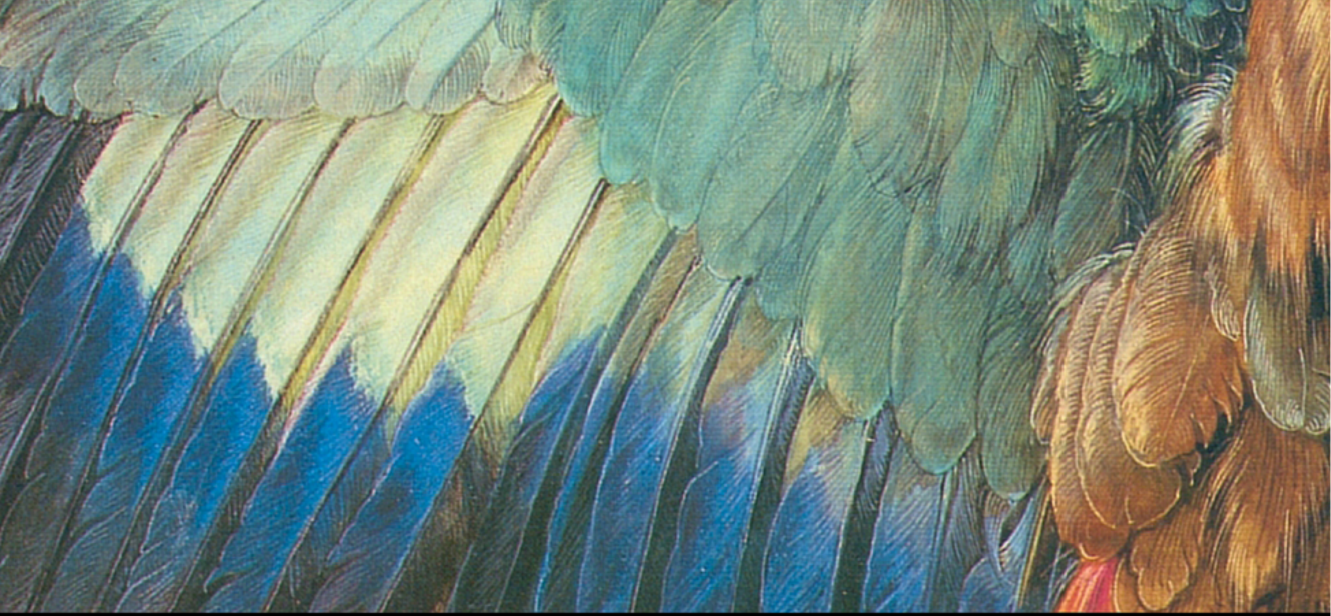

SELECCIÓN DE HÁBITAT Y ECOLOGÍA DEL MOVIMIENTO EN UN MIGRANTE TRANSAHARIANO

CONTRIBUCIÓN A LA CONSERVACIÓN DE LA CARRACA EUROPEA

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Tesis Doctoral

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Memoria presentada por el Licenciado en
Ciencias Ambientales Juan Rodríguez Ruiz para optar
al título de Doctor por la Universidad Pablo de Olavide

Fdo: Juan Rodríguez Ruiz

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CERTIFICAN

Que los trabajos de investigación desarrollados en la **Memoria de Tesis Doctoral** “Selección de Hábitat y Ecología del Movimiento en un Migrante Transahariano: Contribución a la Conservación de la Carraca Europea”, son **aptos** para ser presentados por el **Ldo. Juan Rodríguez Ruiz** ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad Pablo de Olavide.

Y para que así conste, y en cumplimiento de las disposiciones legales vigente, extendemos el presente certificado a 18 de marzo de 2016.

Firma Director: Dr. Jesús Avilés Regodón

Firma Directora: Dra. Deseada Parejo Mora

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Firma Tutor: Dr. David Serrano Larraz

Serrano

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RESUMEN

La carraca europea *Coracias garrulus* es un ave migradora de larga distancia que ha experimentado un fuerte declive poblacional en las últimas décadas. Es un ave cavernícola no excavadora asociada principalmente a hábitats agrícolas, áridos y esteparios. Las principales amenazas que sufre esta especie en sus zonas de cría son la reducción y degradación del hábitat óptimo de alimentación y la pérdida de lugares de nidificación. Fuera de las zonas de reproducción, el conocimiento sobre sus problemas de conservación es muy escaso. Su clasificación como especie amenazada ha sufrido diversos cambios en los últimos años a pesar de la falta de información existente acerca de su situación poblacional, tendencias y patrones de movimiento, tanto dispersivos como migratorios. El objetivo de esta tesis doctoral es identificar los factores que pueden determinar la eficacia biológica de la carraca en todos los momentos de su ciclo vital para contribuir de manera efectiva a su conservación. Para ello se profundiza en el estudio de la historia vital de la especie, tanto durante su etapa reproductora, en una población asentada en cajas-nido en el sudeste español mediante el estudio de individuos marcados individualmente, como durante la migración e invernada en África, a partir de datos obtenidos mediante dispositivos de seguimiento por satélite y geolocalizadores colocados en diversas poblaciones ibéricas.

En el capítulo I de esta tesis, se estudian los factores que afectan a la probabilidad de ocupación y el éxito reproductor de las carracas en cajas-nido durante un período de tres años. Los resultados muestran que el grado de exposición o visibilidad de la caja-nido y su orientación, así como el grado de transformación del hábitat circundante son los factores más importantes que determinan la preferencia de uso de las cajas-nido por las carracas. En concreto, las carracas tendieron a ocupar cajas-nido más expuestas, en localizaciones más apartadas de la autovía y en zonas menos transformadas, y con una preferencia en orientación estacional hacia el noroeste al principio de la temporada y al sureste hacia el final. Sin embargo, el análisis de la productividad de las carracas reveló un desajuste entre

las preferencias por determinadas características de las cajas y el posterior éxito reproductor en las mismas. En las cajas-nido más expuestas y preferidas por las carracas, estas mostraban un éxito reproductor menor que en cajas-nido menos expuestas, lo cual sugiere la posibilidad de que las cajas-nido instaladas puedan funcionar como trampas ecológicas, ejerciendo una atracción hacia zonas menos favorables para la reproducción de la especie.

El estudio de las causas y consecuencias de la dispersión en relación a la edad y el sexo de los individuos es imprescindible para entender la dinámica de una población y establecer medidas concretas de conservación. En el capítulo II, estudiamos las causas y consecuencias de la dispersión natal y reproductiva mediante el seguimiento de individuos marcados en la población de estudio durante un período de ocho años. Los resultados de este capítulo muestran que la probabilidad de dispersión reproductiva en las carracas depende de su edad relativa, siendo más fieles a sus territorios de reproducción los individuos de edad mayor. Además, los factores que influyen en la probabilidad de dispersión son distintos para cada sexo, y no se encontró evidencia de que los eventos dispersivos dentro de la población llevaran asociado un cambio en el éxito reproductor. Destacamos también un reclutamiento extraordinariamente bajo, lo que sugiere que nuestra población podría actuar como una población fuente dentro del sistema metapoblacional del sureste ibérico.

En el capitulo III, presentamos por primera vez una descripción precisa de las rutas migratorias de la especie, sus paradas y cuarteles de invernada, además de su comportamiento durante la migración. Mostramos dos rutas migratorias alternativas para las carracas ibéricas durante la migración otoñal, una ruta directa hacia el sur desde las poblaciones del noreste, y un desvío hacia la costa atlántica africana desde las poblaciones del suroeste, lo cual demuestra estrategias diferentes según el origen al afrontar grandes barreras generadas por ambientes extremos como el desierto del Sáhara. Identificamos áreas clave para las paradas de repostaje durante el viaje en la zona del Sahel, concretamente en

los alrededores del Lago Chad, y durante la invernada en Angola, Botswana y Namibia. Además, encontramos una conectividad migratoria débil en la escala espacial estudiada, sugiriendo que los individuos de las poblaciones ibéricas confluyen en invierno en un área restringida, lo que podría determinar una alta vulnerabilidad de la metapoblación ibérica a cualquier cambio ambiental.

A continuación, evaluamos el efecto causado por los dispositivos de seguimiento empleados en los capítulos III y V sobre las carracas y encontramos evidencias de efectos negativos causados tanto en el corto plazo, sobre la reproducción en la misma temporada de colocación de los dispositivos, como a largo plazo, sobre la tasa de recaptura al año siguiente de los individuos equipados con los dispositivos. Señalamos la necesidad de realizar una evaluación previa de estos efectos en las aves migradoras, además de la importancia de considerar un grupo control antes de cualquier estudio de este tipo y sugerimos como medida cautelar para esta especie un límite de 2.5% como máximo del peso relativo de estos dispositivos respecto al peso corporal del individuo para reducir el impacto producido.

En el último capítulo, empleamos modelos de distribución de especies para analizar el uso del hábitat y su rango de distribución y evaluar las posibles amenazas y el grado de protección de las áreas donde inverna. Mostramos que el área de invernada de las carracas ibéricas supone una pequeña porción al noroeste del área total estimada para la especie. Encontramos diferencias entre los factores que caracterizan el nicho ecológico para las carracas ibéricas y para el total de la especie que inverna en el sur de África. Además, el grado de protección de las zonas de invernada ocupadas por las carracas ibéricas y por el total de la población invernante en el sur de África difiere de manera notable, siendo inferior para la especie general que para las carracas ibéricas. En ambos casos la convergencia con zonas degradadas es mayor de la esperada por azar. En global, estos resultados sugieren la necesidad de enfocar los esfuerzos de conservación en África en aquellas zonas degradadas

situadas fuera de las áreas protegidas, donde la transformación de usos, la intensificación agrícola y el mal uso de pesticidas pueden afectar negativamente a la especie.

Por último, presentamos una serie de recomendaciones derivadas de este estudio dirigidas a contribuir en la elaboración de futuras medidas para la reversión de la tendencia poblacional de la carraca y la recuperación de esta carismática especie migradora.

INTRODUCCIÓN

INTRODUCCIÓN

La conservación de las aves migradoras

De las aproximadamente 10,000 especies de aves conocidas en el mundo el 12.5% de ellas se encuentran amenazadas (BirdLife International 2015a). En Europa la situación es comparativamentemente peor, llegando esta proporción al 18% (BirdLife International 2008). El declive poblacional es más acusado entre las aves migradoras europeas, mostrando el 40% de las mismas una tendencia poblacional negativa entre 1970 y 2000 (Sanderson *et al.* 2006). Las especies migradoras se ven afectadas por un amplio rango de condiciones ecológicas durante un ciclo anual, a menudo a distintas escalas geográficas y temporales y, por tanto, son susceptibles de sufrir amenazas de muy diversa índole (Newton 2004, Thaxter *et al.* 2010). Por tanto, la conservación de especies migratorias resulta una tarea compleja que, para ser efectiva, implica la aplicación de medidas en diferentes momentos y lugares. Hasta la fecha, los planes de conservación sobre especies amenazadas han estado sesgados positivamente hacia la especies no migradoras (Pressey *et al.* 2007). De hecho, a nivel mundial, tan sólo un 9% de especies migradoras encuentran refugio en áreas protegidas en todas las fases de su ciclo anual, frente a un 45% de las aves sendentarias (Runge *et al.* 2015). En el caso particular de las aves invernantes en África la situación es igualmente preocupante (Beresford *et al.* 2011). Así, entre las especies migradoras europeas, aquellas que realizan migraciones de larga distancia han experimentado un mayor declive poblacional (Vickery *et al.* 2014), y, de manera más pronunciada, las asociadas a hábitats agrícolas y aquellas que migran a ambientes más áridos (Vickery *et al.* 2014). Este hecho apunta, como causas del declive, principalmente a la pérdida o degradación de hábitat de cría en Europa (Chiron *et al.* 2014) y al efecto de la sequía, en especial en zonas como el Sahel, junto con los intensos cambios en el uso del suelo para aprovechamiento agrícola en África (Zwarts *et al.* 2009).

La creciente preocupación por el estado de conservación de las aves europeas ha traído consigo el desarrollo de una Directiva Europea, directiva Aves, dedicada exclusivamente a mejorar su estado de conservación (Unión Europea 2009). Esta directiva se fundamenta en la toma de medidas de conservación en los lugares de reproducción, y su aplicación ha tenido un efecto desigual en la recuperación de las especies incluídas en su Anexo I

(Sanderson *et al.* 2015). Aunque muchas especies han mejorado su situación significativamente, las aves migradoras de larga distancia no han experimentado cambios positivos en su tendencia poblacional, lo que sugiere que las presiones que afectan a su declive podrían tener lugar fuera de la época reproductora, durante la migración o en sus áreas de invernada (Sanderson *et al.* 2015). En este sentido, algunas evidencias apuntan a que la tasa de mortalidad de las aves migradoras sería mayor durante las fases de migración que en las fases estacionarias de cría e invernada (Sillett y Holmes 2002, Klaassen *et al.* 2014), lo que podría tener consecuencias sobre la dinámica poblacional a largo plazo. Esto sugiere que una mejora en la calidad de los hábitats de cría podría no ser suficiente para compensar los efectos negativos producido por los cambios ambientales o antropogénicos sufridos en las áreas de invernada (Saino et al 2010, Ockendon *et al.* 2012). Por todo ello, la conservación de especies migradoras requiere un conocimiento exhaustivo de todos los factores que puedan influir en la dinámica poblacional a lo largo de un ciclo anual, tanto en las áreas de cría como en las zonas de paso y áreas de invernada.

La carraca Europea: status y tendencia

La carraca europea *Coracias garrulus* es un ave migradora de larga distancia que se encuentra en declive. Es un ave de tamaño mediano, similar a un arrendajo *Garrulus glandarius*, predominantemente insectívora, y nidificante secundario (no excavadora) en agujeros en árboles, taludes o construcciones humanas (Cramp 1998). Es la única especie europea de la familia Coraciidae y presenta dos subespecies: una subespecie nominal *C. g. garrulus* reproductora en Marruecos, sur de Europa y en Asia Menor hasta Irán y el suroeste siberiano, y otra subespecie *C. g. semenowi* reproductora en Irán (sin solapamiento con *C. g. garrulus*), Iraq, este de Cachemira y norte de Turkmenistán, sur de Kazajistán y noroeste de China (Fry y Fry 1999) (Figura1).

Las poblaciones europeas de carraca han sufrido un drástico declive en las últimas décadas. Aunque a principios del siglo XX la especie se extendía como reproductor por casi toda Europa (Glutz y Bauer 1980), fue desapareciendo en el siglo pasado en Alemania, Dinamarca, Suecia (Snow y Perrins 1998) y Finlandia (Avilés *et al.* 1999). Además sus poblaciones han sufrido fuertes declives en otras regiones de distribución norteña: en

Figura 1. Mapa de Distribución de la Carraca europea (BirdLife International 2015)

Austria (de 300-500 parejas reproductoras en 1960-70 a 7-15 en 1980; Sackl 2004), Eslovenia (actualmente sólo individuos errantes; Rubinić 2008), Estonia (de 50-100 parejas a ninguna; Kovacs *et al.* 2008), Hungría (extinta al oeste y fuertemente reducida la población en el este, aunque recuperándose ligeramente en años recientes; Kiss *et al.* 2004), Lituania (de 1,000-2,000 parejas en 1970 a 20 en 2004; Kovacs *et al.* 2008) y Polonia (alrededor de 1,000 parejas en 1977-1980 a 60-80 parejas en 2008; Grzybek 2009). En Europa se concentra entre el 50-74% de la población global, estimándose en unos 75,000-184,000 individuos reproductores, principalmente localizados en España (2,000 – 6,000 parejas) y Francia (800 – 1,000) en la región más occidental, y en Turquía (12,000 – 30,000), Rusia (7,000 – 10,000), Azerbaiyán (2,000 – 10,000), Bulgaria (2,000 – 8,000), Rumania (4,600 – 6,500) y Chipre (1,000 – 3,000) en la región oriental de su distribución (BirdLife International 2015b; Figura 2).

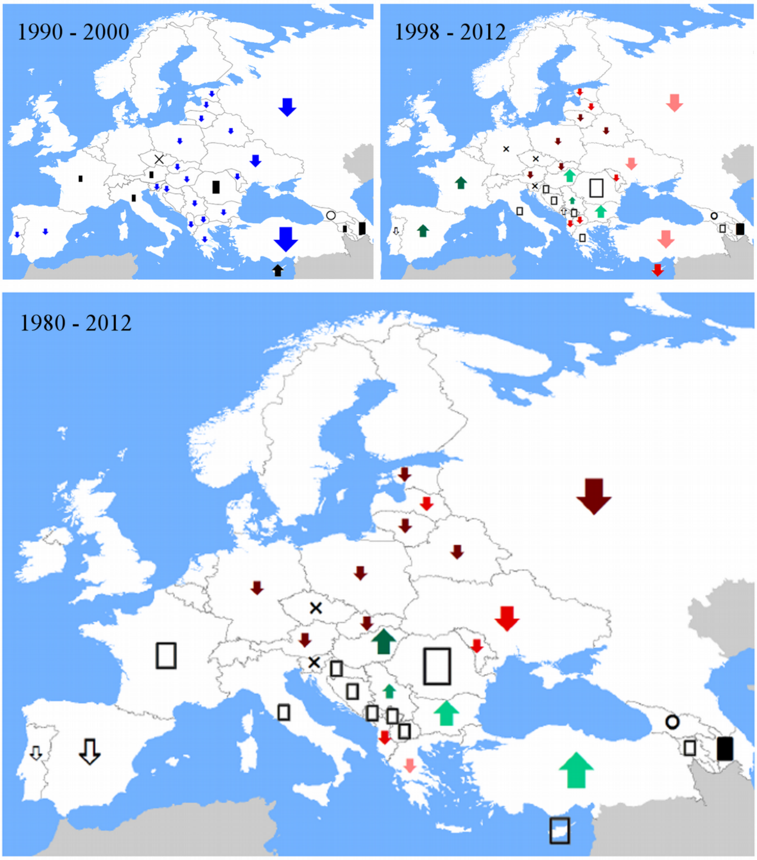

Figura 2. Tendencias poblaciones a corto (arriba) y largo plazo (abajo) de la carraca en Europa. (BirdLife International 2004; BirdLife International 2015c)

La clasificación de la carraca como especie amenazada ha sufrido diversos cambios en muy poco tiempo pese al desconocimiento sobre su situación poblacional, demografía y tendencias, y a que las estimas obtenidas en la mayoría de los países prospectados son de muy baja calidad. De hecho, tan sólo en 4 de 17 países europeos se realizó una estimación de tendencia poblacional fiable y la mayoría eran en poblaciones relictas de la especie (BirdLife International 2015b). En 2005 se incluyó la especie en la categoría de *Casi Amenazada* por estimarse un declive poblacional global mayor de 30% en 15 años (IUCN 2008) y *Vulnerable* en la Unión Europea (BirdLife International 2004). Una posterior evaluación ha catalogado la especie como de *Preocupación Menor,* considerando un declive de entre el 5 y el 20% en 16.8 años (BirdLife International 2015b). En España, se catalogó como *Vulnerable* por considerarse una población de pequeño tamaño con un declive mayor del 10 % en 10 años (Avilés y Folch 2004), pero recientemente se ha detectado un incremento moderado (Ministerio de Agricultura, Alimentación y Medio Ambiente 2011) que ha llevado a su descatalogación como especie amenazada (Real Decreto 139/2011; http://www.boe.es/).

Problemas de conservación de la Carraca

Hasta la fecha la identificación de los problemas de conservación para la carraca se ha basado en el análisis de la presencia de la especie en relación a tipos de hábitat en zonas de reproducción, fundamentalmente en el sur de Europa. Así se ha apuntado que las principales amenazas en sus zona de cría serían la reducción y degradación del hábitat óptimo de alimentación y la pérdida de lugares de nidificación (Avilés y Folch 2004). La densidad de aves cavernícolas no excavadoras como la carraca está estrechamente relacionada con la disponibilidad de agujeros naturales (Newton, 1994). De esta manera, la intensificación agrícola y la consecuente eliminación de árboles viejos, que proporcionan un abundante número de agujeros, es una amenaza importante para la conservación de especies que dependen de este recurso (Gibbons *et al.*, 2008). La disminución en la población ibérica de carraca se ha relacionado con la escasez de estos agujeros (Avilés *et al.*, 2000), habiéndose visto que las zonas agrícolas con baja disponibilidad de árboles afectan negativamente a su éxito reproductor (Avilés y Parejo, 2004). La carraca depende en gran medida de la presencia de especies excavadoras que realizan las cavidades, tales como el pito real *Picus viridis*, (Bouvier et al 2014) que en España se encuentra también en una preocupante situación de declive (Ministerio de Agricultura, Alimentación y Medio Ambiente 2011), aunque también puede aprovechar agujeros en taludes o en edificios abandonados (Avilés y Folch 2004). Por todo ello, las prácticas forestales intensivas, como los clareos, eliminación de árboles viejos, talas de árboles ribereños, eliminación de setos en zonas agrícolas de mosaico e intensificación agrícola han reducido enormemente el número de agujeros disponibles.

La instalación de cajas-nido como medida para incrementar la disponibilidad de lugares de nidificación ha tenido un efecto positivo en la tendencia poblacional de la especie en muchos lugares (Avilés y Sánchez 1997, Sackl 2004, Kiss *et al.* 2014; sin embargo, ver Sosnowski y Chmielewski 1996). Sin embargo no está suficientemente claro si este efecto es debido a un incremento de la población o a la atracción de individuos desde otras zonas con baja disponibilidad de agujeros, ya que se desconocía el estado previo de la poblaciones de carraca antes de la colocación de los nidales (Avilés y Sánchez 1997, Václav 2010). En este sentido, podría resultar aventurado concluir que las cajas tienen un efecto beneficioso para la especie sin evaluar previamente sus efectos a más largo plazo y particularmente sobre su productividad (Gottschalk *et al.* 2011). En caso contrario, se podría estar cometiendo el error de atraer a las aves a lugares no adecuados para la nidificación, generando accidentalmente trampas ecológicas (Schlaepfer *et al.* 2002, Mänd *et al.* 2005, Klein 2007).

Los hábitats de nidificación y alimentación de la carraca en Europa se encuentran fundamentalmente en regiones templadas y esteparias del arco mediterráneo (Cramp 1998). En el suroeste español, muestran una preferencia por campos de cultivo de regadío, olivares y zonas de cereal adehesadas frente a los campos de cereal sin encinas (Avilés *et al.* 2000). En Francia la especie muestra preferencia por parches de baja diversidad de usos agrícolas, con predominancia de cultivos en barbecho y praderas (Bouvier 2014), mientras que en Hungría parecen tener mejor éxito reproductor en zonas de cultivo en mosaico que en pastizales secos (Kiss 2014). Estos estudios demuestran una predilección por hábitats abiertos que dispongan de lugares adecuados desde donde cazar (perchas) como árboles, vallados, postes y tendidos eléctricos (Avilés y Costillo 1998, Cramp 1998). Su asociación con este tipo de hábitat agrícola la hacen especialmente vulnerable a los cambios de prácticas agrícolas, transformaciones a monocultivos y al uso de pesticidas (Kovacs *et al.* 2008, BirdLife International 2015).

Fuera de la época de reproducción, el conocimiento sobre los problemas de conservación de la carraca es, hasta la fecha, anecdótico. La carraca es una especie migradora de larga distancia que pasa el invierno en las zonas comprendidas entre Senegal hacia el este hasta Camerún y de Etiopía hacia el oeste, hasta el Congo y hacia el sur hasta Sudáfrica (del Hoyo *et al.* 2001). Su ruta migratoria es muy poco conocida y la información disponible en enciclopedias se basa en escasas recuperaciones de anillas y en información sesgada hacia las poblaciones del este de Europa (Brown y Brown, 1973, Ash y Miskell, 1980, Feare, 1983). Recientemente, se han realizado trabajos con geolocalizadores en poblaciones de Francia (Emmenegger *et al.*, 2014) y Portugal (Catry *et al.*, 2014), que proponen la existencia de dos rutas migradoras alternativas, pero basados en un número muy bajo de individuos y en estos dispositivos de poca resolución espacial. Debido a esta falta de información, es posible que se esté infravalorando el alcance de las amenazas que pudieran afrontar las carracas durante su migración. Existen informes de caza ilegal en su paso por Serbia, Croacia, Chipre, Arabia Saudita y Libia (http://www.birdlifecyprus.org/, Kovacs *et al.* 2008; Figura 3). Además es habitual la caza en lugares de invernada, o en zonas de paso, como Omán (del Hoyo *et al.* 2001), Chipre, Líbano y Siria (Brochet *et al.* 2016). Igualmente, por su apariencia atractiva y exótica, la especie se enfrenta al problema de la recolección y comercio ilegal para uso como mascota o coleccionismo (existe un caso en 2008 de contrabando en la frontera serbio-húngara; Convention on Migratory Species, 2014). La identificación de los lugares de migración e invernada preferentes para la especie resulta crucial para ayudar a la conservación de la especie ya que las carracas europeas sólo pasan cuatro meses al año en sus cuarteles de reproducción y no existe información cuantitativa sobre los hábitats que seleccionan durante su invernada en África.

Más allá del conocimiento de los movimientos a larga distancia de una especie, es muy importante conocer sus movimientos dispersivos e identificar las causas y consecuencias de los mismos. La dispersión, definida como los movimientos que los individuos hacen entre su lugar de nacimiento o lugar de reproducción y el siguiente evento de reproducción (Greenwood y Harvey 1982) puede afectar a la dinámica y estructura demográfica de las poblaciones (Greenwood y Harvey 1982, Hanski y Gilpin, 1997, Clobert 2009) y puede influenciar enormemente la eficacia biológica (Clobert *et al.*, 2001). La dispersión puede venir mediada por factores intrínsecos del individuo (i.e. edad, sexo, calidad individual, éxito reproductor) o extrínsecos (i.e. calidad de hábitat, densidad poblacional, información social, depredadores) (Clobert *et al.*, 2001) y su entendimiento es crucial para establecer medidas de conservación adecuadas (Ronce 2007, Serrano y Tella 2012). Hasta la fecha los patrones de dispersión en la carraca y sus determinantes no han sido estudiados.

Figura 3. Individuos de carraca, junto a oropéndolas y tórtolas turcas, cazados en Arabia Saudí durante su paso migratorio (http://www.mme.hu/)

OBJETIVO GENERAL

El objetivo último de esta tesis doctoral es identificar los factores que pueden determinar la eficacia biológica de la carraca en todos los momentos de su ciclo vital para poder contribuir así a su conservación. Con este fin, se pretende profundizar en el estudio de la historia vital de la especie, tanto durante su etapa reproductora, para lo que estudiamos una población asentada en cajas-nido en el sudeste español, como durante los periodos migratorios y de invernada en África, para lo que se usan datos obtenidos mediante dispositivos de seguimiento por satélite y geolocalizadores. En concreto, esta tesis se marca los siguientes subobjetivos, englobados en dos partes bien diferenciadas:

Fase Reproductora:

1. Analizar la influencia de factores antrópicos y del paisaje en la elección y posterior éxito reproductor de las cajas-nido (*Capítulo I*). La colocación de cajas nido es un recurso muy extendido para suplir la carencia de lugares adecuados para la nidificación de especies cavernícolas no excavadoras (Lindenmayer *et al.*, 2009). Sin embargo, los estudios centrados en sus efectos sobre la ocupación y éxito reproductor son generalmente escasos, pudiendo darse la paradoja de que cajas-nido instaladas para favorecer a una especie en realidad atrajeran a las aves a zonas menos ventajosas para criar, actuando como trampa ecológica (Schlaepfer *et al.*, 2002). En este capítulo estudiamos los factores que afectan a la probabilidad de ocupación y el éxito reproductor de las carracas en cajas-nido instaladas en una población durante un período de 3 años.

2. Identificar los patrones de dispersión natal y reproductiva, sus determinantes y sus consecuencias (*Capítulo II*). En este capítulo estudiamos qué factores afectan la probabilidad y distancia de dispersión natal y reproductiva y sus consecuencias en términos de éxito reproductor en una población de carraca asentada en cajas-nido durante un período de 8 años. El conocimiento de las causas proximales que motivan la dispersión puede ayudar a entender las presiones selectivas que afectan este proceso. Por otro lado, el estudio de las consecuencias a nivel de eficacia biológica de las diferentes estrategias dispersivas puede ayudar a entender el significado adaptativo de este comportamiento. Por todo ello,

entender los patrones de dispersión de la especie es crucial para entender su dinámica poblacional (Clobert 2009) y poder desarrollar acciones de conservación eficaces (Ronce 2007, Serrano y Tella 2012).

Fase No Reproductora:

3. Estudio de la migración de las poblaciones ibéricas de carraca (*Capítulo III*). En este capítulo queremos identificar de manera precisa la ruta migratoria de la especie para las poblaciones españolas, sus paradas y zonas de invernada, así como estudiar su comportamiento migratorio, con el fin de establecer áreas importantes para su conservación en su período no reproductor. Para lograr este objetivo usamos los datos obtenidos mediante la colocación de dispositivos de seguimiento por satélite y geolocalizadores en individuos ibéricos pertenecientes a distintas poblaciones reproductoras.

4. Explorar los posibles efectos negativos del empleo de dispositivos de seguimiento para el estudio de la migración en la carraca europea (*Capítulo IV*). El uso extensivo de los dispositivos de seguimiento ha contribuido enormemente a nuestro conocimiento sobre la migración de las aves (Stutchbury *et al.*, 2009, Bairlein *et al.*, 2012, Schmaljohann *et al.*, 2012), aunque sus efectos sobre el bienestar de los animales son controvertidos (Rodríguez *et al.*, 2009, Barron *et al.*, 2010, Arlt *et al.*, 2013, Bridge *et al.*, 2013, Costantini y Moller, 2013, Scandolara *et al.*, 2014). En este apartado nos proponemos explorar si la aplicación de estas técnicas de marcaje de común aplicación en ornitología produce efectos negativos sobre la supervivencia o el éxito reproductor de esta especie en una población donde realizamos un seguimiento de más del 70% de los individuos reproductores y las tasas de recapturas son conocidas. Además, compararemos nuestros resultados con otros estudios realizados sobre la misma especie.

5. Caracterizar los hábitats idóneos de invernada de las carracas ibéricas y de toda la especie en África e identificar las variables de hábitat que más contribuyen a su idoneidad mediante la elaboración de modelos de distribución (*Capítulo V*). Para entender mejor la ecología de las especies migradoras durante el periodo no reproductor, se hace necesario

definir el uso del hábitat y las variables ambientales que determinan su distribución en las zonas de invernada (Martin *et al.*, 2007). Los modelos de nicho ecológico son una herramienta muy útil para identificar las áreas más propicias para la invernada de las aves migradoras (Beresford *et al.*, 2011, Jiguet *et al.*, 2010) y así poder definir un plan adecuado para su conservación (Martin *et al.*, 2007). En este capítulo, se desarrolla un modelo de nicho ecológico basado en características topográficas y variables climáticas y de hábitat para identificar las áreas de invernada adecuadas para la carraca en África y, posteriormente, se corrobora con los datos disponibles de individuos marcados con dispositivos satélite.

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MÉTODOS GENERALES

MÉTODOS GENERALES

Este trabajo tiene lugar principalmente en la Hoya de Guadix-Baza (37.22º N, 3.03º O). Representa un altiplano erosivo muy característico, situado a una altura media en torno a los 1,000 metros sobre el nivel del mar y cercado por la Sierra de Baza, Sierra de Castril y Sierra Nevada. El paisaje árido y subdesértico de la zona se halla cortado por numerosas cárcavas y barrancos, lo cual da origen a ramblas o cauces abiertos por la escorrentía del agua durante las lluvias intensas. Estos cauces, por su encajonamiento, adquieren un microclima de carácter más húmedo que permite el crecimiento de vegetación ripícola. Las zonas dedicadas a agricultura intensiva de cereal se alternan a modo de mosaico con almendrales en las zonas altas y medias, tendiendo gradualmente al matorral y encinar de repoblación y posteriormente a zonas baldías en las más bajas. Toda la región se encuentra salpicada de encinas a densidades variables. En nuestro área de estudio, de aproximadamente 135 km^2 de extensión, se han instalado de forma progresiva y aleatoria 249 cajas-nido de corcho sobre encina y álamo principalmente, con unas dimensiones de 24 x 24 cm de base, 40 cm de altura y entrada de 6 cm de diámetro. Las principales especies de aves distintas a la carraca que han ocupado estas cajas fueron la abubilla (*Upupa epops*), autillo (*Otus scops*), carbonero (*Parus major*), grajilla (*Corvus monedula*) y mochuelo (*Athene noctua*). La población de carraca ha variado de 42 individuos reproductores en 2007 a 54 en 2014 (Figura 1).

Los individuos adultos se capturaron a mano o con trampas en la caja-nido durante la incubación o el periodo de crianza de los pollos. Una vez capturados se les tomaron muestras de sangre para el sexado y medidas de peso y longitud de ala y tarso como estima de condición corporal. También se marcaron todos los individuos para su posterior identificación con anilla metálica en el tarso izquierdo y una combinación única de tres anillas de colores (una en el tarso izquierdo y dos en el derecho). Los pollos se procesaron de forma similar, excepto en la asignación de un código de anillas de colores, que sólo se colocaban en caso de ser recapturados como adultos reproductores en años siguientes.

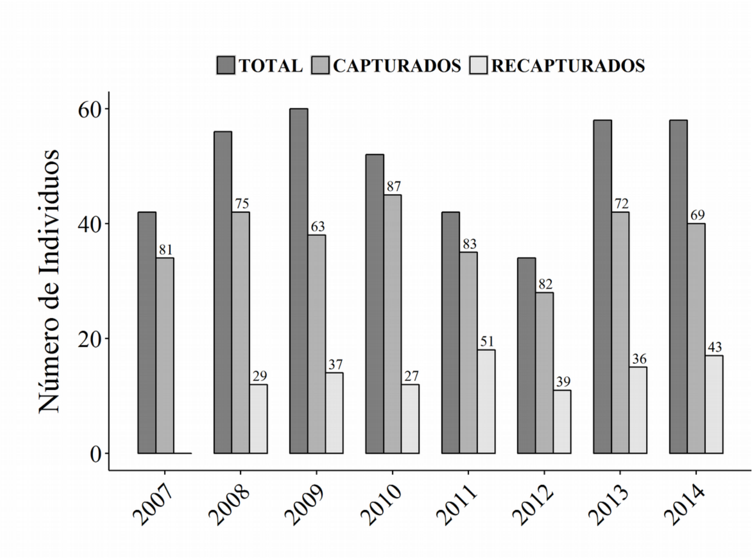

Figura 1. Número de individuos totales, capturados y recapturados por año en la población de la Hoya de Guadix-Baza en el período 2007-2014. Las cifras sobre las barras muestran el porcentaje de individuos capturados respecto al total de individuos en la población, y el porcentaje de individuos capturados que ya fueron capturados en años anteriores (recapturados).

A un grupo de individuos seleccionados de esta población se les equipó, utilizando para su colocación arneses de tipo mochila, con dos tipos de dispositivos de seguimiento que se describen en detalle en el Capítulo 3 (Figura 2). Para lograr los objetivos 3, 4 y 5 también se realizaron capturas de carracas en otras poblaciones de la Península Ibérica. En concreto, se capturaron individuos en Castro Verde (Portugal), Almería, Badajoz, Ciudad Real, Girona, Granada, Huesca, Lleida y Madrid para su posterior colocación de dispositivos de seguimiento. De esta forma, logramos obtenemos una muestra representativa de la población ibérica en toda su distribución. Tanto las especificaciones técnicas del dispositivo empleado, como el método de colocación se describen en detalle en los capítulos 3 y 4.

Figura 2. Carracas equipadas con dispositivo satélite (arriba) y geolocalizador (abajo).

CHAPTER I

The Value of Nest-boxes in the Conservation of Eurasian Rollers *Coracias garrulus* in Southern Spain

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ABSTRACT

The installation of nestboxes is a widely used conservation measure for enhancing habitat suitability for cavity-nesting birds wherever natural holes are scarce. However, nestboxes may attract birds to unsuitable breeding places or induce a non-random distribution of individuals in relation to their qualities. We investigated the factors influencing nestbox selection and the quality of breeding territories for the globally near-threatened Eurasian Roller in a semi-arid area of southeast of Spain over a 3-year period. Rollers preferentially used exposed nestboxes that were placed far from highly modified areas. However, breeding success was significantly lower in exposed nestboxes. Early breeders preferred nestboxes oriented to the northwest over any other orientation. Exposure had opposite effects on nestbox use and breeding success, suggesting that nestboxes installed in exposed sites could function as ecological traps for Rollers.

INTRODUCTION

Recent changes in forest management practices and the alteration of farmland, particularly the removal of isolated trees and hedges, have led to the decline of many cavity-nesting birds across Europe (BirdLife International 2008). The density of hole-nesting birds in their natural habitats is closely correlated with the availability of natural cavities (Newton 1994), so the widespread removal of old trees, which have the highest abundance of natural holes, is a key threat to the conservation of cavity-dependent birds (Linder and Ostlund 1998, Gibbons *et al.* 2008). Conservationists have often resorted to nestbox provisioning as the fastest and most suitable way of conserving cavity-dependent bird populations (Lindenmayer *et al.* 2009). Nestboxes can improve the efficacy of research on cavity-dependent birds by allowing easier access to breeding animals (Griffith *et al.* 2008) and by reducing the risk of losing data due to predation (Llambias and Fernandez 2009) and/or parasitism (Møller 1989). Furthermore, provision of nestboxes can aid the conservation of cavity-dependent birds (Fiehleret al. 2006) and mammals (Beyer and Goldingay 2006, Flaquer *et al.* 2006, Harley 2006, Lindenmayer *et al.* 2009), promoting colonization of habitats from which people have removed trees (Fiehler *et al.* 2006, Harley 2006). For example, provision of nestboxes has been shown to elicit an immediate population explosion in the Hoopoe *Upupa epops* in Central Europe (Arletazz *et al.* 2010). From a conservation perspective, it is necessary to assess the productivity of occupied nestboxes to obtain the best return on investment in terms of conservation gain (Gottschalk *et al.* 2011), otherwise conservationists could be attracting birds to unsuitable breeding places that could be ecological traps (Schlaepfer *et al.* 2002, Mand *et al.* 2005, Klein *et al.* 2007). It also remains largely unknown whether nestbox selection is influenced by individual quality. The distribution of individuals in relation to their innate qualities is a central issue in habitat selection (Fretwell and Lucas 1969) but has rarely been considered in conservation plans for cavity-dependent species. Therefore, it seems necessary to consider occupancy, breeding success and individual quality simultaneously to assess the efficacy of nestbox provisioning programmes.

The Eurasian Roller *Coracias garrulus* (hereafter Roller) is a medium-sized insectivorous bird, the sole European member of the Coracidae, which breeds throughout temperate, steppe and Mediterranean zones from northwest Africa to the western Himalayas (Cramp 1986). In Europe, Roller breeding populations are fragmented and generally declining (Tucker and Heath 1994). Roller populations have shown a marked decline in 18 of 29 European countries (BirdLife International 2008), and the whole European population was estimated to have declined by 30% in the last 10 years (BirdLife International 2004). The loss of suitable breeding habitats has been suggested as the main factor affecting Roller decline throughout Europe (Tucker and Heath 1994). The decline in the Spanish region of Extremadura has been primarily attributed to a shortage of natural cavities (Avilés *et al.* 2000). Also in Spain, the degree of agricultural intensification was negatively associated with Roller breeding success in tree-cleared habitats provisioned with nestboxes (Avilés and Parejo 2004). Rollers are obligate secondary cavity-nesters (i.e. they do not excavate their own cavities) (Cramp 1986). Consequently, throughout their distributional range Rollers depend for nesting on holes excavated by woodpeckers and other birds in trees and / or sandy banks, and on holes in walls of farm buildings and/or bridges (Avilés and Folch 2004). Local and regional conservation plans have often relied on nestbox provisioning to improve Roller breeding populations (Sosnowski and Chmielewski 1996, Avilés *et al.* 1999, Bohus 2007), although patterns of nestbox occupancy and breeding success have never been explored for this species.

Here we analyse nestbox habitat selection of Rollers with a spatially multi-scaled approach using a Geographic Information System (GIS) in an area that represents the upper altitudinal limit of the global distribution of this species. To contribute to the efficacy of Roller conservation through nestbox provisioning, our specific objective was to identify factors influencing nestbox occupancy and habitat quality for Rollers.

METHODS

Study area

The study area is a plateau covering approximately 100 km2 located in Granada province in southern Spain (37.22º N, 3.03º E) with an average altitude above 1000 m asl. It is an extensive agricultural landscape with scattered Holm Oak *Quercus ilex* and is crossed by numerous dry riverbeds (ramblas). Study population Over a 3-year period (2007–2009), we studied the Roller population established in 183 cork oak nestboxes attached to trees (mainly Holm Oaks) or to artificial supports (electric pylons or walls). Nestboxes had a base and roof surface of 24x24 cm, a height of 40 cm and an opening 6 cm in diameter. Nestboxes were randomly distributed over the available habitats and in relation to a motorway crossing the study area (Fig. 1); the mean (± sd) distance between neighbouring nestboxes was 115.46 ± 161.12 m.

We monitored 21, 28 and 31 breeding pairs in nestboxes in 2007, 2008 and 2009, respectively. Although at least three pairs may have established in natural holes (these were not considered in this study due to accessibility problems), we were confident that the majority of Rollers breeding in our study area were sampled. In the few cases where natural holes and nestboxes were simultaneously available, Rollers always occupied nestboxes. During the 3 years of the study, nestboxes were checked at least once a week to determine occupancy and to record reproductive parameters. A nestbox was defined as occupied if at least one egg was laid in it. Rollers started to lay eggs during the first half of May and the mean (sd, n) number of eggs per nest was 4.93 (1.07, 60). Clutches that were abandoned or predated before completion were not considered for the calculation of mean clutch size. Chicks were weighed at day 20 using a Pesola balance to a precision of 0.5 g. to estimate body condition at fledging.

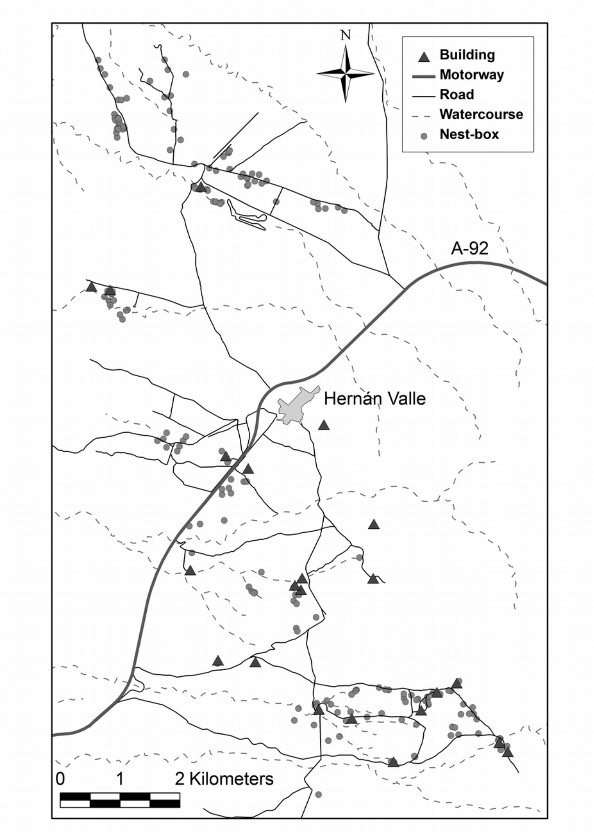

Figure 1. Study area and distribution of nestboxes.

Field data collection

For each nestbox, we estimated in the field: (1) height (in cm) as the distance from the nest entrance to the ground; (2) the opening orientation (in degrees with respect to north), transformed into a categorical variable as follows: 1–90 = NE; 91–180 = SE; 181–270 = SW; 271–360 = NW; and (3) visibility, estimated visually from a randomly selected point placed at 10 m distance from the nestbox, expressed on an ordinal scale where 1 = completely exposed, 2 = up to 25% concealed, 3 = 25–50% concealed, 4 = 50–75% concealed and 5 = totally concealed.

Environmental data

We used GIS software ARCGIS version 9.3 (Environmental System Research Institute 2008) to process environmental data based on aerial photographs and 2003 Vegetation Cover and Land Use Databases for the Province of Granada that were freely available from Junta de Andalucía (Consejería de Medio Ambiente, Junta de Andalucía 2003, Junta de Andalucía 2006). For each nestbox, we derived the following variables: (1) altitude above sea level (m), (2) distance to the nearest road (m), (3) distance to the motorway (miles, m), (4) distance to the nearest building (m) and (5) distance to the nearest watercourse (m). Our study area represents the altitudinal limit of the species in Europe, so we also considered whether altitude was limiting the occupation of nestboxes by Rollers. The study area is crossed by a heavily used motorway and there are other minor roads throughout the area that could also potentially cause disturbance (Reijnen and Foppen 1994). Buildings are represented by isolated farmhouses, most of them abandoned or little-used, one small village, and watercourses by ramblas. Buildings and watercourses were included in the analysis as they may be positively selected by breeding Rollers (Cramp 1986). Additionally, we estimated the average slope, number of Holm Oaks and the percentage of the surface occupied by grassland/herb crop, almond grove, pine plantation, scrubland and other uses within a circular area with a radius of 100 m centred on each nestbox. This radius was based on a previous study which reported that foraging flight distances of Rollers rarely exceed 100 m during nestling provisioning (Avilés and Parejo 2004).

Preliminary analyses revealed that some environmental variables were highly inter-correlated, so we simplified the data by performing a principal components analysis (PCA) on the set of environmental variables. The first three PCA axes explained 27.22, 21.25 and 19.79% of the variance, respectively (Table 1). The first PCA axis was identified as a gradient of farming activity, which classified nestboxes according to altitude and surface of grassland/herb crop *vs.* the surface of scrubland and distance to buildings (Table 1). Thus, nestboxes with negative loadings for the first axis were situated in high, cultivated areas close to buildings and with a low shrub cover. The second axis was identified as a gradient of slope steepness, distance to roads and also the occurrence of watercourses (Table 1). Indeed, very steep areas are those closely associated with watercourses and are unsuitable for road building. Nestboxes with negative values on this axis were situated in relatively flat areas with high densities of Holm Oaks and close to roads. The third axis classified nestboxes according to the density of almond groves and pine plantations and proximity to the motorway. Hence this axis can be regarded as a gradient of land transformation (Table 1). Factor scores derived from the PCA were used in subsequent analyses. Among occupied nestboxes, the mean (± sd) distance to the nearest neighbour nestbox was 319.14 ± 305.08 m. As nestboxes were relatively close to one another, it was possible that the occupation of a given nestbox may have had consequences for the occupancy of nearby nestboxes. We tested for possible spatial autocorrelation in nestbox occupancy using the Moran's I Index as implemented in the spatial statistics package of ARCGIS 9.3. There was no clustering or dispersion in the observed pattern (Moran's I Index = 0.04, $P > 0.1$), and therefore we assume a random distribution, where nestbox occupation is not affected by neighbouring nestboxes.

Table 1. Results of principal component analysis performed on environmental variables (n = 183 nestboxes). Loadings in bold indicate the most important factors (score > |0.50|).

Variable	Factor 1: Farming activity	Factor 2: Slope steepness	Factor 3: Land transformation
Altitude	**-0.81**	-0.15	0.38
Average slope	0.02	**-0.8**	-0.08
Distance to road	-0.02	**-0.56**	-0.34
Distance to watercourse	-0.17	**0.73**	0.12
Distance to building	**0.75**	0.25	0.24
Distance to motorway	0.23	0.01	**0.85**
Density of holm oaks	-0.35	0.43	0.43
Surface of almond groves and pine plantations	-0.14	0.5	**-0.71**
Surface of scrublands	**0.88**	-0.2	0.31
Surface of grassland/herb crop	**-0.72**	-0.3	0.39
Variance explained (%)	27.22	21.25	19.79

Data analyses

In a first analysis, we modelled the probability that a given nestbox was occupied in at least 1 year during the 3-year study period using a generalized linear model (GLM) assuming a binomial error distribution and logit link function (occupied *vs.* unoccupied). Independent variables were nestbox attributes (i.e. height, orientation and visibility) and the three PCA factor scores (i.e. farming activity, slope steepness and land transformation). In a second analysis, performed only on the subset of nestboxes that were occupied by Rollers in at least 1 year, we assessed whether the extent to which a nestbox was occupied for 1, 2 or 3 years (Roller preference hereafter) was related to nestbox attributes and/or environmental variables with a GLM assuming a binomial error distribution and logit link function and using an events/trials response (i.e. number of occupancies out of the 3 years).

Occupied nestboxes may vary greatly in their suitability and, consequently, in productivity. A large number of studies have reported a correlation between some characteristics of the environment (e.g. food resources or presence of predators) and nest productivity in terms of fledglings (Part 2001, Maguire 2006). Therefore, in a third analysis, we used a GLM with a binomial error distribution and a logit link function to assess whether the probability that a given nestbox produced at least one fledging during the 3 years could be explained by environmental and⁄or nestbox attributes.

Finally, we assessed the possibility that Rollers differing in quality were not randomly distributed in relation to habitat and⁄or nestbox attributes. Laying date was fitted as the dependent variable, as it was assumed that it was a reliable sign of individual quality given that, in general, better fed females often lay their eggs earlier in the breeding season (Price and Liou 1989). Previous work has supported this contention for Rollers, too, as earlier breeders produce more fledglings than late breeders in the south of Spain (Avilés *et al.* 1999). These analyses were restricted to 2008 data to avoid the possible confounding effect of study year, and, due to the low sample size, were made separately for environmental and nestbox attributes.

Nestbox occupancy patterns could be a byproduct of early occupation of nestboxes by other hole-nesting-dependent species if nestbox availability was low and those bird species showed a marked preference for particular nestbox features. In our study area, Little Owls *Athene noctua* are the only common breeding bird species laying their eggs earlier than Rollers. Mean (sd, n) lay date of Little Owls and Rollers in 2009 was 120.49 (8.61, 13) and 149.51 (5.29, 23) in Julian days from 1 January onwards, respectively. To test for a possible effect of Little Owl occupation on the observed patterns for Rollers, we re-examined patterns of Roller occupation after discounting nestboxes occupied by Little Owls in 2008.

We used the Akaike information criterion (AIC) to select the model best describing response variables among all the possibilities given the explanatory set of variables (Burnham and Anderson 2002). All subsets were evaluated using the corrected value of AIC (AICc; Hurvich and Tsai 1989) recommended for small samples, and classified according to the difference in AICc with respect to the model with the lowest AICc (ΔAICc). Following Burnham and Anderson (2002), in assessing the relative merits of models in the set, only models with ΔAICc < 2 were considered to provide substantial evidence of being in the best model set and hence to explain variation in the dependent variable. We also used model averaging (Burnham and Anderson 2002) to identify more accurately the relative importance of each model term in predicting nestbox use and productivity for Rollers. (Full details of the models considered in each analysis are given in appendices in the online Supporting Information). Statistical analyses were performed with software STATISTICA 7.1 (StatSoft Inc. 2005) and SAS 9.1 (SAS Institute 2001).

RESULTS

Nestbox occupancy and preference

Of 183 nestboxes, 55 were used in at least 1 year; 34 were used in only 1 year, 16 were occupied in 2 years and five were occupied in all 3 years of the study. We identified five possible models that provided substantial support for nestbox occupation (ΔAICc < 2; Table 2, Supporting Information Appendix S1). Model averaging showed that the most important factors affecting nestbox occupancy were nestbox visibility and the land transformation PCA axis (Table 3). Occupied boxes were more exposed (Fig. 2a) and were situated in less modified areas (i.e. further from the motorway and with lower surface area devoted to almond groves or pine plantations, Fig. 2b).

A second analysis on the subset of occupied nestboxes revealed that seven different models had ΔAICc lower than two for nestbox preference (Table 2, Supporting Information Appendix S2). However, model averaging revealed that there was no single outstanding factor that explained nestbox preference by Rollers (Table 3).

Probability of successful breeding

Seven models provided substantial support for the probability of successful breeding in a nestbox (Table 2, Supporting Information Appendix S3). The most relevant factor determining probability of successful breeding in a nestbox was visibility; the probability of successful breeding was higher in concealed nestboxes (Fig 3).

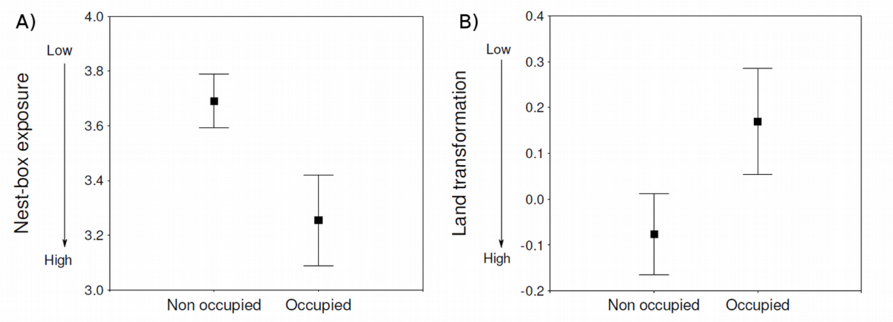

Figure 2. Nest-box exposure (a) and land transformation (b) in relation to nest-box occupation by Rollers. Whiskers correspond to standard error around the mean. Sample size is 55 and 128 occupied and non-occupied nest boxes, respectively.

Table 2. The best ranked models explaining variation in occupation (i.e. used vs. non-used), the probability of success (at least one chick fledged) and variation in lay date (2008 data) in nestboxes occupied by Rollers over a period of 3 years.

Model	K	AICc	ΔAICc	Akaike weights
Nest-box Occupation				
Visibility, Farming activity, Land transformation	5	216.1	0	0.143
steepness	6	216.7	0.63	0.104
Visibility, Land transformation	4	216.9	0.89	0.092
Visibility, Land transformation, Slope steepness	5	217.5	1.46	0.069
Visibility, Farming activity	4	217.9	1.83	0.057
Nest-box Preference				
Land transformation	3	121.55	0	0.123
Slope steepness	3	122.15	0.61	0.091
Farming activity	3	122.8	1.26	0.066
Visibility	3	122.86	1.31	0.064
Height	3	122.99	1.44	0.06
Land transformation, Slope steepness	4	123.19	1.64	0.054
Land transformation, Farming activity	4	123.28	1.73	0.052
Breeding Success				
Visibility, Height	4	67.6	0	0.076
Visibility	3	67.6	0.02	0.076
Visibility, Slope steepness	4	68.4	0.85	0.05
Visibility, Slope steepness, Height	5	68.5	0.98	0.047
Visibility, Land transformation	4	68.8	1.24	0.041
Visibility, Land transformation, Height	5	69.3	1.74	0.032
Visibility, farming activity	4	69.4	1.85	0.03
Slope steepness	3	69.5	1.9	0.029
Laying date (nest-box attributes)				
Orientation	3	173.49	0	0.371
Orientation, Height	4	175.15	1.66	0.162
Orientation, Visibility	4	175.16	1.67	0.161
Laying date (environmental attributes)				
Farming activity	3	174.98	0	0.326
Slope steepness	3	176.24	1.26	0.174
Land transformation	3	176.41	1.42	1.16

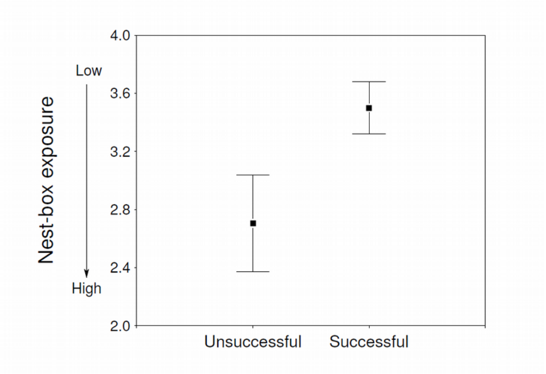

Figure 3. Nest-box exposure in relation to nest-box success by Rollers (i.e. boxes in which at least one chick fledged versus boxes in which no chick fledged) in occupied nest-boxes. Whiskers correspond to standard error around the mean. Sample size is 38 and 17 successful and unsuccessful nest boxes, respectively.

To explore the possibility that the few individuals raised in exposed nestboxes may have a better body condition that could compensate for the low breeding success, we also ran a GLM with our 2008 data in which average weights of nestlings per nest on the day of fledging were used as the dependent variable and variables related to habitat and/or nestbox attributes were used as predictors. There was no significant effect of any environmental variable on nestling body mass at fledging, suggesting that compensation was unlikely at least in terms of nestling body condition (Table 4). However, the effect of orientation approached significance ($P < 0.073$), with the highest weights in boxes facing northwest.

Individual quality and nestbox use

Three models considering nestbox attributes as predictors and three models considering environmental attributes as predictors had strong support in explaining lay date (Table 2, Supporting Information Appendix S4). The most important variable explaining lay date at the nestbox scale was hole orientation (Table 3). Early breeders biased selection toward nestboxes with the hole oriented towards the northwest (Fig. 4). Model averaging revealed that no environmental variable showed a significant contribution to the laying date model (Table 3).

Table 3. Model-averaged parameter estimates derived from model-averaging. Akaike weights and estimates for each factor in the best models explaining occupation, probability of success and variation in laying date of nestboxes occupied by Rollers are given. Bold text indicates variables where 95% confidence intervals of the estimate do not overlap zero. For laying date, parameter estimates for orientation are relative to SW, which is set at zero.

Term	Akaike weight (95%)	Model-averaged estimate (±95% CI)
Occupation		
Visibility	**1**	**0.34 (0.06 to 0.62)**
Land transformation	**0.88**	**-0.36 (-0.72 to -0.01)**
Farming activity	0.65	0.30 (-0.04 to 0.64)
Slope steepness	0.37	0.22 (-0.13 to 0.57)
Preference		
Land Transformation	0.45	-0.21 (-0.56 to 0.13)
Slope steepness	0.28	-0.15 (-0.51 to 0.20)
Farming activity	0.23	-0.10 (-0.42 to 0.22)
Visibility	0.13	-0.05 (-0.29 to 0.18)
Height	0.12	-0.001 (-0.008 to 0.006)
Breeding Success		
Visibility	**0.92**	**-0.50 (-0.99 to -0.001)**
Height	0.41	-0.01 (-0.02 to 0.01)
Rugosity	0.33	-0.45 (-1.16 to 0.26)
Intensification	0.19	-0.28 (-1.02 to 0.45)
Human Activity	0.08	0.16 (-0.46 to 0.77)
Laying date (nest-box attributes)		
Orientation (NW)	**1**	**-7.55 (-13.24 to -1.85)**
Orientation (SE)	**1**	**8.81 (0.53 to 17.09)**
Orientation (NE)	1	0.50 (-5.63 to 6-64)
Height	0.23	0.02 (-0.05 to 0.09)
Visibility	0.23	1.08 (-2.18 to 4.33)
Laying date (environmental attributes)		
Farming activity	0.49	3.53 (-1.92 to 8.99)
Slope steepness	0.26	-0.99 (-6.31 to 4.32)
Land transformation	0.24	1.29 (-3.31 to 5.88)

Table 4. Results of a general linear model using average weight of nestlings per nest on the day of fledging as the dependent variable and variables related to habitat and/or nestbox attributes as predictors.

	Estimate	Standard Error	Wald Stat.	*P*
Intercept	11.288	2.193	26.494	0
Farming activity	0.125	0.478	0.068	0.794
Slope steepness	0.11	0.252	0.189	0.663
Land transformation	-0.193	0.316	0.373	0.541
Height	-0.001	0.006	0.01	0.921
Visibility	0.133	0.235	0.319	0.572
Orientation: SW	-0.341	0.482	0.499	0.48
Orientation: NE	0.105	0.459	0.052	0.82
Orientation: NW	0.842	0.47	3.215	0.073
Scale	0.868	0.141	38	0

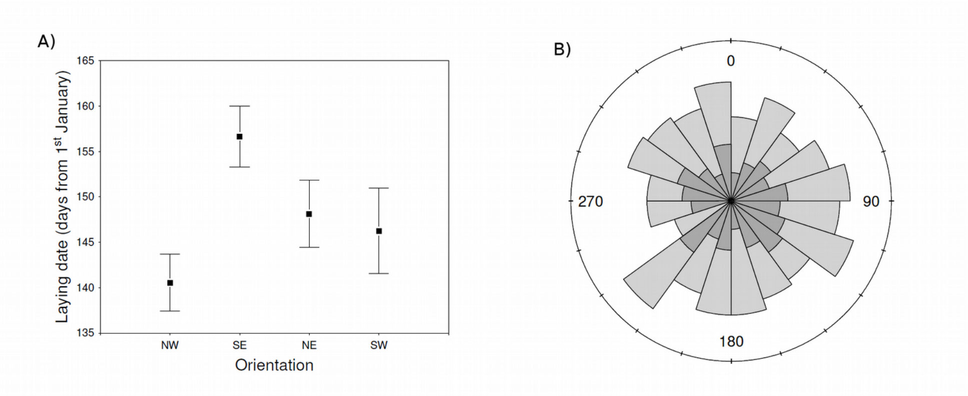

Figure 4. (a) Average value and standard error of laying date in Julian calendar days related to the nest box entrance orientation, (b) Rose diagram representing orientation distribution in degrees of available nest-boxes (pale grey) and occupied nest-boxes (dark grey).

Effect of nestbox occupation by Little Owls

Considering all available nestboxes in 2008, seven models explained nestbox occupation by Rollers (Supporting Information Appendix S5), whereas five explained Roller occupation after discounting those nestboxes previously occupied by Little Owls (Supporting Information Appendix S6). The models with the strongest support were the same models in both cases and revealed that farming activity was the variable that contributed significantly to Roller occupation. Thus, patterns of nestbox occupation by Rollers were not affected by Little Owl presence.

DISCUSSION

Local and regional conservation programmes have often resorted to nestbox provisioning as a tool to improve Roller breeding populations across Europe (Sosnowski and Chmielewski 1996, Avilés *et al.* 1999, Bohus 2007). Here we aimed to contribute to the understanding of the efficacy of Roller conservation through nestbox provisioning by identifying factors influencing occupancy and breeding success in a 3-year period. The most important factors determining nestbox utilization were the visibility of the nestbox and habitat transformation. Nestboxes that were exposed had a higher chance of being occupied by Rollers than more concealed ones (Fig. 2a). However, Rollers breeding in nest-boxes that were in relatively concealed sites had higher breeding success than those settled in relatively more visible sites (Fig. 3). It could be argued that more exposed, and thus accessible, nestboxes could act as an ecological trap attracting birds to unsuitable breeding sites. Indeed, the three lines of evidence listed by Robertson and Hutto (2006) as evidence for the existence of an ecological trap are fulfilled in our Roller system in that: (1) individuals preferred exposed over concealed nestboxes; (2) a surrogate of individual fitness (reproductive success) differed between exposed and concealed nestboxes; and (3) the fitness outcome (reproductive success) for individuals settled in exposed nestboxes, the preferred habitat, was lower than the fitness attained in concealed nestboxes. However, although our results tentatively support an ecological trap scenario, it should be noted that breeding success constitutes only one estimator of fitness, and our data were collected during a relatively short time frame of 3 years, which precluded the possibility of examining other factors contributing to birds fitness (e.g. survival, recruitment of offspring to the breeding population, lifetime reproductive success) which may also have a bearing on whether the situation can be definitively regarded as an ecological trap.

The observed mismatch between preference and productivity may arise if high-quality breeding Rollers showed a marked preference for more concealed nestboxes and were displacing the worst breeding pairs toward more visible nestboxes. However, active nestbox selection linked to individual quality seems unlikely because only 16.9% of nestboxes were occupied in 2009 (the year with the highest breeding Roller population), which would suggest that nestbox availability is not a limiting factor. More importantly, we failed to find a relationship between laying date and nestbox visibility, which suggests that Rollers breeding in both exposed and concealed sites have similar individual quality. Alternatively, the observed patterns may arise if the probability of accessing/finding a nestbox is similar for Rollers and predators. Although Rollers breeding in exposed and concealed nestboxes had similar laying dates, nest failures were significantly more frequent in exposed nestboxes, which could be explained by predation. Previous work has shown that the risk of snake predation is a main factor affecting nest-site selection by cavity-nesting birds in our nestboxes (Parejo and Avilés 2011). Although prey location by snakes is mainly based on olfactory cues, evidence suggests that visual stimuli may also help location of nests by foraging snakes (Mullin and Cooper 1998).

Rollers avoided highly transformed areas, those relatively closer to the motorway and with a higher density of almond groves and pine plantations (Fig. 2b). Previous work has shown a reduction in bird density in areas near roads with high traffic loads (Reijnen *et al.* 1997). Also, it has been shown that traffic noise can interfere with conspecific communication, hindering territory establishment and mating in birds (Parris and Schneider 2009). Rollers may avoid disturbance by actively selecting nestboxes that are further away of the motorway. However, because the axis of habitat transformation united proximity to the motorway and high density of cultivated trees (Table 1), we decided to compare models using these variables separately to assess which was more closely associated with nestbox occupancy. Results of univariate models revealed that density of cultivated trees (AICc = 220.2) provided a more parsimonious explanation of the occupation pattern than the distance to the motorway (AICc = 223.4), suggesting that the negative effect of tree plantations may be more decisive for Rollers than the disturbance produced by the motorway. Indeed, previous studies on commercial tree plantations have revealed that hole-nesting bird abundance is negatively affected in the young stages of the plantation due to a reduction in the number of holes (Donald *et al.* 1998, Malan 2001). In the case of Rollers, a high density of trees may also conflict with their hunting habits, as Rollers need open areas with perches for foraging (Avilés and Costillo 1998).

Earlier-breeding Rollers preferred nestboxes with a northwest orientation (Table 3, Fig. 4). Early preference for northwest-oriented nestboxes is striking, considering previous results in the northern hemisphere showing a preference for southeast-orientated nests (Wiebe 2001, Ardia *et al.* 2006, Magaña *et al.* 2010). In our study site, nestboxes oriented to the northwest were less exposed to cold winds coming from the nearby Sierra Nevada and Sierra de Baza mountain ranges that border the study area. Later in the season after snow-melt in the mountains, conditions are warmer and a southeast orientation may be preferred. There was also some suggestion (although non-significant) that fledglings were heavier in boxes with a northwest orientation. Our results thus suggest that Rollers show a preference for nestboxes with a certain orientation only when it influences microclimate, suggesting that higher nest temperature may provide fitness benefits for Rollers at their upper altitudinal limit.

Besides the physical elements of the landscape, biological factors such as inter-specific competition for nestboxes and⁄or the use of social information coming from heterospecifics (Parejo *et al.* 2005) may also influence nestbox use by Rollers. Patterns of nestbox preference by Rollers were not influenced by the exclusion of nestboxes already occupied by Little Owls. In addition, there was a surplus of nestboxes in our study area, suggesting that the effect of Little Owl presence on Roller settlement patterns was negligible.

Implications for conservation and management

The Eurasian Roller is considered a target species in the LIFE08NAT/E/000068 programme, being the only endangered bird species fully dependent on holes for breeding

(Environment DG 2008). Here, we provide the first study investigating the efficacy of nestbox provisioning for this species by analysing nestbox selection for breeding and reproductive performance. It was noteworthy that nestbox exposure had opposite effects on nestbox use and breeding success, suggesting that nestboxes installed in exposed sites could exert a deceptive effect on Rollers. Nestboxes should not be installed in easily detectable locations, where breeding failure is more likely, or in highly concealed locations, which are probably undetectable for prospecting Rollers. Future conservation plans for this hole-dependent species should assess carefully the fitness consequences of nestbox choice, rather than developing indiscriminate plans of nestbox installation that are justified on the basis of short-term occupancy data.

The key role of nestbox exposure may also have implications for Holm Oak forest management. It can be inferred from our results that pruning could have a direct effect on habitat selection, modifying the structure of branches surrounding the Roller nests and nearby areas, and hence visibility, thereby influencing the preference and fitness of Rollers using nestboxes.

Finally, as we detected avoidance of highly transformed areas (i.e. further from the motorway and with less land devoted to almond groves or pine plantations) by Rollers, future conservation plans for this species should aim to avoid placing nestboxes in these relatively disturbed and intensive landscapes. Instead, conservation plans should promote combined plans of nestbox provisioning with the creation of a mosaic of alternating herb crops and woody groves to enhance the probability of colonization by Rollers.

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SUPPORTING INFORMATION

Appendix S1. The full set of models for Roller nestbox occupation (presence in at least one of 3 years), ordered according to AICc values.

Appendix S2. The full set of models for annual Roller nestbox occupation (presence per year using an events/trials model syntax), ordered according to AICc values.

Appendix S3. The full set of models for the probability of successful breeding, ordered according to AICc.

Appendix S4. The full set of models for variation in laying date using 2008 breeding data, and ordered according to AICc values.

Appendix S5. The full set of models for occupation using 2008 breeding data, ordered according to AICc values.

Appendix S6. The full set of models for occupation using 2008 breeding data and ordered according to AICc values. Only nestboxes not occupied by Little Owls *Athene noctua* were considered for the analysis.

Appendix S1.

The full set of models for Roller nest-box occupation (presence in at least one of three years), ordered according to AICc values.

Model	**K**	**AICc**	**Δ**	**w**
Occupation ~ Farming activity + Land transformation + Visibility	5	216.06	0.00	0.143
Occupation ~ Farming activity + Slope steepness + Land transformation + Visibility	6	216.69	0.63	0.104
Occupation ~ Land transformation + Visibility	4	216.95	0.89	0.092
Occupation ~ Slope steepness + Land transformation + Visibility	5	217.52	1.46	0.069
Occupation ~ Farming activity + Visibility	4	217.89	1.83	0.057
Occupation ~ Farming activity + Land transformation + Height + Visibility	6	218.26	2.20	0.048
Occupation ~ Farming activity + Slope steepness + Visibility	5	218.50	2.44	0.042
Occupation ~ Land transformation + Height + Visibility	5	218.64	2.58	0.039
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Visibility	7	218.97	2.91	0.033
Occupation ~ Slope steepness + Land transformation + Height + Visibility +	6	219.27	3.21	0.029
Occupation ~ Visibility	3	219.33	3.27	0.028
Occupation ~ Farming activity + Slope steepness + Land transformation	5	219.71	3.65	0.023
Occupation ~ Farming activity + Height + Visibility	5	219.78	3.72	0.022
Occupation ~ Farming activity + Slope steepness	4	219.90	3.84	0.021
Occupation ~ Slope steepness + Visibility	4	219.95	3.89	0.020
Occupation ~ Height + Visibility	4	220.21	4.15	0.018
Occupation ~ Farming activity + Slope steepness + Height + Visibility	6	220.71	4.65	0.014
Occupation ~ Slope steepness + Land transformation	4	220.69	4.63	0.014
Occupation ~ Farming activity	3	220.77	4.70	0.014
Occupation ~ Farming activity + Land transformation	4	220.91	4.85	0.013
Occupation ~ Slope steepness + Height + Visibility	5	221.15	5.09	0.011
Occupation ~ Farming activity + Slope steepness + Height	5	221.18	5.12	0.011
Occupation ~ Slope steepness	3	221.01	4.95	0.012
Occupation ~ Farming activity + Slope steepness + Land transformation + Height	6	221.46	5.40	0.010
Occupation ~ Orientation + Farming activity + Land transformation + Visibility	6	221.60	5.54	0.009
Occupation ~ Slope steepness + Land transformation + Height	5	221.60	5.54	0.009
Occupation ~ Slope steepness + Height	4	221.61	5.55	0.009
Occupation ~ Land transformation	3	221.63	5.57	0.009
Occupation ~ Farming activity + Height	4	221.93	5.87	0.008
Occupation ~ Orientation + Farming activity + Slope steepness + Land transformation + Visibility	7	222.40	6.34	0.006
Occupation ~ Farming activity + Land transformation + Height	5	222.30	6.24	0.006
Occupation ~ Height	3	222.18	6.12	0.007
Occupation ~ Orientation + Land transformation + Visibility	5	222.57	6.51	0.006
Occupation ~ Land transformation + Height	4	222.57	6.51	0.006
Occupation ~ Orientation + Slope steepness + Land transformation + Visibility	6	222.83	6.77	0.005
Occupation ~ Orientation + Farming activity + Land transformation + Height + Visibility	7	223.59	7.52	0.003

Occupation ~ Orientation + Farming activity + Visibility	5	223.63	7.57	0.003
Occupation ~ Orientation + Farming activity + Slope steepness + Land transformation + Height + Visibility	8	224.18	8.12	0.002
Occupation ~ Orientation + Land transformation + Height + Visibility	6	224.20	8.14	0.002
Occupation ~ Orientation + Farming activity + Slope steepness + Visibility	6	224.24	8.18	0.002
Occupation ~ Orientation + Slope steepness + Land transformation + Height + Visibility	7	224.70	8.64	0.002
Occupation ~ Orientation + Farming activity + Slope steepness + Land transformation	6	224.90	8.84	0.002
Occupation ~ Orientation + Visibility	4	225.11	9.05	0.002
Occupation ~ Orientation + Farming activity + Slope steepness	5	225.26	9.20	0.001
Occupation ~ Orientation + Farming activity + Height + Visibility	6	225.44	9.37	0.001
Occupation ~ Orientation + Slope steepness + Visibility	5	225.67	9.61	0.001
Occupation ~ Orientation + Slope steepness + Land transformation	5	225.78	9.72	0.001
Occupation ~ Orientation + Farming activity + Slope steepness + Height + Visibility	7	226.34	10.28	0.001
Occupation ~ Orientation + Farming activity + Land transformation	5	226.10	10.04	0.001
Occupation ~ Orientation + Farming activity	4	226.12	10.06	0.001
Occupation ~ Orientation + Height + Visibility	5	226.28	10.22	0.001
Occupation ~ Orientation + Farming activity + Slope steepness + Land transformation + Height	7	226.61	10.55	0.001
Occupation ~ Orientation + Farming activity + Slope steepness + Height	6	226.59	10.53	0.001
Occupation ~ Orientation + Slope steepness	4	226.69	10.63	0.001
Occupation ~ Orientation + Slope steepness + Height + Visibility	6	227.02	10.96	0.001
Occupation ~ Orientation + Slope steepness + Land transformation + Height	6	227.14	11.08	0.001
Occupation ~ Orientation + Farming activity + Height	5	227.23	11.17	0.001
Occupation ~ Orientation + Slope steepness + Height	5	227.36	11.30	0.001
Occupation ~ Orientation + Land transformation	4	227.26	11.20	0.001
Occupation ~ Orientation + Farming activity + Land transformation + Height	6	227.63	11.57	0.000
Occupation ~ Orientation	3	227.85	11.79	0.000
Occupation ~ Orientation + Height	4	227.95	11.89	0.000
Occupation ~ Orientation + Land transformation + Height	5	228.09	12.03	0.000

Appendix S2.

The full set of models for annual Roller nest-box occupation (presence per year using an events/trials model syntax), ordered according to AICc values.

Model	K	AICc	Δ	w
Preference ~ Land transformation	3	121.55	0.00	0.123
Preference ~ Slope steepness	3	122.15	0.61	0.091
Preference ~ Farming activity	3	122.80	1.26	0.066
Preference ~ Visibility	3	122.86	1.31	0.064
Preference ~ Height	3	122.99	1.44	0.060
Preference ~ Slope steepness + Land transformation	4	123.19	1.64	0.054
Preference ~ Farming activity + Land transformation	4	123.28	1.73	0.052
Preference ~ Land transformation + Visibility	4	123.79	2.24	0.040
Preference ~ Land transformation + Height	4	123.79	2.24	0.040
Preference ~ Farming activity + Slope steepness	4	124.22	2.68	0.032
Preference ~ Slope steepness + Height	4	124.33	2.79	0.031
Preference ~ Slope steepness + Visibility	4	124.34	2.79	0.030
Preference ~ Farming activity + Visibility	4	124.79	3.24	0.024
Preference ~ Farming activity + Height	4	124.89	3.34	0.023
Preference ~ Height + Visibility	4	124.98	3.43	0.022
Preference ~ Farming activity + Slope steepness + Land transformation	5	125.12	3.58	0.021
Preference ~ Slope steepness + Land transformation + Visibility	5	125.50	3.96	0.017
Preference ~ Slope steepness + Land transformation + Height	5	125.51	3.96	0.017
Preference ~ Farming activity + Land transformation + Height	5	125.57	4.02	0.017
Preference ~ Farming activity + Land transformation + Visibility	5	125.60	4.05	0.016
Preference ~ Orientation	3	125.93	4.38	0.014
Preference ~ Land transformation + Height + Visibility	5	126.11	4.57	0.013
Preference ~ Land transformation + Orientation	4	126.32	4.77	0.011
Preference ~ Farming activity + Slope steepness + Height	5	126.42	4.87	0.011
Preference ~ Farming activity + Slope steepness + Visibility	5	126.47	4.92	0.011
Preference ~ Slope steepness + Height + Visibility	5	126.58	5.03	0.010
Preference ~ Farming activity + Height + Visibility	5	126.83	5.28	0.009
Preference ~ Farming activity + Slope steepness + Land transformation + Height	6	127.51	5.96	0.006
Preference ~ Farming activity + Slope steepness + Land transformation + Visibility	6	127.55	6.00	0.006
Preference ~ Slope steepness + Orientation	4	127.58	6.03	0.006
Preference ~ Visibility + Orientation	4	127.82	6.28	0.005
Preference ~ Slope steepness + Land transformation + Height + Visibility	6	127.93	6.38	0.005
Preference ~ Farming activity + Land transformation + Height + Visibility	6	127.96	6.41	0.005
Preference ~ Height + Orientation	4	128.27	6.72	0.004
Preference ~ Farming activity + Orientation	4	128.29	6.74	0.004
Preference ~ Slope steepness + Land transformation + Orientation	5	128.40	6.85	0.004
Preference ~ Farming activity + Land transformation + Orientation	5	128.62	7.07	0.004

Preference ~ Farming activity + Slope steepness + Height + Visibility	6	128.68	7.13	0.003
Preference ~ Land transformation + Visibility + Orientation	5	128.75	7.21	0.003
Preference ~ Land transformation + Height + Orientation	5	128.84	7.29	0.003
Preference ~ Slope steepness + Visibility + Orientation	5	129.81	8.27	0.002
Preference ~ Slope steepness + Height + Orientation	5	130.02	8.47	0.002
Preference ~ Farming activity + Slope steepness + Land transformation + Height + Visibility	7	130.04	8.49	0.002
Preference ~ Farming activity + Slope steepness + Orientation	5	130.07	8.52	0.002
Preference ~ Height + Visibility + Orientation	5	130.13	8.58	0.002
Preference ~ Farming activity + Visibility + Orientation	5	130.25	8.70	0.002
Preference ~ Farming activity + Height + Orientation	5	130.67	9.12	0.001
Preference ~ Farming activity + Slope steepness + Land transformation + Orientation	6	130.88	9.33	0.001
Preference ~ Slope steepness + Land transformation + Visibility + Orientation	6	131.00	9.45	0.001
Preference ~ Slope steepness + Land transformation + Height + Orientation	6	131.03	9.48	0.001
Preference ~ Farming activity + Land transformation + Visibility + Orientation	6	131.15	9.60	0.001
Preference ~ Farming activity + Land transformation + Height + Orientation	6	131.22	9.67	0.001
Preference ~ Land transformation + Height + Visibility + Orientation	6	131.36	9.81	0.001
Preference ~ Slope steepness + Height + Visibility + Orientation	6	132.26	10.72	0.001
Preference ~ Farming activity + Slope steepness + Visibility + Orientation	6	132.39	10.85	0.001
Preference ~ Farming activity + Height + Visibility + Orientation	6	132.53	10.99	0.001
Preference ~ Farming activity + Slope steepness + Height + Orientation	6	132.58	11.03	0.000
Preference ~ Farming activity + Slope steepness + Land transformation + Visibility + Orientation	7	133.58	12.04	0.000
Preference ~ Farming activity + Slope steepness + Land transformation + Height + Orientation	7	133.59	12.04	0.000
Preference ~ Slope steepness + Land transformation + Height + Visibility + Orientation	7	133.73	12.18	0.000
Preference ~ Farming activity + Land transformation + Height + Visibility + Orientation	7	133.80	12.25	0.000
Preference ~ Farming activity + Slope steepness + Height + Visibility + Orientation	7	134.87	13.32	0.000
Preference ~ Farming activity + Slope steepness + Land transformation + Height + Visibility + Orientation	8	136.38	14.84	0.000

Appendix S3.

The full set of models for the probability of successful breeding, ordered according to AICc.

Model	K	AICc	Δ	w
Breeding success ~ Height + Visibility	4	67.58	0.00	0.076
Breeding success ~ Visibility	3	67.60	0.02	0.076
Breeding success ~ Slope steepness + Visibility	4	68.43	0.85	0.050
Breeding success ~ Slope steepness + Height + Visibility	5	68.56	0.98	0.047
Breeding success ~ Land transformation + Visibility	4	68.83	1.24	0.041
Breeding success ~ Land transformation + Height + Visibility	5	69.33	1.75	0.032
Breeding success ~ Farming activity + Visibility	4	69.43	1.85	0.030
Breeding success ~ Slope steepness	3	69.48	1.90	0.029
Breeding success ~ Farming activity + Height + Visibility	5	69.79	2.21	0.025
Breeding success ~ Land transformation	3	69.60	2.01	0.028
Breeding success ~ Slope steepness + Land transformation + Visibility	5	69.84	2.26	0.025
Breeding success ~ Slope steepness + Land transformation	4	69.81	2.23	0.025
Breeding success ~ Height + Visibility + Orientation	5	69.94	2.36	0.023
Breeding success ~ Slope steepness + Height + Visibility + Orientation	6	70.11	2.53	0.021
Breeding success ~ Farming activity + Slope steepness + Visibility	5	70.09	2.51	0.022
Breeding success ~ Slope steepness + Orientation	4	70.16	2.58	0.021
Breeding success ~ Slope steepness + Visibility + Orientation	5	70.35	2.77	0.019
Breeding success ~ Visibility + Orientation	4	70.26	2.68	0.020
Breeding success ~ Slope steepness + Land transformation + Height + Visibility	6	70.61	3.03	0.017
Breeding success ~ Farming activity + Slope steepness + Height + Visibility	6	70.63	3.04	0.017
Breeding success ~ Farming activity + Land transformation + Visibility	5	70.73	3.15	0.016
Breeding success ~ Slope steepness + Height + Orientation	5	70.83	3.25	0.015
Breeding success ~ Farming activity + Slope steepness	4	70.75	3.17	0.016
Breeding success ~ Slope steepness + Land transformation + Orientation	5	70.97	3.39	0.014
Breeding success ~ Slope steepness + Height	4	70.87	3.28	0.015
Breeding success ~ Land transformation + Orientation	4	71.20	3.62	0.012
Breeding success ~ Height	3	71.17	3.59	0.013
Breeding success ~ Orientation	3	71.19	3.61	0.013
Breeding success ~ Farming activity + Slope steepness + Land transformation	5	71.42	3.84	0.011
Breeding success ~ Land transformation + Height	4	71.32	3.74	0.012
Breeding success ~ Farming activity + Land transformation + Height + Visibility	6	71.60	4.02	0.010
Breeding success ~ Slope steepness + Land transformation + Height	5	71.49	3.91	0.011
Breeding success ~ Farming activity + Land transformation	4	71.39	3.81	0.011
Breeding success ~ Land transformation + Height + Visibility + Orientation	6	71.65	4.07	0.010
Breeding success ~ Land transformation + Visibility + Orientation	5	71.55	3.97	0.010
Breeding success ~ Farming activity + Slope steepness + Land transformation + Visibility	6	71.71	4.13	0.010
Breeding success ~ Farming activity	3	71.38	3.80	0.011
Breeding success ~ Slope steepness + Land transformation + Height + Orientation	6	71.76	4.18	0.009

Breeding success ~ Slope steepness + Land transformation + Height + Visibility + Orientation	7	72.04	4.46	0.008
Breeding success ~ Slope steepness + Land transformation + Visibility + Orientation	6	71.93	4.35	0.009
Breeding success ~ Farming activity + Height + Visibility + Orientation	6	71.98	4.40	0.008
Breeding success ~ Farming activity + Slope steepness + Orientation	5	71.87	4.29	0.009
Breeding success ~ Farming activity + Slope steepness + Height + Visibility + Orientation	7	72.37	4.79	0.007
Breeding success ~ Height + Orientation	4	72.07	4.49	0.008
Breeding success ~ Farming activity + Slope steepness + Visibility + Orientation	6	72.34	4.75	0.007
Breeding success ~ Land transformation + Height + Orientation	5	72.28	4.70	0.007
Breeding success ~ Farming activity + Visibility + Orientation	5	72.39	4.81	0.007
Breeding success ~ Farming activity + Slope steepness + Height	5	72.45	4.87	0.007
Breeding success ~ Farming activity + Slope steepness + Land transformation + Height + Visibility	7	72.78	5.20	0.006
Breeding success ~ Farming activity + Slope steepness + Land transformation + Orientation	6	72.81	5.23	0.006
Breeding success ~ Farming activity + Slope steepness + Height + Orientation	6	72.90	5.32	0.005
Breeding success ~ Farming activity + Height	4	72.96	5.38	0.005
Breeding success ~ Farming activity + Slope steepness + Land transformation + Height	6	73.38	5.80	0.004
Breeding success ~ Farming activity + Land transformation + Height	5	73.32	5.74	0.004
Breeding success ~ Farming activity + Orientation	4	73.25	5.66	0.004
Breeding success ~ Farming activity + Land transformation + Orientation	5	73.37	5.79	0.004
Breeding success ~ Farming activity + Land transformation + Height + Visibility + Orientation	7	73.76	6.18	0.003
Breeding success ~ Farming activity + Land transformation + Visibility + Orientation	6	73.65	6.06	0.004
Breeding success ~ Farming activity + Slope steepness + Land transformation + Height + Orientation	7	73.85	6.27	0.003
Breeding success ~ Farming activity + Slope steepness + Land transformation + Visibility + Orientation	7	73.85	6.27	0.003
Breeding success ~ Farming activity + Slope steepness + Land transformation + Height + Visibility + Orientation	8	74.08	6.50	0.003
Breeding success ~ Farming activity + Height + Orientation	5	74.28	6.70	0.003
Breeding success ~ Farming activity + Land transformation + Height + Orientation	6	74.53	6.95	0.002

Appendix S4.

The full set of models for variation in lay date using 2008 breeding data, and ordered according to AICc values.

A) Nest-box characteristics.

Model	K	AICc	Δ	w
Laying date ~ Orientation	3	173.49	0.00	0.371
Laying date ~ Height + Orientation	4	175.15	1.66	0.162
Laying date ~ Visibility + Orientation	4	175.16	1.67	0.161
Laying date ~ Height + Visibility + Orientation	5	176.34	2.85	0.089
Laying date ~ Height	3	176.15	2.66	0.098
Laying date ~ Visibility	3	176.45	2.96	0.084
Laying date ~ Height + Visibility	4	178.23	4.74	0.035

B) Environmental characteristics.

Model	K	AICc	Δ	w
Laying date ~ Farming activity	3	174.98	0.00	0.326
Laying date ~ Slope steepness	3	176.24	1.26	0.174
Laying date ~ Land transformation	3	176.41	1.42	0.160
Laying date ~ Farming activity + Slope steepness	4	177.00	2.02	0.119
Laying date ~ Farming activity + Land transformation	4	177.07	2.08	0.115
Laying date ~ Slope steepness + Land transformation	4	178.24	3.26	0.064
Laying date ~ Farming activity + Slope steepness + Land transformation	5	179.11	4.13	0.041

Appendix S5.

The full set of models for occupation using 2008 breeding data, ordered according to AICc values.

Model	K	AICc	Δ	w
Occupation ~ Farming activity + Visibility	4	139.68	0.00	0.098
Occupation ~ Farming activity	3	140.54	0.87	0.063
Occupation ~ Farming activity + Visibility + Orientation	5	140.71	1.04	0.058
Occupation ~ Farming activity + Slope steepness	4	141.25	1.57	0.044
Occupation ~ Farming activity + Slope steepness + Visibility	5	141.25	1.58	0.044
Occupation ~ Farming activity + Orientation	4	141.29	1.61	0.044
Occupation ~ Farming activity + Height + Visibility	5	141.65	1.98	0.036
Occupation ~ Farming activity + Land transformation + Visibility	5	141.77	2.10	0.034
Occupation ~ Visibility	3	142.12	2.44	0.029
Occupation ~ Farming activity + Height	4	142.17	2.49	0.028
Occupation ~ Farming activity + Slope steepness + Orientation	5	142.24	2.56	0.027
Occupation ~ Farming activity + Land transformation	4	142.35	2.67	0.026
Occupation ~ Farming activity + Slope steepness + Visibility + Orientation	6	142.46	2.78	0.024
Occupation ~ Farming activity + Height + Visibility + Orientation	6	142.49	2.81	0.024
Occupation ~ Farming activity + Height + Orientation	5	142.56	2.88	0.023
Occupation ~ Farming activity + Land transformation + Visibility + Orientation	6	142.85	3.17	0.020
Occupation ~ Farming activity + Slope steepness + Height	5	142.98	3.30	0.019
Occupation ~ Farming activity + Slope steepness + Land transformation	5	143.12	3.44	0.017
Occupation ~ Farming activity + Slope steepness + Height + Visibility	6	143.26	3.59	0.016
Occupation ~ Farming activity + Land transformation + Orientation	5	143.28	3.60	0.016
Occupation ~ Farming activity + Slope steepness + Land transformation + Visibility	6	143.37	3.70	0.015
Occupation ~ Height + Visibility	4	143.44	3.77	0.015
Occupation ~ Height	3	143.58	3.91	0.014
Occupation ~ Farming activity + Slope steepness + Height + Orientation	6	143.63	3.96	0.013
Occupation ~ Slope steepness	3	143.65	3.97	0.013
Occupation ~ Slope steepness + Visibility	4	143.71	4.04	0.013
Occupation ~ Farming activity + Land transformation + Height + Visibility	6	143.75	4.08	0.013
Occupation ~ Farming activity + Land transformation + Height	5	143.90	4.23	0.012
Occupation ~ Visibility + Orientation	4	143.95	4.27	0.012
Occupation ~ Land transformation + Visibility	4	144.18	4.50	0.010
Occupation ~ Orientation	3	144.20	4.53	0.010
Occupation ~ Farming activity + Slope steepness + Height + Visibility + Orientation	7	144.27	4.59	0.010
Occupation ~ Farming activity + Slope steepness + Land transformation + Orientation	6	144.28	4.61	0.010
Occupation ~ Farming activity + Land transformation + Height + Orientation	6	144.45	4.78	0.009
Occupation ~ Slope steepness + Height	4	144.53	4.85	0.009
Occupation ~ Height + Orientation	4	144.55	4.87	0.009
Occupation ~ Farming activity + Slope steepness + Land transformation + Visibility + Orientation	7	144.62	4.94	0.008

Occupation ~ Farming activity + Land transformation + Height + Visibility + Orientation	7	144.65	4.97	0.008
Occupation ~ Farming activity + Slope steepness + Land transformation + Height	6	144.80	5.13	0.008
Occupation ~ Land transformation	3	144.88	5.20	0.007
Occupation ~ Height + Visibility + Orientation	5	144.97	5.30	0.007
Occupation ~ Slope steepness + Height + Visibility	5	145.08	5.40	0.007
Occupation ~ Slope steepness + Orientation	4	145.17	5.49	0.006
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Visibility	7	145.39	5.71	0.006
Occupation ~ Land transformation + Height	4	145.54	5.87	0.005
Occupation ~ Land transformation + Height + Visibility	5	145.55	5.88	0.005
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Orientation	7	145.62	5.94	0.005
Occupation ~ Slope steepness + Visibility + Orientation	5	145.62	5.95	0.005
Occupation ~ Slope steepness + Height + Orientation	5	145.69	6.02	0.005
Occupation ~ Slope steepness + Land transformation	4	145.71	6.04	0.005
Occupation ~ Slope steepness + Land transformation + Visibility	5	145.79	6.12	0.005
Occupation ~ Land transformation + Visibility + Orientation	5	145.91	6.24	0.004
Occupation ~ Land transformation + Orientation	4	146.29	6.62	0.004
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Visibility + Orientation	8	146.45	6.78	0.003
Occupation ~ Slope steepness + Land transformation + Height	5	146.56	6.89	0.003
Occupation ~ Land transformation + Height + Orientation	5	146.63	6.95	0.003
Occupation ~ Slope steepness + Height + Visibility + Orientation	6	146.70	7.02	0.003
Occupation ~ Land transformation + Height + Visibility + Orientation	6	147.08	7.40	0.002
Occupation ~ Slope steepness + Land transformation + Height + Visibility	6	147.21	7.54	0.002
Occupation ~ Slope steepness + Land transformation + Orientation	5	147.28	7.60	0.002
Occupation ~ Slope steepness + Land transformation + Visibility + Orientation	6	147.60	7.93	0.002
Occupation ~ Slope steepness + Land transformation + Height + Orientation	6	147.82	8.14	0.002
Occupation ~ Slope steepness + Land transformation + Height + Visibility + Orientation	7	148.82	9.14	0.001

Appendix S6.

The full set of models for occupation using 2008 breeding data and ordered according to AICc values. Only nest-boxes not occupied by Little Owls *Athene noctua* were considered for the analysis.

Model	**K**	**AICc**	**Δ**	**w**
Occupation ~ Farming activity + Visibility	4	136.91	0.00	0.103
Occupation ~ Farming activity	3	137.51	0.60	0.076
Occupation ~ Farming activity + Slope steepness	4	138.18	1.27	0.055
Occupation ~ Farming activity + Slope steepness + Visibility	5	138.45	1.54	0.048
Occupation ~ Farming activity + Visibility + Orientation	5	138.57	1.66	0.045
Occupation ~ Farming activity + Height + Visibility	5	138.94	2.03	0.037
Occupation ~ Farming activity + Orientation	4	138.98	2.07	0.037
Occupation ~ Farming activity + Land transformation + Visibility	5	139.02	2.11	0.036
Occupation ~ Farming activity + Height	4	139.25	2.33	0.032
Occupation ~ Visibility	3	139.47	2.56	0.029
Occupation ~ Farming activity + Land transformation	4	139.47	2.56	0.029
Occupation ~ Farming activity + Slope steepness + Orientation	5	139.86	2.95	0.024
Occupation ~ Farming activity + Slope steepness + Height	5	140.02	3.11	0.022
Occupation ~ Farming activity + Slope steepness + Land transformation	5	140.19	3.28	0.020
Occupation ~ Farming activity + Slope steepness + Visibility + Orientation	6	140.27	3.35	0.019
Occupation ~ Farming activity + Height + Orientation	5	140.35	3.43	0.019
Occupation ~ Farming activity + Height + Visibility + Orientation	6	140.40	3.49	0.018
Occupation ~ Farming activity + Slope steepness + Height + Visibility	6	140.51	3.60	0.017
Occupation ~ Farming activity + Slope steepness + Land transformation + Visibility	6	140.59	3.68	0.016
Occupation ~ Slope steepness	3	140.65	3.74	0.016
Occupation ~ Farming activity + Land transformation + Visibility + Orientation	6	140.67	3.76	0.016
Occupation ~ Height	3	140.69	3.78	0.016
Occupation ~ Height + Visibility	4	140.82	3.91	0.015
Occupation ~ Slope steepness + Visibility	4	141.03	4.11	0.013
Occupation ~ Farming activity + Land transformation + Orientation	5	141.05	4.14	0.013
Occupation ~ Farming activity + Land transformation + Height + Visibility	6	141.08	4.16	0.013
Occupation ~ Farming activity + Land transformation + Height	5	141.17	4.25	0.012
Occupation ~ Farming activity + Slope steepness + Height + Orientation	6	141.37	4.46	0.011
Occupation ~ Visibility + Orientation	4	141.41	4.50	0.011
Occupation ~ Land transformation + Visibility	4	141.46	4.55	0.011
Occupation ~ Orientation	3	141.46	4.55	0.011
Occupation ~ Slope steepness + Height	4	141.64	4.73	0.010
Occupation ~ Height + Orientation	4	141.90	4.99	0.009
Occupation ~ Land transformation	3	141.93	5.02	0.008
Occupation ~ Farming activity + Slope steepness + Land transformation + Orientation	6	141.97	5.06	0.008

Occupation ~ Farming activity + Slope steepness + Land transformation + Height	6	142.02	5.10	0.008
Occupation ~ Farming activity + Slope steepness + Height + Visibility + Orientation	7	142.14	5.22	0.008
Occupation ~ Slope steepness + Orientation +	4	142.35	5.43	0.007
Occupation ~ Farming activity + Land transformation + Height + Orientation	6	142.36	5.45	0.007
Occupation ~ Farming activity + Slope steepness + Land transformation + Visibility + Orientation	7	142.39	5.48	0.007
Occupation ~ Slope steepness + Height + Visibility	5	142.43	5.52	0.007
Occupation ~ Height + Visibility + Orientation	5	142.46	5.55	0.006
Occupation ~ Farming activity + Land transformation + Height + Visibility + Orientation	7	142.56	5.64	0.006
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Visibility	7	142.68	5.76	0.006
Occupation ~ Land transformation + Height	4	142.73	5.81	0.006
Occupation ~ Slope steepness + Land transformation	4	142.74	5.83	0.006
Occupation ~ Land transformation + Height + Visibility	5	142.91	5.99	0.005
Occupation ~ Slope steepness + Height + Orientation	5	142.98	6.07	0.005
Occupation ~ Slope steepness + Visibility + Orientation	5	143.01	6.10	0.005
Occupation ~ Slope steepness + Land transformation + Visibility	5	143.04	6.13	0.005
Occupation ~ Land transformation + Visibility + Orientation	5	143.25	6.34	0.004
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Orientation	7	143.46	6.55	0.004
Occupation ~ Land transformation + Orientation	4	143.53	6.62	0.004
Occupation ~ Slope steepness + Land transformation + Height	5	143.73	6.82	0.003
Occupation ~ Land transformation + Height + Orientation	5	144.01	7.09	0.003
Occupation ~ Slope steepness + Height + Visibility + Orientation	6	144.13	7.22	0.003
Occupation ~ Farming activity + Slope steepness + Land transformation + Height + Visibility + Orientation	8	144.32	7.40	0.003
Occupation ~ Slope steepness + Land transformation + Orientation	5	144.42	7.51	0.002
Occupation ~ Land transformation + Height + Visibility + Orientation	6	144.51	7.60	0.002
Occupation ~ Slope steepness + Land transformation + Height + Visibility	6	144.54	7.63	0.002
Occupation ~ Slope steepness + Land transformation + Visibility + Orientation	6	144.87	7.96	0.002
Occupation ~ Slope steepness + Land transformation + Height + Orientation	6	145.12	8.21	0.002
Occupation ~ Slope steepness + Land transformation + Height + Visibility + Orientation	7	146.19	9.28	0.001

CHAPTER II

Causes and Consequences of Dispersal in the European Roller

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ABSTRACT

Studying the causes and consequences of dispersal is critical to achieve a better knowledge of population dynamics and to develop meaningful conservation actions for endangered species. The European Roller *Coracias garrulus* experienced a drastic decline through their breeding distributional range in Europe, and, although their long-distance migratory movements have been recently described, dispersal patterns within breeding populations are yet fully unexplored. Here we studied causes and consequences of natal and breeding dispersal in a population of European Rollers during 8 years. Older individuals were less dispersive than younger ones and males than females. In males we found that individuals with more brilliant heads, occupying more visible nest-boxes and breeding in highly productively patches were less prone to disperse. In females we found that those with more yellow-red chroma in their backs, and those breeding in territories where their neighbours were less successful dispersed farther to breed in the following year. Concerning settlement decisions, females, but not males, moved to nest-boxes where density of rollers was lower than that at the nest-box of origin. Dispersal decisions had no obvious fitness consequences at the studied scale, and recruitment probability was extraordinary low, which may globally suggest that our population was acting as a source within the meta-population of rollers in the south of Spain.

INTRODUCTION

Dispersal is the movement of individuals between their birth and first breeding site (natal dispersal) or between sites in two consecutive breeding events (breeding dispersal) (Greenwood and Harvey 1982, Clobert *et al.* 2001, Clobert *et al.* 2009). Knowing the proximate causes motivating dispersal may show the selective pressures affecting this process. In addition, the study of the fitness consequences of different dispersal strategies may help us to understand the adaptive significance of this behaviour (Serrano and Tella 2012). Therefore, understanding the dispersal patterns of species is crucial to comprehend their population dynamics (Greenwood and Harvey 1982, Hanski and Gilpin 1997, Clobert 2009) and to develop meaningful conservation actions for populations (Ronce 2007, Serrano and Tella 2012).

In birds, dispersal is a complex process affecting survival chance, breeding performance and, ultimately, the fitness of an individual (Greenwood and Harvey 1982, Stamps *et al.* 2005, Gienapp and Merilä 2011, Bonte *et al.* 2012, Bonte *et al.* 2014). Theoretical and empirical studies have shown that the costs and benefits of dispersal may be affected by several factors along the different phases of the dispersal event (i.e. departure, transfer and settlement) (Bowler and Benton 2005, Clobert *et al*. 2009). Dispersal may respond to intrinsic factors inherent to the individual, as for instance its body condition, individual quality and/or age (Nilsson and Svensson 1996, Cichon and Dubiec 2005, Bonte *et al.* 2014), or to environmental variables, either abiotic or biotic, such as climate, habitat quality, neighbour competition or mate choice (Danchin *et al.* 1998, Serrano and Tella 2003). Indeed, among phenotypic traits, age and sex are well-known determinants of site-fidelity. In general, fidelity to breeding territories tends to increase with age (Greenwood and Harvey 1982, Paradis *et al.* 1998, Newton 2001), and, in territorial species, females are the sex that disperses more often and to farther distances (Greenwood 1980, Greenwood and Harvey 1982, Wiklund 1996). Besides individual traits, breeding dispersal may also respond to previous breeding experience, with dispersal being more frequent after a reproductive failure (Greenwood and Harvey 1982, Haas 1998, Forero *et al*. 1999, Serrano *et al*. 2001). The social environment may affect dispersal as well. Thereby, the presence and performance of conspecifics might provide information about the quality of close patches (Muller *et al*. 1997, Doligez *et al*. 2002, Parejo *et al*. 2007a). And this extra-information on local resources may tip the balance towards settlement or dispersal.

European Rollers *Coracias garrulus* are socially monogamous (Sánchez-Tójar *et al*. 2016) long-distance migratory and territorial hole-nesting birds that generally breed in solitary pairs, although they can occur in small loose groups (Cramp 1998, Václav *et al*. 2010, Rodríguez *et al*. 2011). A number of studies have shown that many nest-sites and territories are occupied by rollers in consecutive years (Cramp 1998, Sosnowski and Chmielewski 1996, Václav *et al*. 2010), and found correlative support for a role of social information in habitat choice (Parejo *et al*. 2005, Václav *et al*. 2010). However, individuals were not identified in these studies and thus it is unknown whether occupation patterns are due to the same birds repeatedly using the same areas or because these areas are consistently attracting different individuals. Although the long-distance migratory movements of this species have been recently described (Third chapter: Rodríguez-Ruiz *et al*. 2014, Finch *et al*. 2015), dispersal patterns at the individual level are yet fully unexplored.

Here we studied causes and consequences of natal and breeding dispersal in a population of European Rollers settled in nest-boxes in the south of Spain. For this purpose, we followed this roller breeding population during 8 years, and we explored the effect of a set of 18 variables sorted in four well-defined groups: individual traits, reproductive traits, nest-box characteristics and social environment. More concretely, we aimed to identify the factors determining probability of dispersal from one territory and dispersal distance between two consecutive breeding sites. We expect that relatively older individuals were more faithful to a territory than younger ones. In addition, as individual condition usually explains competitive ability, we expect that all positively-related individual traits to quality and/or condition (body measurements, plumage coloration and reproductive indexes) were related to faithfulness to breeding sites. Similarly, we expect individuals dispersing more from less preferred nest-boxes, i.e. concealed nest-boxes close to the highway (Rodríguez *et al*. 2011). Regarding the effects of social characteristics, in low competitive environment we expect rollers to remain faithful to nest-boxes located in areas with high conspecific breeding performance and high local conspecific density. Also, we analysed the fitness consequences of breeding dispersal. In addition, for dispersive birds we aimed to identify factors affecting the settlement in a certain nest-box. We expected dispersing birds moving towards more preferred nest-boxes, i.e. more visible ones far from the highway, and surrounded by successful conspecifics (Rodríguez *et al*. 2011). Finally, for nestlings born in the study area we studied individual and parental factors affecting their recruitment in the population, predicting a higher recruitment probability for nestlings in better condition and/or having being raised in nests of higher quality.

METHODS

This work was conducted in “La Hoya de Guadix” (Granada, Spain; 37º 18’ N, 3º 11’ W) during 2007-2014. The area covers approximately 135 km^2 of an agricultural landscape with sparse Holm Oaks *Quercus ilex*, where a set of 249 nest-boxes are held. Every nest-box was monitored once per week since mid April until registering occupation by rollers. Then, we collected data on breeding performance by recording laying date, breeding success, number of fledglings and weight of fledglings at day 20 of the biggest one in the nest.

Breeding dispersal

Adults were captured by hand or using net traps during incubation or nestlings' period through the eight years of study. Individuals were measured (weight and wing) and marked with coloured and metal rings for their identification in subsequent years. We also took blood samples via braquial vein for sexing individuals (as in Parejo *et al*. 2007b) and three feathers respectively from the head, back and scapular areas for colour measurement. Feather colour measurements were obtained using an Ocean Optics DH 2000 spectrophotometer, measured over a black background in total darkness (more details in Silva *et al.*, 2008). As we could not know the exact age of the non-native adult birds recruited in our study area, we assigned a minimum age of 2 years to every bird at the first time of capture and calculate their relative age from that moment. We considered a dispersal event when an individual bred in different nest-boxes in two consecutive years. A few individuals contributed with more than one dispersal event in our data (N = 16 out of 56), however, for analyses, we only considered one random dispersal event per individual. Dispersal distance is the linear distance between two nest-boxes consecutively used by and individual and was calculated using QGIS 2.12 (QGIS D.T. 2015).

We explored the effect of a set of 18 variables to determine causes affecting breeding dispersal (i.e. dispersal probability and dispersal distance (see Table 1) in rollers. These variables were analysed separately in four groups: individual traits, reproductive traits, nest-box characteristics and social environment (Table 1). Individual traits were sex, relative age, morphometric measures and descriptors of structural and melanin-based plumage coloration (see description in Table 1). As reproductive variables we included laying date and breeding success (i.e. probability that at least one chick fledged in a given nest) in a first analysis, anda second analysis including productivity (as the number of fledglings per nest) and total brood mass, as the sum of all fledglings weights at day 20th (Table 1). Only successful nests were used in the second analysis of reproductive variables. From our previous study on rollers' habitat selection (First chapter: Rodríguez *et al*. 2011) we knew that orientation, visibility and distance from the nest-box to the highway are nest-box attributes affecting roller occupation, therefore we targeted on these nest-box attributes as measured in Rodríguez *et al*. (2011) to study dispersal as well (Table 1). Regarding social environment, we calculated breeding densities and productivity of conspecifics (Table 1) by performing heatmaps using QGIS. Heatmaps are often used to identify clusters or hotspots where there is a high concentration of certain activity (Bojko 2009). Here, we elaborate a heatmap of occupation per year of study, associating to each occupied nest-box a circular buffer with a radius of 1000 meters around it. This circular area has a decreasing value from the centre (value=1) to the edge (value=0) that expresses the influence of the roller occupation on its surroundings. Those areas where two or more circles overlap obtain a value that is the sum in the values of each circle. The same method was followed to elaborate maps of productivity per year. In this case, value in the centre of the circular buffer is the number of fledglings raised in the corresponding nest-box. A more detailed description of the entire set of variables and units used to model roller dispersal can be found on Table 1.

Color measurements

Feather colour measurements were obtained using an Ocean Optics DH 2000 spectrophotometer, measured over a black background in total darkness (more details in Silva *et al.*, 2008). Previous studies have shown that most of variation in structural and melanin based coloration of rollers are due to changes in UV-blue chroma (in heads and scapulars) and yellow-red chroma (in the back), respectively. Chroma, was calculated as the ratio of the total reflectance in the range of interest and the total reflectance of the entire spectrum (300–700 nm; Montgomerie 2006). We also considered the brightness of the head as further color descriptor calculated as the summed reflectance from 300 to 700 nm.

Table 1. List detailing all response and explanatory variables used in models of roller dispersal.

Variable	Description
Dispersal Probability	Binomial. Probability of changing nest-box in the next year
Dispersal Distance	(meters) Distance between the nest-box in year t and nest-box in year t+1
Individual Traits	
Age	Relative age in years from capture. Birds were assigned an age of 2 when captured the first time
Wing Length	(centimetres)
Body Weight	(grams)
Scapulars (UV-Blue Brightness)	Total amount of light reflected by the feathers from the scapulars in the wavelength range of 300 - 475nm
Head (UV-Blue Brightness)	Total amount of light reflected by the feathers from the head in the wavelength range of 300 - 475nm
Head (Green-Yellow Brightness)	Total amount of light reflected by the feathers from the head in the wavelength range of 475 - 625nm
Back (Yellow-Red Chroma)	Ratio of reflectance in the wavelength range of 550 - 700nm and the total reflectance of the entire spectrum by feathers from the back
Reproductive traits	
Laying Date	Date of laying of the first egg in Julian calendar
Breeding Success	Binomial. Probability to fledge at least one chick in a nest
Productivity	Number of fledglings raised per nest
Fledglings Weight	(grams) Average weight of fledglings in day 20th of the oldest chick
Nest-box Characteristics	
Orientation	Categorical. Nest-box opening orientation with respect to north
Visibility	Categorical. Estimated visually from 10 metres in a scale of 1 (exposed) to 5 (fully concealed)
Distance to Highway	(meters) Shortest distance in a straight line to the highway
Social Characteristics	
Density of Rollers	Number of nest-boxes occupied by rollers in a radius of 1000m, weighed by relative distance from the centre.
Rollers Productivity	Number of fledglings produced by rollers occupying nest-boxes in a radius of 1000m, weighed by relative distance from the centre.

Natal dispersal

Approximately at day 20th of age of the oldest nestling in a nest, nestlings were measured (weight and wing), their blood sampled for molecular sexing and marked with coloured and metal rings for their subsequent identification, which allowed us to estimate recruitment. All chicks born in the study area that recruited in the population bred in a different nest-box from their natal one. Moreover, only a small portion of these nestlings recruited in the population (see below). Therefore, natal dispersal was studied by analysing the effects of variables, which were likely to affect nestlings' condition (nestling body weight and wing length at fledging time, nestling sex and plumage characteristics as individual traits and laying date and brood size at fledging of the natal nest), on the probability of recruitment of nestlings into the natal population.

Statistical analysis

Statistical analyses were performed using R 3.1.2 (R Core Team 2014). For breeding dispersal, first a binomial generalized linear model was used to assess whether the probability of dispersal was affected by the sex of the bird, its relative age or their interaction. Then, a general linear model was fitted to study whether the dispersal distance was influenced by these two factors or their interaction. Male and females share nest attributes and reproductive outcome and, thus, females and males breeding in the same nest are not independent for an analyses of dispersal. Unfortunately, we failed to capture some of the two adults in many nests through the eight years of study and thus we could not use nest-id as a random intercept in our analyses. Therefore, we opted to analyze sexes separately: first, binomial generalized linear models were performed to explore the effect of the four sets of variables (Table 1) on the probability of dispersal, and second, these sets of variables were introduced again on general linear models to assess their effects on dispersal distance. For the dispersal distance, only events when the bird disperses from one nest-box to another in the next year were included in the models (i.e. we disregarded movements not occurring between consecutive years). Models considering the set of reproductive traits only included dispersal events that succeeded in their reproduction.

To analyse the fitness consequences of breeding dispersal we performed general linear mixed models with laying date, breeding success, brood size, and total brood mass at fledging as dependent variables and dispersal probability as the explanatory factor in each model. In these models the year was introduced as a random factor to account for the fact that proxies of fitness may widely vary with years. Finally, for dispersive individuals we also analysed whether nest-box and social characteristics differed between the nest-box of origin and destination. As nest-box characteristics were the same for a nest-box during all the study period we simply compared these characteristics between the two consecutive nest-boxes used by an individual by means of Student-t tests. However, the social environment around a nest-box changed in different years, therefore we compared these variables by means of Student-t tests between two consecutive nest-boxes used by an individual in both the same and consecutive years.

Natal dispersal was studied by performing generalized linear models to analyse the effects of 1) laying date and brood size at fledging of the natal nest, nestling body weight and wing length and sex; or 2) laying date of the natal nest, nestling body weight and wing length and nestling plumage coloration measurements on the probability of recruitment onto the natal population. The best-fit model was determined following a stepwise backward elimination procedure based on Akaike's information criterion with correction for small sample sizes (AICc; Burnham and Anderson 2002).

RESULTS

Breeding dispersal

We got 56 cases of two successive reproductive events of individuals (25 females and 31 males). In 17 cases rollers did not change nest-box in consecutive years, whereas 39 rollers chose a different nest-box for the second year, which was considered as a reproductive dispersal event. The average distance between the first and the second reproductive event for dispersers was 629.40 ± 607.87 meters.

Probability of Dispersal

We found a significant effect of relative age (relative age effect, $F_{1,54} = 4.09$, $P = 0.05$, Table 2) on roller dispersal probability from a nest-box, with relatively younger individuals being more prone to disperse than older ones (Fig.1A). The effect of relative age on probability of dispersal did not differ between males and females (Interaction relative age*sex effect, $F_{1,52} = 0.86$, $P = 0.36$, Table 2). In addition, male and female rollers showed similar probability of dispersion (sex effect, $F_{1,52} = 1.22$, $P = 0.27$, Table 2).

Male probability of dispersal was influenced by individual and nest-box characteristics, as well as the social environment of the nest-box (Table 2). Specifically, we found that males with more brilliant heads had lower probability of dispersal ($F_{1,29} = 4.19$, $P = 0.05$) (Fig.1B). Moreover, male rollers that occupy more visible nest-boxes tend to disperse less than males breeding in more concealed nest-boxes ($F_{1,29} = 5.43$, $P = 0.03$) (Fig.1C). Regarding social environment, male rollers breeding in nest-boxes surrounded by highly successful conspecifics tended to disperse less ($F_{1,29} = 3.77$, $P = 0.06$, Table 2, Fig.1D). In females, however, we did not find any effect of the considered variables on probability of dispersal. (for a detailed list of the results of all models see Supplementary Material).

Dispersal Distance

Sex had a nearly significant effect on dispersal distance ($F_{1,37} = 3.40$, $P = 0.07$), with females tending to disperse to farther distances (808.0 ± 699.6 meters) than males (459.7 ± 465.9 meters). Dispersal distance was not affected by relative age, neither as a main effect nor in interaction with the sex (Table 2). When sexes were separately analysed, we did not find any significant effect of the considered variables on male dispersal distance. In females, meanwhile, dispersal distance was related to individual features as well as to the social environment: females with more yellow-red chroma in their backs, ($F_{1,17} = 6.756$, $P = 0.02$) and those breeding surrounded by less successful conspecifics ($F_{1,17} = 4.86$, $P = 0.04$) (Table 2) disperse farther away than those with less saturated backs and those breeding surrounded by more successful conspecifics (Fig.2A and 2B) (for a detailed description of the results of all the models see Supplementary Material).

Table 2. Main results obtained from models testing probability of dispersal and dispersal distance in relation to sex and age for both sexes, and individual traits, nestbox characteristics and social environment separated by sex. Only full and most plausible models according to AICc are shown. Significant terms are displayed in bold.

Dependent Variable	Sex	AICc	Explanatory Variable	df	Estimate	Std. Error	F	P
Age and Sex								
Dispersal Probability	*Both sexes*	72.22	Sex	1,52	-1.97	2.03	1.22	0.27
			Minimum Age	1,52	-1.05	0.72	3.93	0.05
			Sex * Minimum Age	1,52	0.64	0.77	0.86	0.36
		69.75	**Minimum Age**	**1,54**	**-0.53**	**0.28**	**4.09**	**0.05**
Dispersal Distance	*Both sexes*	616.64	Sex	1,35	-511.62	746.29	0.47	0.50
			Minimum Age	1,35	126.10	262.20	0.23	0.63
			Sex * Minimum Age	1,35	58.09	318.71	0.03	0.86
		612.90	Sex	1,37	-348.30	188.90	3.40	0.07
Individual Traits								
Dispersal Probability	*Male*	48.72	Minimum Age	1,23	-1.03	0.66	2.22	0.15
			Wing		-0.32	0.16	4.50	0.04
			Weight		0.13	0.10	1.73	0.20
			UV-blue scapulars		-6.77	8.55	0.49	0.49
			UV-blue head		27.13	24.39	1.00	0.33
			Brightness head		0.00	0.00	1.43	0.24
			Yellow-Chroma back		24.95	15.97	2.42	0.13
		40.28	**Brightness head**	**1,29**	**0.00**	**0.00**	**4.19**	**0.05**
Dispersal Distance	*Female*	322.50	Minimum Age	1,11	276.70	295.30	0.88	0.37
			Wing		2.50	26.26	0.01	0.93
			Weight		15.14	14.67	1.07	0.32
			UV-blue scapulars		-3909.00	2449.00	2.55	0.14
			UV-blue head		7986.00	4699.00	2.89	0.12
			Brightness head		-0.04	0.15	0.06	0.81
			Yellow-Chroma back		8943.00	2981.00	9.00	0.01
		302.89	**Yellow-Chroma back**	**1,17**	**6015.00**	**2314.00**	**6.76**	**0.02**
Nestbox and Landscape								
Dispersal Probability	*Male*	45.25	Orientation (NW)	3,23	-2.73	1.84	1.35	0.28
			Orientation (SE)		-0.73	1.65		
			Orientation (SW)		-0.63	1.69		
			Visibility	1,25	1.21	0.56	5.92	0.02
			Distance to Highway		0.00	0.00	0.06	0.81
		38.78	**Visibility**	**1,29**	**0.90**	**0.42**	**5.43**	**0.03**
Social Environment								
Dispersal Probability	*Male*	43.15	Density of Rollers	1,28	0.07	0.47	0.02	0.89
			Productivity of Rollers		-0.23	0.12	3.63	0.07
		40.71	**Productivity of Rollers**	**1,29**	**-0.23**	**0.12**	**3.77**	**0.06**
Dispersal Distance	*Female*	307.03	Density of Rollers	1,16	-103.29	133.47	0.60	0.45
			Productivity of Rollers		-104.47	56.87	3.37	0.08
		304.47	**Productivity of Rollers**	**1,17**	**-117.93**	**53.51**	**4.86**	**0.04**

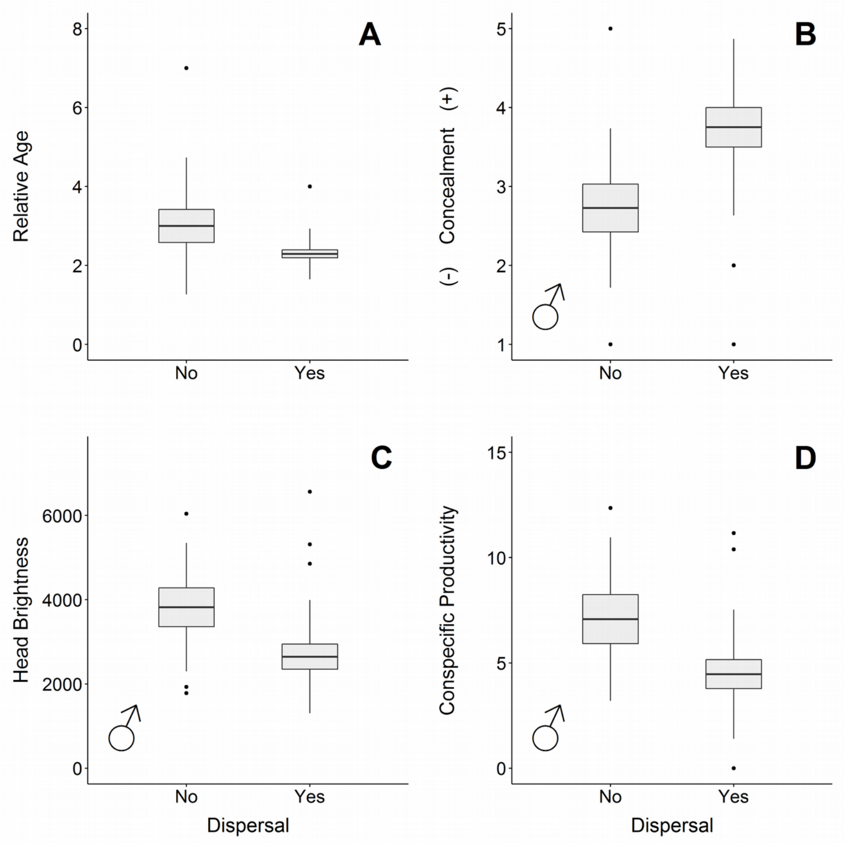

Figure 1. Boxplot showing probability of dispersal in relation to: A) Relative age of rollers (for both sexes). Individuals were assigned an age of 2 years when first captured; B) Concealment of the nest-box in the year before the dispersal event (for males); C) Brightness of the head (for males); and D) Conspecific productivity, as number of fledglings (corrected by relative distance to the nest-box) raised by neighbour conspecifics in a circular area of 1000 metres (for males).

Consequences of Dispersal

We failed to find any significant difference in laying date, breeding success, number of fledglings raised or total brood mass between those reproductive events of dispersive and non-dispersive birds. In addition, dispersal distance did not relate to any of the considered fitness proxies neither in females nor in males (Table 3).

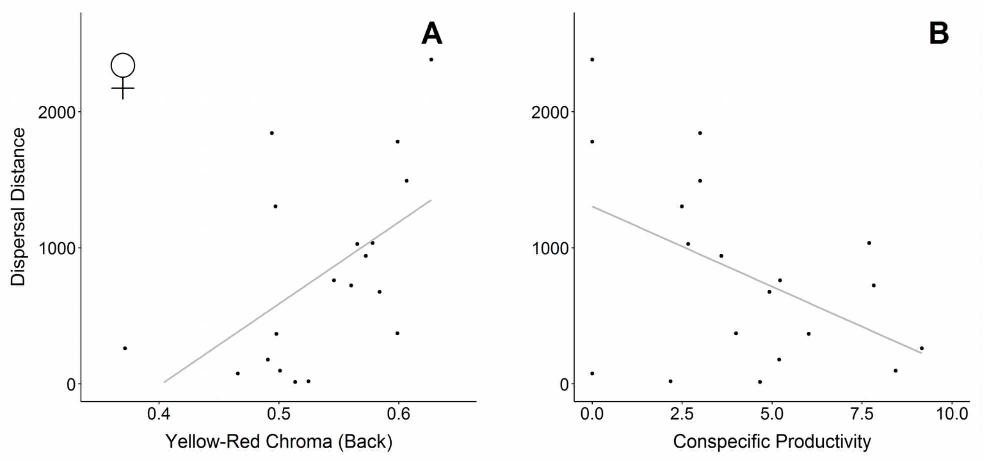

Figure 2. Dispersal distance of females in relation to: A) yellow-red chroma of the back; and B) Conspecific productivity, as number of fledglings (corrected by relative distance to the nest-box) raised by conspecifics in a circular area of 1000 metres.

	Female				**Male**			
Response Variable	**F**	**Df**	**Df.res**	**P-value**	**F**	**Df**	**Df.res**	**P-value**
Breeding Success	0.13	1	14.89	0.73	0.06	1	17.56	0.81
Laying Date	0.09	1	14.89	0.77	0.81	1	16.47	0.38
Number of Fledglings	0.09	1	16.99	0.77	0.00	1	18.00	1.00
Difference in Number of Fledglings	0.33	1	14.89	0.58	0.00	1	15.67	0.98
Total Brood Mass	0.37	1	8.06	0.56	1.78	1	9.14	0.21
Difference in Total Brood Mass	2.28	1	2.52	0.25	0.08	1	6.76	0.79

Table 3. Results from general linear mixed models exploring consequences of dispersal in year of destination.

Settlement

For dispersive males, there were not significant differences in characteristics of the nest-box or the social environment of origin and destination next-boxes (i.e. comparing the nest-box chosen to breed the year t and the year t+1, after the dispersal event) (Table 4). For females, however, we found that conspecific density prior to dispersion in the destination nest-box was significantly lower than that in the next-box of origin (t = 2.15, df = 18, p = 0.05) (Table 4, Fig.3).

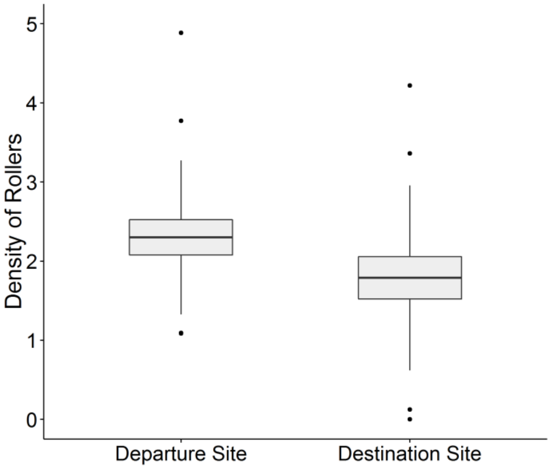

Figure 3. Boxplot showing density of conspecifics in a circular area of 1000 metres around the nest-box occupied before the dispersal event (year t) and density of conspecifics in year t around the nest-box of destination in year t + 1.

Natal Dispersal

From 337 nestlings ringed during the period 2007-2012, only 12 (3.56%) were recruited as breeders in the following years. Eight were females and four males. The average time between the year of birth and year of first detected breeding was 2.5 years [range: 2-4]. We failed to find any effect of the variables considered on natal dispersal (Table 5).

Dispersal Distance	Males 459.7 ± 465.92			Females 808 ± 696.59		
	Previous Site	**Destination Site**	**Destination Site in Previous Year**	**Previous Site**	**Destination Site**	**Destination Site in Previous Year**
Orientation	181.2 ± 98.54	196.85 ± 107.01 T = -0.54 df = 19 P = 0.60		199.63 ± 99.71	220.79 ± 102.93 T = -0.61 df = 18 P = 0.55	
Visibility	3.75 ± 1.12	3.3 ± 1.42 T = 1.92 df = 19 P = 0.07		3.63 ± 1.54	3.42 ± 1.26 T = 0.43 df = 18 P = 0.67	
Distance to Highway	3956.8 ± 1356.16	4087.03 ± 1278.16 T = -1.07 df = 19 P = 0.30		3815.51 ± 981.56	3884.61 ± 597.5 T = -0.38 df = 18 P = 0.71	
Density of Conspecifics	2.08 ± 0.97	1.95 ± 1.01 T = 0.58 df = 19 P = 0.57	1.83 ± 1.2 T = 0.49 df = 19 P = 0.63	2.14 ± 1.19	2.3 ± 0.97 T = -0.51 df = 18 P = 0.62	1.79 ± 1.17 T = 2.15 df = 18 P = 0.05
Productivity of Conspecifics	4.46 ± 3.07	4.51 ± 2.8 T = -0.06 df = 19 P = 0.96	4.18 ± 3.21 T = 0.38 df = 19 P = 0.71	4.21 ± 2.78	5.65 ± 3.02 T = -1.92 df = 18 P = 0.07	3.95 ± 3.52 T = 1.68 df = 18 P = 0.11
Density Heterospecifics	1.27 ± 1.57	1.21 ± 1.6 T = 0.17 df = 19 P = 0.87		1.08 ± 1.22	1.18 ± 1.7 T = -0.21 df = 18 P = 0.83	
Productivity of Heterospecifics	1.75 ± 2.82	1.94 ± 3.01 T = -0.23 df = 19 P = 0.82		1.25 ± 1.81	1.54 ± 3.6 T = -0.35 df = 18 P = 0.73	

Table 4. Analysis of settlement in rollers. Differences in characteristics of the nest-box and social environment between breeding sites before and after a dispersal event. Student-t results under each mean ± SD correspond to the comparison of the variables between that site and the previous site before dispersal.

DISCUSSION

Factors affecting breeding dispersal

As expected, we found that relatively older rollers are more faithful to their territories than younger ones. The effect of age on territoriality and dispersal is a widely reported pattern among avian species (Greenwood and Harvey 1982, Pärt and Gustafsson 1989, Payne and Payne 1993, Forero *et al.* 1999). Higher fidelity of older individuals is probably due to their experience obtained after repeatedly breeding in the same area, which gives older individuals extended knowledge and advantages in the territory and, therefore, a higher proneness to defend its preferred place against competitors. Also, younger birds could be of worse condition and/or lack abilities to compete with older ones, which would expel and force them to move to other places (Forslund and Pärt 1995).

Our results suggest that probability of dispersal is mediated by different factors in female and male rollers. While the decision of changing territories in males is determined by a combination of multiple causes, more concretely by individual quality (i.e. estimated by the brightness of the structural blue colour of the head), nest-box characteristics (nest-box concealment) and local conspecific productivity, female dispersal probability did not respond to

	AICc	Explanatory Variable	Df	Estimate	Std. Error	F	P-value
Full Model 1	110.85	Laying Date	1,319	0.07	0.05	2.09	0.15
		Weight	1,319	-0.01	0.02	0.27	0.61
		Wing	1,319	0.00	0.00	0.14	0.71
		Sex	1,319	-0.66	0.63	1.11	0.29
		Fledglings	1,319	0.17	0.23	0.50	0.48
Best Model 1	104.59	Laying Date	1,323	0.06	0.04	2.14	0.14
Full Model 2	39.86	Laying Date	1,71	0.62	0.36	12.02	0.001
		Weight	1,71	0.01	0.04	0.20	0.65
		Wing	1,71	0.08	0.04	12.70	0.00
		UV-blue scapulars	1,71	10.82	18.53	0.68	0.41
		UV-blue head	1,71	0.17	21.68	0.00	0.99
		Brightness head	1,71	0.00	0.00	2.24	0.14
		Yellow-Chroma back	1,71	-18.09	17.79	2.07	0.15
Best Model 2	30.9	Laying Date	1,76	0.56	0.31	9.25	0.003
		Wing	1,76	0.06	0.03	8.66	0.004

Table 5. Main results of models testing for probability of recruitment in relation to individual traits, nest success and coloration. Only full and most plausible models according to AICc are shown. Significant terms are displayed in bold.

any of these factors. Head brightness in male rollers is correlated with individual condition and breeding productivity (Silva *et al.* 2008). Therefore, higher quality males would tend to maintain territories, whereas lower quality individuals disperse. This may be related to the fact that territory defence is responsibility of roller males (Cramp 1998), and males in good conditions are better competitors than individuals of lower quality. In relation to nest-box characteristics, our results are also in accordance with previous results obtained in the study area showing that rollers preferentially use exposed nest-boxes (Rodríguez *et al.* 2011), even though visibility of these nest-boxes might act as an ecological trap (Rodríguez *et al.* 2011). In addition, males tended to remain in good quality sites indicated by local conspecific reproductive success. The use of information derived from the reproductive performance of neighbour conspecifics to assess local habitat quality has already been demonstrated in previous studies in birds (e.g. Doligez *et al.* 2002, Parejo *et al.* 2007a), and rollers (Parejo *et al.* 2005, Václav *et al.* 2011). Social information, as that provided by the performance of neighbours, allows individuals rapid and inexpensively evaluating local resources and threats (Seppänen *et al.* 2007, Schmidt *et al.* 2010). Here, however, due to the correlative nature of the study, it is not possible to tease apart this possibility from the alternative of individuals being attracted to better territories that lead to better conspecific performance. Surprisingly, however, none of the individual reproductive variables seemed to affect dispersal probability in any of the sexes. Low reproductive success has been pointed out as a strong trigger for dispersal (Newton and Marquiss 1982, Blancher and Robertson 1985, Beletsky and Orians 1987, Beletsky and Orians 1991). However, other studies claims that breeding dispersal is linked to age (Pärt and Gustafson 1989, Newton 1993) and both site-fidelity and breeding success would be the consequences of experience gained with age and the importance of previous reproductive success in determining dispersal.

Considering dispersers only, the distance travelled between two breeding sites tended to be higher in females. This result agrees with many other studies suggesting a female sex-bias in dispersal distance (Greenwood and Harvey 1982, Clarke *et al*. 1997, Gienapp and Merilä 2011). Moreover, females moved farther between breeding sites when their back feathers showed higher yellow-red chroma and when conspecific productivity in the departure site was low (Fig. 2). That is, as for probability of dispersal of males, the determinants of the magnitude of the movement of dispersing females are individual quality and local conspecific productivity. It seems that good-quality females living in good sites (estimated by local conspecific reproductive success) may remain nearer from their previous breeding site. Meanwhile, lower-quality females breeding in low quality sites would be either forced to move from their former breeding site due to competition or failure or would prefer to leave the site and look for any other better place. In males, we did not find any significant relationship between the considered variables and the distance of dispersal, maybe due to insufficient sample size to detect any pattern in this issue.

Consequences of breeding dispersal

We failed to find any cost or benefit of the decisions of staying or leaving. Dispersal is considered to be an adaptive response in which an individual tends to remain in the previous breeding site only when it could overperform the previous breeding event (Sedgwick and Grubb Jr. 2004). However, in our study, faithful individuals do not seem to get any benefit in terms of improved reproductive performance by occupying the same nest-box through consecutive years. On the contrary, defending territories have costs (Gill and Wolf 1975, Krebs 1982, Peres 1989, Wingfield *et al*. 2001) that should be compensated somehow. In black kites, fidelity to breeding sites is explained by antagonistic selective pressures acting in different stages of the life cycle. Thereby, larger birds are better in competing for nest-boxes, while smaller birds are better in raising their broods (Sergio *et al*. 2007), compensating the fact that they breed in worse site-quality conditions. Other reasons may also explain site-fidelity. For instance, familiarity with a breeding site may cause other indirect benefits that would improve fitness in the long term. Extended knowledge about a certain territory could lead to more efficient foraging (Davies and Houston 1981), or to decrease the chances of suffering predation (Yoder *et al*. 2004). Also keeping a territory would increase the probability of being surrounded by known neighbours (Picman 1987), which is less costly than confronting new ones (Eason and Hannon 1994). Unfortunately, we do not have enough data to support these hypotheses, which would require further testing to unveil the benefits of site-fidelity or dispersal.

Factors affecting settlement

As dispersal decisions did, settlement decisions differ between sexes. In fact, while characteristics of the nest-box or the social environment of origin and destination did not differ in males, social factors acquire more importance in females. Females showed an attraction to sites where local conspecific densities were low. Therefore, females seem to show a density-dependent breeding dispersal strategy, avoiding crowded areas, probably as a response against intraspecific competition or to any correlated trait. Competition brings about several costs derived of aggressions and resource depletion, as reduced growth, fecundity or survivorship (Begon *et al.* 2006). Social cues provide with very valuable information for assessing patch quality for breeding in the following year. Moreover, as the use of social information in fitness-affecting decisions may, under some circumstances, counteract the negative effects of competition, females are attracted by high quality sites indicated by local conspecific reproductive success. This is so even when this information involves the presence of conspecifics and thus a certain level of competition (López-Sepulcre and Kokko 2005, Parejo and Avilés 2016).

Natal dispersal

Knowledge of juvenile movement patterns is critical for understanding population dynamics (Cooch and Cooke 1991), and in developing conservation strategies at the population level (Phillips *et al*. 2005, Shillinger *et al*. 2012). Recruitment was very low in our population, and only 3.56 % of ringed fledglings returned to their birthplace to breed when reached maturity. As far as we know, this is the first report of data on natal dispersal in this species. These numbers could mean a low philopatry of the species, at least in our study area. However, due to the scarce number of cases registered, it seems early to draw any conclusion. Definitions of natal dispersal and philopatry depend strongly on the context and natal dispersal is generally a more extensive phenomenon than breeding dispersal (Greenwood and Harvey 1982, Ferrer 1993, Lindberg *et al* 1995, Mathyssen *et al*. 1995). In such a long-distance migrant species, an area of 135 km^2 like our study site could be suitable to explore patterns of breeding dispersal, but insufficient to properly detect natal dispersal and, therefore, we may be underestimating recruitment. However, surveys made outside our area suggest that the core population is included in our nest-boxes and the presence of other pairs out of their boundaries is very scarce due to the lack of suitable places to breed (Rodríguez *et al*. 2011).

CONCLUSIONS

This is the first study in which long-term monitoring of individuals in a population allowed to explore causes and consequences of dispersal at the population level in rollers. Our study revealed for the first time age and sex-specific patterns of year to year movements within a breeding population. Dispersal decisions had no obvious fitness consequences at the analysed scale, and recruitment probability was extraordinary low, which may globally suggests that our population was acting as a source within the meta-population of rollers in the south of Spain.

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SUPPORTING INFORMATION

Appendix S1. Detailed results obtained from models testing probability of dispersal and individual traits, nestbox characteristics and social environment separated by sex. Only full and most plausible models according to AICc are shown. Significant terms are displayed in bold.

		AICc	*Explanatory Variable*	*df*	*Estimate*	*Std. Error*	*F*	*P*
Dependent Variable			**Individual Traits**					
Dispersal Probability	*Female*	44.85	Minimum Age	1,17	-2.27	1.27	3.41	0.08
			Wing		0.04	0.03	2.42	0.14
			Weight		0.03	0.06	0.18	0.68
			UV-blue scapulars		2.14	10.44	0.03	0.86
			UV-blue head		12.88	24.18	0.22	0.65
			Brightness head		0.00	0.00	0.62	0.44
			Yellow-Chroma back		-15.02	18.15	0.59	0.45
		29.87	Minimum Age	1,23	-1.05	0.72	2.08	0.16
Dispersal Probability	*Male*	48.72	Minimum Age	1,23	-1.03	0.66	2.22	0.15
			Wing		-0.32	0.16	4.50	0.04
			Weight		0.13	0.10	1.73	0.20
			UV-blue scapulars		-6.77	8.55	0.49	0.49
			UV-blue head		27.13	24.39	1.00	0.33
			Brightness head		0.00	0.00	1.43	0.24
			Yellow-Chroma back		24.95	15.97	2.42	0.13
		40.28	**Brightness head**	**1,29**	**0.00**	**0.00**	**4.19**	**0.05**
			Breeding Performance 1					
Dispersal Probability	*Female*	32.92	Laying Date	1,22	-0.05	0.05	0.81	0.38
			Breeding Success		-1.07	1.21	0.86	0.36
		31.23	Laying Date	1,23	-0.05	0.05	0.81	0.38
	Male	40.82	Laying Date	1,27	0.03	0.05	0.43	0.52
			Breeding Success		-18.58	2891.75	5.96	0.02
		43.87	Laying Date	1,29	0.00	0.05	0.01	0.94
			Breeding Performance 2					
Dispersal Probability	*Female*	26.88	Laying Date	1,12	-0.15	0.11	2.04	0.18
			Fledglings		6.92	4.50	3.71	0.08
			Total Brood Mass		-0.05	0.03	3.47	0.09
		24.26	Fledglings	1,14	0.31	0.43	0.47	0.51
Dispersal Probability	*Male*	41.00	Laying Date	1,21	0.03	0.06	0.19	0.67
			Fledglings		0.83	1.72	0.19	0.67
			Total Brood Mass		-0.01	0.01	0.47	0.50
		36.06	Total Brood Mass	1,23	0.00	0.00	2.55	0.12
			Nestbox and Landscape					
Dispersal Probability	*Female*	39.80	Orientation	3,17	-0.40	1.67	0.35	0.79
					-1.84	1.96		
					-0.83	1.49		
			Visibility	1,19	0.68	0.49	2.06	0.17
			Distance to Highway		0.00	0.00	0.02	0.88
		29.02	Visibility	1,23	0.63	0.40	3.42	0.08
Dispersal Probability	*Male*	45.25	Orientation	3,23	-2.73	1.84	1.35	0.28
					-0.73	1.65		
					-0.63	1.69		
			Visibility	1,25	1.21	0.56	5.92	0.02
			Distance to Highway		0.00	0.00	0.06	0.81
		38.78	**Visibility**	**1,29**	**0.90**	**0.42**	**5.43**	**0.03**
			Social Environment					
Dispersal Probability	*Female*	34.25	Density of Rollers		-0.25	0.44	0.30	0.59
			Productivity of Rollers		0.10	0.19	0.27	0.61
		31.95	Density of Rollers		-0.16	0.40	0.14	0.71
Dispersal Probability	*Male*	43.15	Density of Rollers	1,28	0.07	0.47	0.02	0.89
			Productivity of Rollers		-0.23	0.12	3.63	0.07
		40.71	**Productivity of Rollers**	**1,29**	**-0.23**	**0.12**	**3.77**	**0.06**

Appendix S2. Detailed results obtained from models testing dispersal distance and individual traits, nestbox characteristics and social environment separated by sex. Only full and most plausible models according to AICc are shown. Significant terms are displayed in bold.

		AICc	*Explanatory Variable*	*df*	*Estimate*	*Std. Error*	*F*	*P*
Dependent Variable			**Individual Traits**					
Dispersal Distance	*Female*	322.50	Minimum Age	1,11	276.70	295.30	0.88	0.37
			Wing		2.50	26.26	0.01	0.93
			Weight		15.14	14.67	1.07	0.32
			UV-blue scapulars		-3909.00	2449.00	2.55	0.14
			UV-blue head		7986.00	4699.00	2.89	0.12
			Brightness head		-0.04	0.15	0.06	0.81
			Yellow-Chroma back		8943.00	2981.00	9.00	0.01
		302.89	**Yellow-Chroma back**	**1,17**	**6015.00**	**2314.00**	**6.76**	**0.02**
Dispersal Distance	*Male*	331.32	Minimum Age	1,12	198.70	190.00	1.09	0.32
			Wing		8.42	28.73	0.09	0.77
			Weight		14.21	19.30	0.54	0.48
			UV-blue scapulars		1647.00	2131.00	0.60	0.45
			UV-blue head		1855.00	4575.00	0.16	0.69
			Brightness head		0.03	0.11	0.06	0.80
			Yellow-Chroma back		-1012.00	2626.00	0.15	0.71
		306.43	Weight	1,18	18.11	11.54	2.46	0.13
			Breeding Performance 1					
Dispersal Distance	*Female*	309.00	Laying Date	1,16	-4.03	17.44	0.05	0.82
			Breeding Success		-566.94	321.51	3.11	0.10
		305.80	Breeding Success	1,17	-573.00	311.00	3.39	0.08
	Male	297.00	Laying Date	1,16	-7.29	17.03	0.18	0.67
			Breeding Success		-168.82	291.31	0.34	0.57
		293.90	Breeding Success	1,17	-229.00	250.00	0.84	0.37
			Breeding Performance 2					
Dispersal Distance	*Female*	190.00	Laying Date	1,7	28.58	31.76	0.81	0.40
			Fledglings		116.89	882.82	0.02	0.90
			Total Brood Mass		0.02	6.63	0.00	1.00
		179.20	LD	1,9	26.30	21.60	1.49	0.25
Dispersal Distance	*Male*	231.10	Laying Date	1,7	-1.82	25.75	0.01	0.94
			Fledglings		200.57	977.51	0.04	0.84
			Total Brood Mass		-1.70	7.70	0.05	0.83
		222.00	Total Brood Mass	1,9	-0.14	0.92	0.02	0.89
			Nestbox and Landscape					
Dispersal Distance	*Female*	324.53	Orientation	3,11	-43.40 67.03 -120.02	549.45 748.92 471.19	0.04	0.99
			Visibility	1,13	62.90	142.63	0.19	0.67
			Distance to Highway	1,13	-0.17	0.25	0.43	0.52
		308.42	Distance to Highway	1,17	-0.15	0.17	0.76	0.40
Dispersal Distance	*Male*	319.70	Orientation	3,12	449.63 -47.41 -90.18	376.50 361.24 304.55	0.73	0.55
			Visibility	1,14	52.67	124.30	0.18	0.68
			Distance to Highway	1,14	0.02	0.11	0.02	0.88
		308.60	Distance to Highway	1,18	-0.05	0.08	0.37	0.55
			Social Environment					
Dispersal Distance	*Female*	307.03	Density of Rollers	1,16	-103.29	133.47	0.60	0.45
			Productivity of Rollers		-104.47	56.87	3.37	0.08
		304.47	**Productivity of Rollers**	**1,17**	**-117.93**	**53.51**	**4.86**	**0.04**
Dispersal Distance	*Male*	311.91	Density of Rollers	1,17	-50.16	115.66	0.19	0.67
			Productivity of Rollers	1,17	-6.30	36.67	0.03	0.87
		308.78	Density of Rollers	1,18	-49.14	112.35	0.19	0.67

CHAPTER III

Disentangling Migratory Routes and Wintering Grounds of Iberian Near-Threatened European Rollers *Coracias garrulus*

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ABSTRACT

Long-distance migrants are suffering drastic declines in the last decades. Causes beneath this problem are complex due to the wide spatial and temporal scale involved. We aim to reveal migratory routes, stopover areas, wintering grounds, and migratory strategies for the most southwestern populations of the nearthreatened European Roller *Coracias garrulus* in order to identify conservation key areas for the non-breeding stage of this species. To this end, we used tracking data from seven satellite transmitters fitted to birds breeding in different populations throughout the Iberian Peninsula and four geolocators fitted to individuals in a southeastern Iberian population. Precise satellite data were used to describe daily activity patterns and speed in relation to the main regions crossed during the migration. Individuals from the most southwestern Iberian populations made a detour towards the Atlantic African coast whereas those from northeastern populations followed a straight north-to-south route. We identified important stopover areas in the Sahel belt, mainly in the surroundings of the Lake Chad, and wintering grounds on southwestern Africa farther west than previously reported for the species. Concerning the migratory strategy, satellite data revealed: 1) a mainly nocturnal flying activity, 2) that migration speed depended on the type of crossed habitat, with higher average speed while crossing the desert; and 3) that the migration was slower and lasted longer in autumn than in spring. The studied populations showed weak migratory connectivity, suggesting the confluence of birds from a wide range of breeding grounds in a restricted wintering area. Therefore, we suggest to target on defining precisely key areas for this species and identifying specific threats in them in order to develop an appropriate global conservation programme for the European Roller.

INTRODUCTION

Migrant birds are highly vulnerable, as they must cross many different habitats while performing their year-round life cycle. Consequently, migrants are liable to be affected by multiple ecological and social challenges in diverse places and occurring at different times (Newton 2004). Wide continental analyses have revealed that migrant birds are involved in a sustained decline of their breeding populations in Europe, which is even more drastic for long-distance migrants (Sanderson *et al*. 2006, Vickery *et al*. 2014). Therefore, a major challenge for conservation biologists is to investigate whether the observed decline of migrants is related to the loss of breeding or winter habitats, heightened mortality during migration, or some combination of these (Wilcove and Wikelsi 2008). Thus, conservation of migratory birds depends largely on the identification of key areas and threats through the migratory pathway and in their wintering grounds as well as the examination of migratory connectivity among populations (Webster *et al*. 2002, Robinson *et al*. 2010). This urge, together with the decreasing size and cost of tracking technologies have fuelled a growing interest for studying the non-breeding stages of many medium and smallsized migrant birds (López-López *et al*. 2009, Meyburg and Meyburg 2009, Rodríguez *et al*. 2009, Bächler *et al*. 2010, Tøttrup *et al*. 2012), even though the total harmlessness of these techniques is debatable (Barron *et al*. 2010, Bowlin *et al*. 2010, Arlt *et al*. 2013, Scandolara *et al*. 2014).

In this context, identifying migratory strategies is also essential to understand how birds may optimize energy expenditure in relation to foraging and meteorological conditions they experience during their journey (Alerstam 2009). For instance, nocturnal migration allows diurnal foragers to refuel during daylight for travelling by night, when they might evade predators and worst diurnal atmospheric conditions, such as extremely high temperatures and/or air turbulences (Kerlinger and Moore 1989). Alternatively, diurnal migration may be beneficial in terms of orientation, allowing birds to find best habitats to stop and forage, or foraging while flying (Strandberg and Alerstam 2007), and avoiding the negative consequences of sleep deprivation (Schwilch *et al* 2002). Migratory behaviour may also vary between and within species in response to habitat characteristics that pose major challenges at a wide spatial scale. For instance, some trans-Saharan migrants have adapted their pace by increasing their speed and lowering the number of stops (Alerstam 1993, López-López *et al*. 2010), and others by choosing an alternative route (Alerstam 2001).

The European Roller *Coracias garrulus* (Roller, hereafter) has suffered a global decline of its breeding population of about 30% in the past few decades (BirdLife International 2013), classing this species as near-threatened. Indeed, this decline is among the most drastic ones for Afro-Palaearctic migrant farmland birds wintering in open savannahs (Sanderson *et al*. 2006). The knowledge about the migration routes and wintering grounds of Rollers is scant as it comes from a few ringing recoveries of central and eastern European birds at a few African places (Brown and Brown 1973, Ash and Miskell 1980, Feare 1983). The first serious attempts of revealing the migratory route of western Rollers' populations combined field observations, a low number of ringing recoveries and the occasional report of corpses (Mayaud 1985). Based on this disjointed information up to four different routes have been hypothesized: 1) diagonal crossing of the Sahara Desert to eastern Africa (Dorst 1962, Glutz von Blotzheim and Bauer 1980); 2) a detour to the east crossing south towards Tibesti-Uganda (Stresemann 1944); 3) a north-south cross of the Desert to Niger (Mayaud 1985) or; 4) a detour to the west passing through Senegal (Morel 1973, Sauvage and Rodwell 1998). Recently, deployment of geolocators in southern France and Portugal based on three and two individuals respectively, show two alternative routes to reach wintering grounds in southwestern Africa in Angola: the former following a straight track across the Mediterranean Sea and Sahara Desert (Emmenegger *et al*. 2014), and the later taking a more western route (Catry *et al*. 2014). However, these patterns were based on less accurate geolocators, which precluded a precise report of spring migration, and on individuals from a single breeding locality. In this work, by deploying satellite transmitters and geolocators on adult breeding individuals from different Iberian populations, we describe in detail for the first time migratory routes and wintering grounds of the most south-western European populations of this near-threatened species. Moreover, we describe its migratory strategy along different stages of the journey. In addition, we explored migratory connectivity for Iberian Rollers by studying the spatial distribution of individuals in their breeding and wintering grounds.

MATERIALS AND METHODS

Adult Rollers were trapped using nets during the late incubation stage or when they had small nestlings in 2012 and 2013 breeding seasons (June-July) in Spain. Birds were ringed, measured and weighted and most of them were also sexed by molecular methods (Fridolfsson and Ellegren 1999) (Table 1). 5-g solar-powered PTT-100 satellite transmitters (Microwave Telemetry Inc., Columbia, MD, USA) were deployed on twelve individuals as a backpack using a ribbon Teflon harness (Garcelon 1985), although we only recorded seven birds initiating their migration due to death or device malfunction of the other five birds: one female in the southeast (Granada, hereafter PTT-GR), two males and one unsexed individual

Table 1. Migration timing and distances of eleven tracked European Rollers.

	Breeding Location	Sex	Departure Date	Arrival to Lake Chad Basin	Departure from L. Chad Basin	Arrival Date	Wintering Location	Duration (days)	Travelling Days	Total Distance (km)	Avg Speed (km/d)	Stopovers (locations)
Autumn Migration												
PTT-M	Madrid, 40°16′ N, 4° 06′ W	Male	04 Aug 2012	18 Sep 2012	23 Oct 2012	01 Dec 2012	Namibia	119	37.5	9,547	254	11
PTT-L	Lleida, 41°49′ N, 0°37′ E	Male	06 Sep 2012	23 Sep 2012	03 Nov 2012	21 Nov 2012	Botswana	76	20.5	8,338	406	7
PTT-C	Ciudad Real, 39°19′ N, 3°18′ W	Male	25 Aug 2012	23 Sep 2012	24 Oct 2012	03 Dec 2012	Botswana	100	36.5	10,095	276	12
PTT-GR	Granada, 37°19′ N, 3°02′ W	Female	04 Aug 2012	07 Oct 2012	26 Oct 2012	17 Nov 2012	Namibia	105	36.5	9,986	273	9
PTT-G	Girona, 42°17′ N, 3°07′ E	Male	12 Sep 2013	Not reached	-	Not reached	Not reached	-	8.5*	2,763*	329	1*
PTT-H	Huesca, 41°47′ N, 0°11′ E	Male	8 Sep 2013	19 Oct 2013	19 Nov 2013	22 Dec 2013	Namibia	105	28	8,996	318	12
PTT-B	Badajoz: 38°42′ N, 6°54′ W	Unidentified	27 Aug 2013	5 Oct 2013	21 Oct 2013	13 Nov 2013	Angola	78	40	8,651	218	5
GLS-1	Almería, 37° 05′N, 2° 21′W	Female	21 Jul 2012	27 Sep 2012	16 Oct 2012	31 Oct 2012	Angola	102	22	9,380	426	4
GLS-2	Almería, 37° 05′N, 2° 21′W	Female	19 Aug 2012	18 Oct 2012	29 Oct 2012	09 Nov 2012	Namibia	82	21.5	9,471	348	4
GLS-3	Almería, 37° 05′N, 2° 21′W	Male	21 Jul 2012	16 Sep 2012	26 Oct 2012	07 Nov 2012	Botswana	109	24	9,406	392	5
GLS-4	Almería, 37° 05′N, 2° 21′W	Female	19 Aug 2012	27 Sep 2012	01 Nov 2012	19 Nov 2012	Namibia	92	37.5	8,719	232	2
								101 (20.5)	*32.25 (14.75)*	*9,393 (739.75)*	*348 (141.5)*	*6 (6.25)*

Table 1. Cont.

	Breeding Location	Sex	Departure Date	Arrival to Lake Chad Basin	Departure from L. Chad Basin	Arrival Date	Wintering Location	Duration (days)	Travelling Days	Total Distance (km)	Avg Speed (km/d)	Stopovers (locations)
Spring Migration												
PTT-H	Huesca, 41°47′ N, 0°11′ E	Male	13 Mar 2014			-	Namibia	-	-	-	-	-
PTT-L	Lleida, 41°49′ N, 0°37′ E	Male	10 Mar 2013			12 May 2013	Botswana	63	23	9,884	426	7
GLS-2	Almería, 37° 05′N, 2° 21′W	Female	23 Feb 2013			06 May 2013	Namibia	72	19.5	10,679	545	3
GLS-3	Almería, 37° 05′N, 2° 21′W	Male	10 Feb 2013			14 Apr 2013	Botswana	63	18	8,712	484	2
GLS-4	Almería, 37° 05′N, 2° 21′W	Female	01 Apr 2013**			06 May 2013	Namibia	35	20.5	7,999	390	1
								63 (9.25)	*20 (2)*	*9,298 (1,549)*	*455 (82.25)*	*2.5 (2.25)*

Total distance refers to the entire migratory journey estimated as the sum of migration segments length (one point per day). Duration is the time (in days) spent by each individual from their departure from breeding sites to their arrival to wintering grounds (or vice versa for spring migration), including time spent in stopovers (which are excluded in Travelling Days). Average flight speed is the total distance divided by the number of travelling days excluding days spent in stopovers. Last rows values are the median and interquartile range (in parentheses) per season (*Route incomplete. Excluded from median and IQR) (**Equinox interference does not allow to determine precise departure date. Thus date shown is considered the latest possible departure date).

in the middle zone (Madrid, PTT-M; Ciudad Real, PTT-C; and Badajoz, PTT-B) and three males in the northeast (Lleida, PTT-L; Girona, PTT-G; and Huesca, PTT-H) (Table 1).

Satellite transmitters were programmed with an about 8-h ON/15-h OFF duty cycle. Cycles started at different time of the day allowing to get a rough representation of the complete daily pattern of activity. For each duty cycle, the satellite transmitter sent a variable number of locations of different quality. High quality locations (classified according to their accuracy as LC 3 (up to 250 m), 2 (up to 500 m), 1 (up to 1.5 km); Argos 2007) were preferentially used. However we relied on lower quality locations (> 1.5 km) to define important data points (i.e. precise arrival or departure dates) when higher quality data were not available. We got (mean ± SD) 1127 ± 563 locations per device on average, of which a 46.2 ± 17.4% were high quality data (LC 3, 2 and 1). To describe individual migratory routes we built a dataset by selecting one of the highest quality locations per hour and individual. PTT-L reached its breeding area in 2013 and, therefore, provided us with a complete record of its annual cycle. PTT-H performed its autumn migration and was still recording by the time this work was done. The signal of PTT-G was lost at some point during its autumn migration, whereas PTT-M and PTT-C signals were lost during their spring migrations. Finally, the signals of PTT-GR and PTT-B were lost once they arrived at their wintering quarters. Moreover, during the 2012 breeding season, 12 adults settled in a population located in the southeast of Spain (Almería) were tagged with 2.5 gram light-level geolocators (model MK4490C manufactured by Biotrack Ltd., United Kingdom). Geolocators use ambient light to estimate latitude and longitude (2 positions per day), determined by day and night lengths and time of local midday or midnight, respectively (Hill 1994). Although precision of locations is considerably lower for geolocators than satellite transmitters, they have proved to be an efficient technique for assessing long-distance movements for small and mediumsized birds (Rodríguez *et al*. 2009, Stutchbury *et al*. 2009, Bächler *et al*. 2010, Schmaljohann *et al*. 2012), including Rollers (Emmenegger *et al*. 2014, Catry *et al*. 2014). Half of the geolocators were fitted with a ribbon Teflon leg-loop harness (Rappole and Tipton 1991) and half with a backpack harness (Garcelon 1985). Four birds equipped with geolocators were recaptured the next year, two of each attachment design (named as GLS-1 to GLS-4) (Table 1). For unknown reason GLS-1 stopped recording locations at the wintering grounds.

Geolocators were calibrated for one week before deployment at a location close to breeding sites. Light-level curves were generated and supervised using BASTrack software (British Antarctic Survey 2010), inferring latitude from length of daylight and darkness periods, and longitude from local time for midday and midnight. We used a threshold value of 2, and values of solar angle obtained for each device from calibration period (angles ranging from 24.9 to 24.5). A confidence value was assigned to each dusk/dawn according to interferences and uncertainty in the light curve and timing.

After obtaining geographic coordinates data, we evaluated the reliability of each position according to days from equinox and confidence values. An iterative forward/backward averaging velocity filter was applied to remaining positions (McConnell *et al* 1992). The speed limit index was set as the 95th percentile of the speed index (Austin *et al* 2003). After filtering, we discarded on average 34% of positions for each individual. Location data from geolocators collected between the 1st September and 12th October and between 28th February and 10th April were estimated only from longitude, as estimations of latitude during the equinoxes are highly imprecise. In addition, latitudinal deviations are higher when locations are close to the equator (Lisovsky *et al*. 2012). Therefore, when departure or arrival from one stopover or wintering area was influenced by equinox, producing unreliable locations, we trusted on previous or late reliable positions to estimate latitude. Next, we looked on their corresponding longitude coordinate to determine movement according to position variation or stabilization in the horizontal axis. If the period of longitude stabilization extended beyond the equinox, we assumed that no movement happened either in longitudinal and latitudinal axis during that period. Hence, departure or arrival date was assigned when longitude varied. However, results derived from these periods and latitudinal range should be considered as approximations.

Onset of migration was identified by abrupt changes in movement pattern, directionality and stability of travelled distance following Limiñana *et al*. (2008). End of migration was identified when we detected a stop longer than 10 days once the bird had crossed the equator. From satellite data, stopovers were assigned when we detected less than 20 km of displacement in at least 24 hours. From geolocators data, stopovers were identified when at least five consecutive points were included within an area with a diameter of 300 km (given that the average error ± SD of geolocators is 185 ± 115 km (British Antarctic Survey 2010)). For clarity in the maps, we used the average values of latitude and longitude coordinates from locations assigned to each stopover. To represent the wintering grounds of satellite-tracked birds, we calculated average coordinates per individual using only one random of the highest quality positions for each 24 hour period. For geolocators, we used Home Range Tools for ArcGIS 9.3 (Rodgers *et al*. 2005) and estimated kernel density areas which comprised 50, 70 and 90 percent of the wintering locations.

Migratory strategy

From the data set extracted from satellite transmitters we selected pairs of high quality locations for each individual (excluding inactive locations corresponding to stopovers and wintering grounds) yielding a subset of 132 segments of 1 to 8 hours duration. As distance travelled and time lapse for each segment are known, we were able to estimate the speed of flight of each bird in these segments. This allowed us to study flight activity of each bird in relation to time of day and region overflown. We classified every segment attending to a threshold of 5 km/h (Strandberg *et al*. 2009a) into stationary, when speed was below 5 km/h, and travelling, when speed was above 5 km/h. We also classified segments according to latitude in four regions: Sahara Desert (from Mediterranean Sea to 19°N), Sahel (from 19°N to 7°N), Equator (from 7°N to 15°S) and Southern Savannah (15°S to wintering grounds). Finally, segments were classified according to light conditions as daylight and darkness in relation to dusk and dawn local hours.

Speed of migration

To estimate the average speed during migration we calculated duration and distance for each migratory step for both geolocator and satellite-tracked birds. One step was defined as the movement between two consecutive stops. Duration was calculated using the starting and ending locations of the movement. Distance was differently estimated depending on the type of stop: for breeding grounds we used the known capture location; for stopovers we used the average location calculated from high quality data; for wintering grounds we used the first high quality location as the final destination in autumn migration and the last one as the starting point in spring migration in order to avoid likely itinerancy during winter (Moreau and Monk 1972). Speed of migration from geolocators data around the equinoxes was derived using the average of those locations within the stopover that were not affected by equinox (thus we are assuming that latitudes does not vary while longitude is constant), and duration was estimated from changes in longitude. Each step was classified in regions as indicated for short segments. As steps can be long and include more than one region (Fig. 1), we assigned the step to the region that represented a major proportion of its length. Movements outside Africa (i.e. across the Mediterranean Sea or the Iberian Peninsula) were discarded in analyses of differences among regions.

Statistical methods

Statistical analyses were performed with the software SAS, version 9.2 and R 2.15.3 (R Core Team 2014). Mann-Whitney tests were used to analyze differences in duration and speed of migration between autumn and spring seasons. We fitted a generalized linear model by stepwise procedure to model variation in Roller flight activity based on segments as a binomial dependent variable (stationary *vs.* travelling, logit link function; PROC GLIMMIX procedure in SAS) in relation to time of day (daylight *vs.* darkness) and overflown region as fixed terms. The interaction between these two factors was also entered to test whether patterns of flight activity between day and night changed over regions. A previous analysis in which we entered individual identity as a random intercept to this model to control for nonindependence of segments from different individuals revealed that the variance component for individual identity was zero and, thus, that individual identity could/should be removed from the model (Searle *et al.* 1992). Results remained the same after the removal of this random intercept. The square-root transformation of speed data for migratory steps was fitted to a general linear mixed model to explore its variation in relation to region using bird identity as a random factor. Analyses were done separately for data based on satellite transmitters and geolocators due to their different error and accuracy. Post-hoc Scheffé multiple comparison tests were performed to look for differences in speed between regions.

To study migratory connectivity we have followed a method similar to the one proposed by Ambrosini *et al.* (2009). A Mantel test was performed to explore the correlation between distance matrices of breeding and wintering areas of tracked birds using the R package ‘ecodist’ (Goslee and Urban 2007). Distances were measured along loxodromes and were calculated using centroids to represent wintering areas, and locations of capture for breeding grounds. High level of correlation between distance matrices between breeding and wintering locations would suggest high migratory connectivity. The significance of Mantel test was checked using permutations with estimations of p-values after 10,000 randomizations. Although ringing recoveries may provide very useful information on this respect, we confirmed that there are not reported ringing recoveries of Spanish rollers outside Spain by checking the Spanish Ringing Scheme database (SEO/BirdLife, http://www.anillamientoseo.org/).

Ethic Statement

The deployment of geolocators and satellite transmitters did not take more than 20 minutes and had no obvious effects on the reproduction of tagged birds. This study was approved by the relevant authorities (regional governments of Andalucía, Aragón, Castilla-La Mancha, Cataluña y Extremadura; research permits CGL2008-00718 and CGL2008-00562). Hence, all necessary permits were obtained for the study, which complied with the national legislation of Spain concerning animal handling and tagging. Study areas are privately owned and permission to use the areas was acquired from the land owners.

RESULTS

Migratory routes and wintering grounds

Departure from the breeding areas occurred between the 21st July and the 6th September in 2012 and between 27th August and 12th September in 2013. These interannual differences may be associated to differences among sampled populations, which differ between years (see Table 1), and/or to isolated cases of breeding failure (e.g. the bird that started migration on July 21st failed to raise any fledgling). Crossing to Africa occurred in three ways (Fig. 1). Birds breeding in central Spain headed south towards the Gibraltar Strait. Meanwhile, birds breeding in the south-east of Spain arrived to Africa crossing the Mediterranean Sea usually following a straight line, through the Alboran Sea. The three birds from the northeastern populations, however, crossed the Mediterranean Sea through the Balearic Islands or near them to enter Africa by Algeria and Tunisia, with short stopovers near the coast (3 and 5 days). After reaching Africa, birds either continued southeast through the Sahara Desert or southwest following the coastal line to their first stops in the Sahel Belt in Senegal, Guinea and the southern regions of Mauritania and Mali, where they stayed between 4.8 and 39 days. In two cases, Rollers had first stopped along the southern face of the Atlas Mountain Range in Morocco (7.5 and 19.5 days). We also detected one important stopover in Burkina Faso of 16.5 days. Next, they followed the northern border of the Sahel Belt to the East to reach Chad, Niger and Nigeria, making short stopovers on the way, where they generally spent less than a week, except for the bird GLS-1 that apparently took a southern route to Ghana, where it spent 35.5 days. Bird PTT-L reached Chad from Algeria flying through Tunisia and Libya without any stopover on the way. Bird PTT-H travelled first to a short stopover in the east of Libya (1 day) and turned south to Chad making an important stopover in the north of Chad (26 days). In Chad, Niger and Nigeria, we identified long stopovers for every bird taking place from 16th September to 7th November and staying between 11 and 41 days. Central Iberian birds took 29 and 44 days to complete this first stage of the migration, whereas southeastern birds ranged from 39 to 68 days. On the other hand, northeastern birds spent 17 and 41 days to perform their route. From the long stopover in Sahelian areas in Chad, Niger and Nigeria, every bird headed south-southeast to Angola, Namibia and Botswana between 16th October and 19th November, where they established their wintering grounds (Table 1, Fig. 1). Birds arrived there between 31st October and 22nd December and their stay lasted between 66 and 133 days. We detected previous short stopovers in Angola and Congo in satellite-tracked birds, but in the case of geolocator-tracked birds we were not able to identify any stopover close to the wintering grounds due to their lower precision. Spring migration information corresponds only to year 2013 for birds tagged in 2012, as the last date available for those tagged in 2013 was 16th March 2014. Spring migration started from 10th February to 1st April, when birds headed north-northwest to Central African Republic, Chad and Cameroon to make a short stopover of 3 to 18.5 days (Fig. 1).

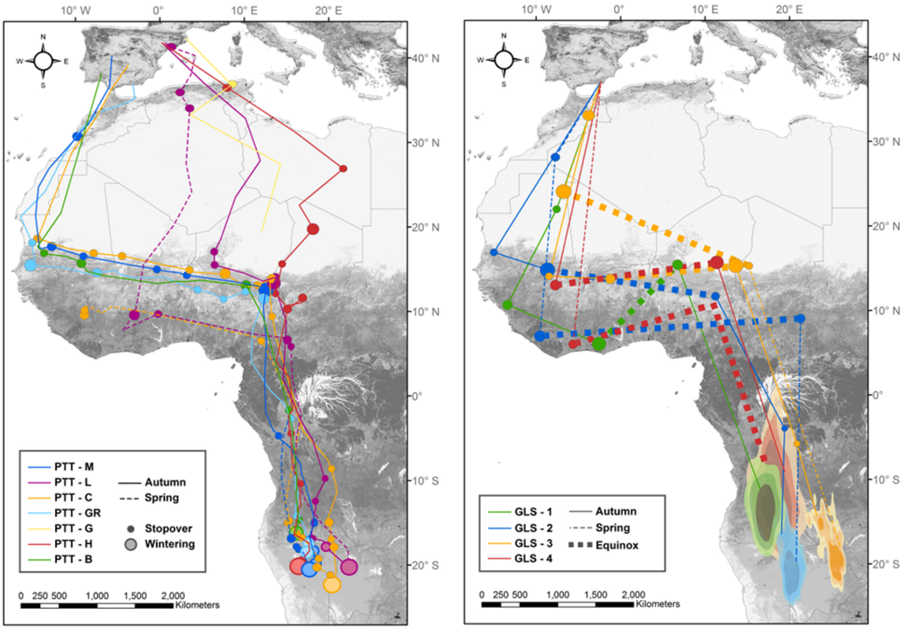

Fig. 1. Migratory routes, stopover sites and wintering grounds of southwestern European Rollers. Tracks recorded by satellite tranmitters (left) and geolocators (right) between breeding sites in the Iberian Peninsula and the wintering grounds (blue dots and blue areas, respectively) in southwestern Africa. Red and green colours correspond, respectively, to autumn and spring migrations. Dots represent stopovers, and their sizes are relative to time spent (the longer the period, the bigger the spot). Dotted lines indicate uncertainty provoked by the equinoxes. Locations assigned before and after dotted lines are partially based on longitudinal data and should be considered as approximations. Geolocators data for latitudes close to the equator have high associated deviations and thus should be interpreted carefully (Lisovski *et al.* 2012). Wintering grounds for satellite-tracked birds were located by calculating average coordinates, whilst for geolocators they were calculated by kernel density estimation for 50, 70 and 90% of the locations.

Next, they headed to the West mainly following the southern border of the Sahel Belt to stop in Ivory Coast, Liberia, Ghana and Guinea for 13.5 to 24.5 days. From these points they changed their directions to the north, heading towards the Alboran Sea to arrive to the Iberian Peninsula in cases of birds GLS-2 and GLS-4 and towards north Algeria in the case of PTT-L, to cross again the Mediterranean Sea to Menorca Island, where it turned west to its breeding ground. Bird GLS-3 travelled by a northern route from Chad to Mauritania, where it stayed 37.5 days, and then joined the western route to the Alboran Sea. No bird entered the Iberian Peninsula through the Gibraltar Strait, but we lacked returning information from Rollers from the most western breeding populations. Rollers arrived at their breeding grounds between the 14th April and 12th May. Comparison of duration and speed of migration between autumn and spring seasons revealed that autumn migration lasted significantly longer when we considered time spent in stopovers (Table 1, Mann-Whitney test: Z-adjusted = 2.83, P = 0.005) and after excluding it (Mann-Whitney test: Z-adjusted = 2.33, P = 0.020). Consequently, autumn migration was significantly slower than spring migration (Table 1, Mann-Whitney test: Z-adjusted = 22.42, P = 0.016), although the number of stopovers did not significantly differ between the two migratory periods (Mann-Whitney test: Z-adjusted = 1.84, P = 0.07).

Migratory strategy: Flight activity in relation to daily time and region

Analysis of segments revealed that travelling movements (< 5 km/h) were significantly more frequent during darkness than during daylight (time of day effect: $F_{1,126} = 27.80$, P < 0.001, Fig. 2). This pattern did not vary between the four regions (time of day*region effect: $F_{3,123} = 0.18$, P = 0.91; region effect: $F_{3,126} = 0.59$, P = 0.62; Fig. 2). Estimated speed in segments was (median [range]) 9.87 [0.12 to 84.31] km/h during the night and 1.31 [0.09 to 46.42] km/h during daylight hours.

Overall speed of migration

Using the data received from satellites, Rollers travelled at a different speed depending on the overflown region (region effect: $F_{3,73} = 15.06$, P < 0.001; bird identity effect: Z = 0.41, P = 0.34, Fig. 3). In particular, we found differences between Sahara and Sahel (Scheffé test: P= 0.013) and between Southern Savannah compared to other regions (Scheffé tests S. Savannah – Sahara: P < 0.001; S. Savannah – Sahel: P < 0.001; S. Savannah – Equator: P < 0.001), but they were not significant when comparing Sahel and Sahara with Equator (Scheffé tests: P = 0.07 and P = 0.96, respectively). Analyses based on less precise geolocators revealed a similar but not significant trend (region effect: $F_{2,19} = 1.39$, P = 0.27; bird identity effect: Z = 0.76, P = 0.22).

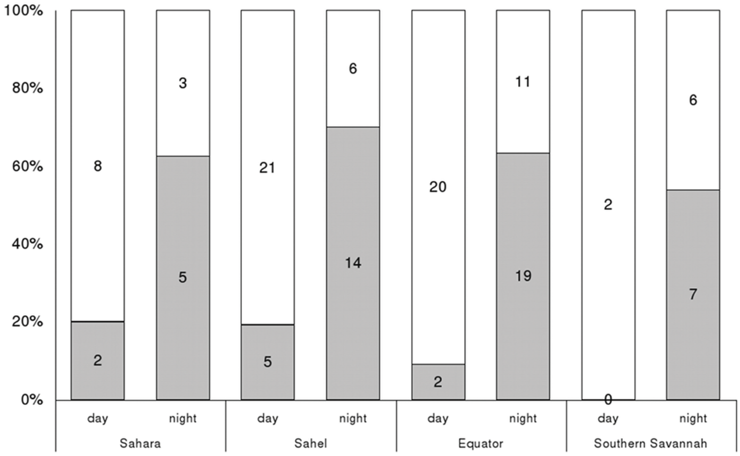

Fig. 2. Travelling activity during migration of Rollers. Percentage of segments flying faster than 5 km/h in relation to time of day and overflown region. Numbers on bars indicate the number of segments in each category (grey for travelling segments, white for stationary segments).

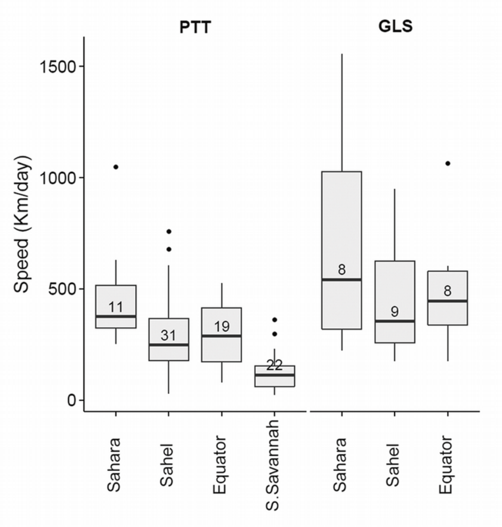

Fig. 3. Migration speed of Rollers in relation to region. Box plot showing median levels of migration speed (km/day) in relation to crossed region, separated by tracking method: satellite transmitters (PTT) and geolocators (GLS). Boxes show interquartile ranges (IQR). Bars represent maximum and minimum values within 1.5 IQR. Dots represent outliers (outside 1.5 IQR). Numbers inside boxes represent sample size (number of steps between consecutive stops, given non-significance of the random factor bird identity; see Results).

Migratory Connectivity

Ten birds were used to build the distance matrices as one individual did not reach the wintering area. Differences in distance among breeding locations did not significantly relate with differences in distance among wintering locations ($r = -0.22$, $P = 0.91$).

DISCUSSION

Migratory routes and wintering grounds

Our results show that Iberian Rollers migrate to Africa using two alternative strategies (Fig. 1). This seems to indicate the existence of a western limit, or a cline, which separates these different strategies. At an intermediate level of this cline would be the southeastern population of Almería which make a moderate western detour but then cross the Sahara desert directly. However, all birds from this population were tracked with geolocators, and thus we cannot discard the possibility that these results are a consequence of the lower precision of this tracking technique compared to satellite-tracking. More detailed sampling is needed to confirm this split of strategies.

Both western and straight paths converge in the Lake Chad surroundings and, from that point, the last phase of migration is common to every bird, in a continuous flight over the tropical forest to their final wintering destination in the savannahs of southwestern Africa, in Angola, Namibia and Botswana (Fig. 1). Our results also show that Iberian Rollers do not spend the non-breeding period in the savannah belt north of the Sahel, as had been previously suggested (Moreau and Monk 1972, Fry 2001), and support the hypothesis of a concentrated passage across the equator for land birds that winter at Southern Hemisphere latitudes in Africa (Strandberg *et al*. 2009b).

In term of distances, birds using the western route that follows the Atlantic African coast covered 9,407 km in average, while the northeastern bird that used the straight route covered 8,667 km. The western route leads to a detour twofold longer than the straighter route (41 per cent more distance than the loxodrome versus 23 per cent, respectively). Detours are widespread when facing with strong barriers to minimize risks related to harsh conditions (Alerstam 2001). In this case, it implies a reduction of the travel segment through the desert of 500 km approximately from about 2,000 km of which birds using the inland way have to deal with. This route may bring benefits due to lower temperatures and lower risks of dehydration by the proximity of the Atlantic Ocean, even though they have to travel an additional distance to reach their wintering grounds.

Regarding the spring migration, we found different routes among individuals compared to autumn migration. Although birds appear to use the same corridor that they used in the autumn migration to cross the rainforest, the spring route seems to diverge into two alternatives as soon as individuals reach the savannah belt (Fig. 1). Nevertheless, it should be taken into account that details of the spring migratory route are based on 3 geolocators and only 1 satellite transmitter and, therefore, it lacks of the same precision of the description of autumn migration.

Migratory strategy and behaviour

Our results also show for the first time in this species flight activity during the migratory stage, revealing a different pattern of migration from what was previously thought. Cramp (1998) describes the species as a diurnal migrant, but here we demonstrate that migration occurs mainly during the night. This is not surprising considering its diurnal foraging habits (hunting from perches (Avilés and Costillo 1998)), as well as its flapping flight (thus, they do not depend on thermal air (Hedenström 1993)).

Birds covering long distances in each step should spend more time in refuelling to be prepared for the journey and, consequently, they probably would start their migration later than birds which use a route that allows them to stop for rest and forage frequently (Alerstam and Lindström 1990). This hypothesis is supported by our data, showing a later onset for northeastern Iberian Rollers (all departures were in September, Table 1), whereas southern Rollers started their migration between July and August (Table 1). Nevertheless, this delay does not happen in the French populations, where the onset of migration occurred in mid to end of July (Emmenegger *et al*. 2014), which could be due to differences in environmental conditions in the breeding habitats. Moreover, the time spent in completing the first stage from the breeding grounds to cross through the hardest part of the travel reveals different strategies on crossing ecological barriers. Birds from northeastern populations took relatively shorter time (17 and 41 days) than the rest (median (IQR)) 51 (22) days to reach the Lake Chad Basin. Furthermore, the northern bird that took 41 days to reach the lake Chad Basin only spent 15 days to cross Sahara desert, although it rested 500 km north of Lake Chad before reaching it at day 41 from departure. This contrast may not be due to the simple variation in distances, but also to climatic factors and the physical incapability to rest along the travel stretches over the sea and the desert.

Migratory Connectivity

A major conservation challenge for studies on migration is to measure migratory connectivity of targeted species (Webster *et al.* 2002, Robinson *et al.* 2010). According to the results of the Mantel test the spatial distribution observed in the breeding grounds does not correlate significantly with the distribution of individuals observed in the wintering areas, which would indicate a weak migratory connectivity for Iberian Rollers. In addition, Portuguese and French southern populations use the same wintering area, suggesting that this weak connectivity could occur in a larger scale. This scenario of weak connectivity of roller populations could be an issue of concern because the confluence of individuals from a wide breeding range in a restricted wintering location might lead to a high vulnerability of the species due to any possible threat in this area.

Implications for conservation

The description of the migratory routes and wintering grounds of the near-threatened Roller highlights the challenge of conserving long-distance Afro-Palaearctic migrants, as many different sites and countries are involved (Fig. 1) (Limiñana *et al.* 2012). An appropriate conservation strategy may involve the definition of "key sites" as sites where different migratory routes converge and Rollers concentrate together. For southwestern Rollers we could define three key sites, namely the Sahel belt, the Lake Chad and the wintering sites among Angola, Namibia and Botswana to which conservation actions should target. The Sahel seems to be a key factor in the decline of long-distance migrants. This big belt gives shelter to many bird species during the migratory and winter periods, and it has suffered an enormous human population growth in the last half of the twentieth century

(Zwarts *et al*. 2009), which has led to the deforestation of several areas and drainage of wetlands in favour of agricultural areas. On the other hand, Lake Chad basin is a crucial stopover for every tracked Roller. This area is also important for other trans-Saharan species that are sustained by grasshoppers and locust pulses (Mullié 2009, Mellone *et al*. 2013, Trierweiler *et al*. 2013), highlighting the concern about the fast rate of degradation of this relevant stopover (Gao *et al*. 2011). Finally, although no major conservation problems seem to be in the wintering grounds, a common problem affecting every key site is the use of pesticides to control locust plagues (Pepler 2000, Zwarts *et al*. 2009), which would negatively affect Rollers attracted to these agricultural areas following the outbreaks of locusts. Furthermore, other problems such as removal of roost trees (Pepler 2000) or illegal shooting (BirdLife Botswana 2014) should not be underestimated.

In this scenario, the development of an appropriate global conservation programme for the European Roller would need to focus on the following issues: 1) Defining precisely core populations and the geographical division, if it does exist, for the different migratory routes, and the connectivity between and within them by more exhaustive sampling; and 2) Identifying specific threats at the identified key stopover sites during migration and wintering areas to establish conservation priorities and target objectives in a local scale. Roller shares these problems with many other species (Sanderson *et al*. 2006, Vickery *et al*. 2014) but being such a spectacular bird it could act perhaps as a "flagship" species in the aim of detecting conservation concerns for trans-Saharan migrants.

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AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: JR JP DP JMA. Performed the experiments: JR JP DP FV MAC AB JMA. Analyzed the data: JR JMR ZZ JMA. Wrote the paper: JR DP JMA. Contributed with comments to the manuscript: JP FV MAC JMR ZZ AB.

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CHAPTER IV

Short- and Long-term Effects of Tracking Devices on the European Roller *Coracias garrulus*

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ABSTRACT

Tracking devices have contributed enormously to our knowledge of avian migration, although their effects on birds are controversial. Here, we study the short- and long-term effects of deploying geolocators on European Rollers *Coracias garrulus* and assess the optimal weight of tracking devices to use. In nests in which both parents had geolocators, brood mass was lighter than in nests where only one or neither parent had a geolocator. The year-to-year recapture rate for Rollers tagged with geolocators was lower than that for control birds and the recapture rate in different populations was negatively related to the device-to-bird weight ratio, decreasing greatly when the weight ratio exceeded 2.5%.

INTRODUCTION

Progressive reduction in the weight and size of animal attached tracking devices has considerably enhanced our knowledge of avian migration (e.g. Ropert-Coudert and Wilson 2005, Bächler *et al*. 2010, Bairlein *et al*. 2012). However, their effects on birds are still unclear (Bridge *et al*. 2013, Costantini and Møller 2013) and generally have been overlooked (Cooke 2008, Vandenabeele *et al*. 2011). Most studies do not test for device effects (Godfrey and Bryant 2003) and, among the studies in which they have been tested, both short- and long-term effects (Rodríguez *et al*. 2009, Arlt *et al*. 2013), and no effects (Phillips *et al*. 2003, Schmaljohann *et al*. 2012, Van Wijk *et al*. 2015), have been reported.

We studied the effects of deploying geolocators in the European Roller *Coracias garrulus*, a species classed as Near-Threatened (BirdLife International 2012). Recent studies have located the wintering grounds of the western European populations in southwestern Africa (Emmenegger *et al*. 2013, Catry *et al*. 2014, Rodríguez-Ruiz *et al*. 2014). These studies have used geolocators and satellite transmitters to track Roller movements, and have relied on the conventional rule of 5% device-to-bird weight ratio (Kenward 2001) without prior knowledge of the possible effects of attaching devices on Rollers. We assessed the short-term effects of geolocator deployment on reproduction in two Spanish populations. We also assessed long-term effects by comparing recovery rates of control and tagged birds in two populations. In addition, we reviewed the published literature and compared our results with other studies that used tracking devices in Rollers to identify a safe weight threshold for the species.

METHODS

The study was performed in two breeding populations in southeast Spain, one in Granada (Rodríguez *et al*. 2011) and another in Almerıa (Václav et al. 2011); and in one breeding population in the south of Portugal, in Castro Verde (Catry *et al*. 2014). In Granada in 2011, we trapped 35 adult Rollers at clutch completion or during the nestling period. Of these, 17 (10 females and seven males) were tagged with MK14S geolocators (British Antarctic Survey (BAS); Fox 2010). The remaining 18 birds (eight females and 10 males) were ringed but not tagged, and thus acted as controls. Four nests had both parents carrying devices, nine nests had only one tagged parent and eight nests had untagged parents. In Almerıa, in 2012, 12 MK4490C geolocators (BAS) were deployed, resulting in three nests with two tagged parents and six nests with only one. No birds were captured as controls in this population, but breeding was monitored in 42 nests. Reproductive success in these two populations was estimated by measuring the number of fledglings and their weight to estimate total brood mass per nest. Weight of nestlings was measured at different developmental stages in the two localities: on day 20 (of the oldest nestling) in Granada and on day 11 in Almeria. In Castro Verde, in 2013, 10 MK5790C or MK7490C geolocators (BAS) were deployed. An additional 30 birds were ringed but not tagged, and thus acted as controls. All adult birds were captured and weighed during the nestling period. Breeding data were not collected in this population. In the three populations, individuals were randomly assigned to the geolocator group along the breeding season to avoid bias due to time of reproduction and, thus, concerning individual quality.

Trapping protocols were repeated in Granada in 2012, 2013 and 2014 and in Castro Verde in 2014 with an effort of capture equivalent to deployment years. Weight of deployed geolocators and birds, and method of attachment used are shown in Table 1. To our knowledge, three published studies (including our own, Rodríguez-Ruiz *et al.* 2014) have used tracking devices to investigate Roller migration. Details on the number of transmitters deployed and recovered, year of deployment, recovery rate, method of attachment and weight of devices in each study are reported in Table 1.

Table 1. Number of geolocators and satellite transmitters deployed and recovered (or seen but not recovered), year of deployment, recovery rate, method of attachment to Rollers, weight of devices including harnesses, average weight of tagged Rollers, percentage of weight of the device in relation to marked Rollers' average weight, and the reference of the known studies using these devices on Rollers.

Locality	Device	Year	Deployed	Recovered	Recovery rate (%)	Attachment	Device weight (g)	Rollers average weight (g)	Weight ratio (%)	Reference
Diverse (Spain)[a]	Satellite transmitters	2012–2013	12	1	8.33	Back-mounted harness	5.9	138.64	4.3	Rodríguez-Ruiz *et al.* (2014)
Granada (Spain)	Geolocators	2011	17	0 (1)	5.89	Back-mounted harness	3.6	140.09	2.6	This study
Granada (Spain)	None	2011	18	8	44.4	–	0	140.09	0	This study
Almería (Spain)	Geolocators	2012	12	5[b]	41.67	6 leg-loop and 6 back-mounted harnesses	2.8–3.4	143.33	2–2.4	This study
Castro Verde (Portugal)	Geolocators	2013	10	2	20	Leg-loop harness	2.4	136.5	1.8	This study
Castro Verde (Portugal)	None	2013	30	14	56.7	–	0	136.5	0	This study
Rousillon (France)	Geolocators	2011	10	5 (2[c])	50	Leg-loop harness	1.4	NA	1	Emmenegger *et al.* (2013)

[a] Return rate was estimated based on satellite data. [b] One of the five recovered geolocators was recovered 2 years after deployment. [c] These two birds were neither captured nor their colour rings identified with certainty, so they were not included in the calculations.

Statistical analysis

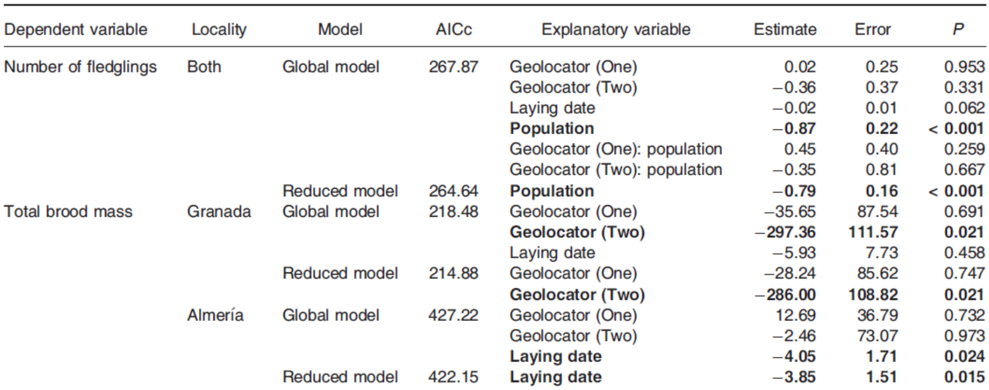
Statistical analyses were performed using R 3.1.2 (R Development Core Team 2014). A Poisson generalized linear model was used to assess whether the number of fledglings per nest was affected by the geolocators as a fixed term with three categories (i.e. no parent tagged, one parent tagged or both parents tagged), and population and the interaction between geolocator and population as other fixed terms. In addition, we used separate general linear models for each population to study variation in total brood mass in relation to the attachment of geolocators (as a categorical fixed term, see above). Models were conducted separately for the Granada and Almeria populations because brood mass was measured at different times after hatching in each area. Nests that failed in their breeding attempt were not included in these models. Laying date was also entered as a covariate in the models to account for seasonal variation. The best-fit model was determined using Akaike's information criterion with correction for small sample sizes (AICc; Burnham and Anderson 2002). We used logistic regression to assess whether the probability of recapture of individual Rollers was affected by the condition of being fitted with geolocators (fixed term) in Granada and Castro Verde. Locality was also entered as a fixed factor to check for differences in recapture rates related to breeding population. We tested for an association between the device-to-bird weight ratio and recovery rate at the population level by conducting a Spearman rank correlation using averages of the data available for the five localities. The control and tagged groups in Granada and Castro Verde were considered separately. Finally, we performed a logistic regression with the probability of recapture of each individual as the dependent variable and the weight ratio as a fixed term (coded as < 2.5% or > 2.5%). In this last analysis, locality could not be included as a random factor to account for site-specific recapture rate because device weight is related to locality, leading to no weight variation within locality.

RESULTS

Short-term effects

All tagged birds resumed their breeding activities immediately after being tagged in the two localities where reproductive success of tagged individuals was recorded. In these sites, the number of tagged adults per pair did not affect the number of fledglings produced, either on its own or in interaction with the population (Table 2). However, broods from nests in which the two parents were tagged had significantly lower weights than those from nests with one or no tagged individuals in Granada (Table 2, Fig. 1). We did not find differences in total brood mass in relation to tagging in Almerıa (Table 2).

Table 2. Short-term effects of geolocators on Rollers from populations in Granada and Almería (southeast Spain). Results of Poisson generalized linear model and general linear mixed models to analyse short-term effects of wearing a geolocator on, respectively, the number of fledglings and fledging body mass. Significant terms are given in bold. Non-significant terms were removed following a stepwise backward elimination procedure based on AICc.



Dependent variable	Locality	Model	AICc	Explanatory variable	Estimate	Error	P
Number of fledglings	Both	Global model	267.87	Geolocator (One)	0.02	0.25	0.953
				Geolocator (Two)	−0.36	0.37	0.331
				Laying date	−0.02	0.01	0.062
				Population	**−0.87**	**0.22**	**< 0.001**
				Geolocator (One): population	0.45	0.40	0.259
				Geolocator (Two): population	−0.35	0.81	0.667
		Reduced model	264.64	**Population**	**−0.79**	**0.16**	**< 0.001**
Total brood mass	Granada	Global model	218.48	Geolocator (One)	−35.65	87.54	0.691
				Geolocator (Two)	**−297.36**	**111.57**	**0.021**
				Laying date	−5.93	7.73	0.458
		Reduced model	214.88	Geolocator (One)	−28.24	85.62	0.747
				Geolocator (Two)	**−286.00**	**108.82**	**0.021**
	Almería	Global model	427.22	Geolocator (One)	12.69	36.79	0.732
				Geolocator (Two)	−2.46	73.07	0.973
				Laying date	**−4.05**	**1.71**	**0.024**
		Reduced model	422.15	**Laying date**	**−3.85**	**1.51**	**0.015**

Long-term effects

In Granada in 2012, we captured 82% of the individuals of the whole breeding population. Only one bird tagged in 2011 was seen at an early stage of the breeding season and was not located again. Of 18 untagged birds in 2011, eight (44%) were recaptured in 2012. In Castro Verde, two of the 10 tagged birds in 2013 were recovered in 2014, and four additional birds that had lost their geolocators were identified (three recaptured and one recorded with a camera). In this last locality, 14 of the 30 untagged birds were resighted in 2014. Thus, irrespective of the locality (interaction locality*geolocator: v21 = 0.87, P = 0.35; locality effect: v21 = 0.38, P = 0.54), we found a significant effect of geolocators on recapture rate of Rollers (geolocator effect: v21 = 10.43, P = 0.001) in Granada and Castro Verde, the two localities where control birds were followed in consecutive years: tagged individuals were less likely to return the following year (mean se (n): 0.46 0.07 (48) and 0.11 0.06 (27) for untagged birds and tagged birds, respectively).

Recovery rate and device characteristics

At the population level, we found that recovery rate decreased with device-to-bird weight ratio (rs = 0.81, P = 0.027, n = 7; Fig. 2). Furthermore, birds with geolocators of < 2.5% of their weight returned significantly more often the following year than those with a higher weight ratio (30.0%, n = 47, vs. 9.0%, n = 23; v21 = 4.42, P = 0.036). We chose a weight ratio of 2.5% for two reasons: (1) it is half of the recommended 5% threshold; and (2) it is the upper limit weight ratio in which we found a recovery rate similar to that found for the control groups monitored in this study (Fig. 2).

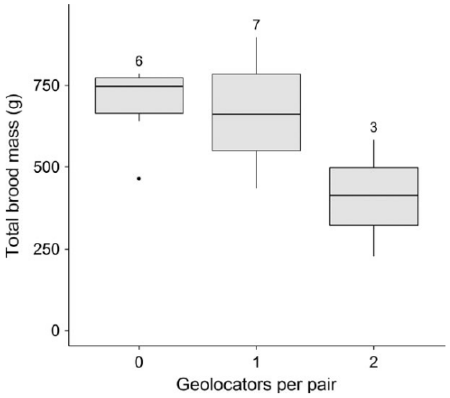


Figure 1. Boxplot showing brood weight at day 20 in relation to the number of geolocators carried per adult bird in Granada. Numbers above each box are sampled nests. *Post-hoc* Tukey tests showed significant differences in brood weight between nests with both parents wearing geolocators and nests without any tagged parent ($P < 0.001$), and nests with one tagged parent ($P < 0.001$), but not between nests with one tagged parent and nests without tagged parents ($P = 0.75$).

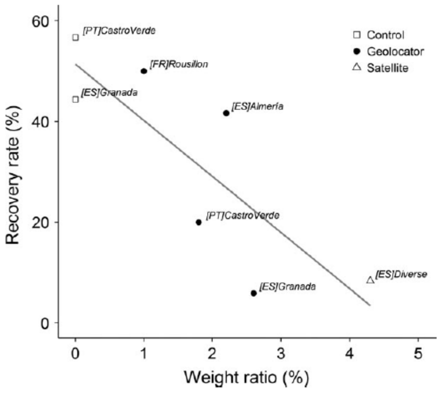


Figure 2. Relationship between device-to-bird weight ratio and recovery rate of Rollers in each locality.

DISCUSSION

Short-term effects

We found evidence of a negative short-term effect of geolocator deployment on the growth of the nestlings in the Granada population, as fledglings from nests with two tagged parents had significantly lower weights. We did not find, however, evidence of short-term effects in Almerıa, although they may have gone unnoticed due to the low sample size (only one of three nests with both parents tagged succesfully raised chicks) and/or to differences in developmental stage of chicks when measured (see Methods). This may suggest that the negative effects of geolocators appeared only late in the chick-rearing period, and that the effect of nuisance and/or increased drag produced by carrying a geolocator (Bowlin *et al.* 2010) cannot be adjusted with extra work by the parents when both are wearing geolocators. The total effect in effort reduction does not seem to be strong enough to affect the number of fledglings raised in our case. These findings suggest that breeding success on its own may underestimate the real effects of geolocators and should be complemented with a more informative estimation of breeding performance, as chicks with tagged parents could fledge in worse condition and therefore have less chance of surviving.

Long-term effects

Results from Granada and Castro Verde also suggest a long-term effect that can be inferred from a clear difference between recapture rates of tagged and untagged Rollers. Other studies that deployed geolocators on Rollers, as well as the Almerıa population, observed higher recovery rates for tagged birds than those reported in Granada and Castro Verde, even when compared with untagged individuals from these two populations (Table 1). These differences may reflect differences in migration and wintering patterns (Rodríguez-Ruiz *et al.* 2014), habitat quality (Rodríguez *et al.* 2011, Vaclav *et al.* 2011) and/or particular climatic conditions in the years of study at each locality (Table 1). However, a control group of untagged birds was lacking in these studies and thus we cannot ascertain the generality of the reported effect in Granada and Castro Verde.

The most plausible explanation for differences in return rate among individuals from different populations is the weight of devices, with higher return rates in those populations where birds were tagged with lighter devices (Fig. 2). Previous studies demonstrated that even small changes in device weight could lead to differences in survival rate and breeding performance of migrant birds (Scandolara *et al*. 2014, Casas *et al*. 2015). Our results would also suggest that the widely applied rule of thumb of 5% would not be advisable for Rollers either. In our case, we suggest that this limit should be set at around 2.5%, above which the recovery rate seems to decrease significantly (Table 1, Fig. 2).

Therefore, although sample sizes were small, we believe that the results are indicative of potential negative effects of geolocators, and we therefore follow the precautionary principle in recommending that geolocators no heavier than 2.5% of body mass should be employed to reduce the impact on return rates of Rollers. Finally, we encourage an in-depth evaluation of the effects of a tracking technique on the target species before a massive deployment of devices to quantify any possible detrimental effect that it may provoke.

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CHAPTER V

Important habitats and areas for the European roller during their non-breeding season in southern Africa, with particular emphasis on the Iberian population

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ABSTRACT

The identification of threats to migratory species of conservation concern is often biased towards breeding areas, with insufficient knowledge on non-breeding areas. The European Roller *Coracias garrulus* is a near-threatened long-distance migrant experiencing a global decline throughout its Eurasian breeding range, which has been attributed to the degradation of open agricultural habitats. However, conservation threats in non-breeding areas in Africa remain largely unstudied. Here we used occurrence data during the non-breeding season and ecological niche models to identify key habitats and areas used by European rollers in Southern Africa. We used data from satellite-tracked birds breeding in Spain to describe suitable non-breeding areas for the Iberian population (westernmost part of the Eurasian breeding range). We also used occurrence data in southern Africa from open-access databases and bird atlases to characterize the overall non-breeding range of the species there. Spanish Rollers occupied a relatively small area in the northwestern part of southern Africa, and a relatively narrow range of habitats compared with the overall non-breeding range. The most important habitat variables determining suitable areas were distance to roads and tree cover for Iberian birds, and tree and herbaceous cover for the overall population. Suitable areas for Iberian rollers were reasonably well included within current protected areas in southern Africa, but not those of the global population. Moreover, suitable non-breeding areas overlapped with degraded areas more than expected by chance. The moderate overlap between suitable and protected areas for European rollers in southern Africa suggests a need to prioritize conservation efforts in degraded non-protected areas.

INTRODUCTION

Afro-Palaearctic long-distance migrant birds are declining faster than sedentary birds with which they share breeding habitats (Vickery *et al*. 2014). The most likely causes of differential decline are the particular conditions affecting migrants in their wintering grounds and/or in their passage areas. In long-distance migratory birds, mortality rates can be considerably higher during migration than during stationary periods (Sillett and Holmes 2002, Terraube *et al*. 2013, Klaassen *et al*. 2014) and reproductive success can be influenced by the quality of habitats located thousands of kilometres away in their non-breeding ground (e.g. Norris *et al*. 2004). It is therefore critical to improve our knowledge of the ecology, distribution and habitat use of migratory birds outside their breeding season in order to elaborate more effective, holistic conservation programs (Martin *et al*. 2007, Wilcove and Wikelski 2008).

In recent years, breeding populations of the European Roller *Coracias garrulus* (Roller, hereafter) have suffered among the most drastic declines for Afro-Palaearctic migrant farmland birds wintering in open savannahs (Sanderson *et al*. 2006). Rollers distribute their annual cycle among their breeding grounds (April-August), non-breeding grounds (November-February) and migratory pathways (August-November for autumn migration and February-April for spring migration) (Finch *et al*. 2015, Rodríguez-Ruiz *et al*. 2015). In Europe, which includes most of its global breeding range, the species has become extinct in several countries. The global population decline of Rollers have been softened but not stopped in the last decade, and its conservation status changed from Vulnerable to Least Concern (Burfield and van Bommel 2004; Kovacs *et al*. 2008). Reasons for this decline point to a loss of suitable habitats, agricultural intensification and misuse of pesticides in breeding areas (BirdLife International 2012). However, there is yet an important lack of information on the threats faced by European rollers during migration and on their non-breeding grounds, preventing us to identify where and why bottlenecks are actually occurring.

Recently, the use of geolocators and satellite telemetry has allowed locating the non-breeding grounds of birds breeding in Spain, in the westernmost part of the Eurasian breeding range. Iberian birds spend the non-breeding season in an area located in south Angola, north and central Namibia and north Botswana (Emmenegger *et al*. 2013, Catry *et al*. 2014, Rodríguez-Ruiz *et al*. 2014). Rollers breeding in central Europe (Bulgaria, Cyprus, Latvia and Montenegro), however, spend the non-breeding season further east, between Botswana, Zambia, Zimbabwe, Tanzania and Kenya (Finch *et al*. 2015). Bird Atlases extend the European roller non-breeding distribution towards the south, with highest densities in the northeast of South Africa, and exclude the most arid areas in the south west of Africa (Fry *et al*. 1988, Herremans *et al*. 1993). On the other hand, migratory connectivity (i.e. to what extent individuals from a given breeding population could migrate to the same areas) has proved to be weak for the most south western European populations (Rodríguez-Ruiz *et al.* 2014), and only moderate for populations breeding further east (Finch *et al.* 2015). This suggests that separate breeding populations might use different areas and habitats during the non-breeding season. Under such a scenario, it is critical to identify roller habitat use and the environmental variables that determine species' distribution during the non-breeding season in order to identify potential threats and deliver effective conservation actions for this endangered species.

For that purpose, we use satellite-tracking data obtained from individuals breeding in Spain to describe non-breeding areas and habitat use in southern Africa. We then develop ecological niche models based on topographic, habitat and climate variables to identify suitable wintering areas for rollers in southern Africa from two different perspectives: first using satellite telemetry data obtained from individuals marked in Spain, to represent specific requirements and range of the Spanish breeding population, and, second, using online open-access databases on roller occurrences as input for the model to identify the requirements and distribution range for the entire species. Finally, we use the model outputs to evaluate to what extent the most suitable non-breeding areas and habitats are included within the current network of protected areas in southern Africa or affected by land degradation.

METHODS

Occurrence data from satellite tracking

We used satellite-tracking occurrence data from six adult birds (four males, one female and one unsexed individual) that were trapped during the 2012 and 2013 breeding seasons in Spain at six different locations (provinces of Badajoz, Ciudad Real, Girona, Granada, Lleida and Madrid; Table 1). Each tagged bird recorded only one wintering event. Birds were equipped with 5-g solar-powered PTT-100 satellite transmitters (Microwave Telemetry Inc., Columbia, MD, USA) that were fitted with a backpack Teflon harness (Garcelon 1985).

Table 1. Summary data of non-breeding events from the six satellite tracked rollers from Spain. The non-breeding residency period was defined as in Rodríguez-Ruiz *et al.* (2014). One non-breeding event was incomplete (marked with an asterisk) as the transmitter stopped emitting before the return migration.

								Habitat		
Bird	**Sex**	**Breeding population**	**Non-breeding residency period**	**Country**	**Locations (1 loc/day)**	**Locations (1 loc/cell)**	**Locations in Protected Areas**	**Grassland**	**Savanna**	**Shrubland**
#115861	M	Madrid	01/12/12 - 07/02/13	Namibia	74	28	32.4%	78.4%	20.3%	1.4%
#115862	M	Lleida	21/11/12 - 10/03/13	Botswana	106	33	74.5%	10.4%	89.6%	0.0%
#115863	M	Ciudad Real	03/12/12 - 07/02/13	Botswana	56	12	5.4%	0.0%	0.0%	100.0%
#115864	F	Granada	17/11/12 - 03/02/13	Namibia	62	13	4.8%	35.5%	29.0%	35.5%
#123744	M	Girona	22/12/13 - 13/03/14	Namibia	58	9	29.3%	81.0%	12.1%	6.9%

Satellite transmitters were programmed with an about 8-h ON/ 15-h OFF duty cycle. We used only high quality locations (classified according to their accuracy as LC 3 (up to 250 m), 2 (up to 500 m) or 1 (up to 1.5 km); Argos 2007) to describe non-breeding areas. The starting of the wintering period was identified when we detected a stabilization of the migratory movement pattern and an absence of bird displacement for more than 10 days. 20 kilometres movement in a day together with a marked north directionality were used as indication of the end of the wintering period (more details in Rodríguez-Ruiz *et al*. 2014). We filtered locations to avoid pseudo-replication due to several locations for a given individual and elaborated two different datasets: a) a first dataset to define roller habitat use, for which we selected one random location per day and per bird, obtaining a total of 374 locations; b) a second dataset to model the suitability of Spanish rollers for which we overlapped a grid of 2.5 arc-min (roughly 4.5 x 4.5 km) cell size and selected one random location per cell, obtaining a total of 100 locations (5 to 33 locations per bird; Table 1).

Occurrence data from online databases

In order to describe the non-breeding areas used by European rollers in southern Africa, we used available occurrence data from the open source database GBIF (Global Biodiversity Information Facility; http://www.gbif.org/). From these data, we discarded every record from collections and filtered with the following criteria: we retained data i) with reported location accuracy; ii) from 2000 to 2014 in order to depict recent roller distribution, iii) collected between 1st December and 28th February to ensure that observations belong to individuals residing on their non-breeding area (Rodríguez-Ruiz *et al*. 2014, Table 1) and iv) occurring within the southern Africa range (Latitude: -15º to -36º N; Longitude: 11º to 34º W). We completed this dataset with available records from the Southern African Birds Atlas Project (SABAP; Harrison *et al.* 1997). In total, we built a dataset of 1217 presences from these sources in order to model the habitat suitability of the species in southern Africa.

Environmental data

We used 14 environmental variables to model the ecological niche of the species (Table 2). We obtained climatic variables from the WorldClim database (Hijmans *et al*. 2005), which includes 19 bioclimatic predictor layers summarizing annual trends, seasonality and extremes in temperature and precipitation. As many of these variables were correlated, we extracted the values from all the 19 bioclimatic predictors corresponding to our occurrence records and selected six independent climate variables for analyses (using regression trees and variance inflation factor analyses to avoid multi-collinearity among selected variables). These six uncorrelated predictors were: (1) Annual Mean Temperature (Bio1), (2) Mean Diurnal Range (Bio2), (3) Driest Quarter Temperature (Bio9), (4) Precipitation Seasonality (Bio15), (5) Driest Quarter Precipitation (Bio17), and (6) Warmest Quarter Precipitation (Bio18). We also considered four additional variables that described topography-related traits: (7) slope, (8) aspect, and (9) distance to rivers and (10) distance to roads. Slope is the maximum change in elevation over the distance between a cell unit of the map and its eight neighbour cells. Aspect represents the direction to which the plane conformed by a cell and its eight neighbours faces. Distance to rivers and roads were included for their *a priori* biological relevance, as these are known to influence habitat preferences of rollers during breeding (Cramp, 1986, Rodriguez *et al*., 2011). Finally, four more variables were used to describe habitat characteristics: (11) percentage of herbaceous vegetation, (12) percentage of tree cover, (13) land cover and (14) land cover diversity. These layers were obtained from the GlobCover global land cover map V.2.3 (ESA Glob-Cover Project; http://ionia1.esrin.esa.int/), which uses satellite image data from 2009 to map land cover in raster format at 300m resolution.

Table 2. Variables used in the Ecological Niche Models.

Layers	Variable	Source
Climatic variables	Annual Mean Temperature (ºC)	BioClim database (http://cres.anu.edu.au/outputs/anuclim/doc/bioclim.html)
	Mean Diurnal Range (ºC)	
	Mean Temperature of the Driest Quarter (ºC)	
	Precipitation of the Driest Quarter (mm)	
	Precipitation of the Warmest Quarter (mm)	
	Precipitation Seasonality (coefficient of variation of monthly precipitation).	
Topographic variables	Slope (degrees)**	Derived from the Digital Elevation Model from BioClim data base*
	Aspect (continuous variable between 0 and 360º)***	
	Distance to Roads (km)	UNEP/FAO Desertification Assessment and Mapping Project (http://www.fao.org/geonetwork/)
	Road Density (% of surface covered by roads per cell of size 15 arc-min)	
	Distance to Rivers (km)	
Habitat	Land Cover	GlobCover
	Land Cover Diversity	
	Tree Cover (%)	

* Calculated with QGIS (QGIS 2015)

** Calculated according to the eight surrounding pixels for every grid cell

*** Pixels with a slope less than 2º were considered as flat (no aspect)

Spatial resolutions

All environmental variables were rescaled to two different spatial resolutions by overlaying them with two grids. First, a wide scale grid (see coordinates range considered above) and a resolution of 15 arc-min (approximately 25 x 25 km) that included almost all sub-equatorial Africa. This scale was chosen to fit the resolution of the SABAP census method that includes most of the locations of wintering rollers in Africa. Second, a finer scale grid from -15º to -26º latitude and 12º to 30º longitude and a resolution of 2.5 arc-min (4.5 x 4.5 km). This fine scale was used to model the more accurate occurrence data obtained from the satellite tracking of Spanish rollers, and is similar to that previously used in similar studies that also used satellite-tracking positions (e.g. Jiguet *et al.* 2011, Liminana *et al.* 2012). The resampling of the data to adjust to each scale was performed using the nearest-neighbour method for the categorical variable "landcover" and the bilinear interpolation method for the continuous variables. For the “distance to roads” variable, we used the distance to roads at the fine scale resolution and the density of roads per cell at the wider scale resolution.

Habitat use

We used the dataset with one randomly selected location per day to calculate the proportion of locations from satellite-tracked birds that occurred in a given habitat type. For this, each individual location was assigned to its corresponding habitat type by superposing it to the land cover layer obtained from the GlobCover map using ArcGIS 9.3 (ESRI 2008).

Ecological Niche models

We modelled the ecological niche of rollers in southern Africa using the MaxEnt software (version 3.3.3k; Phillips *et al*. 2006), which uses presence-only data to estimate the probability distribution of a species and a maximum entropy modelling approach (Phillips *et al*. 2006, Elith *et al*. 2011). This method works under two key assumptions: a) sampling is either random or representative throughout the landscape, and b) detection probability is constant across sites (Yackulic *et al*. 2013). By using satellite-tracking data these two assumptions are met, as tracked birds represent a random sample of the breeding population. These conditions are also complied with data from online databases, as the SABAP had a constant effort along the area considered in this study and rollers are conspicuous birds with almost invariably perch in exposed places (i.e. trees and/or pylons) close to bush-cleared grassland in the south of Africa (Herremans *et al*. 1993), thus making their detection an easy task. The models were run using logistic output format, with 10 replicates and 500 iterations set for model convergence. Variable importance was measured using the Jackknife method.

MaxEnt produces a map showing the relative suitability of species occurrence, giving a value for every grid cell that ranges from 0 to 1. Cells with values above 0.5 were considered as “suitable” for the species (Limiñana *et al*. 2012). We evaluated the relative contribution of variables to the model and how they affected the model predictions attending to the response curves given by *MaxEnt*. However, these curves should be considered carefully as they may depend on possible correlations between variables (as defined in the

MaxEnt results). Models performances were evaluated using the area under the receiver-operating curve (AUC) (Fielding and Bell 1997), for which values above 0.75 are usually considered as good performance and values above 0.90 are considered very good.

Protected areas and land degradation

We assessed the extent to which suitable areas (occurrence probability > 0.5) for the species overlapped with extant protected areas, using nationally recognized protected areas listed in the 2010 World Database on Protected Areas (WDPA; UNEP-WCMC 2010). We also evaluated the level of land degradation of identified suitable areas, using the map of global trend in NDVI adjusted by rain-use efficiency (RUE, i.e. the ratio of net primary productivity (NPP) per rainfall unit). This adjustment accounts for distinguishing the NPP loss caused by land degradation from those caused by other reasons such as climatic fluctuations or land use changes (Bai *et al*. 2008).

We used Mann-Whitney U tests to investigate whether the overlap between suitable and degraded areas was greater than expected by chance. For this, we compared the proportion of points that were within degraded areas from a set of 200 points taken randomly within the identified suitable areas and from another, randomly selected, set of points within the extent area considered for Spanish rollers or for the overall roller population.

RESULTS

Habitat Use by Spanish rollers

During the non-breeding season (December-February), satellite-tracked rollers from Spain used areas covered by savannas (40.9 %), grasslands (36.9 %) and shrublands (22.2 %). Two individuals used almost exclusively savannas (#115862 and #128720), two used mostly grasslands (#115861 and #123744), one used only shrublands (#115863) and one used the three habitat types indistinctly (#115764) (Table 1). Considering the overall non-breeding areas used by tracked rollers, the main habitat types were mostly savannas (65.95 %) and mosaics of croplands and grasslands (13.14 %).

Ecological Niche Models

The identified suitable area for tracked birds from Spain was relatively narrow and located in the south of Angola and north of Namibia and Botswana (Fig. 1). It ranged from a latitude of -15.7 to -23 and a longitude of 14.2 to 26.3 and covered an area of 91, 405 km^2. The climatic variables that contributed most to the model (>10%) were 'Precipitation in the Warmest Quarter' and 'Mean Annual Temperature' (Table 3). The non-climatic variables that contributed more to the model were 'Distance to Roads' and 'Tree Cover' (6 % and 5 %, respectively; Table 3). The discrimination power of the model for the Spanish rollers was very high, as assessed by the area under the curve (AUC = 0.925).

Table 3. Contribution (%) of environmental variables to the ecological niche models. Two separate models were developed to identify suitable areas for the overall European roller population and for a sub-population of birds from Spain. Five most important variables in each model are shown in bold.

Variable	**European rollers model (% contribution)**	**Spanish rollers model (% contribution)**
Annual Mean Temperature	4.5	**23.7**
Mean Diurnal Range	5.4	**6.9**
Mean Temperature in the Driest Quarter	**14.3**	4.7
Precipitation in the Driest Quarter	**9.3**	3.4
Precipitation in the Warmest Quarter	**13.4**	**35.6**
Precipitation Seasonality	**6.5**	2.7
Aspect	0.7	1.9
Distance to Rivers	0.1	1.9
Slope	0.5	2.1
Road density / Distance to Roads	4.5	**6**
Herbaceous Cover	4.7	1.2
Land Cover	1.4	2.7
Land Cover Diversity	0.1	2.1
Tree Cover	**34.5**	**5**

The identified suitable wintering areas for the species (irrespective of breeding origin) was much broader, and consisted mainly the east of southern Africa, Zimbabwe, Eastern Botswana and the northeast and east coast of South Africa, as well as isolated patches in the north of Namibia (Fig. 1). It ranged from a latitude of -16.7 to -34.3 and a longitude of 14.8 to 33.2 and represented an area of 1 185 985 km2. The most important variables contributing to this model were "Tree Cover" and "Temperature in the Driest Quarter" (Table 3). The model for European rollers also performed well (AUC = 0.805).

When both predicted suitable areas were overlapped, 33 405 km^2 of suitable area for Spanish rollers coincided with identified suitable areas for the overall European roller population, representing 36.55 % of the identified suitable area for Spanish rollers. The identified suitable area for Spanish rollers represented only 2.82 % of the suitable area for the species in southern Africa.

Protected Areas and Land Degradation

Only 20.36 % of the predicted suitable surface for European Rollers was included within protected areas (683 protected areas; 23.94 % of the considered whole extant protected area). By contrast, 36.86 % of the identified suitable area for Spanish Rollers was included within protected areas (103 protected areas; 4.51 % of the considered extant protected area; see Table 4 for details on most relevant protected areas). Considering satellite-tracking location data, a similar proportion (33.69 %) fell within protected areas, although there were significant individual differences in the use of protected areas ($\chi^2_5 = 63.69$, P < 0.001).

Non-breeding areas for Spanish Rollers overlapped with degraded areas in 47.85 % of the total predicted suitable area. For the overall European roller population, the overlap with degraded areas was very similar (47.35 % of the total predicted suitable area). This overlap was significantly greater than expected by chance for both Spanish (Mann-Whitney U test: $U = 17088$, $P = 0.01$, N = 400) and European rollers (Mann-Whitney U test: $W = 17313$, $P = 0.02$, N = 400).

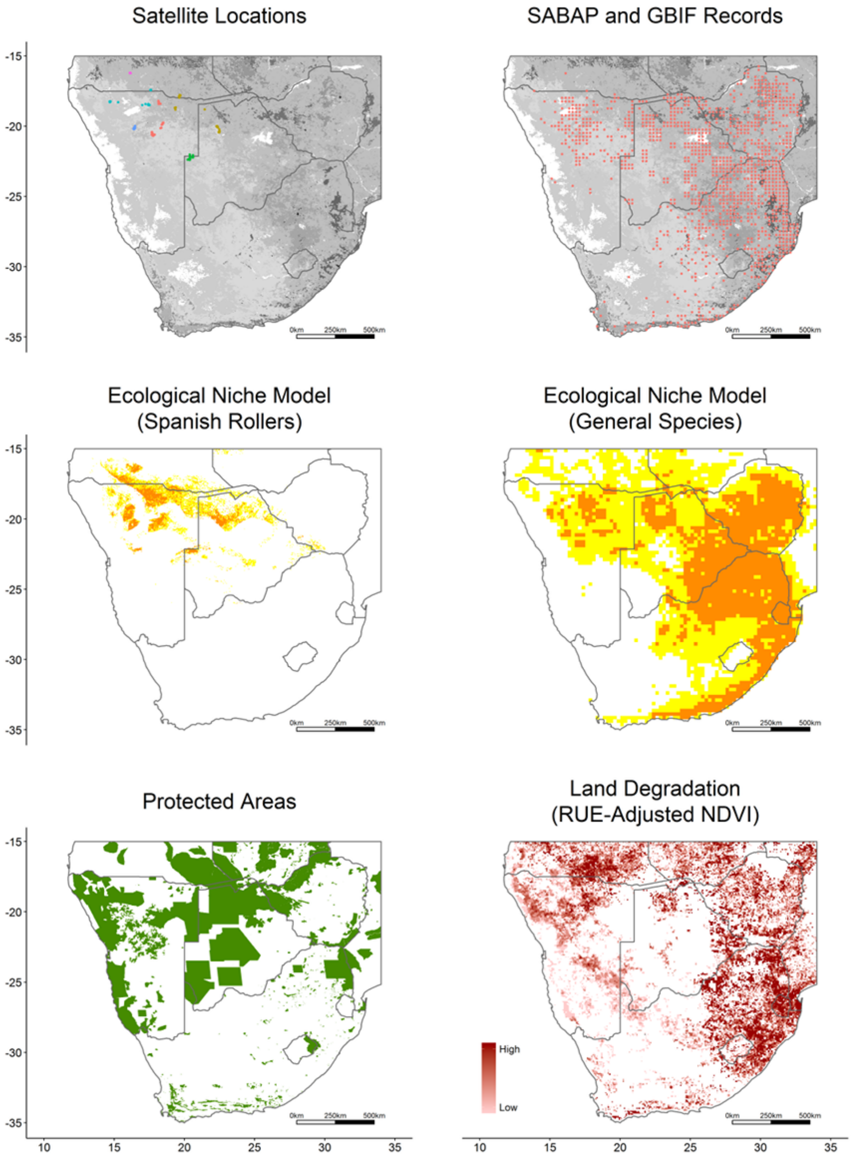

Figure 1. Results of the ecological niche model for Spanish rollers (left) and the general species (right) in Southern Africa with the existing protected areas overlapped (UNEP-CMC 2010) (green). Probability of occurrence per cell is indicated as: white = < 25%; yellow = 25 to 50% and orange = above 50%. Black dots in the left panel show satellite locations of tracked individuals.

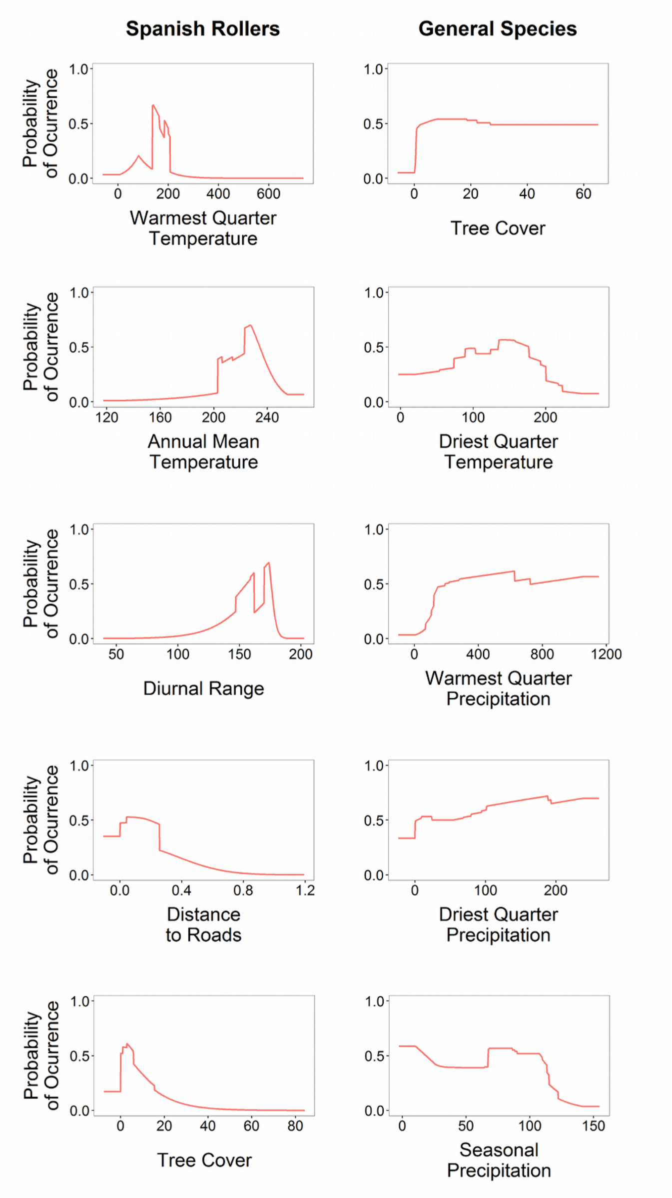

Figure 2. Partial response curves representing the relation between probability of occurrence of Spanish rollers (left) and the global species (right) and the five most important factors contributing to the models (in descending order of contribution). Units are given in Table 2.

Table 4. List of the most important protected areas contributing to the predicted suitable areas for the species and for a sub-population of birds from Spain.

Protected Area	Category	Country	Overlapping Area (km^2)
Overall European roller population			
Okavango Delta System	Ramsar Site	Botswana	52 919
Kruger to Kanyons	UNESCO Biosphere Reserve	South Africa	33 020
Kruger	National Park	South Africa	25 447
Central Kalahari	Game Reserve	Botswana	11 367
Waterberg	UNESCO Biosphere Reserve	South Africa	5 371
Limpopo	National Park	Mozambique	4 183
Etosha	National Park	Namibia	4 076
Moremi	Game Reserve	Botswana	3 075
Gonarezhou	National Park	Zimbabwe	3 019
Selati	Game Farm	South Africa	2 728
European rollers from Spain			
Okavango Delta System	Ramsar Site	Botswana	15 257
Etosha	National Park	Namibia	6 123
Otjituuo	Communal Conservancy	Namibia	2 207
Ngamiland Statelands	Wildlife Management Area	Botswana	1 712
Nyae Nyae	Communal Conservancy	Namibia	1 150
Ngarangombe	Freehold Conservancy	Angola	1127
Ozonahi	Communal Conservancy	Namibia	1 108
Luengú	Hunting Reserve	Angola	917
Omirunga	Freehold Conservancy	Namibia	885
Okawi	Freehold Conservancy	Namibia	839

DISCUSSION

Roller habitat use in southern Africa

During the non-breeding season (December-February), Spanish rollers used habitats characterized by a high proportion of natural vegetation (savannas, grasslands and shrublands), more than in the habitats used by the species across southern Africa. One possible explanation for this difference is that Spanish rollers spend the non-breeding season in the western part of southern Africa, which differs in habitat availability from the east. In the eastern part of southern Africa, a higher proportion of savannahs, grasslands and shrublands have been progressively converted into crops due to a higher human population density (Lambin *et al*. 2001, Linard *et al*. 2012). In these low-intensive farming areas, the replacement of natural savannahs leads to large increases in the availability of prey species for insectivorous birds (e.g. grasshoppers), which might be viewed as positive for birds (Hulme 2007). However, this also means more insect pests for crops and a greater use of pesticides in cultivated areas to combat these, which may indirectly affect insectivorous birds in general, and rollers in particular (Everts 1990, Mullié and Keith 1993, Newton 2004).

Suitable non-breeding areas for rollers

The optimal non-breeding distribution areas for the Spanish tracked rollers were located in the northwestern part of the overall non-breeding range of the species, with surprisingly little overlap between them. This suggests that birds from the Spanish breeding population may spend the winter in a specific area within the global wintering distribution of the species. A possible explanation is that birds from different breeding populations spend their winter in separated areas. From our data, it seems clear that birds breeding in southwestern populations migrate to the northwestern part of the total non-breeding range area for the species. Therefore, birds from other breeding populations (i.e. Central or Eastern Europe) are probably those spending the non-breeding season further east (see Figure 1, map of all rollers). This idea is supported by a recent study of the migration of European rollers breeding in central Europe (Bulgaria, Cyprus, Latvia and Montenegro) showing that these rollers spend the non-breeding season in southern Africa further east than Iberian rollers (Finch *et al*. 2015). Under such a scenario, we would predict that the European roller subspecies *C. g. semenowi*, which occupies the easternmost part of the species breeding range, would also occupy the easternmost part of the wintering range in southern Africa. *C. g. semenowi* represents an estimated 40 % of the species population in southern Africa (Fry *et al*. 1988, Harrison *et al*. 1997). Unfortunately, the information provided by atlases and censuses does not allow distinguishing between the two subspecies. Future studies including satellite-tracked individuals of the *C. g. semenowi* subspecies might help to determine its non-breeding range and obtain a clearer picture of the ecological requirements and conservation status of the two European roller subspecies.

The ecological niche models indicate that the non-breeding distribution of rollers is strongly influenced by climatic variables. Both precipitation and temperature had an important weight when predicting the distribution of Spanish and European rollers. Therefore, changes in the general patterns of these climatic variables might affect the extent of suitable areas for the species through indirect changes in habitat or in prey abundance (Huntley *et al*. 2006, Huntley *et al*. 2008, Chen *et al*. 2011). For example, changes in rainfall during the wettest months could modify the timing of locust outbreaks and their synchronization with the roller non-breeding season.

Beside climatic variables, tree cover appears as an important factor that influences the ecological niche and distribution of the species in general and, although to a lesser extent, of the Spanish population. Habitat suitability is higher when tree cover is low for Spanish birds, while for the species in general the tree cover threshold appears to be higher (Fig. 2). Rollers usually use open landscapes with sparse trees in their breeding grounds (Avilés and Costillo 1998) and this preference seems also to occur during the non-breeding season. This landscape would provide rollers with places to perch with enough visibility to find preys. A similar interpretation could be done for the relative importance of the proximity to roads found for the Spanish rollers. The road network is usually associated with power lines, where pylons and cables represent attractive perching elements for rollers (Herremans and Herremans-Tonnoeyr 1994). We have found, however, that the relevancy of road density vanishes when considering a bigger spatial scale, perhaps because in such a case road density may reflect more human activity than number of perches.

Different variables (Table 3) and response curves (Fig. 2) characterized the ecological niche of the Spanish roller and of the overall species in southern Africa. This implies that the habitat threats and conservation requirements likely differ between sub-populations of the European roller.

Roller Conservation in southern Africa

Our results show that the current network of Protected Areas (PAs) covers only a fifth of the non-breeding areas identified as most suitable for European rollers in southern Africa.

The modelled optimal distribution of Spanish rollers, however, benefited from a greater degree of protection, with almost 40 % of most suitable areas being currently included within PAs. The overlap between optimal distribution and PAs is consistently reflected in the habitat use and locations of the tracked Spanish rollers (24.4 % of all locations included in PAs). Among tracked birds, one bird spent most of the non-breeding season inside a PA and two others spent some time (one third of their locations) inside PAs (Table 1). The relatively high occurrence of European rollers outside protected areas has several mutually non-exclusive explanations: 1) current protected areas are mainly designed with the aim of protecting charismatic megafauna, and, therefore, have an insufficient coverage of suitable habitats for long-distance migrant birds; 2) unprotected areas are attracting rollers due to their high availability of perches for hunting. A previous study has found that availability of perch sites is a factor favouring breeding territory choice for Spanish rollers (Avilés and Costillo 1998). Protected areas in Africa are less densely human populated, and, therefore have a reduced network of roads and associated power lines and may provide rollers with relatively lower perch opportunities (see above); 3) unprotected areas might be attracting rollers because competition with resident insectivores could be lower than inside protected areas (Herremans 1998) or 4) because the higher agricultural intensification in unprotected areas leads to an increase of plant material that facilitates the accidental introduction of foreign insect arthropod pests (Abate *et al*. 2000) that constitutes new feeding opportunities for rollers.

Among the PAs of southern Africa, the Okavango Delta System in Botswana appears as the most important one for rollers (Table 4), being the site that contributes most suitable areas for Spanish and European rollers. This PA is catalogued as a Ramsar site considered in a good condition, although its status is vulnerable and categorized as of first priority of conservation due to increasing pressures to satisfy the demand on water and grazing lands of a growing surrounding population. Targeting on rollers, threats that may compromise the suitability of this area are overgrazing, clear-cutting and the use of insecticides that could cause negative impacts on prey availability (Thieme *et al*. 2005). The Etosha National Park, in north-western Namibia, also contributes to a large extent in protecting suitable areas for rollers and enjoys a good conservation status. The general predicted distribution of rollers overlaps with other important PAs, such as Kruger, Central Kalahari and Limpopo. In the case of Spanish rollers, some birds are linked to communal conservancies (Table 4), small protected areas that aim the social-economic development and environment restoration by delegating the management to local communities (Fabricius *et al*. 2013, Boudreaux and Nelson 2011).

We have also found that suitable areas for Spanish and European rollers overlapped with degraded lands more than expected by chance. This could be a consequence of the poor overlap of suitable areas for rollers with PAs, where land use is likely to be under less or no management and the exposure to agricultural intensification, pesticides, and overgrazing should be lower. But, irrespective of the original cause, this high overlap between suitable areas for rollers and degraded areas represents a major concern for roller conservation. Degraded areas are continuously modified by agricultural intensification and deforestation, and natural prey removed by the use of pesticides. Therefore, conservation of rollers and other insectivorous migrants must rely on measures taken in degraded non-protected areas where the efforts should focus on improving habitat management (for instance through the use of natural alternatives to control crop pests that do compromise neither prey availability for insectivorous birds nor crop production). Summing up, protected areas in southern Africa cover, on average, a low proportion of the suitable habitat for threatened species (Beresford *et al*. 2011) and this seems to be also the case for the European Roller, until very recently considered as Vulnerable by the IUCN. The different requirements of the Spanish populations and the general species suggest that a conservation plan that focuses on the most suitable areas for the species in general may not be sufficient to protect all breeding sub-populations.

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DISCUSIÓN GENERAL

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La carraca europea, al igual que muchas otras especies migradoras de larga distancia, ha sufrido un drástico descenso poblacional en las últimas décadas (Sanderson *et al.* 2006, Vickery *et al.* 2014). Aunque en los últimos años la toma de conciencia a nivel europeo ha promovido actuaciones que han permitido una moderación en la caída de sus efectivos (BirdLife International 2015), la especie continúa teniendo problemas de conservación. Las medidas dirigidas a mitigar este declive han tenido como objetivo la mejora de sus hábitats de cría (Avilés *et al.* 1999, Sackl *et al.* 2004, Bohus 2007, Kiss *et al.* 2014), principalmente mediante la colocación de cajas-nido en hábitats adecuados para la especie pero carentes de agujeros naturales para su nidificación (Kovacs *et al.* 2008). Sin embargo, las lagunas de conocimiento que aún existen sobre aspectos básicos de la historia vital de la especie, principalmente acerca de las fases de su ciclo anual que tienen lugar fuera de sus áreas de reproducción, no permiten tener en consideración todos los procesos ambientales y antrópicos que pudieran estar influyendo en la dinámica poblacional de la especie durante la migración o la invernada, y que en último término podrían estar detrás del declive general que sufre la especie.

En la presente tesis se pretende contribuir a la conservación de la carraca mediante el estudio de los diversos factores que determinan la selección de hábitat tanto en su área de cría como en las zonas de invernada. Se analizan las causas y las consecuencias de estas decisiones, así como de los patrones de movimiento de la especie a diferentes escalas espaciales. Los resultados obtenidos en los distintos capítulos de esta tesis contribuyen a un mejor conocimiento del ciclo vital de esta especie migradora en declive.

Etapa Reproductora

En el capítulo I analizamos los factores que afectan a la probabilidad de ocupación y el éxito reproductor de las carracas en cajas-nido. La instalación de cajas-nido es una medida recurrente en los planes de conservación de aves cavernícolas no excavadoras que se encuentran limitadas por la disponibilidad de agujeros (Lindenmayer *et al.* 2009). Uno de los principales problemas que presentan estas actuaciones es la ausencia de estudios previos que permitan evaluar sus efectos sobre las tendencias poblaciones, y una evaluación poca exhaustiva de las actuaciones que generalmente se basa en el análisis de la ocupación de las cajas durante períodos de tiempo cortos. En este capítulo mostramos que el grado de exposición o visibilidad de la caja-nido y su orientación, así como el grado de transformación del hábitat circundante son los factores más importantes que determinan la preferencia de uso de las cajas-nido por las carracas en una población reproductora del sur de España que se estudió durante varias temporadas. Mostramos una tendencia de las carracas a seleccionar como lugar de nidificación localizaciones más apartadas de la autovía y de zonas agrícolas transformadas, sugiriendo una preferencia de la especie por zonas menos humanizadas en el área de estudio. Estudios anteriores han mostrado que la orientación de las cajas juega un papel importante en la preferencia y éxito en la reproducción de las aves que las utilizan a través de la regulación de la temperatura (Wiebe 2001, Ardia *et al.* 2006, Butler *et al*. 2009). Sin embargo, el efecto de la orientación suele ser estacional (Ardia *et al.* 2006) y depende de cada especie (Goodenough *et al.* 2008). De acuerdo con ésto, en las carracas encontramos una preferencia por cajas-nido orientadas hacia el noroeste al principio de la temporada y hacia el sureste al final, lo que podría explicarse por la disposición geográfica de la zona de estudio respecto a la altitud media y a las cadenas montañosas que la rodean. Por otra parte, el análisis de la productividad de las carracas reveló un desajuste entre las preferencias por determinadas características de las cajas y el posterior éxito reproductor en las mismas. Las parejas que criaban en las cajas más visibles fracasaban con mayor frecuencia que aquellas que lo hacían en cajas-nido más escondidas. Este resultado sugiere la posibilidad de que en la población estudiada las cajas-nido instaladas puedan funcionar como una trampa ecológica al atraer a las parejas de carracas a zonas que pueden no ser las más óptimas para la reproducción de la especie (Schlaepfer *et al.* 2002, Mänd *et al.* 2005, Klein *et al.* 2007, Torres-Orozco *et al.* 2016).

Tan importante como identificar los factores más importantes a la hora de elegir un territorio de nidificación, es identificar las causas principales que motivan la fidelidad a dicho territorio durante reproduciones sucesivas. El estudio de las causas y consecuencias de la dispersión es imprescindible para entender la dinámica de una población (Greenwood y Harvey 1982) y poder implementar medidas adecuadas para su conservación (Ronce 2007, Serrano y Tella 2012). En el capítulo II, encontramos que la probabilidad de dispersión reproductiva en las carracas depende de la edad relativa de los individuos, siendo más fieles a sus territorios de reproducción los individuos de edad relativa mayor. Además se encontró que los factores que influyen en la probabilidad de dispersión son distintos para cada sexo. Los machos de carraca de coloración más brillante en su cabeza fueron más fieles a sus territorios cuando sus cajas se encuentraban en zonas más expuestas y de elevada productividad para las carracas. La probabilidad de dispersión de las hembras de carraca, por su parte, no se relacionó con ninguno de los factores analizados. Sin embargo, encontramos que, entre las hembras que permanecieron en la población, aquellas con coloraciones menos saturadas en su espalda se dispersaron una menor distancia entre eventos consecutivos de reproducción. Además las hembras que criaron en zonas muy productivas para los congéneres tendieron a reproducirse cerca de esos territorios al año siguiente. Estudios anteriores han mostrado que la coloración del plumaje en la carraca está correlacionada con varios indicadores de calidad individual y éxito reproductivo, y que podría revelar el estatus social (Silva et al. 2008). Es decir, que parece que aquellos individuos de mejor calidad, estimada aquí indirectamente a través de su coloración, son los que mantienen los territorios durante más de una reproducción. Estos resultados apuntan a que el mantenimiento de los territorios de reproducción se debería fundamentalmente a los machos (Cramp 1998), mientras que las hembras competirían por quedarse cerca de los territorios dominados por estos machos de mejor calidad. Se corrobora en este capítulo la querencia por las cajas-nido más expuestas (Capítulo I). Los resultados de este capítulo apoyarían también la hipótesis de la atracción por el éxito de los conespecíficos (Danchin *et al.* 1998, Doligez *et al.* 2002), sugiriendo que las carracas podrían valorar la calidad de un territorio no sólo en función de su propia experiencia, sino también a través de la productividad en los nidos próximos de su misma especie. Sin embargo, a partir de este estudio correlativo no es posible descartar que las carracas estuvieran evaluando directamente la calidad de los territorios en vez de la productividad de sus carracas vecinas. Por otro lado, encontramos que estos patrones de movimiento no parecen tener consecuencias para la reproducción posterior, sugiriendo que los costes derivados de este proceso (la competencia por mantener un territorio o el coste energético de buscar nuevos recursos y parejas) son pequeños o no pueden detectarse en este estudio porque se manifiestan en futuras temporadas reproductivas. En último lugar, analizamos en aquellos individuos que se movieron entre temporadas dentro de la zona de estudio las diferencias entre los territorios de destino y partida, no encontrando diferencias en las características de dichos territorios para los machos. Sin embargo, las hembras, se movieron hacia territorios donde la densidad de conespecíficos era menor, lo cual puede indicar un estrategia de dispersión denso-dependiente en las hembras de nuestra población. De esta manera, las hembras podrían buscar zonas que fueron productivas en el año previo a la dispersión, buscando a la vez una baja densidad de congéneres, es decir, evitando la competencia.

Etapa No Reproductora

Los problemas que afectan a una especie migradora de larga distancia pueden ser de naturaleza muy diversa y de muy amplio ámbito geográfico y temporal (Newton 2004). Hay evidencia de que los factores que influyen en el acusado descenso poblacional de las poblaciones de aves migradoras pueden ejercer su influencia fuera de sus áreas de cría (Sanderson *et al.* 2015). Hasta hace muy pocos años, la información disponible sobre la etapa no reproductora de la carraca era muy escasa y basada en avistamientos y recuperaciones anecdóticas de anillas, estando además muy sesgada hacia las poblaciones al este de su rango de distribución (Brown y Brown 1973, Ash y Miskell 1980, Feare 1983). Esta carencia de información supone un problema a la hora de implementar medidas adecuadas de conservación para mejorar la tendencia de sus poblaciones. En esta tesis presentamos por primera vez una descripción precisa de las rutas migratorias de la especie, sus paradas y cuarteles de invernada, y su comportamiento durante el largo trayecto que realizan hasta llegar a ellos mediante un estudio en el que se combina el marcaje de individuos de varias localidades de cría que definen un amplio rango latitudinal en España (Capítulo III). Mostramos que en las carracas de la Península Ibérica tienen dos rutas migratorias alternativas durante la primera mitad del trayecto migratorio. La primera de ellas una ruta directa desde las poblaciones que se reproducen en el noreste, y una segunda ruta alternativa hacia el oeste por la costa atlántica africana desde las poblaciones del centro y sur hasta el oeste. De esta manera, las carracas que se reproducen en las poblaciones occidentales españolas lograrían sortear la barrera del desierto del Sáhara y los riesgos que conllevan atravesar un ámbiente árido extremo (Alerstam 2001). Ambas rutas confluyen en una importante zona de repostaje en los alrededores del lago Chad para continuar al sur hacia los cuarteles de invernada en Angola, Botswana y Namibia. El lago Chad es una región vital no sólo para las carracas, sino para millones de aves migradoras que buscan refugio en este lugar desde toda Europa (Zwartz et al. 2009). Además, se demuestra por primera vez una actividad migratoria fundamentalmente nocturna en una especie previamente descrita como migradora diurna (Cramp 1998). Nuestros resultados también muestran evidencia de plasticidad en el comportamiento migratorio en relación con el tipo de hábitat atravesado, observándose que las carracas viajaron más rápido al atravesar el desierto del Sáhara que otros tipos de hábitat, como la selva tropical o el cinturón del Sahel. Por último, encontramos una conectividad migratoria débil en la escala espacial estudiada. Individuos de poblaciones diversas confluyen en invierno en un área restringida, lo que muestra la vulnerabilidad de la metapoblación ibérica a cualquier cambio ambiental y remarca la necesidad de definir áreas clave para su conservación.

El estudio de la migración en las aves ha experimentado una expansión muy importante en la última década gracias al desarrollo progresivo de dispositivos de seguimiento de menor peso, tamaño y coste (Bächler *et al.* 2010, Bairlein *et al.* 2012). Sin embargo, el efecto producido por estos dispositivos sobre los individuos marcados es aún un tema de debate, con evidencias a favor y en contra (Rodríguez *et al.* 2009, Arlt *et al.* 2013, Bridge *et al.* 2013, Costantini y Møller 2013, Van Wijk *et al.* 2015, Blackburn *et al.* 2016, Matyjasiak *et al.* 2016). En el Capítulo IV evaluamos el efecto a corto y largo plazo causado sobre las carracas por estos dispositivos de seguimiento, que fueron empleados para lograr los objetivos planteados en los Capítulos III y V, además de otros colocados en individuos de otras poblaciones. Encontramos evidencia de efectos negativos causados tanto en el corto plazo sobre la reproducción en la misma temporada de colocación de los dispositivos, como a largo plazo sobre la tasa de recaptura al año siguiente de los individuos equipados con los dispositivos. El peso total de los pollos en nidos criados por dos individuos equipados con dispositivos fue significativamente menor que el de nidos criados por sólo uno o ningún individuo equipado. Además, la tasa de recaptura de individuos equipados con los dispositivos fue menor que la de individuos no equipados. Asimismo, al comparar las tasas de recaptura de diferentes poblaciones en las que se habían colocado dispositivos observamos que estas tasas fueron mayores cuando los dispositivos eran menos pesados, observándose que la tasa de recaptura disminuye drásticamente cuando el peso de los dispositivos colocados superó el 2.5 % del peso corporal del individuo equipado. Este trabajo, por tanto evidencia la importancia del seguimiento de individuos control en este tipo de actuaciones y la necesidad de realizar una evaluación exhaustiva de los potenciales efectos negativos de estos dispositivos antes de valorar su colocación masiva en cualquier especie migradora.

Una vez conocida la ruta migradora e identificados los lugares de invernada de las carracas ibéricas, el paso siguiente es analizar el uso del hábitat y su rango de distribución y evaluar las posibles amenazas y el grado de protección de las áreas donde inverna la especie. Estos aspectos son tratados en el último capítulo de esta tesis (Capítulo V), donde analizamos por primera vez las características de hábitat de las áreas seleccionadas para la invernada por las carracas ibéricas seguidas en el capítulo III y lo comparamos con la distribución adecuada para la especie en general, estimada a partir de registros tomados de bases de datos online y censos realizados en el sur de África (SABAP, Harrison *et al.* 1997). Para ello usamos modelos de distribución de especies, que es una técnica muy efectiva para caracterizar el rango de distribución de las especies, predecir cambios ante diferentes escenarios y tomar medidas enfocadas a su conservación (Elith y Leathwick 2009, Guisan *et al.* 2013). Los resultados de esta comparativa revelan, en primer lugar, que el área de invernada de las carracas ibéricas supone tan sólo una pequeña parte al noroeste del área total estimada para la especie. También se muestra un uso de hábitats menos antropizados por las carracas ibéricas, quizás debido a las diferencias en la densidad de población entre el oeste y el este, ya que en la zona más oriental las sabanas y praderas se han transformado progresivamente en campos de cultivo (Lambin *et al.* 2001, Linard *et al.* 2012). En general, encontramos factores de naturaleza e importancia relativa diferentes en la caracterización del nicho ecológico para las carracas ibéricas y para el total de la especie que inverna en el sur de África. Por otro lado, tanto para las carracas que se reproducen en la Península Ibérica como para el total de la especie los factores climáticos influyeron de manera sustancial en la distribución de las áreas de invernada, sugiriendo que la especie podría ser particularmente susceptible a variaciones producto del cambio climático en una zona donde han ido potenciándose las temperaturas extremas en las últimas décadas (Kruger y Sekele 2013). La cobertura arbórea resultó ser otro factor de gran relevancia para la especie, de forma que cuando ésta es baja se favorece la presencia de carracas, lo cual está en consonancia con la querencia vista en las áreas de reproducción de esta especie por hábitats abiertos con disponibilidad de puntos dispersos desde donde cazar (Avilés y Costillo, 1998).

El grado de protección de las zonas de invernada ocupadas por las carracas ibéricas y por el total de la población invernante en el sur de África difieren de manera notable. Mientras que el area de invernada de las carracas ibéricas presentó una cobertura protegida moderada, con un 40 % de la distribución incluída en zonas protegidas, tan sólo un 20 % de la distribución de la especie se encontraba en zonas protegidas. De nuevo, las diferencias en densidades de población humana entre el este y el oeste tienen una repercusión en la distribución y disponibilidad de tipos de hábitat, con un porcentaje más alto de terrenos dedicados a la agricultura en el este. Es posible que el propio diseño de la red de parques nacionales existente en África, con una tendencia clara a la protección de la megafauna amenazada, no sea favorable para las especies migradoras asociadas a hábitats áridos como la carraca. Estas especies pueden encontrar en las zonas agrícolas no incluídas en los espacios protegidos una mayor disponibilidad de recursos, aunque, por contra, se pueden ver también sometidas a los impactos producidos por los tratamientos pesticidas y la degradación del hábitat. De hecho, al superponer las distribuciones óptimas con mapas de evaluación de la degradación causada por factores antrópicos en África, mostramos que la convergencia con zonas degradadas es mayor de la esperada por azar. En esta tesis sugerimos que las actuaciones de conservación dirigidas a ésta y otras especies migradoras de requerimientos ecológicos similares deberían focalizarse en estas áreas degradadas fuera del ámbito de protección de la red actual de espacios protegidos africanos, donde amenazas tales como la intensificación agrícola, la deforestación o el uso de pesticidas podrían poner en peligro su supervivencia.

PERSPECTIVAS FUTURAS E IMPLICACIONES PARA LA CONSERVACIÓN

A nivel de población, son varias las implicaciones que los resultados de esta tesis tienen en relación a la conservación de la carraca:

1. En primer lugar, los futuros planes de conservación para esta especie cavernícola no excavadora deben analizar las consecuencias en términos de fitness de la elección de cajas-nido y no llevar a cabo instalaciones indiscriminadas basadas tan sólo en datos de ocupación a corto plazo.

2. Recomendamos tener en cuenta las preferencias de hábitat mostradas en este estudio, evitando la colocación de cajas-nido en paisajes degradados, muy antropizados y de usos intensivos. Además, fomentando el desarrollo de un paisaje agrícola en mosaico, con alternancia de usos de cultivo herbáceos y leñosos, con especial atención a la disponibilidad de posaderos para descansar y cazar.

3. Se recomienda evitar la colocación de cajas-nido demasiado expuestas, pues aunque la especie muestra predilección por lugares despejados a la hora de elegir cajas-nido, éstos presentan una mayor tasa de fracasos . Sin embargo, si las cajas-nido son instaladas en lugares demasiado cubiertos, esto podría hacerlas indetectables para individuos en prospección, mermando la eficacia de la instalación.

4. Es importante considerar la orientación de las cajas en relación a las condiciones climáticas de la zona de actuación. Las cajas-nido son más frías y con oscilaciones térmicas más amplias que otro tipo de cavidades (Amat-Valero et al. 2014) y, por tanto, los factores que afecten a la temperatura podrían ser más importantes en estos sistemas. En nuestra zona de estudio se ha observado que la orientación preferida durante el período más frío de la temporada es diferente al habitualmente visto en otras especies en el hemisferio norte (Rohrbaugh Jr. y Yanner 1997, Ardia *et al.* 2006, Goodenough *et al.* 2008, López *et al.* 2010) debido a las condiciones geográficas particulares. No obstante, la población estudiada supone una población limítrofe respecto al rango

altitudinal de la especie y muy dependiente de sus condiciones climáticas particulares. Por tanto, cualquier extrapolación a otras zonas debe realizarse con precaución.

5. En cuanto a la dinámica de nuestra población, destacan dos aspectos que pueden tener repercusiones muy importantes a largo plazo y sería necesario estudiar en el futuro. En primer lugar, la alta tasa de renovación de la población. A lo largo de 8 años de seguimiento, hemos registrado un porcentaje de entre el 38 y el 57% de individuos nuevos por año (Introducción, Figura 3). Es decir, aproximadamente la mitad de la población se renueva cada año. Resulta intrigante cuál es el origen de estos individuos nuevos debido a la ausencia de otras poblaciones próximas de densidad importante. Por otro lado, la tasa de reclutamiento de los individuos nacidos en la población es extremadamente baja. Aún queda por explorar cuáles son los mecanismos que determinan la dispersión natal y cuál es el destino de los juveniles. Es posible que nuestra población resulte ser una población sumidero dentro del sistema metapoblacional del sureste ibérico por encontrarse al borde de la distribución altitudinal y, por tanto, representar unas condiciones climáticas extremas dentro del rango de tolerancia de la especie (Huntley *et al*. 2007).

6. Respecto a la etapa no reproductora, mostramos la importancia de tres lugares claves en la ruta migratoria de las carracas ibéricas: el cinturón del Sahel, el lago Chad y las áras de invernada comprendidas entre Angola, Botswana y Namibia. Tanto el Sahel como la cuenca del Lago Chad son zonas de refugio y abastecimiento muy importante para ésta y otras especies migradoras europeas. Es preocupante la fuerte presión antrópica en esta región debido al crecimiento humano exacerbado reciente que ha tenido como consecuencia un fuerte proceso de deforestación, transformación y drenaje de zonas húmedas para la generación de cultivos (Zwarts *et al.* 2009). Por otro lado, la cuenca del Lago Chad lleva décadas en proceso de retroceso, lo que podría poner en riesgo su persistencia y la de tantas especies que dependen de él (Gao et al. 2011). En cuanto a las áreas de invernada, según estudios recientes, la efectividad de las zonas protegidas africanas podría verse alterada debido al calentamiento global, que puede causar un desajuste con el desplazamiento de las distribuciones óptimas para las diferentes

especies de aves que actualmente encuentran refugio en ellos (Hole *et al.* 2009). Es muy importante estimar el grado de resiliencia de la especie en concreto y de las diferentes poblaciones europeas de carraca en particular. En esta tesis vemos que las carracas ibéricas ocupan un área muy reducida dentro del rango de distribución óptimo para la especie y que esta distribución está correlacionada con las condiciones climáticas, lo cual podría repercutir muy negativamente ante un escenario de cambio climático. Además la conectividad migratoria para las poblaciones ibéricas es débil, lo que podría ser precupante al confluir un rango amplio de poblaciones europeas en un área restringida en África. Un estudio colaborativo a escala europea ha revelado un conectividad migratoria moderada que podría otorgarle cierta resiliencia ante la pérdida localizada de hábitat (Finch *et al.* 2015), sin embargo se hace necesario ahondar más profundamente en el estudio de la conectividad migratoria, la identificación de localizaciones clave, las condiciones a las que están sometidas las carracas en ellas y cuáles podrían ser las amenazas bajo un escenario de cambio climático.

7. Por último, el análisis de los efectos a corto y largo plazo de la colocación de dispositivos de seguimiento para el estudio de la migración en la especie revela efectos negativos de los dispositivos a las dos escalas temporales. Esto nos lleva a hacer en primer lugar una recomendación sobre la necesidad de evaluar los efectos de cada técnica de seguimiento en cada especie estudiada antes de la colocación masiva de dispositivos. Además, para el caso de la carraca recomendamos usar dispositivos con un peso inferior al 2.5% del animal para reducir el impacto negativo de estos sobre las tasas de retorno de los individuos marcados.

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CONCLUSIONES

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1. La selección de cajas-nido por las carracas en la población estudiada revela un posible efecto de trampa ecológica, pues el uso preferente de cajas-nido más expuestas va acompañado de un menor éxito reproductor para la especie.

2. La orientación de las cajas preferida por las carracas cambió estacionalmente, evitando la exposición a los vientos más fríos provenientes de las sierras al principio de la reproducción. Además, las carracas evitan ocupar cajas-nido colocadas en hábitats altamente antropizados, lo cual sugiere que éstos son hábitats desfavorables para la especie.

3. En relación con los patrones de dispersión ,se concluye que los individuos de mayor edad relativa son más fieles a sus territorios de reproducción, y que los condicionantes de la dispersión reproductiva difieren entre machos y hembras. La probabilidad de dispersión en machos viene determinada por la calidad individual, las características de la caja-nido y la productividad del parche. Las hembras se dispersan más lejos que los machos y la distancia está correlacionada con la calidad individual y la productividad de carracas vecinas. Las hembras se dispersaron a lugares con una menor densidad de conespecíficos. Las decisiones de dispersión no tuvieron consecuencias obvias para el fitness de los individuos.

4. El reclutamiento de individuos nacidos en la poblacion fue extraordinariamente bajo sugierendo que la población de estudio podría funcionar como una población fuentede otras poblaciones vecinas.

5. Las carracas ibéricas usan dos rutas migratorias diferentes: Aquellas del suroeste de la península se desvían hacia la costa atlántica africana, mientras que desde las poblaciones del noreste siguen una ruta directa hacia el sur cruzando el Mediterráneo. El cinturón del Sahel y, principalmente, los alrededores del lago Chad, son paradas vitales de reabastecimiento para la especie. Además, los lugares de invernada se localizaron en el suroeste africano, más al oeste que lo descrito previamente.

6. Las carracas ibéricas tienen una conectividad migratoria débil en la escala espacial estudiada, puesto que individuos de poblaciones diversas confluyen en un área restringida, lo que remarca la necesidad de definir áreas clave para su conservación.

7. Los datos de seguimiento por satélite revelaron un comportamiento migrador principalmente nocturno y una velocidad de migración dependiente del hábitat atravesado, con velocidades mayores al atravesar zonas extremas, como el desierto.

8. El uso de dispositivos de seguimiento en esta especie reveló posibles efectos negativos a corto y largo plazo sobre los individuos marcados. A corto plazo, los pollos salieron del nido con un menor peso y a largo plazo, la tasa de recaptura fue mucho menor en individuos equipados. La comparativa de dispositivos empleados en diferentes poblaciones sugiere una disminución de la tasa de recaptura cuando estos pesan más de un 2.5% del peso corporal del individuo.

9. Respecto a las zonas de invernada, las carracas ibéricas ocuparon un área muy pequeña al noroeste dentro del área total estimada para la especie al sur de África. Las zonas adecuadas para la invernada de las carracas ibéricas están moderadamente bien representadas por espacios protegidos, aunque no es así para la zona estimada global de la especie. Además, en ambos casos, la zona adecuada para la invernada solapaba con áreas degradadas más de lo esperado por azar, lo cual sugiere la necesidad de priorizar los esfuerzos de conservación sobre las áreas adecuadas degradadas que no se encuentren protegidas por la red de espacios protegidos africanos.

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