period (1st to 31st August) of 2009-2011, at Jaizubia (Fig. 5.1, Table 5.2). Of these, 301 individuals were recaptured at least once within the same year. Rain (≥ 2mm) was registered in 15.2% of the nights and tailwinds were observed to be dominant (66.7% of the nights) over headwinds (33.3%; $\chi^2 = 8.170$, $P < 0.001$) (Table 5.2; Fig. 5.2).

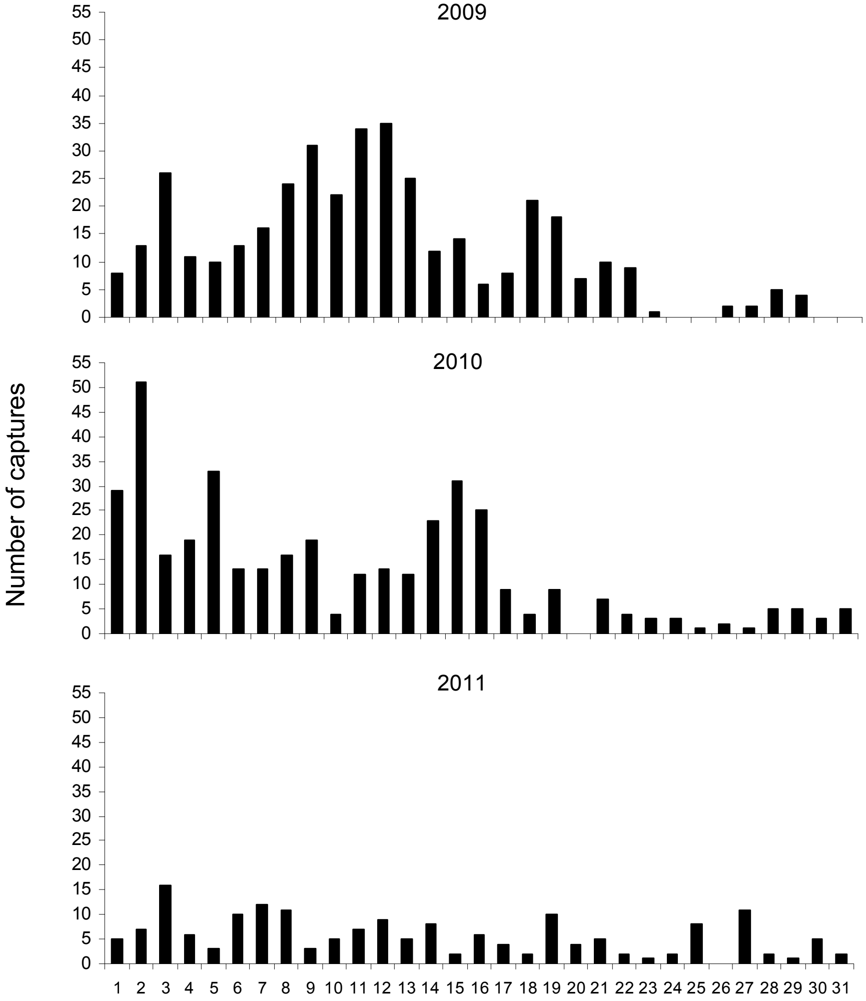

Figure 5.1. Daily number of Sedge Warblers captures, for August 2009-2011.

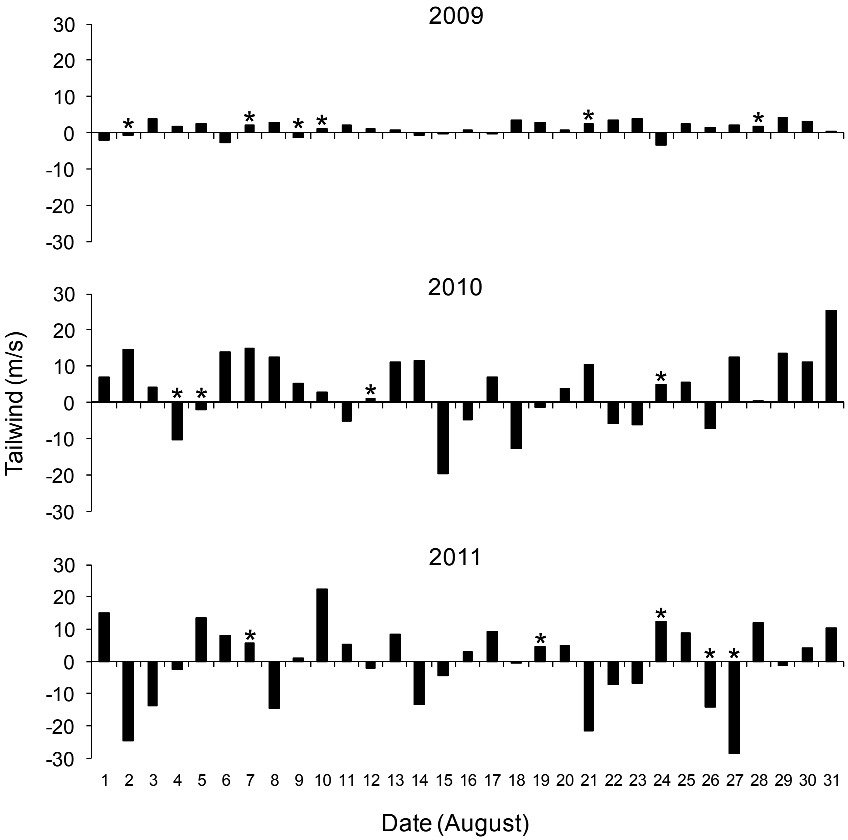

Figure 5.2. Daily tailwind component (*b*) values during an 8 h period, starting at dusk, for August 2009-2011. "*" indicates accumulated rain > 2mm for the same period; "♦" indicates days without Sedge Warblers captures.

Overall, 14 CMR models were tested (Table 5.1). Four models were clearly better supported by the data than the other ones (Table 5.1). Among the variables included in these models, age did not have a significant effect according to the *B* parameters

(Table 5.3). Model 1 (Table 5.1) included the interaction effect of wind and rain (Table 5.3) so birds were more likely to land in rainy nights with headwinds than under no rain and tailwinds. However, after model averaging (we averaged betas from the entire model set according to the models AICc weights, setting betas = 0 in models without the corresponding variable, and then calculated γ for different values of the variables from the averaged equation), only rain showed a significant effect (Fig. 5.3). Thus, Sedge Warblers were more likely to land on rainy nights (Fig. 5.3). Additionally, CMR models showed that first-captures are not always birds which have just arrived, because γ was not zero (Fig. 5.3).

Days with a high number of first captures occurred after nights with rain (Mann-Whitney U = 310.50, $P = 0.010$), whereas wind conditions did not affect the change in number of first captures (Mann-Whitney U = 919.50, $P = 0.830$) (Fig. 5.4).

5.5. Discussion

We studied the landing decision of a European long-distance migratory passerine according to meteorological conditions (wind and rain) and age, as a surrogate of bird’s experience, using CMR models, a methodological approach rarely used to addres this question (Schaub et al. 1999).

Table 5.3. *B*-parameters values, SE and 95% CI of each variable included in the best models according to Table 5.3. Variables are significant if their 95% CI do not span the zero value.

			95% CI	
	B	SE(*B*)	Lower	Upper
Model 1				
wind	+0.058	0.035	-0.01	+0.125
rain	-1.472	0.311	-2.081	-0.863
rain×wind	-0.128	0.051	-0.227	-0.029
Model 2				
age	+0.246	0.137	-0.022	+0.514
rain	-1.256	0.257	-1.759	-0.754
Model 3				
rain	-1.278	0.257	-1.781	-0.775
Model 4				
age	+0.248	0.138	-0.023	+0.519
wind	-0.036	0.034	-0.103	+0.03
rain	-1.444	0.332	-2.095	-0.792

We found that, after rainy nights, the proportion of newly landed birds in the population was higher than after dry nights. This result agrees with the expectation that, under rainy conditions, migrants decide to interrupt their migration (Pyle et al. 1993; Barriocanal et al. 2002; Yaukey & Powel 2008; Arizaga et al. 2011a). Rain has a negative effect on flying performance, because it reduces visibility, hence causing disorientation, and it also wets plumage, hence increasing the costs of flight and making migrants lose heat rapidly (Newton 2007). We found the same result when data on change in number of first captures from one day to the next were analysed, thus validating what we obtained from CMR models. In particular, we registered an increasing number of first captures after nights with rain, indicating that rain forced migrating birds to land.

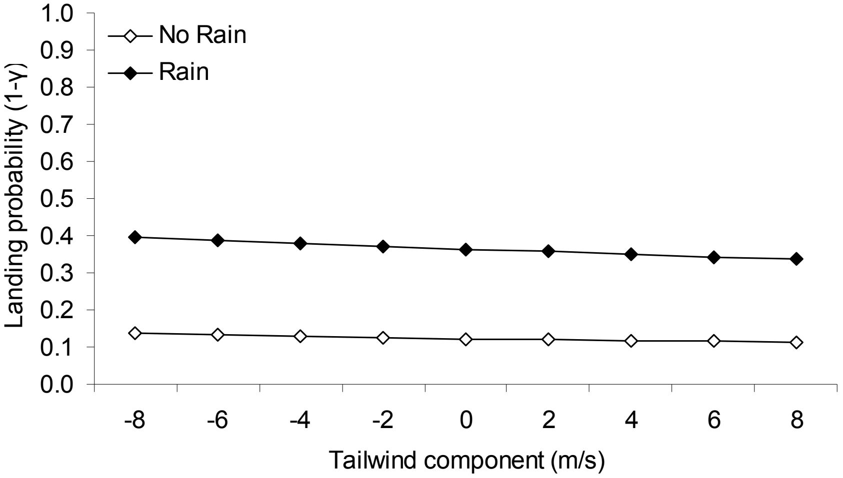

Figure 5.3. Landing probabilities (1-γ) under rainy and no rainy conditions at night for increasing tailwind component values, resulting from averaging according to their AICc weights the 10 alternative models from Table 5.1.

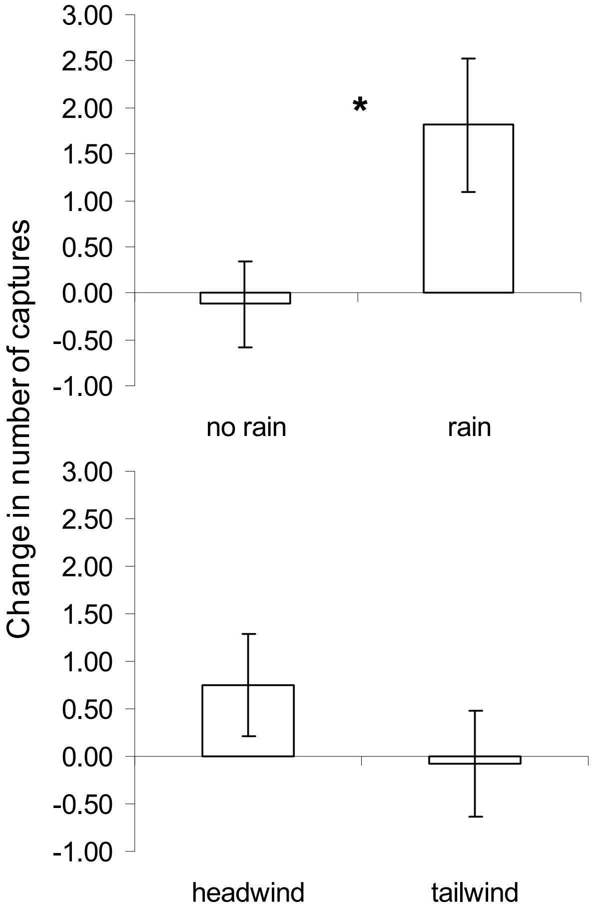

Figure 5.4. Change in number of first captures from one day to the previous one (we show median values ± interquartile ranges) in relation to rain (rainy nights $n = 15$; no rainy nights $n = 78$) and wind conditions (tailwinds nights $n = 62$; headwinds nights $n = 31$) along the night previous to the capture day. "*" indicates significant differences ($P < 0.05$).

Saino et al. (2010) detected a negative effect of tailwind on the presence of migrants on small Mediterranean islands, showing that migrants moving through the Mediterranean continued flying under favourable winds. One of our best models showed a similar wind effect as Sedge Warblers were less likely to land under tailwinds, especially in nights with no rain. However, the average effect of wind on landing decisions was not significant. Wind is known to determine departure decisions (Weber et al. 1998a; Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Åkesson et al. 2002; Arizaga et al. 2011b; Andueza et al. 2013b), and if tailwinds are predominant as in this study (Fig. 5.2), waiting for favourable wind conditions would be preferable as the period to wait may be short (Bulyuk and Tsvey 2013). However, once in flight, the effect of wind conditions on landing could be different, depending on whether migrants are crossing land or large free water surfaces, such as the sea or the ocean. For migrants that minimise the duration of migration (i.e. time-minimisers; Alerstam and Lindström 1990), such as possibly the sedge warbler (Bayly 2007), it is disadvantageous to interrupt the migration in the case of headwinds, especially when tailwinds may blow soon (Fig 5.2). In the proximity of departure sites, flying into headwinds could be better or preferable to stopping over (Erni et al. 2002a).

Finally, we detected no differences in the effect of rain and wind in the landing behaviour between first-year birds and adults.

Biometric differences between juveniles and adults, in particular in wing morphology (Lockwood et al. 1998; Pérez-Tris and Tellería 2001; De Neve et al. 2010), could make juveniles more vulnerable to adverse weather conditions (Saino et al. 2010). However, Sedge Warblers passing through Iberia do not present age-related wing morphology differences (M. Andueza pers. obs.), and, as a result, no differences in flight efficiency would occur between age categories.

In this work we studied landing decisions in a single sampling site, Jaizubia, which can be considered a sub-optimal fuelling site for sedge warblers (Bibby and Green 1981; Grandío 1998; Schaub and Jenni 2000a, b; Wernham et al. 2002). Hence, our stopover site is likely to be used more like as an emergency or secondary stopover site than like a target, strategically relevant place, given that sedge warblers were found to leave Jaizubia under good weather conditions independently of their fuel loads (Andueza et al. 2013b). Our results refer to the influence of rain, wind and age on the interruption of nocturnal migration at a particular sub-optimal stopover site, so whether the relative role of such factors varies along the route or depending on the stopover quality of sites (Dierschke and Delingat 2001; Schaub et al. 2008), it is an aspect which demands further research.

CMR models turned out to be useful for analysing the influence of weather on landing decisions of migrants, particularly in relation to small passerine birds captured abundantly at a stopover site, since our modelling results were consistent with those obtained from a simple analysis on changes in bird abundance. Also, in agreement with previous work (Schaub et al. 2001), we have shown that migrants at our site were not necessarily just-arrived birds on first capture. Thus, CMR models provide more accurate results than changes in bird abundance analyses as capture probabilities, and hence birds which are present in the area but are not seen, are taken into account. Additionally, in contrast to the classic approach, whose results are more limited, CMR allows quantifying the effect of the studied factors at a population level in the form of landing probabilities, as well as inferring the relative importance of such factors.

However, this methodology could only be appropriated to study landing probabilities for certain cases. Particularly, CMR models are appropriate to study the factors that cause nocturnal migration interruption (i.e. under which conditions birds arrived), such as adverse weather conditions, especially at sub-optimal stopover sites where migrants would not have stopped otherwise. However, it may not be suitable to study the factors which determine the selection of stopover sites (i.e. inferring the landing probabilities of birds approaching a stopover site in relation to certain factors), which can be highly influenced by habitat availability and the individual energy reserves. As a result, the use of CMR models may not be appropriate to analyse the effects of several other factors on landing probabilities, such as fuel load or conspecifics abundance. Studying landing probabilities in relation to, for example, Sedge Warbler abundance at a site using this methodology may result in trivial conclusions unrelated to actual nocturnal movements, as landing probabilities are very dependant on passage intensity (e.g. after nights when many Sedge Warblers have landed, their numbers increase at a site, thus resulting in higher γ values for increasing Sedge Warblers abundance). In conclusion, despite the limitations of CMR models to study landing decisions, they can be a suitable methodology for study cases in which alternative biological or ecological determinants may be excluded a priori.

5.6. Acknowledgements

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CAPÍTULO 6

The role of extrinsic and intrinsic factors on the departure decisions of a long-distance migratory passerine

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6.1. Abstract and keywords/Resumen y palabras clave

Abstract: Factors determining departure decisions of migrants from a stopover site can be extrinsic or intrinsic but the relative role of each of these factors on departure decisions is still poorly known. In a long-distance migrant, which is expected to minimize duration of migration, date and wind should be the main factors determining departure decisions. Date was considered as an intrinsic factor and wind as an extrinsic one. We analysed the capture-recapture data of a long-distance European songbird, the Sedge Warbler *Acrocephalus schoenobaenus,* from a stopover site in northern Iberia during the autumn migration period, in order to quantify the relative importance of several factors on emigration likelihood. Cormack-Jolly-Seber (CJS) models were used to estimate the emigration likelihood. From 107 models tested, only the model with an additive effect of date, tailwind assistance and population size substantially supported the data. As expected, Sedge Warblers were more likely to depart with high tailwind values and late in the season and, contrary to expectations, with decreasing Sedge Warbler abundance.

Keywords: Cormack-Jolly-Seber models, date, density, departure decision, Sedge Warbler, tailwind assistance.

Resumen: Los factores que determinan la decisión de abandonar un área de descanso durante el periodo de migración pueden ser extrínsecos o intrínsecos. En las aves que tienden a reducir el tiempo de la migración, tanto la fecha como la meteorología deberían ser los factores principales que determinan las decisiones de partir. Se analizaron datos de captura-recaptura de un migrador transahariano, el carricerín común *Acrocephalus schoenobaenus,* de un área de descanso en el norte de la Península Ibérica durante el periodo de paso posnupcial para cuantificar la importancia relativa de diversos factores en la probabilidad de emigración. La probabilidad de partir se estimó con modelos Cormack-Jolly-Seber (CJS). De 107 modelos, solo uno tenía respaldo suficiente, de acuerdo al criterio AIC. Dicho modelo incluía el efecto aditivo de la fecha, viento y densidad de aves. Como se esperaba, los carricerines comunes tenían más probabilidad de partir con vientos de cola elevados y en fechas más tardías, siendo esta probabilidad más elevada para densidades bajas.

Palabras clave: Asistencia de viento de cola, carricerín común, decisions de partir, densidad, fecha, modelos Cormack-Jolly-Seber.

6.2. Introduction

Migratory birds divide their journey into periods of flight, when fuel store is consumed, and stopovers, where fuel stores are replenished, mostly as fat but also as proteins (Klaassen et al. 1997; Salewski et al. 2009). As a result, most of the time spent by a bird during migration is consumed at stopover sites (Newton 2008). Thus, duration of migration is normally determined by stopover duration, which in turn is conditioned by departure decisions (Schaub & Jenni 2001a, b). Consequently, factors affecting departure decisions from a stopover site are key elements of bird migration strategies (Alerstam & Lindström 1990; Alerstam & Hedenström 1998). Such parameters could be either extrinsic (environmental, such as meteorological conditions, competition, predators, food availability, etc.) or intrinsic (associated to individual internal elements, like endogenous circannual rhythm, age, physiological status, fuel load etc.) (Dänhart & Lindström 2001; Bulyuk & Tsvey 2006; Schaub et al. 2008).

When considering extrinsic parameters, meteorological conditions, especially rain and wind, are considered to be amongst the most important (Richardson 1978; Dänhart & Lindström 2001; Erni et al. 2002b; Erni et al. 2005; Tsvey et al. 2007). Tailwind is advantageous as it allows birds to cover longer distances with the same amount of fuel, hence birds prefer to depart on nights/days when there is tailwind assistance (Åkesson & Hedenström 2000; Dänhart & Lindström 2001; Åkesson et al. 2002). Although wind characteristics on the ground are reported to influence departure decisions (Åkesson et al. 2001, 2002), the topography can modify such characteristics locally (generally wind direction, but also wind velocity). In such a scenario, wind characteristics would be expected to vary with altitude, and departure decisions would depend more on wind aloft (Schaub et al. 2004). Rain is another important environmental factor because it reduces visibility and wets plumage, hence increasing the costs of flight. Thus, birds avoid departing and flying on rainy nights/days (Schaub et al. 2004). Population size (density) of co-specifics at a stopover site is also an extrinsic factor that may condition departure decisions. High densities of co-specific birds at a stopover site, caused by date (migration peak) or by bad weather conditions (Erni et al. 2002b; Ma et al. 2011), could force the departure of weaker birds as a consequence of intra-specific competition (Moore & Yong 1991).

Amongst intrinsic factors, age can play an important role in departure decisions from a stopover site (Woodrey 2000). Adults have been reported to perform shorter stopovers than juveniles (Grandío 1998, 1999; Rguibi-Idrissi et al. 2003), partly because they often refuel more rapidly (Ellegren 1991; Neto et al. 2008). Accordingly, for birds arriving at the same time, adults would be expected to depart before juveniles. Fuel load can also determine the decision to depart from a stopover site. Although fuel load can be determined by several environmental factors, such as food availability, weather, etc. (Bayly 2007), it can be considered as an intrinsic factor as it is associated with the individual physiological status (Schaub et al. 2008). Other things being equal, birds with higher fuel loads would be more likely to depart than those with low ones (Arizaga et al. 2008).

Finally, timing of migration (date), although also associated with external cues such as food availability and fuelling rates at previous stopover sites, is also endogenously controlled, since the scheduling of the annual cycle of birds is mostly internally (genetically) determined (Berthold 1996; Newton 2008). Therefore, it can be considered as either an extrinsic or intrinsic factor. Here, we have included it as an intrinsic one, as a proxy of the circannual migrants' rhythm. The migrants' internal program means that birds migrating later in the season are more time-stressed than those moving earlier (Bayly 2006). Moreover, the longer the stay of a bird at a suitable stopover site with sufficient food the higher its fuel load and, as a consequence, the higher its departure probability (Yosef & Chernetsov 2005).

So far, the effect of these factors on departure decisions has mostly been studied separately (Dierschke & Delingat 2001; Bulyuk & Tsvey 2006; Bolshakov et al. 2007; Arizaga et al. 2008). The development of more sophisticated model techniques for capture-recapture analyses (Schaub et al. 2001; Salewski et al. 2007, Arizaga et al. 2008; Schaub et al. 2008) allows the simultaneous analysis of the influence of all of these factors (Arizaga et al. 2011b). Cormack-Jolly-Seber (CJS) models on capture-mark-recapture data estimate survival (ϕ) and recapture (p) probabilities separately for open populations (Lebreton et al. 1992; Schaub et al. 2001). Assuming that the actual survival, ϕ, of a bird from one day to the next at a stopover site is almost 1, it might be assumed that ϕ in this type of study is the probability of remaining at that stopover site. The emigration likelihood, ε, is therefore $1- \phi$. Our aim was to determine the relevance of both extrinsic (wind, rain and Sedge Warbler density) and intrinsic parameters (date, age and fuel load) on departure probabilities of a long-distance migratory passerine using CJS models.

6.3. Methods

The avian model chosen for this study was the Sedge Warbler *Acrocephalus schoenobaenus*. The Sedge Warbler is an abundant Palaearctic songbird that breeds in most of central and northern Europe (Cramp 1992) and its wintering grounds are located in tropical Africa. During the autumn migration period it accumulates large fuel loads at suitable sites in Europe with superabundant food supply [reed aphids (*Hyalopterus pruni*)], and then reaches its wintering areas south of the Sahara Desert practically without refuelling (Bibby & Green 1981; Schaub & Jenni 2001b). As a typical warbler, it is a nocturnal migrant that initiates migratory flights around sunset (Moore 1987; Åkesson et al. 1996b).

6.3.1. Sampling site and field data

Sedge Warblers were captured during the autumn migration period at Jaizubia, Txingudi marshlands, northern Iberia (43º21´N 01º49´W; 2 m above sea level). The sampling site is located in a tidal-marsh with a c. 25 ha-surface of reedbeds (*Phragmites australis*). Txingudi is situated in a geographic funnel, between the western border of the Pyrenees and the Bay of Biscay, so it is a major natural entry route for birds moving from northern Europe to Iberia and Africa during the autumn migration (Galarza & Tellería 2003). This species did not breed in the area during the study period (Aierbe et al. 2001) so all captures were of migratory birds. Birds were captured in daily trapping sessions with mist nets (204 linear m) that were opened during a period of 4 h starting at dawn, for three consecutive years (2007: 01-31 August; 2008/09: 15 July-31 August). Each bird was individually identified with a numbered metallic ring, aged using wing feather abrasion (first-year birds or adults, according to Svensson 1998), weighed (± 0.1 g accuracy), and had its subcutaneous fat load determined (scaled from 0 to 8, following Kaiser 1993).

6.3.2. Meteorological data

Meteorological data were obtained from Jaizkibel Meteorological Station (525m above sea level), the closest station to the sampling site (3.5 km). Since Sedge Warblers are nocturnal migrants, meteorological conditions around sunset were considered (4 hours before and 4 hours after sunset). Most birds start migratory flights within this time window (Åkesson et al. 2001, 2002). Precipitation was considered as "rain", for values $\geq$ 2mm within the 8 hour period, or "no rain" for values below 2 mm (Schaub et al. 2004). Wind velocity (m/s) and direction (measured as the angle in relation to N, which is 0 or 360º), were available every 10 minutes from the station and were averaged for the 8 hour period. The tailwind component, b, was estimated as: $b = V \times \cos[\alpha_T-(180 + \alpha_W)]$, where V is wind velocity (m/s), α_T is the angle at which the Sedge Warblers depart from Jaizubia, and α_W is the angle which the wind comes from. α_T was assumed to be 225º, according to data from Sedge Warblers ringed at Jaizubia and recaptured along a south-west axis from Jaizubia (J. Arizaga, unpubl. data). High positive values of *b* indicate a strong tailwind, whilst high negative values correspond to a strong headwind.

6.3.3. Statistical analyses

Data were analysed with Cormack-Jolly-Seber (CJS) models, for which MARK software (White and Burnham 1999) was used. Before starting to select models, we explored the fit of the data to CJS assumptions (no transients, no trap dependence) with a goodness-of-fit (GOF) test. The GOF test on a CJS model where both ε (that is 1- ϕ) and *p* (emigration and recapture likelihood, respectively) were time-dependent [ε(t) *p*(t)], as other fitted models were nested within this starting one, was carried out using U-CARE software (Choquet et al. 2001). Neither the global GOF test ($\chi^2_{323} = 223.32$, $P = 0.99$), nor the specific test 3SR to detect transients ($z = 0.92$, $P = 0.36$) nor the test 2CT to detect trap dependence ($z = -1.84$, $P = 0.07$) were significant. Thus, the best model from which to start to model emigration likelihood was the one in which both ε and *p* were time-dependent [ε(t) *p*(t)].

For Sedge Warblers captured more than once within a season, we divided their capture history into individual histories using the capture occasions. Hence, for these birds the first capture event of each individual history was the last recapture of the previous history, except in the case of the last history which contained only the last recapture (i.e. a capture history with an initial capture and two recapture events ‘1001010’ would be split into three histories: ‘1001000 -1;’, ‘0001010 -1;’, ‘0000010 1;’). In MARK the term ‘-1’ indicates that this bird was “removed” from the data set after the last capture. The reasoning behind this was that, if a bird was recaptured, ϕ between the first and second captures was 1 (no departure), and what we were interested in was estimating the departure probability after the last recapture. Capture days were introduced longitudinally in the matrix (from 01 August 2007 to 31 August 2009). ϕ was fixed as 0 between the last day of capture of one year and the first day of capture of the next consecutive year. Days with 0 captures were removed and we specified the number of days between capture occasions. We obtained a matrix with 121 columns (sampling days with captures,) and 1640 rows (capture histories).

The date of the first capture in a season and the number of days stay before the last recapture were introduced as individual covariates. For birds captured once, we assigned 1 day of stay; for recaptured birds the number of days stay for each divided capture history was the number of days since the first capture. Fuel and age were considered as groups. Two age classes were considered: first-year birds and adults. As an indicator of fuel load we used fat scores according to Kaiser (1993), transformed into an ordinal qualitative variable: low (from 0 to 2), medium (2.5 to 5) and high (5.5 to 8). From the combination of age and fuel we obtained 6 groups. Meteorological data and population size are daily variables and not characteristics of each bird, and hence they were not included in the matrix but were introduced during MARK analysis. The number of captures per 100 m of mist net per day was used as an index of Sedge Warbler abundance (or density).

In order to model emigration likelihood, covariates were incorporated into the models and we tested different combinations of these, including additive effects and interactions, using the logit-link function, $\text{logit}(\phi) = B_0 + B$ (covariate). The most complex models included the additive effects of 3 variables. Interactions between models were not considered due to sample size constraints. Akaike´s Information Criterion (AICc) was used to rank and choose the best models fitting to the data (Burnham & Anderson 1998). Two models were considered to have the same support if the difference between their AICc values was less than 2 (Burnham & Anderson 1998). For a given model, the effect of a variable was considered to be significant if the 95% confidence interval (CI

95%) of its *B* parameter did not include 0 within its limits. The AICc weight of a model could be read as the probability of the model to rank best given the data. The sum of the weights of all models including a variable can be used as an indicator of the importance of this variable as a predictor (Burnham & Anderson 1998). We also ran analyses of deviance (ANODEV) to test the effect of covariates (Grosbois et al. 2008). Mean values are given with ± SE.

6.4. Results

6.4.1. Captures and meteorological data

Overall 1145 Sedge Warblers were captured, 346 of which were recaptured at least once within the season. 72.9% of captures were first-year birds and 27.1% were adults. The proportion of each age class did not differ between years ($\chi^2_2 = 2.08$, $P = 0.350$).

The abundance of Sedge Warblers (number of captures per 100 m of net per day) ranged from 3.42 ± 0.27 (2008) to 9.35 ± 1.13 (2007) (mean 6.90 ± 0.50). The mean number of captures per unit effort differed between years ($F_{2,120} = 18.95$, $P < 0.001$), 2008 being the year with the lowest number of captures per unit effort (Fig. 6.1).

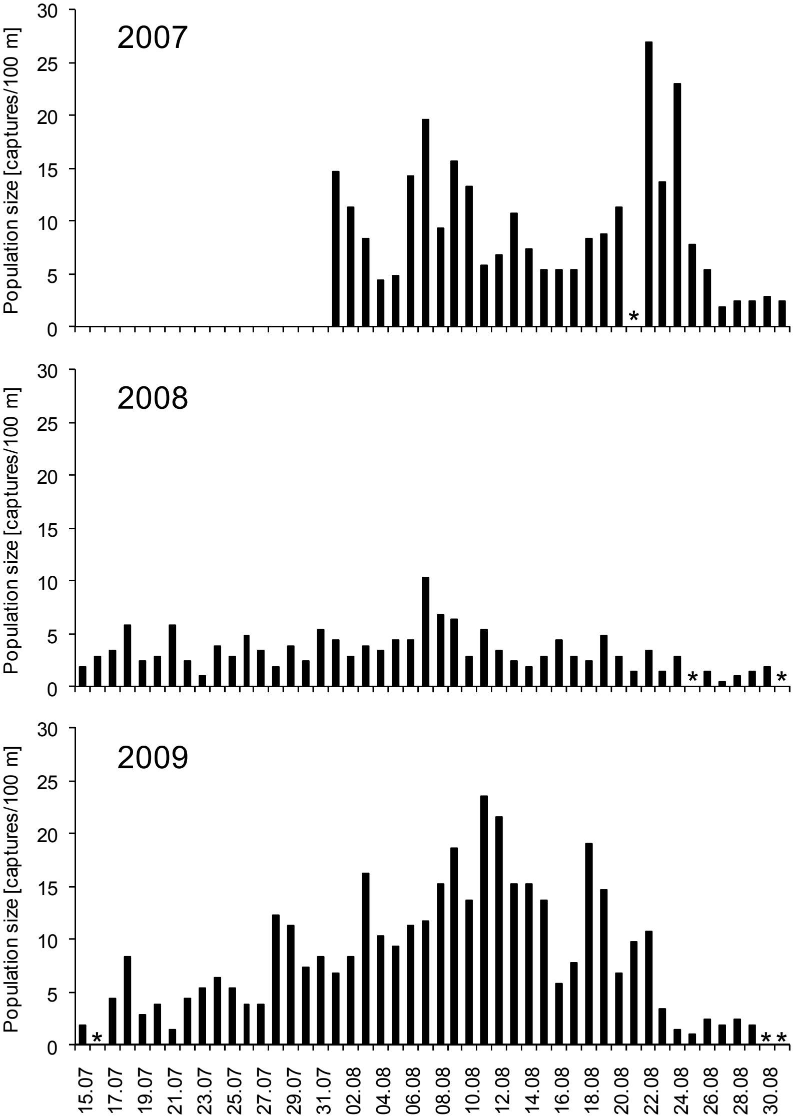


Figure 6.1. Index of abundance (used to assess population size) of Sedge Warblers *Acrocephalus schoenobaenus* at Jaizubia. All captures refer to a sampling period of 4 h starting at dawn. Asterisks (*) indicate no-sampling days (sampling suspended, normally due to poor meteorological conditions). In 2007, the sampling period started on 01 August.

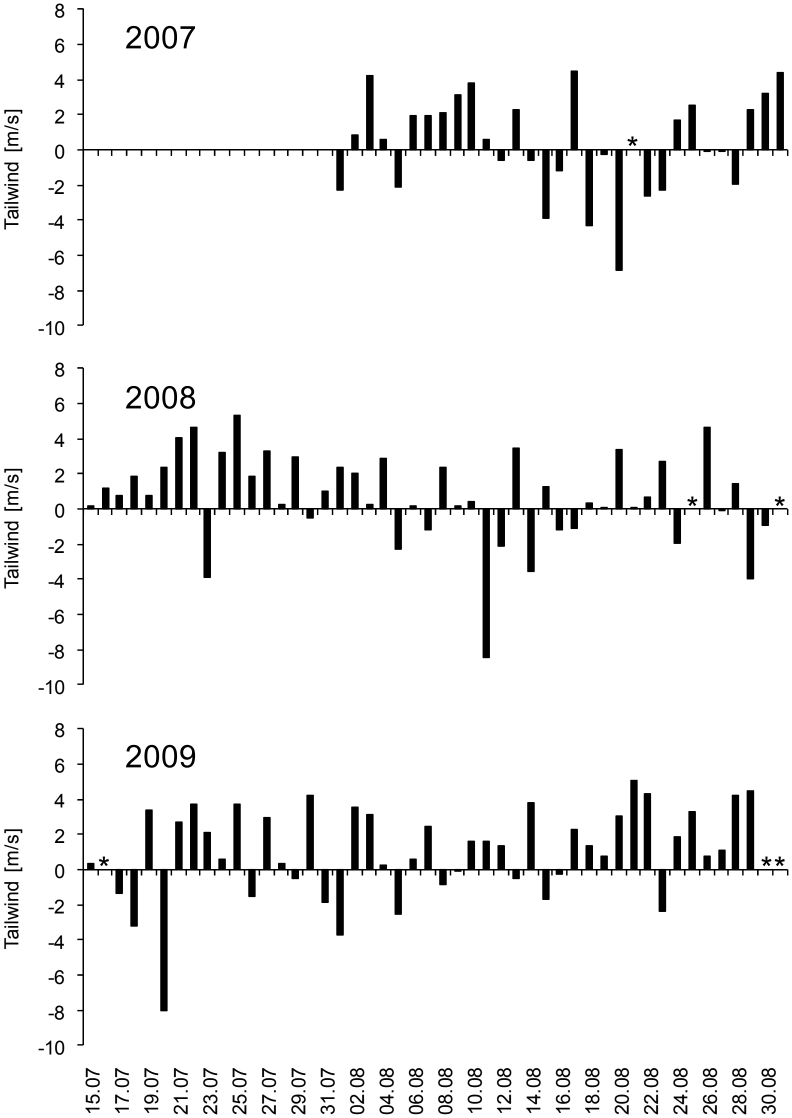


Figure 6.2. Mean tailwind values (m/s) at Jaizubia during the sampling period in 2007, 2008 and 2009 around sunset (sunset ± 4 h). Asterisks (*) indicate no-sampling days (sampling suspended, normally due to poor meteorological conditions). In 2007, the sampling period started on 01 August.

Mean tailwind values ranged from 0.37 ± 0.51 m/s (2007) to 1.03 ± 0.39 m/s (2009), without significant differences between years ($F_{2,120}$ = 0.57, P = 0.570; mean: 0.3 ± 0.24). There were more days with tailwind (66.1%) than with headwind (33.9%; χ^2_1 = 12.57, P < 0.001; Fig. 6.2), without significant differences in that proportion between years (χ^2_2 = 2.99, P = 0.220). It rained on 13 days (10.7%) overall during the three year study period. The mean tailwind value under rainy conditions was -1.59 ± 0.55 m/s, whereas on nights without precipitation it was 1.01 ± 0.25 m/s (t_{120} = 3.45, P = 0.001).

6.4.2. Modelling departure probabilities

From 107 models tested, only one model had substantial support (Model 1), showing an AICc difference >2 with the second best model (Table 6.1). Furthermore, Model 1 showed an AICc weight 10 times greater than Model 2 (Table 6.1), so it was not necessary to do model-averaging. Thus, Model 1 supported a significant, additive effect of date, wind and Sedge Warbler abundance on ε. The *B* parameters of this model were significant for all variables (Table 6.2). In particular, ε values were higher with increasing tailwind values, decreasing bird abundance and proximity to the end of the season (Fig. 6.3). ANODEV analyses showed a significant effect of wind ($F_{1,121}$ = 3.95, P = 0.049) and abundance ($F_{1,121}$ = 9.58, P = 0.003), but not of date ($F_{1,121}$ = 2.64, P = 0.107).

Table 6.1. Emigration models of Sedge Warblers *Acrocephalus schoenobaenus* from a stopover site during the autumn migration period in Northern Iberia. We show the emigration likelihood, ε; Corrected Akaike´s Information Criterion (AICc); difference in AIC values of each model with the first one; AICc weights, number of parameters and deviance. Only the best ten out of 107 models run are shown. Variables: tailwind values (wind), date of passage (date), index of Sedge Warbler abundance (abun), age, fuel load (fuel), and minimum stopover duration before the first capture event (days).

Model	AICc	ΔAICc	AICc Weight	No. Parameters	Deviance
1. ε[wind+date+abun], *p*	4031.431	0.000	0.628	5	4021.394
2. ε[date× abun], *p*	4036.101	4.670	0.061	5	4026.064
3. ε[date+ abun], *p*	4037.285	5.854	0.034	4	4029.260
4. ε[age+fuel+date+days], *p*	4037.387	5.957	0.032	9	4019.277
5. ε[age+fuel+days], *p*	4037.462	6.031	0.031	8	4021.373
6. ε[age+fuel], *p*	4038.238	6.807	0.021	7	4024.169
7. ε[wind× abun], *p*	4038.388	6.957	0.019	5	4028.351
8. ε[days+date+ abun], *p*	4038.397	6.966	0.019	5	4028.360
9. ε[age+ abun +date], *p*	4038.492	7.062	0.018	5	4028.456
10. ε[fuel+date+days], *p*	4038.745	7.314	0.016	6	4026.694

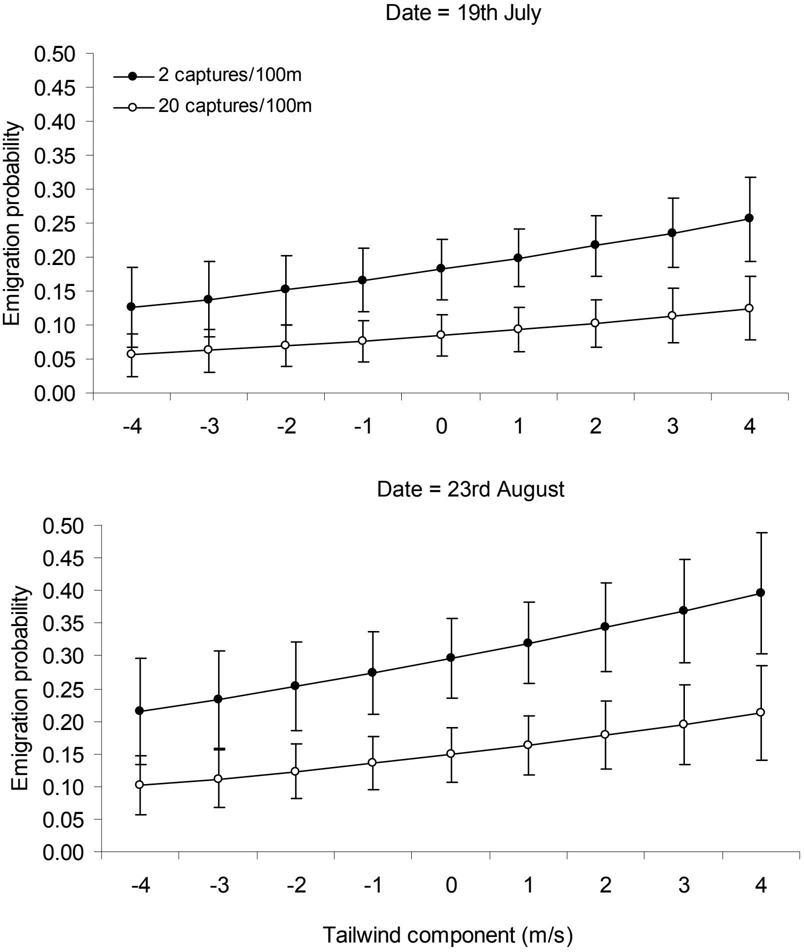
Table 6.2 Standardized *B*-parameters (±SE and the 95% interval of confidence) of Model 1 from Table 6.1.

			95% IC	
Parameters	*Beta*	SE	Lower	Upper
Wind	+0.109	0.042	+0.027	+0.192
Date	+0.018	0.005	+0.008	+0.029
Pop. size	-0.049	0.013	-0.074	-0.024

The importance of date, wind and population size on the departure decisions of Sedge Warblers is also evident when considering the sum of AICc weights of models including these variables (date: 0.847; population size: 0.819; wind: 0.646). The remaining variables had much lower weights (days: 0.135; fuel: 0.054; age: 0.025; rain: 0.018).

6.5. Discussion

Our results indicate that the departure decisions of Sedge Warblers from a stopover site in northern Iberia during the autumn migration seemed to be determined by both extrinsic (wind, abundance of co-specifics) and intrinsic variables (date, used here as a proxy of the circannual rhythm). The most important variables determining departure decisions were date and Sedge Warbler abundance, according to their models AICc sums, followed by wind.


Date = 19th July

Date = 23rd August

Figure 6.3. Estimated emigration probability in relation to tailwind values, population size (number of Sedge Warblers standardized for 4 h and 100 m of mist nets) and date, based on Model 1 from Table 6.1.

Emigration likelihood would be expected to increase with increasing bird densities at a stopover site, owing to intra-specific competition. However, we detected the opposite relationship, since departure probability increased when population size was low. A number of possible explanations may explain our results: (1) Sedge Warblers depend on a superabundance of reed aphids to accumulate sufficient fuel (Bibby & Green 1981; Grandío 1998). If food availability is not high enough to allow birds to accumulate large fuel loads, newly arriving birds ought to depart from the site shortly after arrival and search for more suitable sites where they can gain sufficient fuel (Alerstam & Lindström 1990). Hence, low densities of Sedge Warblers could be used by newly arriving birds as an indicator of poor foraging conditions. (2) Migrants can experience lower rates of fuel accumulation if they have to watch for potential predators (Lind 2004; Bayly 2006). So, high densities of co-specifics would allow Sedge Warblers to reduce their foraging intensity-dependent predation awareness and therefore experience better fuelling rates (Fransson & Weber 1997; Bayly 2006). (3) Later in the season the decline in population size (Fig. 6.1), coincides with the period when birds were more likely to depart, meaning that bird abundance and departure probability may not be independent.

Date was positively correlated with emigration likelihood and, for the same wind conditions, birds arriving later in the season had higher departure probabilities, especially when favourable tailwinds occurred (Fig. 6.3). This result agrees with the idea that Sedge Warblers are under more time-related pressure to arrive in their wintering areas as the season progresses (Bayly 2006, 2007). However, our results also support alternative hypotheses. Sedge Warblers may depart more quickly later in the season due to extrinsic factors, such as seasonal food depletion at stopovers (Grandio 1999), or they may have already accumulated fuel at more northern sites and hence were just passing by our site.

As expected, Sedge Warblers tended to depart on nights with tailwinds, thereby agreeing with previous studies (Weber et al. 1998a; Åkesson & Hedenström 2000; Dänhart & Lindström 2001; Åkesson et al. 2002; Erni et al. 2002b; Erni et al. 2005) and indicating that departure decisions are highly governed by meteorological conditions. Our sampling site, Jaizubia, was located 2 m above sea level whilst the meteorological station was at 525 m, on the top of a coastal mountain (Jaizkibel), so it is unclear whether the meteorological data used is representative of the wind aloft itself or whether it was used as a ground clue by migrants to decide on departure. Tail winds aloft allow birds to maximize the distance of flight and save time and energy. Weber et al. (1998a) introduced wind as an additional factor in time-minimizing models and they assumed that migrants are not sensitive to wind conditions until they are ready to depart. Furthermore, such models show that, if suboptimal weather conditions prevail for a long time period, birds will leave a stopover site independently of wind conditions. However, our results suggest that: 1) both birds with high fuel loads and birds that stayed in the area for long time periods as well as 2) birds with low fuel loads, left the area under favourable wind conditions. In this line of reasoning, neither fuel load nor days of stay showed a significant effect on emigration likelihood as would have been expected. This suggests that wind conditions were considered by migrants independently of their fuel loads and length of stay at this site. Sedge Warblers have recently been reported to carry out two different fuelling behaviours (Bayly 2007): (1) stop over for a few days and accumulate a small amount of fuel, or (2) stop over for longer periods and accumulate sufficient reserves to arrive directly in tropical Africa without the need to refuel. This behaviour is compatible with our results and, consequently, when favourable wind conditions occur, these may be considered opportune by birds which have both large and small fat reserves. Moreover, Jaizubia is located in northern Spain, so birds leaving without sufficient fat loads to cross the Sahara Desert can find suitable places to refuel later, before facing that barrier.

Rain, contrary to expectations, did not show an important effect on departure decisions. In fact, rain was the variable with the lowest value of ∑AIC Weight in the models where it was included. Rain has been reported to have an important influence on the probability of leaving a stopover site since it wets plumage, hence making flight more difficult and increasing energy demands. It also decreases visibility, which makes disorientation more likely and, in general, causes higher mortality associated with migration (Dänhart & Lindström 2001; Schaub et al. 2004). Our results may be explained by the low number of days with rain around the sunset period considered in this study (13 rainy nights only). Ten of these rainy nights coincided with headwinds; thus, although these two meteorological conditions may not be completely independent, the masking effect in our results is probably weak, given the low number of rainy nights in relation to those with headwind values. Hence, the existence of a wind effect independent of rain in explaining departure from a stopover cannot be fully rejected.

In conclusion, the departure decisions of Sedge Warblers from a stopover site in northern Iberia were influenced mainly by extrinsic parameters. However, the relative importance of each of these parameters may differ between sites because birds can consider or give priority to different factors depending on aspects such as facing a geographical barrier nearby. Fuel load was not included in our models, but Sedge Warblers may consider this factor if they are departing from southern Iberia to cross a large area (the Atlantic and the Sahara Desert), with practically no possibilities of refuelling before arriving at their wintering areas in tropical Africa.

6.6. Acknowledgements

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CAPÍTULO 7

Relative influence of different factors on the departure decisions of migrant Reed Warblers *Acrocephalus scirpaceus* in relation to barrier crossing proximity

Este capítulo es una reproducción del artículo: Andueza, M., Barba, E., Cuenca, D., Laso, M., Unamuno, E., Unanue, A., Valkenburg, T. & Arizaga, J. Relative influence of different factors on the departure decisions of migrant Reed Warblers *Acrocephalus scirpaceus* in relation to barrier crossing proximity. Enviado.

7.1. Abstract and keywords/Resumen y palabras clave

Abstract: The importance of different factors in departure decisions at stopover sites could vary depending on the location of the latter along the migration route and the ecological conditions ahead. We studied whether the effects of fuel load and wind conditions on departure decisions varied in relation to the site proximity to a geographic barrier (the sea band between Iberia and Africa) during the autumn migration. For that purpose we analysed data from first-year Reed Warblers using capture-recapture models, obtained at six sampling sites, three in northern and three in southern Iberia. Additionally, we estimated and compared food availability and fuel deposition rates between sites to control the potential effect of these variables on departure probabilities. The proximity of stopover sites to the barrier modified the importance of the factors that migrants take into account when deciding whether to stay or leave. In northern Iberia departure probabilities were independent of fuel load, whereas in southern Iberia birds were more likely to depart with higher body masses. Reed Warblers departed irrespective of wind conditions in both regions. The fuel deposition rates experienced by birds at the different sites were not correlated with food availability or with departure probabilities.

Keywords: Cormack-Jolly-Seber models, food availability, fuel load, sea crossing, stopover, tailwind.

Resumen: La importancia de distintos factores en las decisiones de partir de las áreas de descanso pude variar según su situación a lo largo de la ruta migratoria y las condiciones ecológicas en el siguiente tramo de vuelo. Aquí estudiamos si el efecto de la carga de grasa y las condiciones de viento en las decisiones de partir varían según la proximidad a una barrera geográfica (la franja marítima entre Iberia y África) durante la migración otoñal. Para ello, analizamos datos de carriceros juveniles mediante modelos de captura-recaptura obtenidos en 6 estaciones de muestreo, tres localizadas en el norte y tres en el sur de la Península Ibérica. Adicionalmente, estimamos y comparamos la disponibilidad trófica y las tasas de engorde entre sitios para controlar el efecto potencial de estas variables sobre las probabilidades de partir. La proximidad de las áreas de descanso a la barrera modificó la importancia de los factores que los migrantes toman en cuenta a la hora de decidir si permanecer o partir. En el norte peninsular las probabilidades de partir fueron independientes de la carga de grasa, mientras que en el sur éstas fueron mayores para mayores cargas de grasa. Los carriceros partieron independientemente de las condiciones de viento en ambas regiones. Las tasas de engorde experimentadas por las aves en los diferentes sitios de muestreo no se correlacionaron ni con la disponibilidad trófica ni las con las probabilidades de partir.

Palabras clave: Carga de grasa, cruce del mar, disponibilidad trófica, modelos Cormack-Jolly-Seber, parada, viento de cola.

7.2. Introduction

During migration, birds must often fly over areas such as oceans or deserts, where there is no chance to land and/or gain fuel (Newton 2008). Such geographic barriers force migratory birds to evolve strategies for crossing them safely (Alerstam & Lindström 1990; Lindström & Alerstam 1992; Hedenström

2008). As a result, migrants make decisions about the time to depart from each particular stopover site, taking into account the species-specific migration strategy and the conditions existing at that particular site (Alerstam & Lindström 1990; Weber et al. 1998b). Many studies on the stopover ecology of migrant birds have analysed the role of multiple factors, either intrinsic or extrinsic, on the departure decisions of migrants (e.g. Dänhardt & Lindström 2001; Schaub et al. 2004; Tsvey et al. 2007; Schaub et al. 2008; Navedo et al. 2010; Arizaga et al. 2011b; Morganti et al. 2011; Andueza et al. 2013b). However, the influence of a particular factor on departure decisions could vary depending on the site's location along the migratory route and the ecological conditions ahead (Dierschke & Delingat 2001; Bauer et al. 2008; Schaub et al. 2008). The relative role of several factors on the departure decisions of birds along their route of migration is an aspect which remains relatively unstudied, particularly in passerines (Dierschke & Delingat 2001; Schaub et al. 2008).

A number of studies have shown that many passerines tend to accumulate large fuel loads before facing geographic barriers (Hilgerloh & Wiltschko 2000; Schaub & Jenni 2000a; Rubolini et al. 2002; Fransson et al. 2008; Yohannes et al. 2009; Smolinsky et al. 2013; but see Salewski & Schaub 2007). For instance, the sea crossing between Iberia and Africa implies the accumulation of important fat reserves for a number of passerines, mainly at sites close to the south Iberian coast (Hilgerloh & Wiltschko 2000; Andueza et al. in press). If this were true, we would expect departure decisions from stopover sites close to the barrier edge (e.g., the south coast of Iberia) to be highly influenced by the actual fuel load. Fuel might play a more marginal role in leaving decisions made far from the barrier (Andueza et al. 2013b). Alternatively, fuel load may govern leaving decisions from inland sites if birds accumulate the energetic reserves needed to cross the sea at sites located far from it, for example, if they expect worse fuelling conditions towards the barrier proximities.

Birds have been reported to select favourable wind conditions to depart, since tail winds increase the potential flight distances for given fuel loads, allowing birds to save time and energy (Weber et al. 1998a; Dänhardt & Lindström 2001; Liechti 2006; Andueza et al. 2013b). However, the relative importance of wind conditions on departure decisions could vary along the route. In particular, when migration is performed in a number of short-flights between stopover sites, birds could ignore the wind conditions on departure (Dierschke & Delingat 2001). By contrast, selecting favourable wind conditions (i.e. tailwinds) may be especially relevant before a sea crossing (e.g. between Iberia and Africa). During a sea crossing no landmarks exist for bird orientation (Åkesson 1993) and wind drift, resulting from flying under adverse wind conditions, can lead birds to open oceanic areas where their survival is compromised. This is particularly important in juveniles, who are unable to compensate for wind drift properly (Liechti 2006). Accordingly, our hypothesis is that migrants will preferably select tailwinds to depart before the barrier, whereas they will leave irrespective of wind conditions when suitable areas are expected ahead. Alternatively, the role of wind conditions on departure decisions may not differ depending on the location of stopover sites.

The aim of this work is to test whether the relative influence of fuel load and wind conditions on the departure decisions of the Reed Warbler *Acrocephalus scirpaceus*, a long-distance migrant passerine, vary in relation to proximity to a geographic barrier: the sea band between Iberia and Africa. For that, we compared departure probabilities from a number of stopover sites located in northern and southern Iberia during the autumn migration period, using Cormack-Jolly-Seber (CJS) models.

7.3. Methods

7.3.1. Study species

The Reed Warbler *Acrocephalus scirpaceus* is a widespread Palaearctic, trans-Saharan migrant species, which breeds across most of Europe and overwinters in tropical Africa (Cramp 1992). The species is mainly associated with reed beds

(*Phragmites* spp.), where it feeds opportunistically on invertebrates (Bibby & Thomas 1981; Kerbiriou et al. 2011). Reed Warblers in Europe seem to organize their migration in short steps, accumulating the reserves required to fly over the Sahara Desert mainly in northern Africa (Schaub & Jenni 2000a).

7.3.2. Sampling sites and data collection

Reed Warblers were captured at 6 strategically selected sampling localities in Iberia (Fig. 7.1): (1) 3 localities in northern Iberia (Txingudi, Urdaibai and Salburua), within a region where one of the chief migratory flows of birds entering Iberia is situated and (2) 3 localities in south-west Iberia (Faro, Doñana and Tarifa), where many birds converge before crossing the sea to reach the north of Africa (Cantos 1998; Andueza et al. 2013a).

The main vegetation at all of these sites was Reed beds (*Phragmites* spp.). The sampling period lasted from 15th August to 15th September of 2012. Daily sampling was carried out at each site using mist nets, which remained open for a 4 h period starting at dawn. Once caught, each bird was ringed and aged either as a first-year bird (birds with fresh, juvenile feathers in their wings, a dark brown iris and legs) or adult (with worn feathers in their wings, a clear brown/yellowish iris and legs)

(Svensson 1992). Wing length (± 0.5 mm, according to method III in Svensson 1992), body mass (± 0.1 g accuracy) and moult state (yes or no) were also recorded. Only first-year birds were considered in this paper, given the low number of adults captured. We did not pool both age classes since they might show different stopover behaviour (Moore & Yong 1991; Woodrey 2000; Jakubas & Wojczulanis-Jakubas 2010; Andueza t al. 2014).

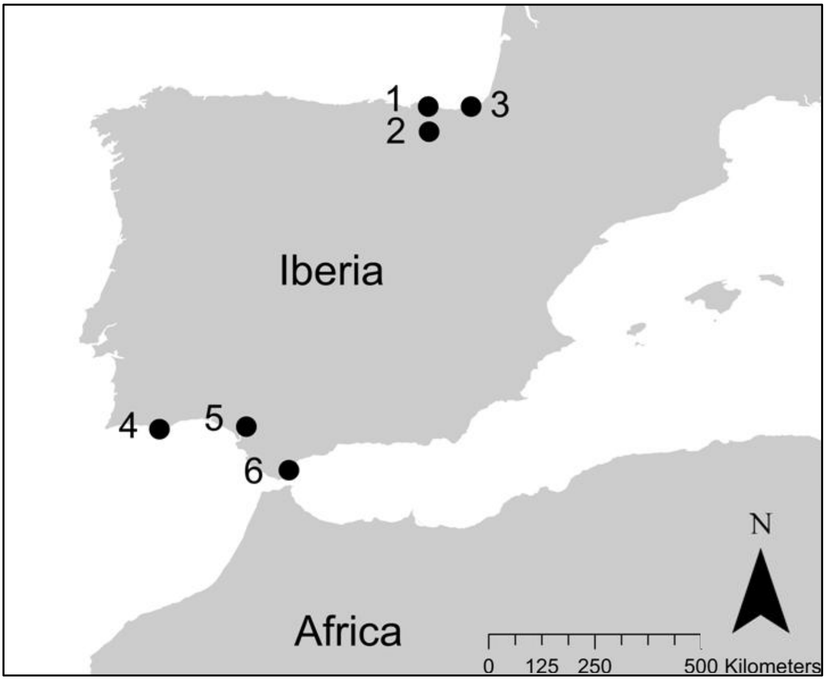


Figure 7.1. Sampling sites in the Iberian Peninsula. Northern Iberia: 1 Urdaibai (43.35N 2.66W). 2 Salburua (42.86N 2.64W). 3 Txingudi (43.35N 1.82W). Southern Iberia: 4 Faro (37.02N 7.92W). 5 Doñana (37.07N 6.22W). 6 Tarifa (36.21N 5.38W).

7.3.3. Capture-recapture models

We were not able to separate migrants and local birds using wing length (as suggested in Bibby & Green 1981) due to the high overlap between the two in Iberia (M. Andueza, pers. obs.). Furthermore, the moult state was not useful in separating these populations, since there is also some overlap between moult and migration (Schaub & Jenni 2000a). We therefore considered that local birds could have been included in our data set. However, since the sampling was carried out during the peak of passage of migrant Reed Warblers in Iberia (Cantos & Tellería 1994), the number of local birds was expected to be relatively low compared to the quantity of migrating birds (Schaub & Jenni 2000a).

Departure decisions were modeled using CJS models in which the following factors were included: sampling site, fuel load, date and wind assistance. To assess fuel load we considered an index of body size-controlled body mass consisting of the residual values from a linear regression of body mass and wing length (Schulte-Hostedde et al. 2005). We included date because departure probability can vary as the migration period progresses. This is due to the fact that migrants often increase their migration speed with date (Schaub & Jenni 2000b; Bayly

2006). Wind assistance was calculated as a tailwind component (*b)* (Åkesson & Hedenstrom 2000):

$$b = V \times \cos(\alpha_t - \alpha_w)$$

where V was the wind velocity; α_t was the (presumed) departure direction [localities in northern Iberia: 220º (Andueza et al. 2013b); localities in southern Iberia 211º (Hilgerloh 1989)], and α_w was wind direction (Åkesson & Hedenstrom 2000). We obtained the wind direction (in degrees) and speed (m/s) at 925 mb, equivalent to a flying altitude of ca. 1000 m above sea level, from NOAA (www.noaa.gov) for each of the 6 sampling sites during the study period (15th August-15th September). We selected the wind conditions at 18:00 h and 00:00 h, since most birds start their migratory flight within this time window (Åkesson et al. 2002) and calculated the mean values of wind velocity and direction for each site. In northern Iberia, the wind direction and speed values were exactly the same for the 3 sites, due to their geographic proximity. The wind values were also highly and positively correlated among the southern Iberian sites (*R* values of the correlations between sites were greater than 0.63 for wind direction and greater than 0.76 for wind velocity). Wind values did, however, differ between the two regions (*R* values of the correlations between northern and southern sites were below 0.40 for wind direction and below 0.66 for wind velocity). Thus, we considered two data sets for the CJS models (i.e., we ran two groups of models), one for each region, since the wind conditions in one region may not be representative of those in the other. For southern Iberia, the tailwind component was calculated using the mean wind direction and speed of the three sampling sites.

If we assume that the survival (ϕ) of a bird from one day to the next at a stopover site is the probability of remaining at that stopover site (Schaub et al. 2001), then the emigration (i.e., departure) probability (ε) is $1-\phi$. Before starting to select models, we tested the fit of our data to CJS assumptions (no transients, no trap dependence) with a goodness-of-fit (GOF) test. The GOF test run with U-CARE software (Choquet et al. 2001) detected the presence of transients in southern Iberia ($z = 3.91$, $P < 0.001$) but not in northern Iberia ($z = 1.75$, $P = 0.080$). No trap-dependence was found in either region ($P > 0.05$). We considered two data sets (northern and southern Iberia) because the wind values within each region were not the same on the same date (see below for further details).

To control for the presence of transients in southern Iberia, we used an age-dependent model structure (Pradel et al. 1997; Salewski & Schaub 2007; Salewski et al. 2007). Its application allowed us to estimate two local survival rates, ϕ_i (i.e., survival from t to $t+1$, where t is the capture day; this rate includes both transients and non-transients), and ϕ_{nt}, (daily survival after the second day; this rate only includes non-transients, i.e. migrants that stay in the area for longer than one day). The probability that a newly caught individual is a transient is τ = 1- ϕ_i/ϕ_{nt}. To test for the effect of the different factors on ε (in this case ε_i and ε_{nt}) we first ran basic models on ε (ε_i and ε_{nt}) and *p* assuming either constant or time-dependent parameters. Both ε_i and *p* were observed to fit to the data better when they were constant (Table 7.1), so these were fixed to be constant when we ran the remaining models, which included body mass and wind assistance (*b*). For northern Iberia, we also ran models considering either constant or time-dependent ε and *p* before running more complex models. In this case, the most complex model from which to start to test additional models was the one where ε and *p* were time-dependent [ε(t) *p*(t)].

CJS models were run using MARK software (White & Burnham 1999). We tested for the effect of each single variable and for combinations of variables, which included both additive effects and interactions. The most complex models included the additive effect of 3 variables and interactions of up to 2 variables. Triple interactions were not included due to sample size limitations. The small sample sizes-corrected Akaike´s Information Criterion (AICc) was used to rank and choose the models best fitting to the data (Burnham & Anderson 1998).

Table 7.1. Basic models run before modelling departure probabilities in relation to sampling site, fuel load, date and wind assistance, in which parameters are considered to be time-dependent (t) or constant. ε: departure probability; ε_i: departure probability from *t* (first capture day) to *t*+1 (following day), including both transients and non-transients; ε_{nt}: departure probability after the second day, including only non-transients; *p*: recapture probability; AICc: corrected Akaike's Information Criterion; ΔAICc: difference in AIC values of each model with the first one.

Models	AICc	Δ AICc
Northern Iberia		
ε, p(t)	1110.879	0.000
ε(t), p(t)	1157.575	46.696
ε, p	1167.236	56.357
ε(t), p	1174.715	63.836
Southern Iberia		
ε_i, ε_{nt}, p	1232.850	0.000
ε_i(t) ε_{nt}, p	1240.620	7.7570
ε_i, ε_{nt}, p(t)	1268.610	35.760
ε_i, ε_{nt}(t), p	1280.983	48.133
ε_i(t) ε_{nt}, p(t)	1283.777	50.927
ε_i(t) ε_{nt}(t), p	1300.234	67.384
ε_i, ε_{nt}(t), p(t)	1325.931	93.081
ε_i(t) ε_{nt}(t), p(t)	1346.793	113.943

Two models were considered to have the same support if the difference between their AICc values was less than 2 (Burnham & Anderson 1998). Within a given model, a particular variable was considered to have a significant effect on ε if "zero" was not included within the 95% Confidence Interval (95% CI) of its *B* parameter.

7.3.4. Food availability estimation and fuel deposition rate analyses

The possible effect of site on our models may be masked by other factors apart from the geographic position of that site. Thus, departure decisions may be associated not with the position of a site in Iberia, nor in relation to the sea and northern Africa, but rather with the conditions provided by that particular stopover site in terms of fuel deposition rates (Schaub et al. 2008) or food availability. The rate at which fuel is accumulated by birds during stopovers can be considered as an indicator of the quality of the site (Grandío 1999) and food availability is one of the main factors influencing fuel deposition rates (Schaub & Jenni 2000b; Bayly 2006; Smith & McWilliams 2010). Therefore, in order to control for their effects on departure decisions, we estimated and compared both weight gain and food availability at the different sites.

The quantity of small invertebrates within the Reed beds was used here as a surrogate of the food available to Reed Warblers. To assess this, we used the approach of Poulin et al. (2002), which consisted of sweeping the Reed beds with a 30-cm insect net. This method allowed us to sample a broad range of invertebrates in a short time. These were mostly arthropods, the main foraging substrate of Reed Warblers (Poulin & Lefebvre 1997). The sampling protocol consisted of sweeping the vegetation 500 times, along a transect parallel with the lines where the mist nets were placed. This was carried out in the period of 2 h before dusk. During each sweep the vegetation was struck from the bottom upwards, with the net wing at an angle of about 45º. Each site was sampled every 10 days (three times overall), starting on 21st August. At Urdaibai and Salburua the first sampling was missed for logistical reasons. The invertebrates were stored in 70% ethanol before being processed in our laboratory. Reed Warblers mostly forage on prey of 1 to 20 mm in length (Bibby & Thomas 1981; Kerbiriou et al. 2011). We therefore selected prey within this size range in order to estimate food availability. From each sample we obtained the dry weight (± 0.01 g accuracy) after a period of 24 h at 50ºC. We compared food availability between regions and sites using non-parametric tests.

To analyse if the fuel deposition rate varied between regions and sites, we conducted a General Linear Model (GLM) on the weight variation (%) between the first and last capture occasion. We included region, sampling sites (nested into regions) and moult as factors and days elapsed between both capture events and date as covariates (Neto & Correria 2012). Individuals recaptured for the last time on the day following the first capture were excluded from analyses so as to avoid a possible handling effect on the fuel deposition rate (Schwilch & Jenni 2001). Additionally, we tested if the slope of the graph of weight increase (%) vs. days (used as an indicator of the fuel accumulation rate) for the different stopover sites depended on the food availability at each, and whether the emigration probability was correlated with the fuel accumulation, by running Spearman correlation tests.

All analyses were made with SPSS v. 15.0.

7.4. Results

Overall, we captured 1190 first-year Reed Warblers, 608 in northern Iberia and 582 in southern Iberia (Table 7.2). Average invertebrate biomass (dry weight) was similar between regions (Mann-Whitney U = 3.50, *P* = 0.658; northern Iberia: 0.63 ± 0.13 g/500 sweeps; southern Iberia: 0.60 ± 0.16 g/500 sweeps), and also between sites (Kruskal-Wallis $\chi^2 = 10.50$, *P* = 0.062) (Table 7.2). Tailwinds occurred on 40.6% and 56.3% of the nights during the sampling period in northern and southern Iberia, respectively.

For northern Iberia, 24 models were tested overall. Only one model was observed to fit to our data much better than the others (Table 7.3). This model considered an effect of site on ε. Thus, Reed Warblers showed a higher departure probability from Salburua (ε = 0.29 ± 0.04), followed by Txingudi (ε = 0.15 ± 0.02) and finally Urdaibai (ε = 0.08 ± 0.03). *p* was time-dependent and ranged from < 0.001 ± < 0.001 to 0.52 ± 0.22.

Table 7.2. Number of captures of first-year Reed Warblers, number of auto-recaptures within the season, and number (and % of the total captures) of moulting individuals at each sampling site. The mean ± SE food availability (dry weight of invertebrates) for the sampling events (500 sweeps) at each sampling site is also shown.

Site	No. Captures	No. Recaptures	No. Moulting Birds	Food Availability
N Iberia				
Txingudi	238	46	36 (15.1%)	0.51 ± 0.19
Salburua	309	15	18 (5.8%)	0.88 ± 0.21
Urdaibai	61	20	0 (0%)	0.89 ± 0.03
S Iberia				
Faro	246	43	60 (24.4%)	0.23 ± 0.09
Tarifa	62	10	14 (22.6%)	1.06 ± 0.26
Doñana	274	29	149 (54.4%)	0.51 ± 0.19

For southern Iberia, 28 models were tested overall. In this case, 4 models fitted to data equally well (Table 7.3). These models included effects of site, fuel and date on ε (Table 7.3; Table 7.4). After averaging the 4 best models (with an accumulated AICc weight of 63.3%) we observed increasing ε values with increasing fuel load (Fig. 7.2). Moreover, Reed Warblers tended to depart more quickly late in the season (Fig. 7.2). However, a detailed analysis on the *B*-parameters of these models showed only a marginal, non-significant effect of date on departure decisions (Table 7.4). Both ε_i and *p* were considered to be constant over time and had a value of 0.54 ± 0.07 and 0.04 ± 0.01, respectively.

The interactions between the days and both region and site for the weight gain (%) were not significant, indicating that the relationship (slope) between weight increase and the number of days elapsed between the first and last capture was similar between groups (Table 7.5, Fig. 7.3). Moreover, neither region nor site showed a significant effect, suggesting that mass gain was similar at all stopover sites independently of the region (Table 7.5, Fig. 7.3). Non-moulting individuals were able to accumulate more fuel than moulting individuals (Table 7.5, Fig. 7.3). In northern Iberia, no relationship was found between the slope of the graph of weight increase (%) vs. days for each site (indicator of the fuel accumulation rate) and the departure probability ($r = 0.500$; $P = 0.667$; $n = 3$).

Table 7.3. Best CJS models used to model departure probabilities from northern and southern Iberia. Abbreviations: ε: departure probability; ε_{nt}: departure probability of non-transients; p: recapture probability; AICc: corrected Akaike's Information Criterion; ΔAICc: difference in AIC values of each model with the first one; +: additive models; ×: models including the interaction between variables.

Models	AICc	Δ AICc	AICc Weight	No. Parameters
Northern Iberia				
1 ε(site), p(t)	1085.852	0.000	1.000	34
2 ε, p(t)	1110.879	25.028	0.000	32
3 ε(site+fuel), p(t)	1121.789	35.937	0.000	5
4 ε(site+date+fuel), p(t)	1123.597	37.746	0.000	6
5 ε(site+wind+fuel), p(t)	1123.818	37.967	0.000	6
Southern Iberia				
1 ε_{nt}(site+fuel+date), p	1226.462	0.000	0.266	7
2 ε_{nt}(site+fuel), p	1227.885	1.423	0.130	6
3 ε_{nt}(site×date), p	1227.887	1.425	0.130	8
4 ε_{nt}(fuel+date), p	1228.288	1.826	0.107	5
5 ε_{nt}(fuel×date), p	1228.969	2.507	0.076	6

Table 7.4. Standardized *B*-parameters (± SE and the 95% CI) of the best models from Table 7.3. for southern Iberia. Variables are significant if zero is not included in their 95% CI. [a] Reference value.

			95% CI	
Parameter	*B*	SE(*B*)	Lower	Upper
Model 1				
Site1	+0.572	0.243	+0.096	+1.049
Site2	+0.301	0.377	-0.438	+1.039
Site3	0[a]			
Fuel	-0.477	0.168	-0.807	-0.147
Date	-0.074	0.043	-0.157	+0.01
Model 2				
Site1	+0.621	0.247	+0.137	+1.105
Site2	+0.372	0.375	-0.363	+1.108
Site3	0[a]			
Fuel	-3.089	0.173	-3.428	-2.75
Model 3				
Site1	+1.106	0.402	+0.318	+1.895
Site2	+1.168	0.644	-0.094	+2.429
Site3	0[a]			
Date	-0.014	0.057	-0.125	+0.098
Interaction: Site1×Date	-0.091	0.045	-0.180	-0.002
Interaction: Site2×Date	-0.128	0.057	-0.241	-0.016
Interaction: Site3×Date	0[a]			
Model 4				
Date	-0.082	0.043	-0.167	+0.003
Fuel	-3.067	0.173	-3.406	-2.729

Table 7.5. GLM results to compare weight gain (%) of first-year Reed Warblers between regions (northern and southern Iberia), sites and moult state. Sampling sites were nested within region. Date and the number of days between the first and last capture were included as covariates.

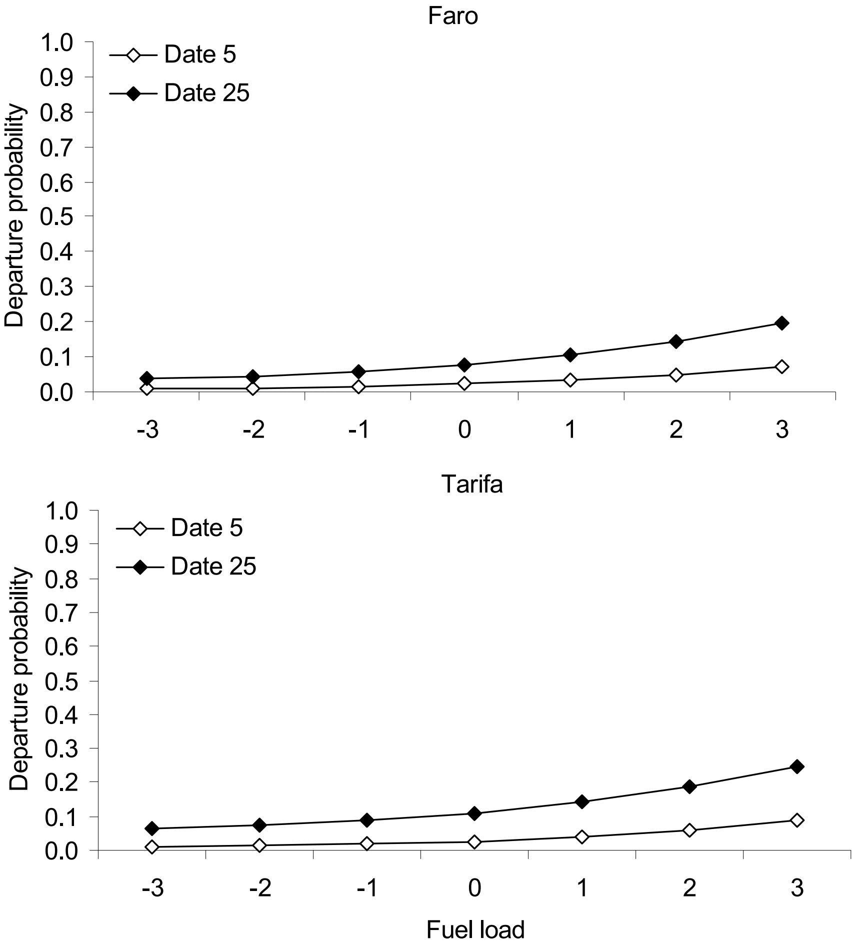
Factor	SS	df	*F*	*P*
Region	1010.051	2	0.488	0.683
Moult	1034.724	1	8.678	0.004
Site (Region)	1087.026	4	2.083	0.093
Date	20.210	1	0.170	0.681
Days	852.542	1	7.150	0.008
Region x Days	65.571	1	0.550	0.459
Site x Days	40.621	4	0.085	0.987

7.5. Discussion

For southern Iberia we found that birds captured with low fuel were less likely to depart than more heavily fuel loaded individuals. However, this was not the case in northern Iberia, where departure decisions were independent of this variable. Thus, Reed Warblers assigned varying importance to their fuel loads depending on their geographic position and the conditions expected ahead (land vs. sea) (e.g. Dierschke & Delingat 2001). Reed Warblers captured in northern and southern Iberia belong to populations following a similar migratory direction (Andueza et al. 2013a). Therefore, the observed differences between regions are likely to be due to variations in the role (weight) of several factors on the departure decision and not to the fact that the study populations could have different migration strategies. Moulting Reed Warblers were more abundant in southern Iberia. However, departure probabilities were of similar magnitudes between sites in northern and southern Iberia, suggesting that moult did not have an important effect on the departure decisions.

Reed Warblers in southern Iberia did not leave a stopover site and cross the sea to Africa until they had accumulated a minimum amount of energy. Thus, especially in early migratory birds, ε values tended to be zero for low-fuel loaded migrants. This supports the idea that even though the sea area between Iberia and Africa is a minor barrier when compared to the Sahara Desert, Reed Warblers stopping over at its northern border prefer to adopt a safety crossing strategy. This implies the accumulation of more reserves than are necessary to cover the sea journey. We have found that the potential flight ranges of Reed Warblers captured in southern Iberia can be more than twice the distance to northern Africa (Andueza et al. in press). These results differ from those found for Pied Flycatchers *Ficedula hypoleuca*, for which departure decisions were independent of fuel stores in southern Iberia (Schaub et al.

2008). This suggests the existence of species-specific fuelling and barrier crossing strategies (Schaub & Jenni 2000a). Additionally, time pressure, and its expected effect on increasing departure probabilities from stopover site in late migrants (Schaub & Jenni 2000b; Bayly 2006), did not seem to be relevant in Reed Warblers, at least in the period when these birds were sampled (from 15th August to 15th September).



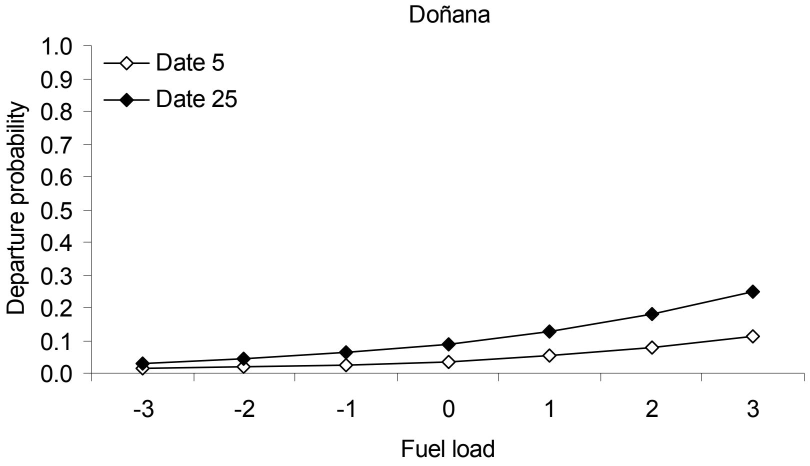
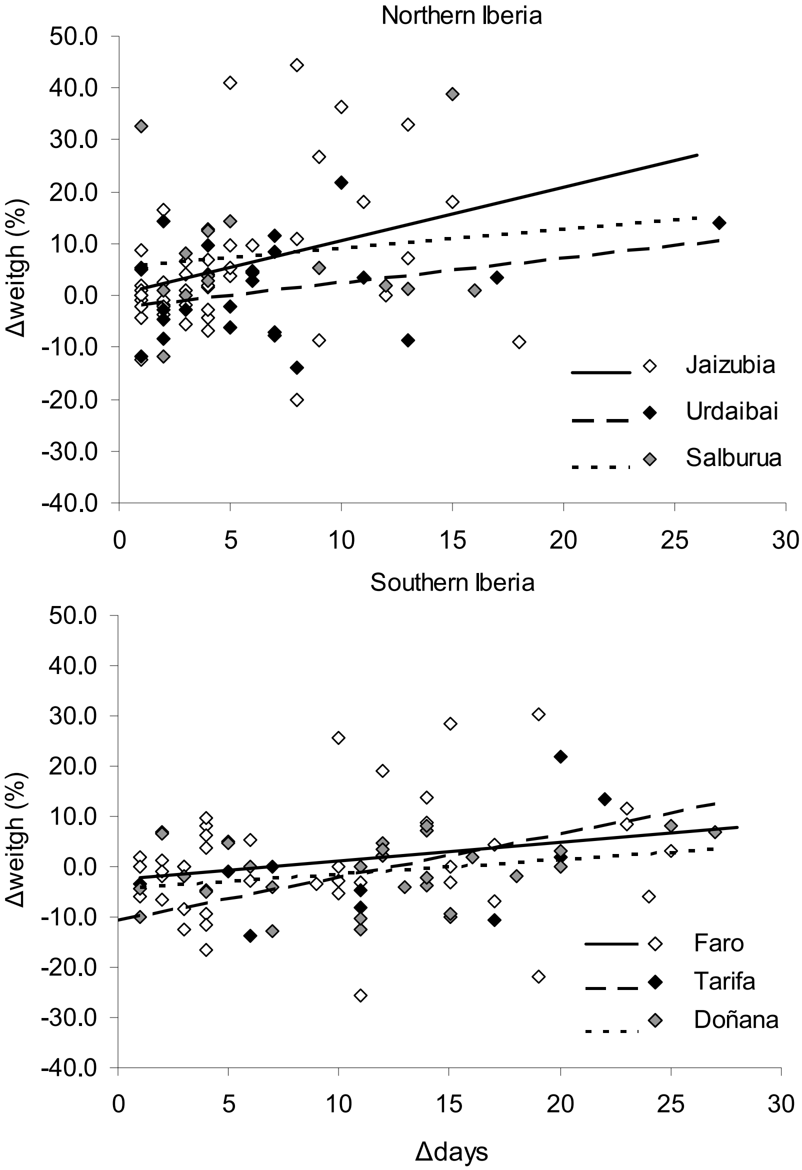


Figure 7.2. Departure probabilities of non-transient Reed Warblers after arrival. ε_{nt}. at the sampling sites in southern Iberia for increasing fuel load (residual values from a linear regression of weight and wing length) for both an early and late date (sampling day) within the migratory season, resulting from averaging the best models according to Table 7.4.

Within regions, departure probabilities varied greatly between sites, especially in northern Iberia, suggesting that departure decisions are shaped by other factors apart from fuel load and location in relation to the barrier. The fuel deposition rate experienced at stopover sites has previously been found to be a key factor affecting departure decisions (Schaub et al. 2008). In northern Iberia no relationship between the average fuel deposition rate experienced by Reed Warblers at a site and their departure probability was found, indicating that departure probabilities were independent of the fuelling conditions at the sites. The time-minimization migration strategy assumes the existence of a positive relationship between departure fuel loads and fuel deposition rates (i.e. the higher the fuel accumulation rate experienced, the higher the departure fuel load) (Alerstam & Lindström 1990). Hence, if departure probabilities are independent of the fuel deposition rate experienced by birds, this would result in birds departing with very different fuel loads. This explains why departure probabilities in northern Iberia were independent of body mass. However, this conclusion should be regarded cautiously given the low number of available sites. In southern Iberia, where the sites were before the sea crossing, departure probabilities were very similar amongst sites, as was the rate of mass gain, so we were unable to establish any relationship between the fuelling conditions provided by sites and departure probabilities. The lack of a significant relationship between food availability and the average fuel accumulation rate at the stopover sites suggests that fuelling rates are modified by other factors than food availability alone. Previous studies have reported how fuel accumulation can be constrained to minimize predation risk and increased despite food depletion (Schaub & Jenni 2000b; Bayly 2006).


Northern Iberia
Δweitgh (%)
50.0
40.0
30.0
20.0
10.0
0.0
-10.0
-20.0
-30.0
-40.0
0
5
10
15
20
25
30
Jaizubia
Urdaibai
Salburua
Southern Iberia
Δweitgh (%)
Faro
Tarifa
Doñana
Δdays

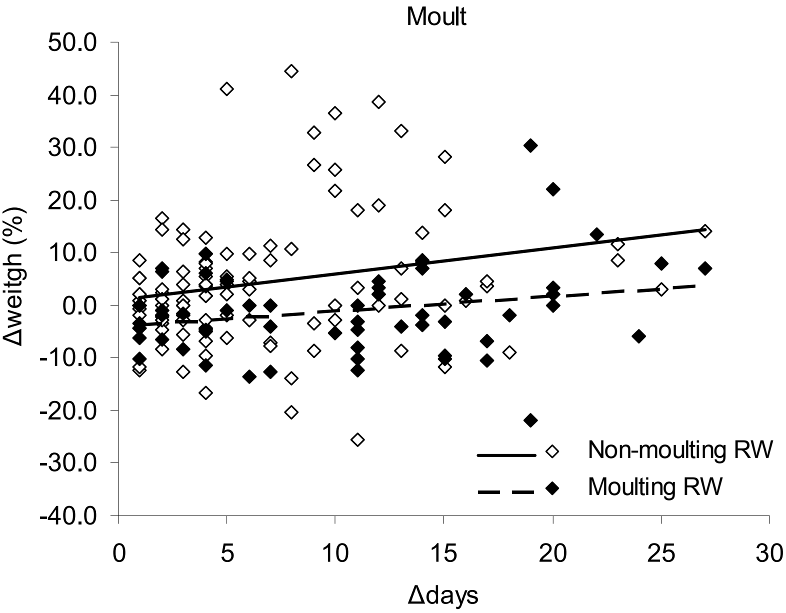


Figure 7.3. Relationship between the weight increase between the first and last capture (%) and the number of days between both capture events for different stopover sites in northern and southern Iberia, and for the moulting and non-moulting fractions of first-year Reed Warblers.

Wind conditions did not affect departure decisions. Migrants have been reported to select tailwinds to depart. This allows them to fly longer distances with the same amount of fuel, thus saving both energy and time (e.g. Åkesson & Hedentröm 2000; Dänhardt & Lindström 2001; Schaub et al. 2004; Tsvey et al. 2007). However, on some occasions, birds do not seem to consider this variable when making departure decisions (Dierschke & Delingat 2001; Karlsson et al. 2011; Smolinsky et al. 2013). This is particularly notable when birds migrate over continental areas in a series of short flights (Fransson 1998b; but see Andueza et al. 2013b). When stopover opportunities are widespread and birds adopt a short-flight-bouts strategy, as is the case with Reed Warblers, low selectivity may be expected if the time and/or energy costs of waiting for certain wind conditions are too high (Karlsson et al. 2011).

Interestingly, this low selectivity for tailwind assistance was detected even in southern Iberia. A sufficient amount of fuel might allow these birds to perform longer flights over the sea in case of drift. The probability of the occurrence of tailwinds may play an important role in the wind selectivity strategy (Thorup et al. 2006). Although days with tailwinds in northern and southern Iberia were common when the study was conducted, there were still a significant number of days with headwinds, which theoretically would promote the selection of tailwinds in relation to departure decisions (Thorup et al. 2006). Perhaps the sea crossing between Iberia and Africa is not of such a magnitude as to force birds to consider tailwind assistance.

In conclusion, the proximity of a stopover site to a small barrier modified the relative importance of the factors that migrants consider when deciding to remain or to depart from a stopover site. In particular, Reed Warblers in southern Iberia (i.e., before crossing the sea area between Europe and Africa) were more likely to depart if they were more fuel loaded, a response not detected in northern Iberia.

7.6. Acknowledgements

We are grateful to the Doñana Biological Station team for providing logistic support to carry out the fieldwork in the Doñana area. The Plaiaundi Ecological Park supported ringing activities in Txingudi. The Basque, Andalusian and Portuguese government administrations authorized the ringing samplings. This research was funded by the Spanish Ministry of Education (pre-doctoral fellowship to MA) and the Spanish Ministry of Science and Innovation (project CGL2010-21933-C02-02; to EB).

7.7. Ethical standards

Ringing activities were authorised by the Basque, Andalusian and Portuguese Administrations, according to their current laws, and were carried out by certified expert bird ringers. We used a safe trapping method, mist nets, which were hourly revised. Captured birds were kept individually in cotton bags until being processed so as to reduce stress, and, once ringed, they were released immediately.

CAPÍTULO 8

Spatial distribution and habitat use of Reed Warblers *Acrocephalus scirpaceus* during the autumn migration

Este capítulo es una reproducción del artículo: Andueza, M., Arizaga, J., Barba, E. & Tamayo-Uria, I. 2014. Spatial distribution and habitat use of Reed Warblers *Acrocephalus scirpaceus* during the autumn migration. *Behaviour* 151: 799-817.

8.1. Abstract and keywords/Resumen y palabras clave

Abstract: Spatial behaviour and habitat selection at stopover sites have a strong influence on the foraging and fuelling performance of migrating birds and hence are important aspects of stopover ecology. The aim of this study was to analyse the spatial behaviour and habitat use of Reed Warblers *Acrocephalus scirpaceus* during the autumn migration. We used radio tracking data from Reed Warblers surveyed at a stopover site in northern Iberia and assigned to three different groups: (1) local adult birds which were still at their breeding site, (2) migrating first-year birds (originating from beyond Iberian peninsula), and (3) migrating adult birds. Overall, migrating first-year birds tended to have larger home ranges than both local and migrating adults and to move more widely in the study area. They also showed lower fat deposition rates than adults. The proportion of habitats in home ranges (reed-beds and tidal flats being the most abundant habitats) was similar amongst groups. The spatial distribution and habitat use of organisms have been theorised to follow an ideal-free or ideal-despotic distribution. However, according to our results, other complex underlying mechanisms may play an important role in shaping the spatial behaviour of birds at stopover sites.

Keywords: Age classes, breeders, fuel deposition rate, ideal-despotic distribution, ideal-free distribution, migrants, radio tracking, reed-beds.

Resumen: El comportamiento espacial y la selección de hábitats en las áreas de descanso tienen una gran influencia en el rendimiento energético de las aves en migración y constituyen, por tanto, aspectos importantes de la ecología migratoria. El objetivo de este trabajo es analizar el comportamiento espacial y el uso de hábitats del carricero común *Acrocephalus scirpaceus* durante la migración otoñal. Empleamos datos de radioseguimiento de carriceros en un área de descanso en el norte de la Península Ibérica, pertenecientes a tres grupos: (1) adultos locales que crían en la zona, (2) juveniles en migración de poblaciones europeas no ibéricas, y (3) adultos en migración, no locales. En general, los juveniles tuvieron áreas de campeo mayores que los adultos, tanto locales como en migración, y se movieron más por la zona de estudio. También mostraron tasas de engorde más bajas que los adultos. La proporción de hábitats en las áreas de campeo (siendo el carrizal y las llanuras mareales los más abundantes) fue similar entre grupos. Se ha teorizado que la distribución espacial y uso de hábitats pueden seguir una distribución libre o despótica. Sin embargo, de acuerdo a los resultados obtenidos, otros mecanismos subyacentes pueden jugar un papel fundamental configurando el comportamiento espacial de las aves en las áreas de descanso.

Palabras clave: Carrizal, clases de edad, criadores, distribución despótica ideal, distribución libre ideal, locales, migradores, radioseguimiento, tasa de engorde.

8.2. Introduction

Bird migration is usually divided into several flights during which energy is consumed, interrupted by stopovers, when energy is normally replenished (Weber at al. 1998b). The success of migration depends largely on the fuelling opportunities en route. Relevant aspects of stopover ecology are spatial behaviour and habitat selection, which have a strong influence on foraging and fuelling performance (Shochat et al.

2002; Lindström 2003; Chernetsov 2006; Ktitorov et al. 2010). Spatial use possibilities include establishing defended territories (Kodric-Brown & Brown 1978; Bibby & Green 1980; Stamps 1994), home ranges (relatively small but non-defended areas in which individuals perform their normal activities; Burt 1943; Titov 1999b; Chernetsov & Mukhin 2006), or moving extensively within an area (Chernetsov et al. 2004). Understanding how migrants distribute in the space and how they use the habitats available is of great importance for the conservation and management of sites used as stopovers (Petit 2000), in particular those which are threatened by human activity and climate change, such as wetlands.

Habitat quality, which can be widely understood as resource availability, is one of the most important factors determining spatial use in birds (Johnson & Sherry 2001; Rodewald & Brittingham 2007; Chandler & King 2011; Smith et al. 2011; Chernetsov 2012). Fretwell & Lucas (1969) theorised on how birds are distributed in heterogeneous habitats, assuming that they settle in habitats based on their quality and the density of individuals. The ideal-free distribution assumes that all individuals have equal fitness and that they distribute in a density dependent way. As population density increases, the quality of best habitats is reduced, equalling fitness in the most and least preferred habitats. The ideal-despotic distribution assumes that dominant individuals displace subordinates to less preferred habitats, resulting in unequal fitness. Both patterns have been used to explain spatial distribution and habitat selection during the breeding period, in different avian species, considering reproductive success as an indicator of individual fitness (Huhta et al. 1998; Weidinger 2000; Zimmerman et al. 2003; Sergio et al. 2007).

When applying the previous ideas to hypotheses related to the spatial use of migrating birds at stopover sites, it can be assumed that the higher the fuel deposition rate of birds the higher the fitness, as the rate at which fuel is accumulated is the best indicator of stopover performance (Chernetsov 2006). During migration, birds arrive and depart from stopover sites in a sequential fashion, temporarily sharing those sites with other migrants, or even with residents or local birds which have not started their migration. Thus, according to the ideal-free pattern, birds would occupy the best available areas as they arrive, independently of their social status, and home range size would be inversely proportional to the quality of the habitat to equalise fitness. By contrast, if habitat selection follows the ideal-despotic distribution, dominant individuals (adults) would displace juveniles to poorer habitats, or prevent them from gaining a home range, forcing them to move broadly in the area (Chernetsov 2006; Tellería & Pérez-Tris 2007). As a result, juveniles would be expected to experience lower fuelling rates. The same hypotheses can be applied to local/migrating birds, considering local individuals as dominant since they have settled in the area previously and thus have a better knowledge of the site (the "resident advantage", as denominated in Piper 2011).

The Reed Warbler, *Acrocephalus scirpaceus*, is a trans-Saharan migrant which breeds widely in Europe and winters in tropical Africa. The species preferred habitat is reed-beds (*Phragmites australis*), although during migration the bird can be found in other habitats (Cramp 1992). Reed Warblers have been described to defend territories at stopover sites, due to the characteristics of their foraging source, which consists of uniformly distributed invertebrates (Bibby & Green 1981). However, the Reed Warbler adopts an opportunistic diet depending on the type of food available, which can vary along the route of migration (Chernetsov & Manukyan 1999; Chernetsov & Titov 2001). As a result, given that the spatial use is related to the foraging habits and the prey distribution (Chernetsov & Manukyan 1999; Chernetsov & Titov 2001; Chernetsov & Bolshakov 2006), Reed Warblers might adopt a different spatial behaviour depending on the feeding conditions found en route.

The aim of this study was to analyse the spatial behaviour and habitat use of Reed Warblers during autumn migration at a stopover site. For that purpose, we used radio tracking data at a stopover site in northern Iberia.

8.3. Methods

8.3.1. Study area

Our study was carried out at the Jaizubia marshlands, in Gipuzkoa, northern Iberia (43º21´N, 01º49´W). The sampling area was situated in a ca. 25 ha tidal marsh, mainly consisting of reed-beds and mud flats with halophytic vegetation (*Aster sp.*, *Salicornia* sp.). Jaizubia is used as a stopover site by numerous passerines during migration, especially in the autumn (Mendiburu et al. 2009). This is due, in part, to its particular geographic location, in a natural funnel between the western edge of the Pyrenees and the Bay of Biscay. One of the most abundant passerines in the area is the Reed Warbler, both as a breeding species and as a stopping over bird during the autumn migration period (Mendiburu et al. 2009). In this period migrating individuals overlap with local breeders which have not yet started migration. Ringing is carried out at Jaizubia each year during the breeding period (from May to August, twice a month) and the autumn migration (from August to October, daily).

8.3.2. Sampling protocol and survey method by radio tracking

We considered two types of analyses in this study, relative to (1) fuel deposition rate estimation, and (2) habitat use and spatial behaviour.

To estimate Reed Warbler fuel deposition rate, we used data from birds captured with mist nets (204 linear m, always placed in the same site for a period of 4 h starting at dawn) during the autumn migration (from 15 July to 30 September) of 2007 to 2011. Mist nets were open daily and visited hourly. Captured Reed Warblers were ringed and their age determined, as first-year birds or adults, according to Svensson (1992). We also recorded wing length (± 0.5 mm, according to method III in Svensson 1992), subcutaneous fat scores (according to Kaiser 1993), body mass (± 0.1 g, digital balance) and moult state (yes or no).

Between the 20th July and the 31th August of 2010 and 2011, 38 of the Reed Warblers captured in the mist nets were equipped with PIP41 transmitters (Biotrack) using a Rappole harness (Rappole & Tipton 1991), in order to localize their position by radio-detection. The size of the harness was calculated according to Naef-Daenzer (2007). The weight of the transmitter and harness was 0.6 g overall. Individuals chosen for this goal were assigned to one of three categories: (1) local adult birds (local breeders which were still at their breeding site), (2) migrating first-year birds (true migrants, coming from abroad), (3) migrating adult birds. We considered as local adults those Reed Warblers captured once or more during the breeding period of 2010 or 2011, or individuals with evident signs of being local birds (repeated recaptures within the season, evidence of active sexual traits such as a brood patch in females). We considered as true migrating Reed Warblers those individuals recovered with a foreign ring. Additionally, given the low number of foreign recoveries, we considered those non-moulting individuals with wing length ≥ 67 mm as being on migration, since only 25% of our captured local birds had wings longer than 67 mm (M. Andueza, unpublished data).

To survey the spatial ecology of Reed Warblers we used Sika receivers (30 MHz) with Yagi antennas from Biotrack. Birds were surveyed during a period of 4 h starting at dawn and 4 h before dusk. We attempted to obtain one location/hour for each bird. Reed Warblers were tagged when caught during the first 4 hour period in the morning but we did not start to track them until the afternoon, to allow birds to come back to their home areas. Reed Warblers were usually tracked for a maximum of 10 days (range: 1-15), allowing us to obtain a mean number of 41.7 ± 3.7 points/bird (range: 3-80). The survey method allows us to obtain directional information of the location of a bird in relation to the observer position, but not the location itself. As a result, we measured almost simultaneously the position angles from two different points on the field and the location of the bird was obtained with a GIS from the intersection of both directional lines (biangulation, Arizaga et al. 2013). We obtained a mean accuracy of 30 m (SE: 7 m), after comparing the estimated location of 6 points using biangulation with their real positions, measured by GPS.

8.3.3. Data analyses

Individual home ranges were calculated with ArcGIS 9.2 ESRI and Gearspace software. Particularly, we calculated Minimum Convex Polygon (MCP), 95% kernel area, and 50% kernel area, this last used as a core area surrogate. These values have been commonly used in similar studies (Baker 2001; Bosch et al. 2010; Arbeiter & Tegetmeyer 2011; Ponjoan et al. 2011; Šálek & Lövy 2012). Two approaches were used to estimate the movement of Reed Warblers during the survey period. Firstly, for each individual, we obtained the centroids of the positions of each day, and thereafter we calculated the longest distance between those daily centroids as an indicator of the overall distance covered within the area. Secondly, for each Reed Warbler, we calculated the mean displacement of the daily centroids from one day to the next to see if birds tended to remain at the same site on consecutive days or move randomly. Reed Warblers with less than 10 locations were excluded from analyses (*n* = 4 out of the 38 Reed Warblers surveyed). All these variables fitted a normal distribution (K-S test: $P > 0.05$). We used Generalized Linear Models (GLMs) on all variables (home range size and distance between centroids) with type of bird group as a factor. The number of locations was included as a covariate when comparing home range size (Chernetsov & Mukhin 2006), whilst the number of sampling days was included as a covariate when comparing the distance between centroids. In both cases, date of collocation of the transmitters for each bird was also included as a covariate, considering the 20th July as day 1 and 30th August as day 41.

To quantify the habitat use we calculated the proportion of habitats for both the 95% and 50% kernel areas, but not for the MCP. Although the MCP includes all the area potentially used by an individual, it might also include areas not used. Hence, kernel areas are more accurate for quantifying the intensity of use (Seaman & Powell 1996). To analyze habitat use, we used a vegetation map, created using a 2009 orthophoto of Jaizubia obtained from the Basque Government. Overall, we considered 7 habitat types: reed-beds (REED; 23.4% of the total surface), tidal flats with lime and halophytic vegetation (FLAT; 20.8%), grassland (GRAS; 20.8%), wooded vegetation (mostly tamarisk *Tamarix* spp., alders *Alnus* spp., and brambles *Rubus* spp.) (WOOD; 18.7%), free-water areas (WATR; 10.9%), man-made structures (roads, buildings, etc.) (MSTR; 6.0%) and orchards

(ORCH; 4.2%). To summarize habitat characteristics we ran a Principal Component Analysis (PCA) on the proportion of each habitat type using a var-covariance matrix for both 95% and 50% kernel areas. The first three Principal Components (PC), with eigenvalues > 1, explaining all together > 95% of the total variance for both the 95% and 50% kernel areas (Table 8.1, Table 8.2), were used to compare habitat use between groups using one-way ANOVA tests. using one-way ANOVA tests.

Table 8.1. Factor loadings of a Principal Component Analysis on the relative surfaces of each habitat type for 95% Kernel Area. Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation). * indicates significant correlation between the factor loading and the variables.

Variable	PC1	PC2	PC3
WATR	+0.153	-0.04	-0.074*
WOOD	+0.065*	-0.014	+0.056*
REED	-0.186*	-0.091*	-0.023
ORCH	+0.008	-0.006	+0.017*
MSTR	+0.018*	+0.006	+0.029*
GRAS	+0.014	+0.005	+0.028*
FLAT	-0.072*	+0.140*	-0.033
Eigenvalue	0.068	0.030	0.012
% Variance	60.1	26.5	10.7

Table 8.2. Factor loadings of a Principal Component Analysis on the relative surfaces of each habitat type for 50% Kernel Area. Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation). * indicates significant correlation between the factor loading and the variables.

Variable	PC1	PC2	PC3
WATR	+0.183*	+0.142*	-0.077
WOOD	+0.035	+0.045*	+0.099*
REED	-0.279*	+0.052	-0.043
ORCH	+0.000	+0.002	+0.003
MSTR	+0.007	+0.007	+0.034*
GRAS	+0.002	+0.003	+0.016*
FLAT	+0.052	-0.252*	-0.034
Eigenvalue	0.115	0.088	0.020
% Variance	50.7	38.8	8.9

For 95% kernel areas, home ranges with positive PC1 scores tended to have a lower proportion of reed-beds and tidal flats, and a higher proportion of woodland and man-made structures. High scores of PC2 were related to a lower proportion of reed-beds and more tidal flats in home ranges. PC3 was positively correlated with a higher proportion of woodland, orchards, man-made structures and grassland, and with less free-water areas. For core areas, high PC1 values indicated the presence of a higher proportion of free-water zones and a low incidence of reed-beds. Core areas with high PC2 scores had a high proportion of free-water surfaces and woods but less tidal flats. Finally, PC3 was related to higher proportions of woodland, man-made structures and grassland.

We also investigated to what extent the home range area depended on (1) habitat, (2) the fuel load of a bird, and (3) the abundance of co-specifics. For that, we ran a stepwise linear regression on the 95% and 50% kernel areas with habitat type (PC1, PC2 and PC3), fuel load (here calculated as a body mass/wing length ratio), and the abundance of co-specifics (here calculated as the mean number of captures of Reed Warblers during the survey period of each individual). The survey initiation date and the number of locations of each surveyed bird was also included as additional independent variables, since home range area is (or can be) positively correlated with the number of locations (Chernetsov & Mukhin 2006) and vary along the migratory season. Stepwise linear regressions were run for each study group (local adult, migrating adult and first-year birds).

Finally, we ran a one-way ANOVA to test whether fuel deposition rate varied between groups. Fuel deposition rate fitted a normal distribution (K-S test: $p > 0.05$). This was calculated as the weight difference between the first and last capture of an individual during the same autumn migration period, divided by the number of days between captures. For that, we used data from Reed Warblers captured daily at Jaizubia following a standardized protocol between mid-July to late September of 2007 to 2011 (see Sampling protocol and survey method by radio tracking for further details). Individuals were assigned to the different groups using the same previously described criteria (see Sampling protocol and survey method). We excluded individuals recaptured the day after the first capture, so as to avoid a possible handling effect on fuel deposition rate (Schwilch & Jenni 2001).

All data analyses were run with SPSS 15.0 and PAST software.

8.4. Results

Overall, we surveyed 12 local adult, 11 migrating first-year, and 11 migrating adult birds (4 Reed Warblers with less than 10 locations excluded). Most of our birds were low-fuelled (fat scores ≤ 3 of a scale ranging from 0 to 8) although three Reed Warblers (two local ones and one migrating adult) showed a fat score of 4 and one migrating adult of 5. The individual survey period ranged from 2 to 15 days (mean ± SE: 7.7 ± 0.5 days) and the number of survey points per bird varied from 11 to 80 (mean: 46.2 ± 3.4 locations). Mean home ranges for each type of bird are included in Table 8.3.

Table 8.3. Mean (± SE) home range (MCP and 95% Kernel Area) and core area (50% Kernel Area) sizes for migrating first-year Reed Warblers, local adults and migrating adults. Also shown are the maximum distance between daily centroids, and the mean distance between centroids on consecutive days.

	Local Adults	Migrating First-year Birds	Migrating Adults
MCP (ha)	1.57 ± 0.34	3.33 ± 0.65	1.45 ± 0.41
	(0.24-3.51)	(0.01-7.70)	(0.14-4.45)
Kernel 95% (ha)	1.94 ± 0.059	5.43 ± 0.30	1.39 ± 0.28
	(0.30-6.22)	(0.86-3.86)	(0.31-2.66)
Kernel 50% (ha)	0.43 ± 0.14	0.52 ± 0.08	0.31 ± 0.06
	(0.06-1.59)	(0.11-0.93)	(0.05-6.57)
Max. Distance (m)	97.4 ± 13.0	232.0 ± 54.0	90.5 ± 20.6
	(21.9-162.9)	(32.6-650.8)	(26.1-241.1)
Mean Distance (m)	31.7 ± 4.3	92.7 ± 28.6	35.2 ± 5.6
	(12.8-57.7)	(32.9-345.6)	(9.6-69.8)

Home range size varied between groups for both the 95% kernel area ($F_{3,34} = 5.599$, $P = 0.004$) and the MCP ($F_{3,34} = 3.578$, $P = 0.026$), with the number of points also having a significant effect for both the MCP ($F_{1,34} = 5.090$, $P = 0.032$) and the 95% kernel area ($F_{1,34} = 4.478$, $P = 0.043$). An *a posteriori* Bonferroni test did not show significant differences between groups for the 95% kernel area, but for the MCP migrating first-year birds had significantly larger home ranges than adults, both local ($P =$

0.015) and in migration (P = 0.029). There were no significant differences between adults (P = 1.000). Core areas varied between groups ($F_{3,34}$ = 5.536, P = 0.004) but we did not detect *a posteriori* differences. The number of locations had a significant effect on core area size ($F_{1,34}$ = 6.581, P = 0.016). Date did not show a significant effect on home ranges (95% kernel area $F_{1,34}$ = 0.873, P = 0.358; MCP $F_{1,34}$ = 1.392, P = 0.248) nor on core areas ($F_{1,34}$ = 0.482, P = 0.493). For Reed Warblers tracked simultaneously during more than 2 consecutive days (one group of 3 local adults and 2 first-year migrants, plus another group of 4 migrating adults and 2 first-year migrants), core areas overlapped amongst individuals from the different groups (Fig. 8.1).

The mean distance between the centroids on consecutive days were larger in migrating first-year birds ($F_{3,34}$ = 7.715, P < 0.001) than in local or migrating adults (Bonferroni test P = 0.003 and P = 0.002 respectively). On average, adults moved similar distances each day (Bonferroni test P =1.000). The same result was obtained for the maximum distance between daily centroids ($F_{3,34}$ = 8.438, P < 0.001) with first-year birds covering longer distances than adults (Bonferroni tests, local adults P = 0.008, migrating adults P = 0.003). The number of surveying days had a significant effect on the maximum distance between daily centroids ($F_{1,34}$ = 8.042, P = 0.008), but not on the mean daily distance between consecutive days ($F_{1,34}$ = 0.457, P

= 0.504), whereas the opposite result occurred for date (maximum distance $F_{1,34} = 5.545$, $P = 0.026$; daily distance $F_{1,34} = 1.749$, $P = 0.196$).

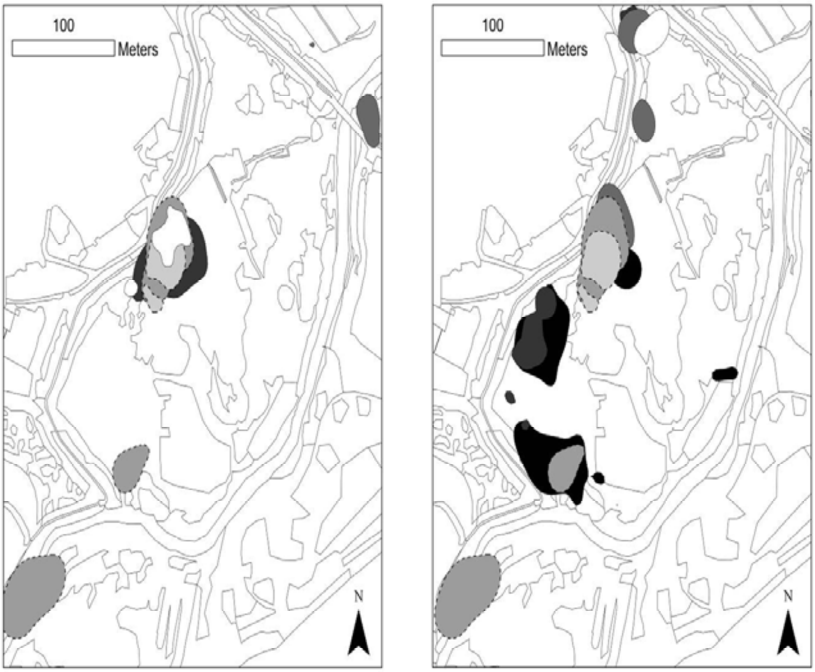


Figure 8.1. Core area (50% kernel areas) overlap for Reed Warblers tracked simultaneously on more than two consecutive days (left, 3 local adults and 2 first-year migrants; right, 4 migrating adults and 2 first-year migrating Reed Warblers). Different colors correspond to the core areas of different individuals. Dotted margins correspond to first-year individuals and continuous ones to adults (left, locals; right, migrating individuals).

The main habitats contained in the home ranges (95% kernel area) and core areas (50% kernel area) of all groups were reed-beds and tidal flats (Fig. 8.2). No significant differences ($P > 0.05$) were found between groups in the 3 main principal component values for home ranges and core areas (Fig. 8.3), indicating that habitat composition in home ranges and core areas did not differ amongst groups.

Stepwise linear regressions on both 95% kernel areas and core areas sizes for the whole data set with their 3 main principal components, body mass (weight/wing length), Reed Warbler abundance, survey initiation date and number of locations as independent variables, did not include any of these variables. However, when considering each group separately, the number of locations and PC1 had a negative effect on core area size for first-year birds (Table 8.4). Hence, larger core areas in first-year birds tended to be related to a higher proportion of reed-beds and a lower proportion of free-water surfaces.

The mean fuel deposition rate (± SE) in migrating first-year birds was 0.06 ± 0.05 g/day, 0.09 ± 0.04 g/day in local adults, and 0.26 ± 0.14 g/day in migrating adults. No significant differences were detected ($F_{1,85} = 1.964$, $P = 0.147$).

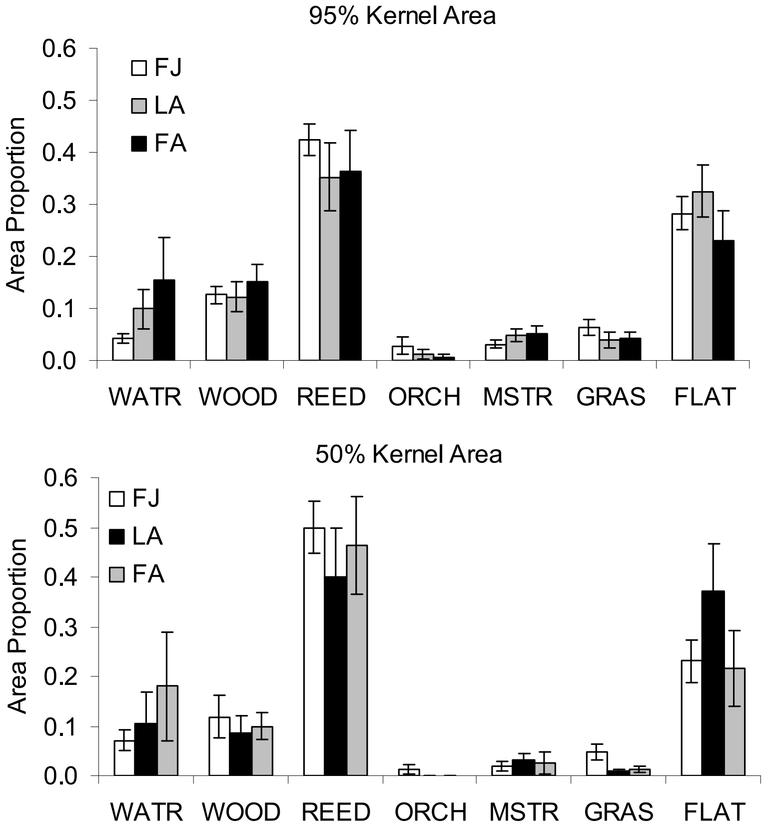


Figure 8.2. Proportion (mean ± SE) of habitat types present in Reed Warbler home ranges. Different types of birds have been considered separately: FY, migrating first-year birds; LA, local adult birds; MA, migrating adult birds. Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation).

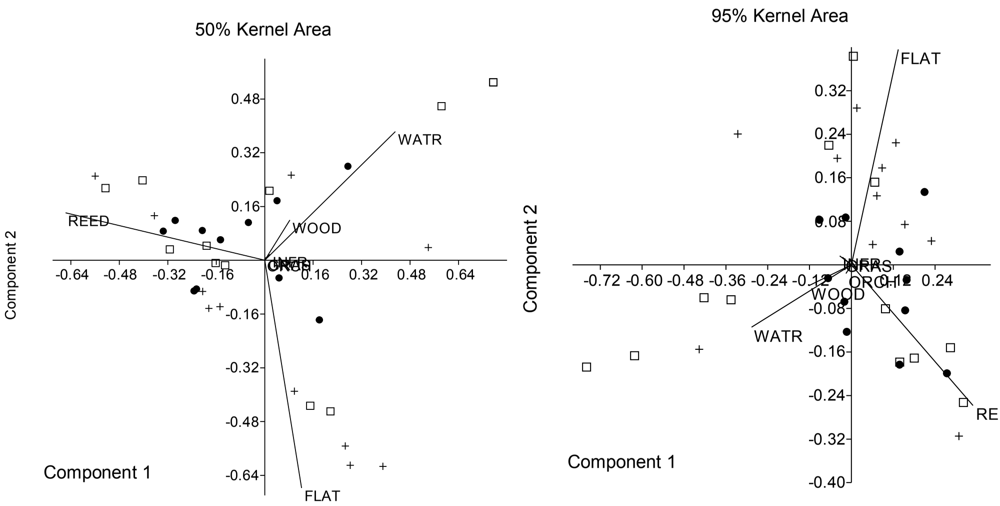


Figure 8.3. Biplots from Principal Component Analyses on the surface proportion of each habitat type for 50% and 95% Kernel Area. Dots, crosses and squares are the home ranges of migrating first-year Reed Warblers, local adults and migrating adults respectively. Abbreviations: WATR, free water area; WOOD, woodlands; REED, reed-beds; ORCH, orchards; MSTR, man-made structures; GRAS, grasslands; FLAT, tidal flats (lime surfaces with halophytic vegetation).

Table 8.4. Variables introduced in a stepwise linear regression predicting core range size in migrating first-year birds, in relation to several factors. Abbreviations: POINTS, number of survey points; PC1, Component 1 obtained from a PCA on the relative habitat surfaces. Excluded variables were: PC2, PC3, body mass, Reed Warbler abundance and date.

Variable	*B*-parameters (non-standardized)	SE(*B*)	*P*
Constant	10194.9	921.811	<0.001
POINTS	-108.7	17.0	<0.001
PC1	-3468.5	717.2	0.002

8.5. Discussion

Spatial ecology is an aspect of stopover ecology which has barely been studied in Reed Warblers to date and the results which have been obtained differ depending on the sites (Bibby & Green 1981; Chernetsov & Titov 2001). Moreover, with the exception of the aquatic warbler *A. paludicola*, a globally threatened species which has been the subject of a few studies (Provost et al. 2010; Arbeiter & Tegetmeyer 2011), no detailed information on home range size at stopover sites exists for other *Acrocephalus* warblers, including Reed Warblers.

Chernetsov & Titov (2001) concluded that, during the autumn migration period, Reed Warblers moved randomly over relatively large areas throughout a stopover site in northern Europe. By contrast, in Portugal, Bibby & Green (1981) observed that stopping-over Reed Warblers tended to move within a very small area [restricted to 80 m away from a fixed point (aprox. 2 ha) during 150 minutes]. In Jaizubia, we found that Reed Warblers occupied smaller areas than the whole stopover site, which would be in agreement with what was described by Bibby & Green (1981). However, the conclusion drawn by Bibby & Green (1981) was obtained from only a short sampling period, so it should be considered very cautiously. There has been discussion that the spatial ecology of migrants at stopover sites is influenced by food availability and the spatial distribution of prey (Chernetsov & Bolshakov 2006). Thus it could be possible that, for Reed Warblers in particular, the use of true home ranges or, alternatively, the vagrancy over relatively large areas could be determined by the type and availability of prey (Chernetsov & Manukyan 1999; Chernetsov & Titov 2001; Chernetsov & Bolshakov 2006). Food availability can change as season progresses (Bibby & Green 1981). However, in this case, home ranges size was not affected by date, although the maximum distance covered during the stopover period varied depending on when birds were captured. If this effect is related to changes in food availability is a hypothesis to be tested in future research.

We observed that adults, either locals or migrants, settled in smaller home ranges than migrating first-year birds. Moreover, first-year birds moved more than adults, indicating more erratic displacements through the study site. This result is in agreement with the idea that first-year birds find problems in settling in a well-defined, small home range. This could be due to the fact that (1) they are less efficient foragers than adults (Heise & Moore 2003) so they must cover wider areas to find sufficient food, and/or (2) they are socially subordinate (Chernetsov 2006), and hence could be displaced by dominant adults. Nevertheless, the core area did not differ between groups. Fuel deposition rates did not differ statistically between migrant first-year birds and adult Reed Warblers (either locals or migrants), suggesting that, despite needing to cover wider areas, migrant first-year birds would able to reach similar rates of fuel accumulation to adult birds. However, first-year individuals showed, on average, considerably lower fuelling rates than adults despite the lack of significant differences, which could be biologically relevant.

Rappole & Warner (1976) reported how territorial behaviour in relation to conspecifics changed depending on their physiological state, with individuals who aimed to accumulate high fat reserves being aggressively territorial. In here, home range size was independent of Reed Warbler density and condition. The lack of density-dependent effects on home range size supports the hypothesis that home ranges are not true territories (as e.g. found in other passerines that also feed on insects; Lindström et al. 1990). This is also demonstrated by the fact that overlapping of home ranges existed amongst all groups, even for core areas. The different results presented here compared with those in Rappole & Warner (1976) are likely to be due to the fact that Reed Warblers do not accumulate massive fuel reserves in northern Iberia (Schaub & Jenni 2000a), and thus competition for resources is lower. Migrant fuel loads have also been shown to influence spatial behaviour at stopover sites in two different ways. Previous works have shown that fat birds are less mobile than lean ones, since they do not aim to refuel, preferring to save energy (Bairlein 1987; Titov 1999a, b). Alternatively, it has been proposed that fat birds might invest more time and energy looking for optimal areas within a stopover site (Chernetsov 2006). In our study we did not find any effect of body condition on spatial behaviour (as in Chernetsov & Mukhin 2006). The lack of a relationship between body condition and stopover behaviour could be the result of the presence of fat Reed Warblers performing both of the above described behaviours (Chernetsov 2006). Also, it must be considered that we did not survey very high-fuelled individuals and hence our conclusions in relation to body mass may be biased.

Habitat use did not differ between first-year birds and adult birds, both when considering the 95% and the 50% range areas. Overall, home ranges were established in zones with both tidal flats and reed-beds. Additionally, the core area size in juveniles was directly related to the proportion of reed-beds and inversely to the proportion of free-water surfaces. This result indicates that when first-year birds settled in a home range, they intensively used the proportion of suitable habitat contained within it. So, if a home range contains a high proportion of reed-beds, the entire surface would be used as core area, whereas if the proportion is low, with a high proportion of free water, only the small suitable habitat surface would be exploited, thus reducing the core area size.

The fact that juveniles had higher mobility than adults and experienced lower fuelling rates could be the result of the existence of an age-related discrimination and hence a despotic component (Fretwell & Lucas 1969). By contrast, the proportion of habitats in home ranges was similar among groups and fitness differences could arise from age-related efficiency differences (Heise & Moore 2003) and not from despotic exclusion, which would be more in agreement with an ideal-free pattern (Fretwell & Lucas 1969). Overall, Fretwell & Lucas′ (1969) ideal models turned out to be too simplistic (or unrealistic) to explain Reed Warblers' spatial distribution in our study case, as has been found previously (reviewed by Newton 1998; Piper 2011), although they constitute a useful theoretical frame to explain the spatial distribution of organisms. Recent studies (reviewed by Piper 2011) are starting to provide clues about other underlying mechanisms that may play an important role in determining the spatial distribution and habitat selection of organisms. One of these is site familiarity, which implies that individuals learn and remember features of an inhabited space and use that information to improve fitness. However, given the difficulties in measuring its impact, the inclusion of site familiarity in spatial use studies is still underrepresented (Piper 2011). The understanding of the mechanisms that determine the spatial distribution and habitat use of birds at stopover sites is a complex issue and this is a field of behavioural ecology which demands further investigation.

8.6. Acknowledgements

We wish to thank A. Mendiburu and R. Piculo, who collaborated in the ringing activities, as well as G. Deán and I. López who assisted us in the radio-tracking surveys. The Gipuzkoa Administration authorized the ringing activities and the radio-tracking. M. Andueza was funded by a doctoral fellowship from the Spanish Ministry of Education. The work was partly supported by the Spanish Ministry of Science and Innovation (project CGL2010-21933-C02-02).

CAPÍTULO 9

Discusión general

En esta Tesis Doctoral se han estudiado diversos aspectos sobre la migración postnupcial de las aves trans-saharianas empleando como modelos dos especies del género *Acrocephalus*, el carricero común y el carricerín común, en una región clave dentro de las rutas migratorias europeas hacia África: la Península Ibérica. Los resultados obtenidos son de utilidad para profundizar en el entendimiento de cómo se organiza la migración y, por tanto, cómo se modelan las estrategias migratorias. Además, un conocimiento más detallado de las estrategias migratorias en la Península Ibérica tiene interés para la gestión y conservación de estas especies y los hábitats empleados por ellas durante la migración, especialmente en un escenario de cambio global en el que se viene observando un avance del desierto del Sáhara hacia el sur (Zwarts et al. 2009), y una progresiva desertificación de la región circum-mediterránea (Puigdefábregas & Mendizabal 1998). Los principales resultados obtenidos se discuten a continuación.

9.1. Organización espacial de la migración

Se ha analizado qué factores explican el patrón espacial y la carga de grasa de los carriceros en la Península Ibérica, siendo los más importantes el origen de las aves (Capítulo 3), la distancia al mar Mediterráneo/Atlántico, y la distribución de las áreas de descanso favorables (Capítulo 4).

9.1.1. Conectividad entre áreas de cría y de descanso

Los carriceros mostraron una segregación de poblaciones en la Península Ibérica durante la migración postnupcial de acuerdo a su origen, de forma que los carriceros capturados en zonas más al este en la Península Ibérica provenían de regiones más orientales y más al sur que aquellos capturados en zonas más al oeste (Capítulo 3). A modo ilustrativo, ningún carricero proveniente de las Islas Británicas se capturó en la vertiente mediterránea de la Península. Este resultado apoya la hipótesis de que los carriceros tienden a seguir rutas paralelas entre sus áreas de cría y de descanso según su origen, siguiendo así las rutas más cortas (Newton 2011).

El carricero común muestra una elevada conectividad entre sus áreas de cría en Europa y sus áreas de invernada en África (Procházka et al. 2008). Sin embargo, durante la migración, el grado de conectividad es moderado, dado que se observó cierto grado de solapamiento de poblaciones de distinto origen. El hecho de que el mar Mediterráneo sea notablemente más estrecho en esta región que en su zona central genera un efecto embudo en la Península Ibérica para los migrantes europeos, lo que se traduce en cierto solapamiento poblacional. Asimismo, las diferentes poblaciones europeas que atraviesan la Península por las distintas rutas tienden a converger en la región suroeste para cruzar el mar y atravesar el Sáhara por su costa occidental, donde las condiciones son más favorables (Hilgerloh 1989, 1990; Cantos 1998), lo que explica la alta concentración de carriceros detectada en esta zona. Estos resultados hacen referencia a la población global de carriceros en la Península durante la migración, sin distinguir clases de edad, debido al tamaño muestral disponible. Sin embargo, sería esperable que los adultos mostraran una conectividad mayor que los jóvenes, dado que estos últimos suelen mostrar mayor variabilidad en las direcciones migratorias (Fransson & Stolt 2005).

Los carriceros provenientes de las zonas más occidentales de Europa, especialmente de Reino Unido e Irlanda, recorren menores distancias que aquellos de origen más oriental, por lo que este hecho debería reflejarse en su morfología alar (García-Peiró 2003; Chernetsov 2004; Förschler & Bairlein 2010). Los carriceros capturados en el oeste peninsular, originarios principalmente del Reino Unido e Irlanda, mostraron alas significativamente más cortas que los capturados en las otras regiones peninsulares, resultados que estarían de acuerdo con lo esperado. Sin embargo, no se detectaron diferencias entre el centro y este peninsular, donde los carriceros capturados provienen mayoritariamente de la Europa continental. Por tanto, parecen existir diferencias biométricas en la longitud alar entre las poblaciones británicas y el resto de Europa, pero no entre las distintas poblaciones de Europa continental.

9.1.2. Variación geográfica en las cargas de grasa

Las cargas de grasa en la primera captura para los carriceros juveniles en la Península Ibérica (Capítulo 4) fueron bajas en comparación con otras áreas de descanso europeas (Chernetsov 1999; Schaub & Jenni 2000a). Lo mismo se observa si se comparan los valores obtenidos en el sur peninsular (Capítulo 4) con los de otros trabajos de la misma zona (Peiro 1995; Schaub & Jenni 2000a; Hilgerloh & Wiltschko 2000). El carricero común puede mostrar una gran variabilidad interanual en las cargas de grasa, incluso en las proximidades de una barrera geográfica (Yosef & Chernetsov 2005) lo que podría explicar las diferencias observadas con respecto a la bibliografía preexistente. Complementariamente, es posible que los individuos más pesados no estén bien representados en nuestra muestra, dado que, debido a su baja movilidad (Bairlein 1987; Titov 1999a, b; Chernetsov 2006), su probabilidad de captura es baja.

Los carriceros capturados en el este peninsular mostraron en promedio una mayor carga de grasa en sitios localizados más al norte, mientras que en el oeste la tendencia observada fue opuesta. En la ruta central, lugares del norte y sur mostraron valores similares y relativamente elevados (Jaizubia y Vejer). Asimismo, lugares muy próximos mostraron cargas de grasa muy diferentes. Por ejemplo, en Manecorro (Doñana), donde la vegetación predominante era arbustiva, y por tanto de calidad sub-óptima para los carriceros, la condición corporal promedio fue notablemente más baja que en un carrizal cercano (Vejer), donde los carriceros mostraron cargas elevadas de grasa. Así, la calidad de las áreas de descanso parece jugar un papel importante, determinando la condición corporal en las mismas (Ktitorov et al. 2008). Por tanto, a un nivel regional, la estrategia de acumulación de grasa puede ser flexible y modelada por otros factores más allá de la distancia a una barrera geográfica, como puede ser la distribución geográfica de las áreas de descanso óptimas. Esto explicaría los diferentes patrones de cargas de grasa observados en las distintas rutas migratorias peninsulares (Moore & Aborn 2000; Fransson et al. 2008; Chernetsov 2013), que podrían estar relacionados, además, con una estrategia diferencial de preparación para cruzar el mar según la ruta migratoria seguida.

En el este peninsular la carga de grasa se incrementó con la fecha, de acuerdo a lo esperado (Schaub & Jenni 2000a; Bayly 2006). Sin embargo, en el centro y oeste peninsular se mantuvo constante. Un paso diferencial de las distintas poblaciones europeas entre rutas migratorias dentro de la Península Ibérica (Capítulo 3) puede ser responsable de las diferencias observadas (Maggini et al. 2013).

Los rangos potenciales promedio de vuelo, desde cada estación, mostraron que, incluso desde el sur de la Península Ibérica, las aves podrían alcanzar el norte de África, pero no el sur del Sáhara, por lo que las reservas para cruzar el Sáhara deben ser acumuladas en el norte de África (Schaub & Jenni 2000a; Neto et al. 2008; Maggini & Bairlein 2011). Este resultado parece contradecir otros trabajos previos sobre esta especie (Arizaga et al. 2011d; Hilgerloh & Wiltschko 2000). Sin embargo, aquí los rangos se han estimado considerando una estrategia de vuelo intermitente (Delingat et al. 2006; Schmaljohann et al. 2007) y teniendo en cuenta el coste energético de las paradas diurnas (Wikelski et al. 2003), lo que se ajusta más a la realidad. De todos modos los rangos reales pueden ser mayores debido a que se calcularon con la carga de grasa en la primera captura y no la de partida. Tampoco se consideró la influencia de las condiciones de viento (Weber & Hedenström 2000; Dänhardt & Lindström 2001; Tsvey et al. 2007; Morganti et al. 2011), de forma que, según la frecuencia de vientos favorables (vientos de cola frente a vientos de cara), estos rangos potenciales pueden verse incrementados o disminuidos. Asimismo, los resultados presentados se refieren a individuos juveniles, por lo que es probable que los adultos presenten rangos de vuelo mayores (Woodrey & Moore 1997). Por tanto, no se puede descartar que haya ejemplares que, bajo condiciones de viento favorables, puedan alcanzar África tropical con las reservas energéticas acumuladas en la Península Ibérica.

9.2. Comportamiento en áreas de descanso

Se ha estudiado qué factores influyen en la estancia de las aves en migración en las áreas de descanso, determinando el efecto de algunos de ellos en las decisiones de parar (Capítulo 5) y abandonar (Capítulo 6) uno de éstos lugares, así como la variación de su importancia relativa según la proximidad a una barrera geográfica (Capítulo 7). Adicionalmente, se ha analizado el comportamiento espacial en un área de descanso (Capítulo 8).

9.2.1. Factores que influyen en las decisiones de parar y abandonar un área de descanso

La lluvia aumentó las probabilidades de parar, e incrementó significativamente el número de carricerines capturados en Jaizubia (Capítulo 5). Estos resultados indican que las aves tienden a interrumpir el vuelo bajo condiciones de lluvia (Pyle et al. 1993; Barriocanal et al. 2002; Yaukey & Powel 2008; Arizaga et al. 2011a), y a parar en lugares que no son áreas de descanso y/o alimentación prioritarias (como Jaizubia para el carricerín común) debido, probablemente, a los efectos adversos de ésta sobre las aves (Newton 2007). Sin embargo, las condiciones de viento, contrariamente a lo registrado por Saino et al. (2010) en islas del Mediterráneo, no mostraron influencia en la probabilidad de parar. Por tanto, una vez iniciados los vuelos migratorios, el efecto del viento podría variar según las características de las regiones a sobrevolar. En el caso del mar abierto (Saino et al. 2010), las aves aprovecharían las escasas islas disponibles para evitar volar sobre éste con vientos desfavorables, lo que podría comprometer seriamente su supervivencia. Por el contrario, al sobrevolar áreas continentales donde las posibilidades de parar en caso de necesidad son constantes, como en este caso, el hecho de continuar volando con vientos de cara no resultaría tan arriesgado para las aves. Así, desde un punto de vista de optimización de la migración, sería mejor seguir volando sobre tierra firme con vientos de cara, que interrumpir la migración y parar en un lugar cercano al de partida (Erni et al. 2002a).

Respecto a las decisiones de abandonar Jaizubia, los factores más importantes que influyeron en las probabilidades de partir para los carricerines fueron la fecha, la densidad de congéneres y las condiciones de viento (Capítulo 6). Contrariamente a lo esperado, la probabilidad de partir fue mayor para bajas densidades de carricerines. Podemos recurrir a tres hipótesis para explicar el resultado observado. En primer lugar, dado que los carricerines se alimentan principalmente de áfidos, que suponen una fuente de alimento superabundante, y por tanto no genera competencia por los recursos tróficos (Bibby & Green, 1981; Grandío 1998), la densidad de individuos puede servir de indicador sobre la disponibilidad de alimento para los recién llegados. Por tanto, una baja densidad implicaría una baja disponibilidad trófica, y los carricerines recién llegados abandonarían pronto la zona en busca de otra mejor (Alerstam & Lindström 1990). En segundo lugar, una alta densidad de individuos reduciría el riesgo de depredación individual, permitiendo disminuir la vigilancia anti-depredación, lo que permitiría a las aves experimentar mejores tasas de engorde (Fransson & Weber 1997; Bayly 2006). Por último, conforme avanza la estación, la población de carricerines en migración tiende a disminuir, a la vez que aumenta la probabilidad de partir, por lo que ambos efectos podrían no ser independientes.

La relación positiva entre la fecha y las probabilidades de abandonar Jaizubia apoya la idea de que la presión del tiempo aumenta conforme avanza el periodo migratorio (Bayly 2006, 2007). Sin embargo, este resultado también podría deberse a otros factores externos, como la disminución estacional de la disponibilidad de alimento (Grandío 1999), o bien que las aves más tardías pasan con suficientes reservas, acumuladas en áreas más al norte, y se detienen únicamente para descansar.

Mientras que el viento no tuvo influencia a la hora de interrumpir los vuelos migratorios (Capítulo 5), sí tuvo un efecto relevante en las decisiones de abandonar el área de descanso estudiada. Los carricerines comunes buscaron la asistencia de viento de cola para proseguir con la migración, lo que está de acuerdo con estudios previos (Weber et al. 1998a; Åkesson & Hedenström 2000; Dänhart & Lindström 2001; Åkesson et al. 2002; Schaub et al. 2004; Morganti et al. 2011). Además, los resultados obtenidos sugieren que, cuando se dan condiciones favorables, éstas son aprovechadas por todos los individuos, independientemente de su carga de grasa (Bayly 2007). La lluvia no mostró un efecto significativo posiblemente debido al escaso número de días con precipitación durante el presente estudio.

El comportamiento adoptado en las áreas de descanso por los carriceros juveniles en la Península Ibérica varió según la proximidad a una barrera geográfica, particularmente a la franja de mar Atlántico/Mediterráneo entre el sur peninsular y África (Capítulo 7). En concreto, en el sur peninsular, los carriceros con menor carga de grasa en su primera captura mostraron menor probabilidad de partir que aquellas aves con mayores reservas energéticas. Por el contrario, en el norte peninsular, las decisiones de partir fueron independientes de la carga de grasa. De los resultados obtenidos se deduce que la importancia de la carga de grasa en las decisiones de partir de un área de descanso en carriceros juveniles depende de las condiciones esperables en el siguiente tramo de vuelo. Como consecuencia, en el sur peninsular los carriceros no proseguirían con la migración hasta no disponer de ciertas reservas energéticas para cruzar el mar (Biebach et al. 1986; Bairlein 1985; Weber at al 1998b; Atkinson et al. 2007), que, de acuerdo al Capítulo 4, pueden suponer rangos potenciales de vuelo muy superiores a la distancia que separa la Península Ibérica del norte de África. Contrariamente a lo esperado (Schaub & Jenni 2000b; Bayly 2006), y a lo obtenido para el carricerín común (Capítulo 6), la fecha no mostró un efecto relevante para el carricero común en el periodo de estudio.

Dentro de cada región y, especialmente en el norte peninsular, las probabilidades de partida variaron notablemente, sugiriendo que otros factores más allá de la situación geográfica en relación al mar influyen en dichas probabilidades. Schaub et al. (2008) determinaron la importancia de las tasas de engorde que las aves experimentan en un área de descanso en las decisiones de abandonarla (Schaub et al. 2008). En el norte peninsular, las probabilidades promedio de partir de cada una de las localidades estudiadas fueron independientes de las tasas de engorde promedio experimentadas por las aves en cada una de ellas. El hecho de que las probabilidades de partir sean independientes de las tasas de engorde, resultaría en aves que abandonan las áreas de descanso con diferentes cargas de grasa (altas, bajas e intermedias), de acuerdo al modelo de minimización del tiempo de la migración, que asume una relación positiva entre las cargas de grasa y las tasas de engorde experimentadas (a mayores tasas de engorde experimentadas, mayores cargas de grasa alcanzadas y viceversa, Alerstam & Lindström 1990). En el sur peninsular, tanto las probabilidades de partida, como las tasas de engorde promedio, fueron similares entre sitios, por lo que no se pudo establecer ninguna relación entre ambas variables. Por otra parte, las tasas de engorde promedio experimentadas en las distintas áreas de descanso ibéricas fueron independientes de la disponibilidad trófica, por lo que otros factores más allá de la cantidad de alimento parecen modificar las tasas de engorde experimentadas por las aves (e.g. riesgo de depredación, Schaub & Jenni 2000b; Bayly 2006).

Contrariamente a lo esperado (Åkesson & Hedentröm 2000; Dänhardt & Lindström 2001; Schaub et al. 2004; Tsvey et al. 2007), y a lo obtenido para el carricerín común (Capítulo 6), las probabilidades de partir en el carricero común fueron independientes de las condiciones de viento, incluso antes de cruzar el mar. De acuerdo con Karlsson et al. (2011), el hecho de que las aves seleccionen o no determinadas condiciones de viento para partir está relacionado con la organización general de la migración. Así, en aves que migran realizando vuelos cortos (e.g. carricero común) sobre áreas con abundantes oportunidades de parar, resultaría más eficiente abandonar un área de descanso independientemente de las condiciones de viento, pues los costes energéticos y de tiempo de esperar condiciones favorables podrían ser más elevados que volar con vientos de cara. El hecho de que las aves no busquen la asistencia del viento para cruzar el mar, puede deberse a que la distancia que separa el sur peninsular del norte de África no sea de tal magnitud como para que sea necesaria una selección de las condiciones de viento en el momento de partir. Asimismo, la acumulación de importantes cargas de grasa antes del mar (Capítulo 4) sería suficiente para compensar posibles derivas debidas a condiciones de viento adversas.

9.2.2. Distribución espacial y selección de hábitat en un área de descanso

En general, los carriceros se movieron en áreas de campeo bien definidas, de menor tamaño que la superficie total de la marisma de Jaizubia (Capítulo 8), lo que apoya lo descrito por Bibby & Green (1981) en Portugal. Sin embargo, este resultado contrasta con lo obtenido por Chernetsov & Titov (2001) en el norte de Europa, donde los carriceros se movieron aleatoriamente por toda el área de estudio. Dado el carácter generalista del carricero común (Bibby & Green 1983; Chernetsov & Manukyan 1999), las diferencias en el comportamiento espacial según zonas pueden estar determinadas por la disponibilidad y distribución de las presas potenciales (Chernetsov 2012). Las áreas de campeo establecidas no fueron territorios exclusivos defendidos, dado que hubo solapamiento entre individuos, tanto locales como en migración, jóvenes y adultos.

Los adultos, locales y en migración, establecieron áreas de campeo de menor tamaño que los juveniles, quienes mostraron unos desplazamientos más erráticos y amplios por la zona de estudio. La dificultad de los jóvenes para establecer áreas de campeo puede deberse a que son menos eficientes a la hora de alimentarse (Heise & Moore 2003) y/o a que socialmente están subordinados a los adultos, y por tanto son desplazados por éstos (Chernetsov 2006). Adicionalmente, los carriceros juveniles experimentaron tasas de engorde inferiores a los adultos, a pesar de que las diferencias no fueron estadísticamente significativas. Por el contrario, el uso de los hábitats disponibles en la zona fue similar entre grupos, de forma que los carriceros, independientemente de su edad, ocuparon principalmente zonas con carrizo y llanuras mareales.

En general, los modelos de Fretwell & Lucas (1696), aunque suponen un buen marco teórico de inicio, resultan demasiado simples para explicar el comportamiento espacial de los carriceros observado en Jaizubia. Las diferencias observadas entre jóvenes y adultos sugieren la existencia de un componente despótico, de forma que los jóvenes serían desplazados por los adultos, socialmente dominantes. Sin embargo, la proporción de hábitats en las áreas de campeo fue similar lo que, sumado al hecho de que las diferencias en las tasas de engorde pueden ser resultado de la ineficiencia juvenil y no de la exclusión social, se ajustaría más a un modelo libre (Fretwell & Lucas 1969). Recientemente se ha empezado a poner de manifiesto la importancia de otros factores para explicar el comportamiento espacial de los organismos, como la capacidad de éstos para aprender y recordar aspectos de un área determinada y aplicar dicho conocimiento en su beneficio (Piper 2011). Sin embargo, aún se desconocen los mecanismos últimos que modelan el uso espacial de las aves en las áreas de descanso.

CAPÍTULO 10

Conclusiones

Las principales conclusiones obtenidas en esta Tesis Doctoral se enumeran a continuación:

1) Durante el periodo de migración postnupcial, existe una segregación espacial con cierto solapamiento de las distintas poblaciones europeas de carricero común en la Península Ibérica según su origen geográfico, que resulta en la existencia de diferencias biométricas (longitud alar) entre los individuos capturados en las distintas rutas ibéricas. Por tanto, esta especie mantiene una conectividad moderada entre sus áreas de cría europeas y las áreas de descanso en la Península Ibérica.

2) La Península Ibérica, principalmente la zona sur, es empleada por los carriceros comunes para acumular las reservas de grasa necesarias para llegar al norte de África, donde deben preparase para cruzar el desierto del Sáhara. Sin embargo, la distancia a la costa sur no es el único factor que modela la estrategia de acumulación de grasa en la Península, dado que parecen existir factores geográficos asociados a la distribución de áreas de descanso favorables.

3) Los modelos de captura-recaptura constituyen una metodología útil para estudiar el efecto de ciertos factores (e.g. condiciones meteorológicas) en las decisiones de parar en un área de descanso. En particular, mostraron que la lluvia incrementa las probabilidades de parar para el carricerín común.

4) Las decisiones de abandonar un área de descanso del N de la Península Ibérica en el carricerín común están gobernadas principalmente por las condiciones de viento, la fecha y la abundancia de congéneres. La probabilidad de partir se incrementó con vientos de cola y conforme avanzaba la estación, mientras que disminuyó al aumentar el número de carricerines.

5) La proximidad de una barrera geográfica modifica la importancia relativa de diversos factores en las decisiones de abandonar las áreas de descanso para proseguir con la migración. En particular, la carga de grasa fue un factor clave en el sur peninsular (esto es, justo frente a la barrera geográfica), mientras que en el norte, al igual que en el caso de los carricerines, los carriceros partieron independientemente de ésta.

6) Las diferencias en la organización de la migración en el carricero y el carricerín común provoca que el efecto del viento en las decisiones de partir para cada especie sea diferente. Al

contrario que en el carricerín común, las decisiones de proseguir con la migración en el carricero común fueron independientes de las condiciones de viento, incluso antes de cruzar una barrera geográfica.

7) Los carriceros comunes establecen territorios no exclusivos (con solapamiento entre individuos) en Jaizubia, que abarcan principalmente carrizo y llanuras mareales. Los jóvenes cubrieron mayores áreas y distancias que los adultos pero no hubo diferencias entre adultos locales y en migración.

8) La distribución espacial observada para el carricero común en Jaizubia no se ajustó con claridad ni a una distribución libre ni despótica. Por tanto, otros mecanismos más allá de la densidad de individuos y calidad de los hábitats disponibles podrían explicar el uso espacial de las aves en las áreas de descanso.

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