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UNIVERSIDAD DE
CASTILLA-LA MANCHA

Junta de Comunidades de
Castilla-La Mancha

IREC Ana Benítez López Tesis Doctoral 2014

Instituto de Investigación
en Recursos Cinegéticos

Ecología y conservación de Pteróclidos ibéricos: una aproximación multiescalar

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Tesis Doctoral

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ECOLOGÍA Y CONSERVACIÓN DE PTERÓCLIDOS IBÉRICOS: UNA APROXIMACIÓN MULTIESCALAR

Memoria presentada por

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para optar al grado de Doctor

2014

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Esta Tesis Doctoral ha sido financiada por la Dirección General de Investigación (proyectos CGL2007-66322/BOS CGL2008-04282/BOS), Consejería de Educación y Ciencia de Castilla-La Mancha (proyectos PAI08-0171-9582 y PAC06-137), la Reserva de la Biosfera de Bardenas Reales (proyectos UCTR09-0268, UCTR110053 y UCTR120308) y la Direction Régionale de l'Ecologie, de l'Aménagement et du Logement de Provence-Alpes-Côte d'Azur.

A mis padres y mi hermana

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Marco conceptual

La actual pérdida de biodiversidad es un problema global que está teniendo lugar a un ritmo sin precedentes (Pimm et al. 1995). Las principales amenazas para la biodiversidad son de origen antrópico, entre las cuales la destrucción de hábitats por cambios en los usos del suelo se ha citado como una de las más importantes (Vitousek et al. 1997). De seguir la tendencia actual, las presiones que ejercen los seres humanos sobre la diversidad debido a los cambios en los usos del suelo serán mucho más fuertes en los próximos decenios (Sala et al. 2000), por lo que existe una creciente urgencia por intentar atenuar o revertir lo que ha venido en llamarse “crisis de la biodiversidad” (Balmford et al. 2005; Hochkirch et al. 2013; Tittensor et al. 2014). En este contexto, aumentar nuestro conocimiento sobre la importancia de las relaciones ecológicas entre las especies y los hábitat que ocupan, así como identificar los procesos que determinan la distribución, abundancia y demografía de las especies se ha convertido en prioritario dentro de la investigación ecológica aplicada.

El ejemplo quizá más paradigmático de la devastación ecológica sufrida durante el último siglo por la acción humana es el debido a las transformaciones en los agrosistemas y la intensificación agraria, responsables de la mayor pérdida de biodiversidad del planeta (Green et al. 2005; Tilman et al. 2001). Este proceso ha sido muy notable en Europa, donde este tipo de ecosistemas son los predominantes, ocupando el 40 % de la superficie del continente (EU-28, Eurostat 2014) y por tanto sostienen buena parte de la biodiversidad que ha conseguido adaptarse a la actividad humana en una de las zonas del planeta con mayor influencia antrópica (50% de las especies de aves europeas, Pain and Pienkowski 1997). En las últimas décadas estos medios agrarios están sufriendo su particular crisis (de biodiversidad) por la modernización agraria desde la segunda mitad del siglo XX (Krebs et al. 1999), y las medidas políticas de la Política Agraria Común (PAC) (Donald et al. 2001; Donald et al. 2002; Donald et al. 2006), causando el descenso poblacional del 23% de la biodiversidad europea en las últimas tres décadas (De Heer et al. 2005), incluyendo un 52% de las especies de aves (PECBMS 2012). Para el año 2050 se prevé un aumento del 70-100% en la producción necesaria para consumo humano (Godfray et al. 2010; Tilman et al. 2011), y consecuentemente un descenso continuado de la biodiversidad de medios agrarios (Butler et al. 2010a). Por lo tanto, la conservación de las especies adaptadas a este tipo de hábitat originados y manejados por el hombre es uno de los principales retos actuales en conservación.

En la presente Tesis Doctoral **se ha investigado sobre cómo determinadas especies propias de los agrosistemas responden a los cambios ecológicos provocados por las alteraciones derivadas del desarrollo humano**. Hemos utilizado para ello dos especies de aves simpátricas: la ganga ibérica (*Pterocles alchata,* Linnaeus 1766) y la ganga ortega (*Pterocles orientalis,* Linnaeus 1758), cuyo origen está asociado a medios desérticos y semi-desérticos, pero que en el contexto europeo, se distribuyen por paisajes eminentemente agrarios, y por tanto sometidos a un alto grado de impacto humano. La investigación se ha abordado desde una aproximación multiescalar, estudiando tanto los factores abióticos, bióticos y antrópicos que determinan la distribución geográfica y nicho ecológico de ambas especies, hasta la selección de hábitat y microhábitat a nivel local, así como estudios de seguimiento a nivel individual que han proporcionando estimas de supervivencia y posibles causas de mortalidad en diferentes contextos geográficos.

Esta Tesis Doctoral no puede, ni quizá deba, ser ajena al escaso conocimiento que aún se tiene de nuestras dos especies de estudio, a su delicado estado de conservación y a la tendencia regresiva de sus poblaciones, por lo que la investigación tiene una eminente vocación de generar conocimiento sobre la ecología de los propios modelos de estudio y de ayudar a su conservación.

Introducción general

1. Biodiversidad, conservación de especies y persistencia de poblaciones

La pérdida de biodiversidad es un problema global que ha adquirido cada vez más interés dentro de la comunidad científica, en especial desde la Cumbre de Río en 1992. Tras la Convención sobre Diversidad Biológica (Convention on Biological Diversity, CBD, http://www.biodiv.org), los países Europeos acordaron unánimemente "*poner fin a la pérdida de biodiversidad para el año 2010*" (Balmford et al. 2005). Este compromiso, lejos de ser logrado (Butchart et al. 2010), ha sido renovado para el 2020, pero hay muchas dudas sobre su viabilidad real y sobre la forma en la que hay que alcanzar tan ambicioso objetivo (Hochkirch et al. 2013). Así mismo, muchos otros países en el mundo se han comprometido a una reducción significativa de la tasa actual de pérdida de biodiversidad a nivel global, regional y nacional (Balmford et al. 2005; Pereira and David Cooper 2006). En el caso concreto de Europa, y dado el grado de modificación del paisaje para el aprovechamiento agropecuario llevado a cabo desde el Neolítico hasta el presente, la conservación de la biodiversidad en estos medios (especialmente la conservación de aves de medios agrarios) es sin duda la que más atención suscita (Donald et al. 2001; Pain and Pienkowski 1997).

A lo largo de las últimas décadas se ha llevado a cabo la identificación de las amenazas más severas para la biodiversidad, que incluyen la destrucción y fragmentación de hábitats, la intensificación (o abandono) de los usos del suelo tradicionales, el cambio climático, la contaminación y las invasiones biológicas (Sala et al. 2000). Todas estas amenazas tienen un origen antrópico, y son consecuencia del rápido y generalizado crecimiento de la población humana y su desarrollo durante el pasado siglo y el actual (McKinney 2006), con aproximadamente un 83% de la superficie terrestre bajo influencia de actividades humanas (Sanderson et al. 2002). De todas las amenazas, la destrucción de hábitat es sin duda la principal causa de pérdida de diversidad de especies (Venter et al. 2006; Wilcove et al. 1998), puesto que implica la reducción de efectivos poblacionales a nivel local y regional, y además supone la fragmentación de hábitats dando lugar a una distribución discontinua de la especies. Todo esto supone mayor vulnerabilidad a las extinciones locales y una inmigración reducida (Kuussaari et al. 2009; Tilman et al. 1994). Otros efectos de la actividad humana son de tipo directo, e incluyen la mortalidad de individuos por persecución y caza ilegal, la sobreexplotación de especies, la electrocución en líneas de alta tensión, o el efecto nocivo de la ingesta de pesticidas y contaminantes (Newton 1998). Aunque muchos de estos procesos tienen lugar a escala local, pueden existir sinergias entre ellos cuyas consecuencias pueden ser percibidas a escala regional o a escala del rango de distribución de una especie (Brook et al. 2008).

Además de los factores antes mencionados (todos ellos extrínsecos), la persistencia de una población también se ve influenciada por factores intrínsecos derivados de las características individuales y los rasgos de la historia de vida ("life history traits") de una especie. Las decisiones individuales y estrategias de la historia de vida afectan a la eficacia biológica ("fitness") de un organismo, por lo tanto, a su habilidad para reproducirse y sobrevivir (parámetros demográficos básicos de una población). Dentro de las decisiones individuales que toma un organismo, la selección de hábitat (el uso desproporcionado de recursos o condiciones) es, sin duda, un aspecto crucial en fenómenos vitales como la regulación de una población, las interacciones entre especies, el ensamblaje de comunidades ecológicas y el origen y mantenimiento de la biodiversidad (Morris 2003). El hábitat de una especie, en su sentido más amplio, comprende todas las condiciones y recursos abióticos y bióticos que permiten la supervivencia, reproducción y presencia de una población. En concreto, la elección de un hábitat particular para el desarrollo de una actividad determinada ha sido frecuentemente descrita como el resultado de un compromiso evolutivo entre presiones selectivas que maximizan la supervivencia y/o el éxito reproductor a lo largo de la vida de un organismo (Krebs and Davies 1993). Así, los organismos no seleccionan un hábitat independientemente del riesgo de depredación (Brown 1988; Brown 1992; Lima and Dill 1990), de la cantidad y calidad de recursos en otros lugares, o de la demanda de esos recursos por otros individuos conespecíficos o heteroespecíficos (Fretwell and Calver 1969; Rosenzweig 1981); y en consecuencia sus historias de vida no evolucionan independientemente de los hábitats que ocupan (Martin 1995; McNamara and Houston 1992). De hecho, los individuos pueden tener diferentes habilidades competitivas y/o diferentes estrategias de historia de vida que pueden resultar en una ventaja adaptativa. Por ejemplo, hay individuos que pueden diversificar sus áreas de invernada y reproducción realizando movimientos exploratorios para aprovechar nuevos recursos que pueden fluctuar en el espacio y en el tiempo (comida, lugares de cría, pareja, etc.) (Dingle and Drake 2007). Estas variaciones individuales pueden ser determinantes en la supervivencia y el éxito reproductivo a nivel individual dependiendo del contexto ambiental. Entender el origen y la persistencia de estas variaciones es, por tanto, de vital importancia en la dinámica de poblaciones y en la conservación.

La selección de hábitat es muy dependiente de la escala a la que se estudie (Johnson 1980; Mayor et al. 2007), y su comprensión requiere información de las condiciones ambientales a toda las escalas espaciales y temporales en las que los organismos operan (Hutchinson 1957).Dado que en ecología los niveles (espaciales y temporales) están organizados (Bissonette 1997) e interconectados (procesos a escalas mayores influyen en procesos a escalas menores, y viceversa), los avances que logren la comprensión del funcionamiento de cada uno de ellos pueden ayudar a explicar parte de los otros. De esta forma, identificar los procesos que determinan la distribución y la dinámica de las especies, comunidades, poblaciones y ecosistemas se ha convertido en un tema central de investigación en ecología, sobre todo dentro del contexto de cambio global en el que nos encontramos, con una gran cantidad de hábitats destruyéndose y desapareciendo a una velocidad sin precedentes. Sin embargo, esta tarea supone un gran reto debido a la compleja naturaleza de los procesos dinámicos que influyen en los rangos geográficos de las especies y los factores relacionados con estos procesos, que actúan a múltiples escalas espaciales (Elith and Leathwick 2007; Guisan and Thuiller 2005; Guisan and Zimmermann 2000). Este reto es aún mayor cuando se trata de especies poco o escasamente estudiadas, en los que los aspectos más generales de su ecología son desconocidos, por lo que hay que dirigir de la manera más eficaz los recursos disponibles para maximizar y diversificar la información científica extraída, de manera que pueda ser integrada y responda preguntas claves que nos ayuden a comprender aspectos básicos de la ecología de la especie en cuestión.

Una posible aproximación para poder abordar y ampliar el exiguo conocimiento científico sobre los aspectos ecológicos fundamentales de una especie poco conocida es utilizar un enfoque multiescalar en la cual los determinantes medioambientales de su distribución, abundancia, preferencias de hábitat, relaciones bióticas y parámetros demográficos sean estudiados desde grandes escalas geográficas, pasando por escalas intermedias y llegando a escalas pequeñas.

2. Distribución de especies y nicho ecológico

El conocimiento de los patrones de distribución y abundancia de las especies y la identificación de los factores que determinan estos patrones son cruciales para la gestión y conservación de la biodiversidad (Krebs 1978). Dichos patrones obedecen a las relaciones entre las especies y su entorno, y son el resultado de su ecología e historia evolutiva (Brown 1995). Además, los factores que determinan la distribución de las especies operan con diferente intensidad y a diferentes escalas espaciales (Gaston 2003), que van desde la distribución geográfica de las especies hasta el uso que éstas hacen de los recursos en un marco local, por ejemplo dentro de su área de campeo (ej.: Johnson 1980; MacArthur 1972). De esta forma, una distribución gradual a gran escala espacial (baja resolución) suele venir determinada por factores climáticos, mientras que una distribución parcheada a escala local (alta resolución) suele ser el resultado de una distribución discontinua de los recursos, debida principalmente a variaciones micro-topográficas o a la fragmentación del hábitat (Guisan and Thuiller 2005; Scott et al. 2002).

En general, los factores que determinan la distribución de una especie se clasifican en (a) factores abióticos, que son las condiciones ambientales favorables para el establecimiento, supervivencia y reproducción de los individuos y que constituyen los límites más amplios del rango de distribución de una especie (Figura 1, región A); (b) factores bióticos, constituidos por competidores, depredadores y patógenos (interacciones entre especies), los cuales determinan la estructura de grano fino de la distribución y que también pueden modificar los límites determinados por los factores abióticos (Figura 1, región B); y (c) la capacidad dispersiva de las especies, ya sea por propios movimientos o por dispersión por agentes externos (p.e. dispersión zoocora o anemócora de propágulos, frutos o semillas), que determina las partes del mundo que son accesible a los individuos de la especie en cuestión (Figura 1, región M) (Guisan and Thuiller 2005; Soberon 2005; Soberón 2007).

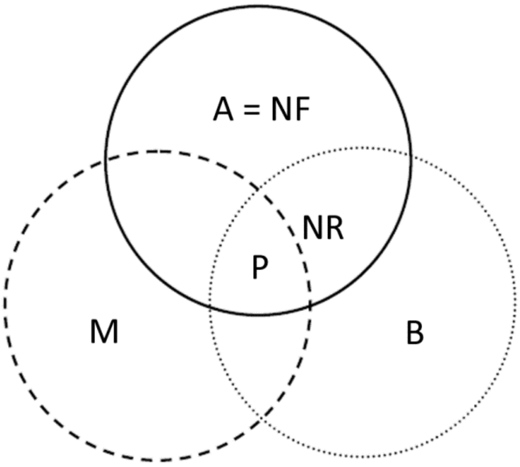


Figura 1. Círculo A: región geográfica donde los factores abióticos son adecuados para la especie (nicho fundamental, NF). Círculo B: región donde se encuentra una combinación de especies tal que permite el asentamiento de la especie considerada. A ∩ B (incluyendo la región P) es la expresión de su nicho realizado (NR). Círculo M: es la parte del mundo accesible para la especie en términos ecológicos, esto es, sin barreras dispersivas. Finalmente A ∩ B ∩ M = P es la región que contiene las peculiaridades tanto abióticas como bióticas y que es accesible para la especie, y equivale a la distribución geográfica de la especie. Adaptada de Soberón y Peterson (2005).

Aunque existen factores adicionales (como los evolutivos, por ejemplo) estos tres son fundamentales para entender la distribución geográfica de una especie y su relación con el nicho ecológico (Soberón 2007). Hutchinson (1957) definió el nicho como un hipervolumen multidimensional en el cual una especie mantiene una población de manera viable, y donde cada dimensión corresponde a los factores antes descritos. Así, para que una especie esté presente en un punto geográfico concreto las condiciones abióticas (A, Figura 1) deben ser favorables para un crecimiento poblacional positivo, y deben darse asimismo las interacciones específicas (B) necesarias para la presencia de la especie, esto es, que las especies mutualistas estén presentes y la presencia de competidores, depredadores y enfermedades debe mantenerse bajo un umbral que resulte en una eficacia biológica positiva. Mientras el rango de condiciones abióticas favorables representa el nicho fundamental (NF) de la especie, este puede ser restringido por las interacciones bióticas, dando lugar al nicho realizado (NR) de la especie (Figura 1) (Hutchinson 1957). Finalmente, este nicho realizado podrá ser observado sólo en aquellas áreas accesibles para la especie desde su origen, teniendo en cuenta la potencialidad del medio (barreras geográficas) y la capacidad dispersiva de la especie para su expansión (Figura 1, región P). Así, dentro del marco de la teoría de metapoblaciones, áreas accesibles pero que no cumplan los requerimientos abióticos y bióticos de la especies alojarían poblaciones "sumidero" (áreas donde el crecimiento poblacional es negativo), mientras que las que sí los cumplan podrían acoger poblaciones "fuente" (con crecimiento poblacional positivo) (Gaston 2003; Pulliam 2000).

En este contexto, los modelos de distribución de especies (*Species Distribution Models*, SDM) han adquirido una relevancia enorme en las últimas décadas debido a su capacidad para cuantificar las relaciones especie-hábitat (nicho de una especie) mediante relaciones estadísticas entre la presencia de especies y las condiciones ambientales (factores abióticos) (Guisan and Thuiller 2005; Guisan and Zimmermann 2000). Los SDM se han utilizado para identificar y gestionar especies amenazadas (Engler et al. 2004; Norris 2004), priorizar áreas para la conservación de la biodiversidad (Araújo et al. 2004; Ortega-Huerta and Peterson 2004), evaluar la propagación potencial de especies invasoras (Peterson and Robins 2003; Thuiller et al. 2005b), y evaluar el impacto potencial del cambio climático sobre los patrones de distribución de especies (Bakkenes et al. 2002; Loiselle et al. 2010; Thuiller et al. 2005a). El desarrollo de este tipo de modelos es particularmente interesante cuando se trata con especies amenazadas (Donázar et al. 1993; Muñoz et al. 2005), pues permiten identificar los factores que están determinando su distribución, identificar áreas de hábitat favorable y elaborar planes de conservación que incluyan estas áreas dentro de la red de espacios protegidos. Además, los SDM permiten construir mapas de idoneidad de hábitat ("habitat suitability maps") que, comparados con la distribución real de la especie, facilitan la identificación de áreas donde la especie está presente pero el hábitat es desfavorable (áreas sumidero, Pulliam 2000) y las poblaciones se mantienen gracias a la dispersión desde áreas fuente, o áreas de alta idoneidad de hábitat pero donde la especie no esté presente debido a causas o eventos históricos.

Entender los mecanismos que determinan el nicho de una especie y los factores que permiten su coexistencia con especies emparentadas es uno de los grandes retos de la ecología, y es crucial para nuestro entendimiento de las implicaciones evolutivas y ecológicas de las interacciones entre especies (Brown 1984; Darwin 1859). El nicho de una especie no solo determina su distribución (potencial), sino también su abundancia de acuerdo a dos hipótesis: la hipótesis de amplitud de nicho, y la hipótesis sobre la posición del nicho (Gaston et al. 1997). La primera postula que hay especies con amplias distribuciones geográficas y alta densidad a nivel local debido a su capacidad para ocupar una variedad más amplia de hábitats y de explotar condiciones ambientales y recursos más diversos (dicotomía generalistas *vs* especialistas, Brown 1984). La segunda defiende, por otro lado, que las especies más abundantes son aquellas que usan los recursos que son comunes en un determinado momento y en un área particular, o que son altamente exitosas (en términos de eficacia biológica y crecimiento poblacional/densidad) bajo un determinado conjunto de condiciones ambientales (esto es, la posición de su nicho se ajusta a las condiciones ambientales imperantes, Devictor et al. 2010), mientras que las especies raras utilizan recursos escasos y restringidos a nivel local (dicotomía comunes *vs* raras, Gaston et al. 1997). Estas dos hipótesis no son mutuamente excluyentes (Heino 2005), y aunque la segunda ha tenido más apoyo en el pasado (Gaston and Blackburn 2000; Gregory and Gaston 2000; Hanski et al. 1993), la primera ha ganado en popularidad recientemente (Brändle and Brandl 2008; Slatyer et al. 2013), y ambas pueden ser complementarias.

Como hemos visto, el rango geográfico de una especie puede verse restringido por interacciones bióticas (depredadores, competidores, parásitos), que reducen su nicho fundamental a una fracción que puede ser explotada de manera estable por la especie. Los requerimientos ecológicos de especies cercanamente emparentadas son similares y pueden impedir su coexistencia en un ambiente donde los recursos son limitados (ej.: MacArthur 1972), por lo que el nicho ecológico de una especie puede quedar restringido por la presencia de otra especie en simpatría. Cuando dos o más especies cercanamente emparentadas –y, por tanto, con similares requerimientos- coexisten en un determinado momento y en un preciso lugar, la pregunta que surge es: ¿cómo pueden coexistir? Por un lado, la adaptación de las dos especies a ambientes abióticos similares puede dar lugar al desarrollo de de preferencias ecológicas similares, y por tanto ambas especies pueden llegar a competir por los mismos recursos (García and Arroyo 2005). Por otro lado, el elevado coste de competir por los mismos recursos ecológicos puede dar lugar a la denominada "exclusión competitiva", limitando la coexistencia de las dos especies (MacArthur and Levins 1967).

Cuando hablamos de nicho ambiental (nicho Grinelliano, Grinnell 1917) a larga escala no existe competición *per se* por recursos (nicho Eltoniano, Elton 1927), o esta no es relevante, es decir, las condiciones ambientales no se consumen, si no más bien éstas restringen la presencia de las especies. Una manera de evaluar por qué especies altamente relacionadas coexisten en regiones simpátricas es comparando las condiciones abióticas de escenarios simpátricos frente a alopátricos. De esta forma podemos ahondar en el entendimiento de hasta qué punto los factores abióticos (en oposición a los bióticos o históricos), marcan los límites de coexistencia entre especies. Así, en alopatría, la posición y amplitud de nicho de una especie respecto a uno o varios gradientes ambientales puede variar respecto a escenarios de simpatría, siendo en el primer caso una aproximación al nicho fundamental de la especie, y en el segundo al nicho realizado. Las variaciones en el nicho de dos especies relacionadas entre ambos escenarios nos proporcionarían evidencia de interacción y segregación del nicho a gran escala (Chunco et al. 2012; Rannap et al. 2009), e hipotéticamente deberían seguir uno de los siguientes patrones (Figura 2): (a) en simpatría las condiciones abióticas son intermedias respecto a regiones alopátricas. Es decir, si los factores abióticos determinan el rango geográfico de las especies, éstas deben coexistir en regiones donde haya condiciones que estén incluidas en el nicho fundamental de ambas especies (Hutchinson 1957); (b) en simpatría, las condiciones abióticas no están en posiciones intermedias entre situaciones alopátricas, si no que se encuentran en un extremo a lo largo de un *continuum* de condiciones ambientales, de forma que son las interacciones bióticas las que median la respuesta de una o ambas especies a las condiciones abióticas (Chunco et al. 2012); (c) las condiciones ambientales en simpatría y en alopatría no difieren, lo que sugeriría que son limitaciones dispersivas (debido al comportamiento o fisiología de las especies, o a barreras físicas) las que están restringiendo las distribuciones de las dos especies (Guisan and Thuiller 2005).

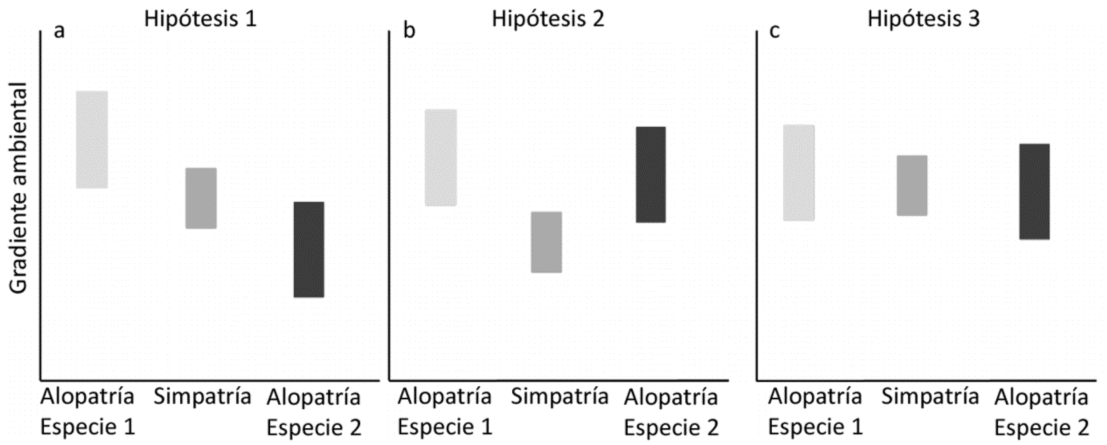


Figura 2. Hipotésis alternativas sobre los patrones de variación ambiental en poblaciones simpátricas y alopátricas de dos especies a lo largo de un gradiente ambiental. (a) Según la hipótesis 1, las especies conviven en condiciones ambientales intermedias donde los nichos de las dos especies solapan. (b) Según la hipótesis 2, los factores bióticos median la coexistencia de tal forma que las especies están presentes a la vez de manera más frecuente cuando las condiciones son extremas. (c) Según la hipótesis 3, la simpatría y la alopatría dependen principalmente de la capacidad dispersiva, resultando en la ausencia de diferencias ambientales entre las poblaciones alopátricas y simpátricas. Adaptada de Chunco et al. (2012).

Aunque en ocasiones puede haber casos en que en áreas de convergencia ecológica de condiciones abióticas (intermedias), una de las especies (o las dos) dependan en gran medida de la presencia y/o densidad de la otra (véase capítulo 2). Algunos ejemplos de cómo las interacciones interespecíficas pueden afectar a la densidad de especies en zonas simpátricas dependiendo de las condiciones ambientales han sido descritos en aves asociadas a medios agrarios (Sanza et al. 2012), incluyendo cambios en el nicho ecológico que permiten el uso de determinados hábitat en simpatría raramente usados en alopatría (Martín et al. 2010a). Por otra parte, los individuos pueden utilizar la presencia de otros de la misma especie para agregarse en áreas tradicionalmente ocupadas o donde la reproducción fue exitosa en el pasado (áreas alopátricas, Osborne et al. 2007); independientemente de si las condiciones ambientales han cambiado. Por tanto, los factores bióticos pueden afectar a las relaciones especie-hábitat tanto de manera positiva como negativa.

Hoy en día, para entender los factores que generan y mantienen la biodiversidad y para poder definir los nichos ecológicos de las especies, se requiere incorporar, además de factores abióticos y bióticos en los modelos, factores antrópicos que estén limitando la distribución y persistencia de las poblaciones (Eriksson 2013). Esto es particularmente oportuno en especies sensibles a la presencia humana, como podrían ser las especies típicas de medios desérticos y áridos, donde la densidad de población humana y el desarrollo asociado son bajos (ver sección 5). De esta forma, será posible predecir la plasticidad ecológica de las especies (en simpatría y alopatría) respecto a los cambios de hábitat y, por tanto, respecto a su vulnerabilidad a cambios de usos del suelo inducidos por la actividad humana (ver sección 3 y 4).

3. Del rango geográfico a la escala de microhábitat: importancia de los estudios multiescalares

Los factores abióticos que actúan a escalas mayores (con resolución de grano grueso, "coarse grain") limitan lo que ocurre a escalas más pequeñas (con resolución de grano fino, "fine grain") (Turner et al. 2001), de manera que la supervivencia de una especie sólo es posible en una región del espacio climático, y la reproducción con éxito será posible únicamente en una zona restringida de esta región, donde entrarán en juego otros factores que actúan a menores escalas (Kearney and Porter 2004). En su trabajo seminal, Johnson (1980) describió un orden natural de procesos de selección que determinan la distribución de las especies, atendiendo tanto a las restricciones fisiológicas que operan a grandes escalas, como a decisiones etológicas adquiridas evolutivamente como un compromiso entre el beneficio y el riesgo de utilizar un determinado hábitat, éstas operando a escalas intermedias y de grano fino. Así, la selección de primer orden puede ser definida como la selección del rango geográfico o físico de una especie (ver sección 2). Dentro del rango de distribución, la selección de segundo orden determina el área de campeo de un individuo o grupo social, mientras que el uso de los componentes del hábitat dentro del área de campeo correspondería a la selección de tercer orden. Por último, si la selección de tercer orden se refiere a un hábitat o lugar de alimentación, el tipo, identidad y cantidad de comida usada respecto a la disponible en ese lugar sería llamada selección de cuarto orden (microhábitat). Aunque estos órdenes se pueden dividir más finamente, los anteriormente definidos son los más ampliamente utilizados en la mayoría de los casos. La selección de hábitat es por tanto un proceso espacial y jerárquico, que puede ser descrito atendiendo a diferentes escalas, tanto espaciales como temporales (Mayor et al. 2009; Morris 1987; Wiens 1989) (Figura 3).

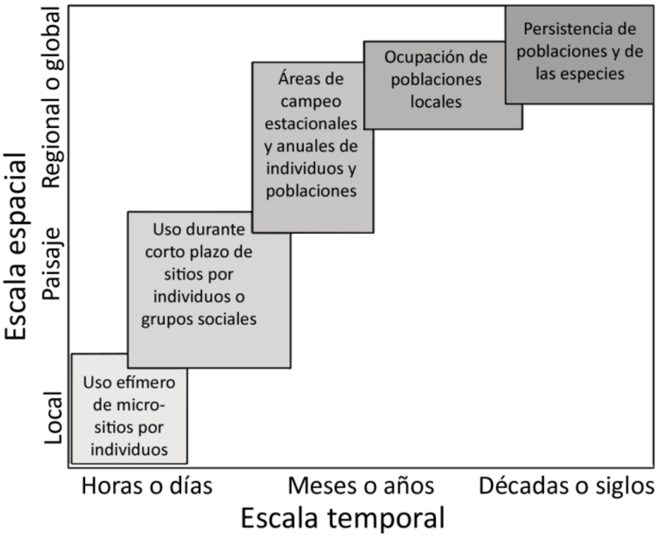


Figura 3. Vínculo entre las escalas espaciales y temporales que actúan en la selección de hábitat. La unidad espacial refleja la movilidad del organismo (adaptado de Mayor et al. 2009)

En el proceso de selección de hábitat, el establecimiento del área de campeo es sin duda la decisión etológica más importante para un organismo puesto que determina la disponibilidad y número de hábitats que pueden ser explotados, y por tanto, la disponibilidad de recursos claves (acceso a pareja, alimento, refugio, lugar de nidificación) y condiciones a escalas más finas (Cody 1985; Indermaur et al. 2009), que son los que afectan de manera más directa al comportamiento individual del individuo (Martin 1998; Rotenberry and Wiens 1980). Es decir, la selección de hábitat de grano fino puede ser modulada por la selección de hábitat a escalas superiores, existiendo interdependencia entre las distintas escalas (Traba et al. 2013). Dado que los ecosistemas y poblaciones no pueden ser descritos adecuadamente a una sola escala, y que el efecto de las condiciones ambientales depende de la escala de estudio (Levin 1992), las aproximaciones multiescalares están ganando popularidad para caracterizar patrones de selección de hábitat (Mateo-Tomás and Olea 2009; Razgour et al. 2011). Además, en el caso de especies simpátricas que coexisten a escala geográfica de grano grueso, la selección de hábitat diferencial es un proceso clave desde el punto de vista ecológico y evolutivo que estabiliza la coexistencia de las especies (MacArthur and Wilson 1967), mediante segregación espacial a escalas más pequeñas (Traba et al. 2013). En este sentido, los estudios multiescalares pueden ser especialmente informativos a la hora de entender partición de hábitat y coexistencia de especies cercanamente emparentadas y, consecuentemente, con similares requerimientos y uso de los recursos (ver sección 5).

El proceso jerárquico de selección de hábitat se entiende como una posible solución para adaptarse a la variación espacial (y temporal) en la disponibilidad de condiciones y recursos (Levins 1968; Orians and Wittenberger 1991), que afectarán a la capacidad de carga y la calidad de los hábitats, y por tanto regulará los niveles poblacionales (Morris 2003; Newton 1998). En medios agrarios, estos procesos vienen íntimamente relacionados con la gestión humana, con variaciones espacio-temporales en los sustratos, estructura del hábitat y disponibilidad de recursos altamente asociadas a los ciclos de siembra y recolección y aplicación de agroquímicos (Butler et al. 2010b); en comparación con medios cuya gestión es más homogénea (medios forestales, por ejemplo). Por tanto, el hombre es el principal agente inductor de los cambios en agrosistemas, y éstos serán más o menos importantes dependiendo de la escala (a escala de parcela agraria o a escala de paisaje), y dependiendo de la actividad antrópica considerada (ver sección 4).

Los animales pueden usar diferentes hábitats dentro de sus áreas de campeo o cambiar radicalmente sus áreas de campeo temporalmente dependiendo de la distribución espacial de los recursos (Cody 1985), y en respuesta a variaciones ambientales introducidas por el hombre (ej.: movimientos inducidos por cambios en el hábitat). Este tipo de decisiones individuales puede repercutir de manera positiva o negativa en la supervivencia y reproducción de los individuos (Parker and Stuart 1976), por lo que explorar la importancia relativa de los factores que determinan la selección de hábitat (incluyendo factores antrópicos) a diferentes escalas puede darnos pistas sobre las decisiones que subyacen al movimiento de los animales (Roshier et al. 2008), y las implicaciones que estas decisiones tienen a nivel individual y poblacional.

4. Paisajes antropizados y amenazas de conservación de aves esteparias

Identificar los requerimientos ecológicos y las características del hábitat que favorecen la supervivencia y reproducción de las especies es crítico para establecer cualquier estrategia de conservación, especialmente para especies que habitan medios sujetos a rápidos cambios antrópicos (Tapia et al. 2008; Tella et al. 1998). Los sistemas agrarios europeos son un ejemplo de este tipo de medios, principalmente debido a la intensificación agraria que está provocando un rápido y severo descenso de las poblaciones de aves asociadas a estos hábitats (Donald et al. 2001; Donald et al. 2006). Como resultado, un gran número de especies típicas de agrosistemas están actualmente amenazadas en Europa, en concreto, un 83% de las especies tienen un estado de conservación desfavorable (BirdLife-International 2004; Burfield 2005).

Muchas de las aves ligadas a medios agrarios en la península ibérica son especies esteparias, que han ocupado esos cultivos por su similitud estructural con las estepas naturales de las que proceden (Santos and Suárez 2005; Suárez et al. 1992). Las poblaciones de aves esteparias (estepas naturales o pseudo-estepas cerealistas) han sufrido un dramático descenso en las últimas décadas, especialmente durante el periodo 1970-1990 (BirdLife-International 2004; Burfield 2005). En España, donde se concentra la comunidad de aves esteparias más diversa y abundante de Europa, estas tendencias negativas están asociadas principalmente con cambios en el uso del suelo que suponen la destrucción o degradación de áreas habitadas por este grupo (Madroño et al. 2004). Entre los cambios de usos del suelo destacan el desarrollo de infraestructuras, la urbanización e industrialización, la intensificación de la agricultura y el abandono masivo de tierras de cultivo que están siendo invadidas por formaciones de matorral (Santos and Suárez 2005; Suárez-Seoane et al. 2002). Estos cambios de usos del suelo son relativamente recientes en España: un marcado incremento en el desarrollo de infraestructuras y líneas de comunicación, con un crecimiento de 900 km lineales de carreteras/año entre 1970-1998 (Rosell et al. 2003); un proceso intenso de urbanización y desarrollo industrial, para el cual se han utilizado 190000 ha de suelo en el periodo 1990-2000; el aumento en la extensión de invernaderos, los cuales ocupaban unas 25000 ha en 1997 en el sureste de España en zonas previamente de carácter estepario; y el incremento en cultivos intensivos de olivar, cuya extensión ha aumentado en 40000 ha entre 1985-2000 (Santos and Suárez 2005; Suárez-Seoane et al. 2002).

Pero es sin duda la intensificación de la agricultura el proceso más importante asociado con el descenso en las poblaciones de aves esteparias de los agrosistemas españoles (Santos and Suárez 2005; Suárez-Seoane et al. 2002). Las estimas más recientes indican un declive general de las especies ligadas a medios agrarios en el periodo 1998-2011 (-17%), mientras que la mayor parte de especies generalistas o asociadas a otros ecosistemas (aves forestales) parecen tener poblaciones estables o en incremento (SEO/BirdLife 2013). El proceso de intensificación agraria, se debe en gran parte a los cambios en el uso del suelos y las prácticas agrarias impulsadas por la PAC (Donald et al. 2001; Donald et al. 2002; Donald et al. 2006), y tiene lugar a tres escalas espaciales: la escala de parcela, escala de paisaje y escala regional (ver Guerrero 2013, Tabla 1). En concreto, en España, este proceso está marcado por un descenso en la superficie de barbecho (en parte por la aplicación de técnicas de mínimo laboreo y siembras directas) y en la de cultivos de leguminosas, un incremento en la producción mediante el aumento de cultivos intensivos de cereal, un uso intensivo de pesticidas, insecticidas y semillas blindadas (reduciendo la cantidad de alimento disponible para aves), la transformación de tierras de secano a regadíos (incluso en áreas áridas y semidesérticas), el uso de variedades de cereal de ciclo corto, un aumento del tamaño de parcela y desaparición de linderos debido a concentración parcelaria (Suárez et al. 1997b).

Tabla 1: Prácticas agrarias y cambios en los uso asociadas con la intensificación agraria a tres escalas espaciales (adaptado de Guerrero (2013).

Escala	**Práctica agraria/cambio uso suelo**
Parcela o campo de cultivo	**uso más intensivo de la maquinaria agrícola**, que faculta una gestión más precisa del cultivo **aumento de las dosis y frecuencia de uso de fertilizantes de síntesis** y **productos fitosanitarios,** incluyendo **semillas blindadas**, que promueve la uniformidad espacio-temporal en el establecimiento, crecimiento y maduración de los cultivos **mayores dosis de simiente** que consiguen mayor densidad y uniformidad en las siembras utilización de **variedades de cultivo de alto rendimiento**, que facultan una mayor productividad simplificación o **desaparición de las rotaciones de cultivos (**técnicas de mínimo laboreo y **siembra directa)** disminución o **desaparición del barbecho** transformación en **regadío**
Paisaje	**simplificación y uniformización de los paisajes agrarios**, como consecuencia tanto de la agregación de los cambios a nivel de parcela, como de las operaciones de **concentración parcelaria** y sus efectos de **disminución de la densidad de linderos** entre parcelas y de otros elementos no cultivados del paisaje (setos, eriales, ribazos, bosquetes o bancales). Esta práctica a su vez provoca una **mayor continuidad espacial de áreas bajo los mismos sistemas de gestión** y / o rotaciones de cultivos a lo largo del ciclo anual
Regional	**polarización del espacio entre grandes áreas de monocultivos intensos (**que han reemplazado el mosaico agrario**)**, y otras **zonas menos productivas** por limitaciones naturales afectadas por la disminución de la actividad o el **abandono**. En última instancia, la PAC y las dinámicas del desarrollo promueven **diferentes tasas de intensificación o abandono entre regiones**, comarcas y orientaciones productivas.

Dado que los cambios en la prácticas o componentes en cada escala ocurren frecuentemente de manera interdependiente, podemos considerar la intensificación agraria como un proceso multiescalar que ha modificado profundamente la gestión de los cultivos a escala de parcela, y la estructura y funcionamiento de los agro-ecosistemas a escala de paisaje y a escala regional (Chamberlain et al. 2000), por lo que las estrategias de conservación en estos medios requieren también de una aproximación multiescalar (Gonthier et al. 2014).

Además de la gestión agraria, otras actividades humanas tienen lugar en medios agrarios (Sastre et al. 2009). En concreto, en zonas rurales menos favorecidas, el aprovechamiento agrícola es habitualmente complementado con otras actividades como la actividad cinegética, la cual genera sustanciales beneficios socioeconómicos (Bernabeu 2000; Martínez et al. 2002). La caza menor (conejo *Oryctolagus cuniculus)* y perdiz roja *Alectoris rufa*) es particularmente importante en España y se practica en la mayor parte del territorio nacional, particularmente en medios agrícolas heterogéneos (Buenestado et al. 2009; Casas and Vinuela 2010). Por tanto, los esfuerzos de gestión cinegética (gestión del hábitat, control de depredadores, aporte de agua o comida, establecimiento de zonas de reserva), junto con la gestión agraria, pueden afectar a la conservación de las aves esteparias (Caro et al. 2014; Estrada et al. en revisión). En particular, el control de depredadores, podría ser un elemento que favoreciera a las aves esteparias, tanto por mortalidad directa como por su sensibilidad a la depredación de nidos por especies generalistas (De Borbón et al. 1999b; Yanes and Suárez 1996). Esta medida podría ser especialmente interesante en agrosistemas cercanos a asentamientos humanos o donde ha habido una paulatina expansión de viviendas recreacionales (urbanización), y donde la densidad de depredadores generalistas suele ser mayor (ej.: por atracción por residuos humanos) (Bino et al. 2010; Contesse et al. 2004; Fedriani et al. 2001). Por último, no se dispone de información precisa sobre el impacto de la caza ilegal o accidental en las poblaciones de aves esteparias.

5. Las gangas (*Pteroclidae*) como modelo de estudio: distribución, ecología básica y estado de conservación

Las gangas (familia *Pteroclidae*) son un grupo de aves del Viejo Mundo (Europa, Asia y África) que se encuentran en terrenos abiertos y climas áridos o semiáridos (Del Hoyo et al. 1997; Johnsgard et al. 1991). Su principal fuente de alimentación son las semillas que encuentran en el suelo, lo que ha condicionado algunas de sus principales características morfológicas, como son el reducido tamaño de su pico, cuello y patas, o la coloración del plumaje sumamente críptica (Del Hoyo et al. 1997). El granivorismo y los medios áridos en los que viven también han condicionado alguna de sus características comportamentales más llamativas, como son el elevado gregarismo que presentan y las visitas regulares a bebederos. Se trata por tanto de un grupo de características anatómicas complejas, pero con un patrón morfológico muy homogéneo, que ha sido adscrito a diversos órdenes como son los Galliformes, Columbiformes, Charadriiformes y Ciconiformes, pero que actualmente constituyen un orden independiente.

5.1 Distribución y abundancia

La familia *Pteroclidae* se considera integrada por dos géneros (*Pterocles* y *Syrrhaptes*) y un total de dieciséis especies (Tabla 2), de las cuales dos se encuentran en territorio español: la ganga ibérica (*Pterocles alchata,* Linnaeus 1766) y la ganga ortega (*P. orientalis,* Linnaeus 1758). Ambas especies presentan una distribución mundial claramente discontinua, con dos núcleos poblacionales muy alejados entre sí. El primero ocuparía la región más occidental de su área de distribución e incluiría a grandes rasgos la península ibérica y el Magreb. El segundo núcleo se encuentra en Oriente Medio y Asia central (principalmente Turquía, Irán, Pakistán, Afganistán, Kazajstán, Uzbekistán y Turkmenistán) (Del Hoyo et al. 1997).

Tabla 2. Especies actuales de gangas y su distribución mundial

Nombre vernacular	**Nombre científico**	**Distribución**
Ganga tibetana	*Syrrhaptes tibetanus*	Asia central (Tíbet)
Ganga de Pallas	*Syrrhaptes paradoxus*	Asia central
Ganga ibérica	*Pterocles alchata*	SO Asia, SO Europa, N África
Ganga namaqua	*Pterocles namaqua*	S África
Ganga moruna	*Pterocles exustus*	S y SO Asia, N y E África
Ganga moteada	*Pterocles senegallus*	S y SO Asia, N África
Ganga ortega	*Pterocles orientalis*	Asia, SO Europa, N África
Ganga gorgigualda	*Pterocles gutturalis*	E y S Africa
Ganga coronada	*Pterocles coronatus*	SO Asia, N África
Ganga decorada	*Pterocles decoratus*	E África
Ganga malgache	*Pterocles personatus*	Madagascar
Ganga de Lichtenstein	*Pterocles lichtensteinii*	SO Asia, N África
Ganga bicinta	*Pterocles bicintus*	S África
Ganga cuadricinta	*Pterocles quadricinctus*	N y E África
Ganga india	*Pterocles indicus*	S Asia (India)
Ganga goteada	*Pterocles burchelli*	S África

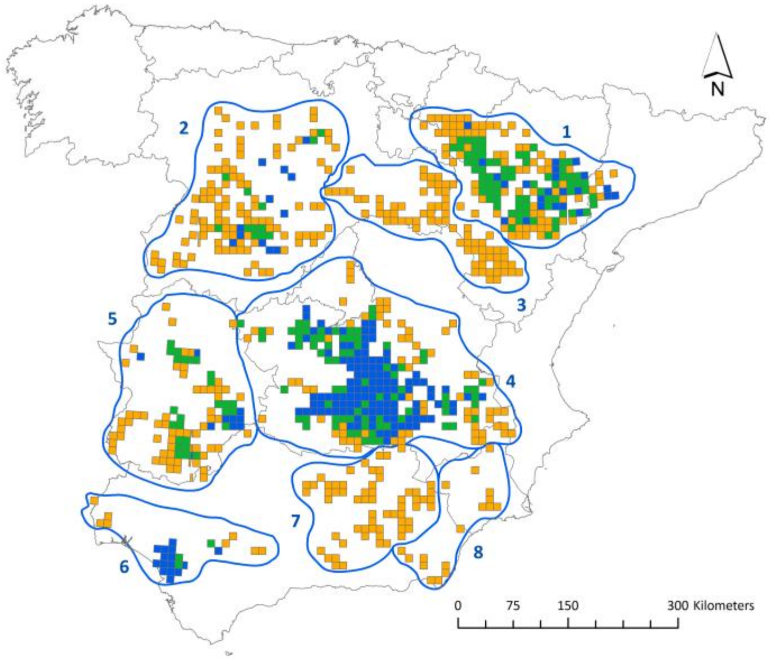
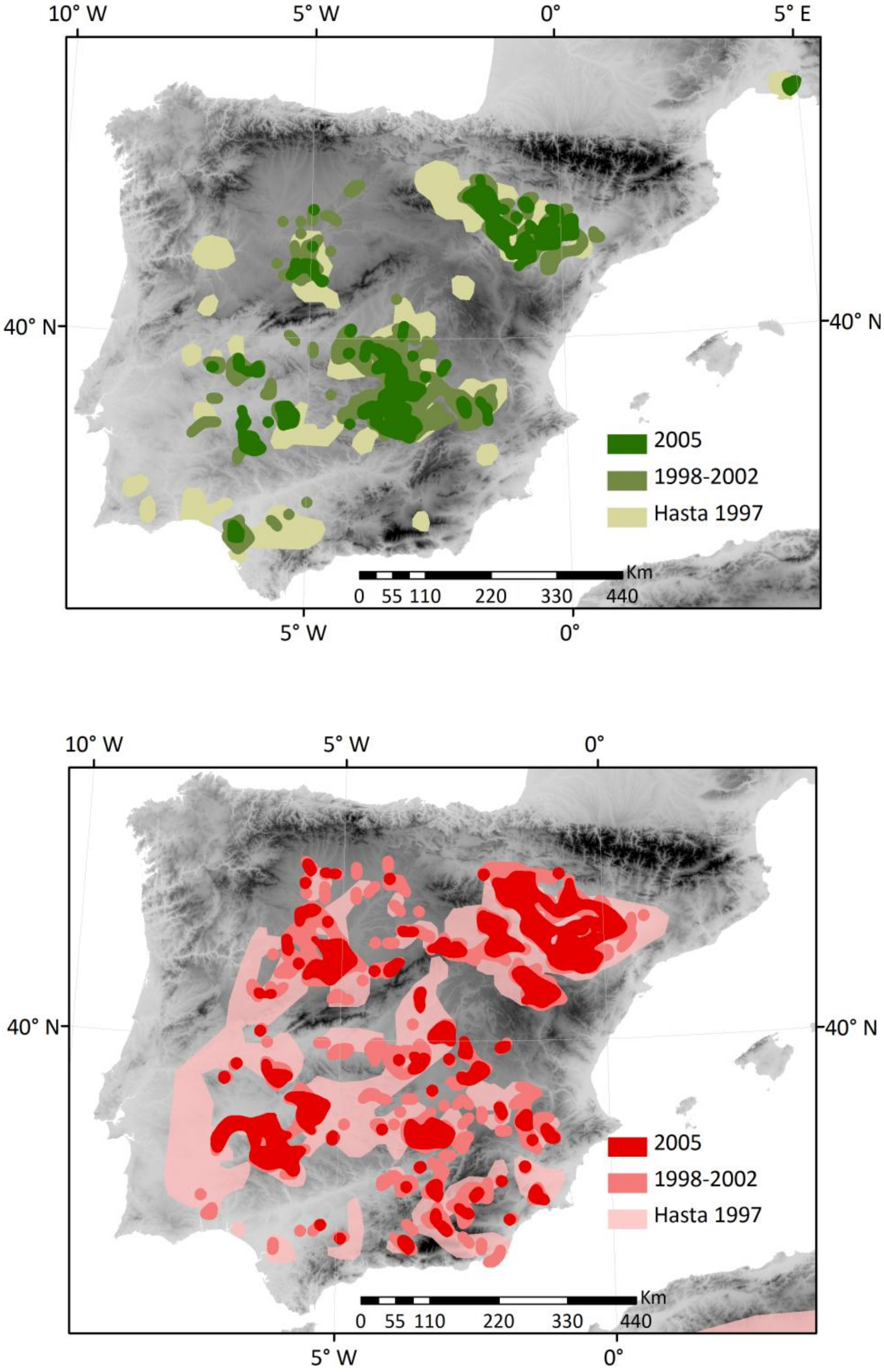


Figura 4. Distribución de Pteróclidos en la península ibérica. Azul: ganga ibérica, naranja: ganga ortega, verde: ambas especies presentes en simpatría. Las principales regiones geográficas son:(1) valle del Ebro, (2) meseta norte, (3) páramos del Sistema Ibérico, (4) meseta sur, (5) Extremadura, (6) valle del Guadalquivir, (7) penillanuras subbéticas and (8) SE semiárido. Adaptado de Suárez et al. (2006).

Las dos especies son simpátricas en gran parte de su rango de distribución, tanto a nivel mundial como a nivel peninsular (Figura 4), y comparten hasta cierto punto sus nichos climáticos, tróficos y de hábitat (Herranz and Suárez 1999). Dentro del ámbito europeo (sin considerar Turquía) la ganga ibérica se localiza exclusivamente en la península ibérica y el sureste de Francia, mientras que la ganga ortega se encuentra sólo en España (incluidas las Islas Canarias) y recientemente ha desaparecido de Portugal (Figura 5).

La ganga ortega está más ampliamente distribuida en la península ibérica pero es más escasa (9000-11000 individuos) que la ganga ibérica (c. 14000), especie que tiende a concentrarse en determinadas áreas (Suárez et al. 1997a) (Figura 4). Estos datos fueron actualizados en el censo nacional más reciente hasta la fecha (Suárez et al. 2006), obteniéndose unas estimas menores para la ganga ibérica (8.500-11.500 individuos), y similares para la de ganga ortega en 7.700-13.000 individuos. Estas estimas reflejan tanto una mayor precisión del censo, como la preocupante tendencia regresiva de las últimas décadas, confirmada en poblaciones locales (Suárez et al. 2006). Las tendencias regresivas de la ganga ibérica han sido especialmente notables en las provincias más septentrionales de la meseta norte (Burgos, Palencia y Zamora), de Ávila, y de los extremos oriental y occidental del valle del Ebro (La Rioja, Navarra y Lérida), del valle del Guadalquivir, a excepción de Doñana, y de un núcleo históricamente importante, Extremadura. En cuanto a la ganga ortega, las tendencias regresivas han sido registradas en las mismas zonas que la ganga ibérica, a las que hay que añadir los páramos del Sistema Ibérico (Suárez et al. 2006) (Figura 4,5).

a)



b)

Figura 5. Distribución de la (a) ganga ibérica y (b) ganga ortega en España hasta 1997 (Del Hoyo *et al*. 1997), en 1998-2002 (Martí y Del Moral) y en 2005 (Suárez et al. 2006)

5.2 Estado de conservación

Aunque ambas especies no están amenazadas a nivel mundial, en Europa tienen un estado de conservación desfavorable (BirdLife-International 2004) y están incluidas en el Anexo I de la Directiva Aves (2009/147/CE, referente a la Conservación de las Aves Silvestres en la Unión Europea), y en el Anexo III del Convenio de Berna, relativo a la Conservación de la Vida Silvestre y el Medio Natural en Europa. España alberga el 90% y 25% de las poblaciones Europeas de ganga ibérica y ganga ortega, respectivamente (BirdLife-International 2004; Suárez et al. 2006), y ambas especies se encuentran amenazadas a nivel estatal. Actualmente están catalogadas como "Vulnerables" en el Libro Rojo de la Aves de España (Suárez and Herranz 2004a; Suárez and Herranz 2004b), y "Vulnerables" en el Catálogo Nacional de Especies Amenazadas (RD 139/2011).

5.3 Aspectos básicos de la ecología de las especies de estudio

Tanto la ganga ibérica como la ganga ortega, son especies altamente **gregarias,** aunque en la primera este comportamiento es mucho más notable que en la segunda (De Borbón et al. 1999a; Martín et al. 2010a). El vivir en bandos puede suponer una serie de beneficios como son mejorar la seguridad ante depredadores, compartir el esfuerzo de vigilancia y disminuir, por tanto, el riesgo de depredación (Bertram 1980; Elgar 1989). También se ha sugerido que el gregarismo puede estar asociado con una distribución irregular de las fuentes de alimento (Perrins and Birkhead 1983), y que puede servir a los individuos para obtener información sobre la localización de los lugares de alimentación y los bebederos (Ward and Zahavi 1973). Los mayores tamaños de bando se dan en la época invernal (con máximos de varias centenas de individuos en la ganga ibérica, y de varias decenas en la ganga ortega), y son mínimos durante la estación reproductiva (De Borbón et al. 1999a).

El uso y la selección de hábitat a gran escala que exhiben estas especies ha sido un tema tratado por Herranz y Suárez (1999), Suárez et al. (2006) y Wolff (2005), aunque estos autores reconocen que aún quedan importantes lagunas de conocimiento en este elemento clave para la gestión de conservación, tanto a escala del rango de su distribución peninsular, como en particular en cuanto a los patrones de selección a menor escala en paisajes agrarios, que constituyen el hábitat más común de estas especies (incluyendo la escala de microhábitat en medios aparentemente homogéneos, como suelen ser las parcelas agrícolas). A grandes rasgos, ambas especies se encuentran en zonas llanas u onduladas, desarboladas y fundamentalmente dedicadas a la agricultura extensiva de cereal de secano (Herranz and

Suárez 1999). Para la ganga ortega, los barbechos de larga duración, eriales y pastizales parecen ser esenciales durante el invierno y la estación reproductora. La ganga ibérica selecciona positivamente los pastizales y los barbechos anuales durante la reproducción, y en el invierno, además, utiliza algunos cultivos de leguminosas (Herranz and Suárez 1999; Martín et al. 2010b). Sin embargo, hasta el momento apenas se han detectado diferencias en los patrones de selección de hábitat entre ambas especies, lo que plantea la interesante cuestión de cómo es posible la coexistencia espacial de dos especies tan similares sin que haya una clara partición de nicho ecológico, al menos en lo que se refiere a selección de hábitat.

En cuanto a **los movimientos estacionales** que llevan a cabo estas especies, y pese a la importancia de los mismos para la dinámica de poblaciones de cualquier especie, hasta el momento permanecen prácticamente desconocidos (Suárez and Herranz 2004a; Suárez and Herranz 2004b; Suárez et al. 2006). Desde una perspectiva ecológica, la dispersión influye en la demografía y persistencia de las poblaciones, y también en la distribución y abundancia de las especies (Johnson and Gaines 1990). Desde una perspectiva evolutiva, la dispersión determina el nivel de flujo genético entre poblaciones, lo que afecta a procesos como la adaptación a ambientes locales y la especiación (Avise 1994). También hay que destacar el importante papel que el conocimiento de los procesos dispersivos juega a la hora de establecer medidas para la conservación de poblaciones de especies amenazadas (Meffe and Carroll 1994). Toda esta falta de información básica sobre la dispersión en estas especies crípticas se debe, en parte, a que apenas se han hecho esfuerzos en el sentido de intentar capturar ejemplares vivos y acometer estudios de marcaje y radioseguimiento necesarios para obtener información relevante en este tipo de especies (Kenward 2001).

5.4 Amenazas de conservación

Las principales amenazas para la conservación de la ganga ibérica y la ganga ortega son similares a las descritas para el conjunto de especies asociadas a medios agrarios (ver sección 4), e incluyen la reducción de la superficie de hábitat adecuado por cambios de uso, la disminución de la calidad del hábitat por intensificación de los cultivos, la contaminación de los bebederos y la elevada depredación de nidos por depredadores generalistas (Herranz and Suárez 1999).

6. Lagunas de conocimiento

A pesar de que el 83% de las especies asociadas a medios agrarios están amenazadas, el conocimiento científico sobre la ecología de la mayoría de estas especies, y sobre el impacto de la actividad antrópica en sus poblaciones es aún escaso en comparación con el que se tiene de aves asociadas a otros medios (forestales, por ejemplo). Esta falta general de conocimiento motivó, en parte, el comienzo de esta Tesis Doctoral. Decidimos utilizar dos especies emblemáticas de medios agrarios pero que habían recibido escasa atención por parte de la comunidad científica: la ganga ibérica (*Pterocles alchata*) y la ganga ortega (*Pterocles orientalis*). Ambas son propias de paisajes desérticos o semidesérticos con vegetación baja y abierta que, secundariamente, han ocupado los medios cultivados, particularmente, la estepa cerealista (Cramp et al. 1985). Así, nos encontramos con un caso paradigmático de especies cuya historia evolutiva está desacoplada de los medios que habitan en la actualidad y que tienen, por tanto, que persistir en medios muy humanizados, de baja productividad, donde los cambios de usos del suelo son frecuentes como consecuencia de políticas agrarias y del desarrollo humano (infraestructuras y urbanización) y donde frecuentemente tienen que coexistir con la gestión agraria y cinegética de estos medios. Debido a la escasez de conocimientos básicos sobre la ecología de ambas especies y sobre los impactos de las actividades humanas en ellas, nos planteamos abordar estas cuestiones mediante una aproximación multiescalar que permitiera contribuir a entender la distribución, abundancia, repartición espacial, selección de hábitat diferencial y dinámica poblacional de estas especies, incluyendo el desarrollo de una metodología de captura y marcaje seguros para estas especies (inexistentes hasta la fecha) que nos permitiera incrementar la cantidad de datos biológicos sobre ambas. Nuestro objetivo final ha sido identificar problemas de conservación propios de aves de medios agrarios y desarrollar medidas de gestión adecuadas para aunar la conservación de la biodiversidad agraria con actividades humanas características de paisajes altamente antropizados (agrosistemas donde confluyen prácticas agrarias, actividad cinegética, actividad lúdica,…).

Estructura de la Tesis y Objetivos

Esta Tesis se divide en dos grandes bloques: 1) estudio comparativo multiescalar de los factores que determinan a la distribución, nicho ecológico y selección de hábitat de ambas especies, con especial atención a la influencia de los factores antrópicos que predominan en ambientes agrarios; 2) desarrollo de una nueva metodología de captura y marcaje para estas especies, evaluación del efecto de la captura en estas especies y estimas de supervivencia dentro de un contexto de la historia de vida. El segundo bloque está desarrollado principalmente sobre la ganga ibérica, mientras que la información sobre la ganga ortega es más escasa (debido a su escasa presencia y baja densidad en la zona de estudio principal, ver capítulos 2 y 3). En última instancia, toda la información obtenida en los capítulos de esta Tesis es combinada para **mejorar el entendimiento sobre los factores, y en particular la importancia de aquellos relacionados con la actividad humana, que determinan la distribución, selección de hábitat y demografía poblacional de los Pteróclidos ibéricos, para identificar posibles causas de su regresión y discutir implicaciones para su conservación**. Por tanto, esta Tesis tiene componentes tanto de investigación básica sobre ecología de especies, como de investigación aplicada, mediante el uso de herramientas de análisis espacial, modelos de distribución de especies, desarrollo de técnicas y modelado de supervivencia, todo ello con el objetivo último de entender y mejorar la gestión de poblaciones de aves asociadas a medios humanizados, y con un claro enfoque hacia su conservación.

Se enumeran a continuación los objetivos específicos planteados en la presente Tesis:

1. Identificar los factores (abióticos, antrópicos y geográficos) que determinan la distribución de la ganga ibérica y la ganga ortega en España, estimar la importancia relativa de los mismos y generar mapas de idoneidad para ambas especies, identificando zonas fuente y sumidero.

2. Describir y cuantificar las variaciones en el nicho ecológico (incluyendo la dimensión humana) y en la densidad de la ganga ibérica y la ganga ortega en regiones alopátricas y simpátricas para entender los mecanismos que permiten su coexistencia.

3. Analizar la influencia de las características del paisaje, los usos del suelo y el microhábitat en la distribución de la ganga ibérica y la ganga ortega a escala local, usando una aproximación multiescalar e integradora que permita identificar similitudes y diferencias en las preferencias de hábitat.

4. Poner a punto un método seguro y no dañino de captura selectiva para especies altamente sensibles y difíciles de localizar (crípticas) que permita la obtención de datos biológicos (morfología, fisiología, comportamiento, muestras para análisis genéticos o análisis bioquímicos….), así como evaluar los efectos a corto plazo para los individuos asociados con la aplicación de dicho método.

5. Proporcionar las primeras estimas de supervivencia y causas de mortalidad en ambas especies de estudio, explorar las variaciones estacionales y geográficas de dichas estimas y evaluar la influencia de características individuales y estrategias de historia de vida en la supervivencia.

Estos objetivos quedan abordados en los próximos capítulos según se detalla a continuación.

En primer lugar (**capítulo 1**) hemos recopilado la información más reciente hasta la fecha sobre la distribución de ambas especies (Censo Nacional de 2005) para actualizar la información del Atlas de las Aves Reproductoras de España (Martí and Moral 2003) y poder determinar (a) la distribución actual de ambas especies, (b) los factores espaciales, abióticos y antrópicos que determinan esta distribución, (c) las variables antrópicas (y por tanto modificables por manejo) que influyen de manera más determinante en la distribución de las dos especies, (d) las áreas donde los esfuerzos de conservación deberían ser prioritarios. Este capítulo trata de discernir si la regresión poblacional de ambas especies tiene lugar sólo en núcleos marginales (poblaciones periféricas) o también en áreas a priori más importantes históricamente. También resalta el papel clave de la PAC, que es el principal motor de la gestión agraria en Europa, tanto en la actual distribución de las dos especies como en los futuros cambios que los usos del suelo derivados de su implementación tengan sobre ambas especies y sobre otras especies asociadas a medios agrarios. Este capítulo, además, nos permitió visualizar diferencias regionales en la distribución de ambas especies, existiendo áreas de clara simpatría y otras totalmente alopátricas. Estas diferencias fueron exploradas en el siguiente capítulo (**capítulo 2**), que ilustra cómo los nichos ecológicos de ambas especies son modulados en situaciones alopátricas (aproximación al nicho fundamental) y simpátricas (aproximación al nicho realizado), y los mecanismos que determinan la expresión del nicho ecológico y sus consecuencias a nivel de distribución espacial (*niche-position vs. niche-breadth hypothesis*, en español: hipótesis de posición de nicho vs hipótesis de amplitud de nicho). Además, como novedad en estudios de este tipo, incorporamos la dimensión humana como parte del nicho realizado, dimensión que entendemos vital para una comprensión adecuada de la distribución de especies asociadas a medios humanizados.

En el **capítulo 3** aumentamos la resolución y bajamos la escala de estudio, para centrarnos en el estudio de las poblaciones locales de un agrosistema estepario manchego, en el que establecemos una selección de hábitat jerárquica a tres niveles (paisaje, usos del suelo y microhábitat), y determinamos las preferencias de hábitat y la influencia de las perturbaciones humanas para ambas especies, y la selección de microhábitat durante el periodo reproductor, dentro de un contexto ecológico de compromiso entre riesgo y beneficio (alimentación y nidificación *vs.* camuflaje y estrategia anti-depredatoria).

Incorporamos dos subcapítulos eminentemente metodológicos que tratan de enfatizar la importancia de desarrollar un método adecuado de captura y marcaje de especies amenazadas (**capítulo 4a**), y la necesidad de evaluar los posibles efectos negativos que ese método puede tener en la especie objeto de estudio (**4b**), de manera que los beneficios obtenidos del procedimiento de captura, marcaje y seguimiento en cuanto a la alta cantidad de parámetros biológicos obtenidos (fenología de la reproducción, éxito reproductivo, supervivencia, causas de mortalidad, dispersión, uso del espacio…) compensen holgadamente el riesgo al que se ve sometido el individuo capturado, sobre todo si se trata de especies amenazadas. Finalmente, en el **capítulo 5**, y gracias al desarrollo de las técnicas expuestas en los **capítulos 4a y 4b**, aportamos las primeras estimas de supervivencia adulta y juvenil en especies de Pteróclidos (específicamente, de la ganga ibérica), dentro del marco de las historias de vida. En este capítulo enfatizamos la ventaja adaptativa (en términos de mayor supervivencia) que supone uno de los mecanismos comportamentales más enigmáticos de las gangas como es el de los movimientos estacionales. Además, establecemos variaciones a nivel geográfico (entre poblaciones centrales y periféricas) y a nivel estacional en la supervivencia, y señalamos el posible efecto que una mortalidad mayor en hembras tiene en la razón de sexos y la estructura demográfica de las poblaciones. Por último, tratamos de establecer un vínculo entre la humanización del paisaje y las causas de mortalidad de la ganga ibérica (depredación y caza ilegal), y proponemos medidas de conservación al respecto. En este último capítulo no aparece la ganga ortega por razones logísticas (baja densidad en nuestras principales zonas de estudio).

Estos capítulos tienen formato estándar de artículo científico y están redactados en inglés. La Tesis se cierra con un capítulo en castellano de **síntesis y conclusiones**, en el que se resumen los resultados más significativos de esta Tesis.

A continuación se enumeran los artículos científicos que componen la presente Tesis Doctoral:

1. Benítez-López A, Viñuela J, Hervás I, Suárez F, García JT (2014) Modelling sandgrouse (*Pterocles* spp.) distributions and large-scale habitat requirements in Spain: implications for conservation. Environ. Conserv. 41: 132-143.
2. Benítez-López A, Viñuela J, Suárez F, Hervás I, García JT (2014) Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species. Oecologia 176: 193-206.
3. Benítez-López A, Viñuela J, Mougeot F, García JT. Integrating landscape, land use and microhabitat preferences of threatened sympatric steppe species for informing conservation needs.

4a Benítez-López A, Mougeot F, Martín C, Casas F, Calero-Riestra M, García JT, Viñuela J (2011). An improved night-lighting technique for the selective capture of sandgrouse and other steppe birds. Eur. J. Wildl. Res. 57: 389-393.

4b Casas, F, Benítez-López A, García JT, Martín CA, Viñuela J, Mougeot F (2014) Assessing the short-term effects of capture, handling and tagging of sandgrouse. Ibis (online). doi: 10.1111/ibi.12222

5. Benítez-López A, Casas F, Mougeot F, García JT, Martín C, Viñuela J. Individual traits and life history strategies influence survival: the case the threatened pin-tailed sandgrouse (*Pterocles alchata*). Biol. Conserv., en evaluación (enviado 23/10/2014).

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CAPÍTULO 1

Modelling sandgrouse (*Pterocles spp.*) distributions and large-scale habitat requirements in Spain: implications for conservation

Foto: Enrique Ruiz Ara (ruizarafoto.es)

Benítez-López A, Viñuela J, Hervás I, Suárez F, García JT (2014) Modelling sandgrouse (*Pterocles* spp.) distributions and large-scale habitat requirements in Spain: implications for conservation. Environ. Conserv. 41: 132-143.

Abstract

Knowledge of the factors determining species distributions is essential for developing conservation strategies. Sandgrouse *Pterocles alchata* and *P. orientalis* are threatened in Spain, the stronghold of European populations. Spatial modelling was used to: (1) assess the relative importance of abiotic, anthropogenic and geographical factors in the distribution of both sandgrouse species, (2) determine the most important anthropogenic predictors for each species occurrence and (3) identify areas where conservation efforts should be prioritized.

Abiotic and anthropogenic factors explained most of the variation in sandgrouse distributions. Both species were associated with arid flatlands, arable land cover being the most important anthropogenic variable determining their distribution. The Common Agricultural Policy (CAP) is the main driver of agricultural management in Europe, and may thus have a direct effect on sandgrouse distributions. *P. orientalis* exhibited broader habitat tolerance than *P. alchata;* the latter species tolerates warmer climates. Consequently, the network of core and marginally suitable areas identified for each species differs, and connectivity between the populations of these areas seems unlikely. Potential future changes in sandgrouse distribution will probably be directed principally by the synergistic effects of climate change and expected land use transformations resulting from the new CAP and ongoing population growth, urbanization and infrastructure development.

Keywords: Biogeography, *Pterocles alchata*, *Pterocles orientalis*, sandgrouse, species distribution models, steppe birds, threatened species, conservation, variation partitioning procedure

Introduction

Knowledge of species distributions patterns and identification of environmental factors influencing these patterns are crucial for managing biodiversity (Krebs 1978). Species distribution models (SDM) have been used to identify management priorities for threatened species (Norris 2004), prioritize areas for biodiversity conservation (Araújo et al*.* 2004), evaluate the potential spread of invasive species (Thuiller et al*.* 2005), and forecast the potential impact of climate change on species distribution patterns (Bakkenes et al*.* 2002). However, species distribution patterns are often the result of interacting factors whose effects are difficult to disentangle. The recent development of analytical methods such as variation partitioning and hierarchical partitioning analyses have proved useful to identify the pure and combined effects of the factors considered (Borcard et al*.* 1992; Hortal et al*.* 2008). Furthermore, SDM's enable construction of habitat suitability maps that, when compared with actual distributions, facilitate the identification of areas with favourable conditions for the species that are currently unoccupied, thus providing clues about possible causes of recent regression, as well as identifying a number of areas where conservation problems should be further investigated (Seoane et al*.* 2003).

Farmland and steppe species are at present the most threatened bird group in Europe, with 83% of species having unfavourable status (Burfield 2005). Among steppe birds, the pin-tailed sandgrouse (*Pterocles alchata*, Linnaeus 1766) and the black-bellied sandgrouse (*Pterocles orientalis*¸ Linnaeus 1758) are two species of conservation priority at European level (conservation category SPEC3) (Madroño et al. 2004). Both species are ground-nesting birds of Palearctic distribution associated with open arid habitats, natural steppes and agricultural 'pseudo-steppes' (see definition in Suárez et al*.* 1997). Both sandgrouse are considered 'vulnerable' in Spain, the stronghold of the European population (Madroño et al. 2004); although the proportion of the total European population of the black-bellied sandgrouse that is Spanish (*c*. 25%) is smaller than that of its counterpart (Madroño et al. 2004; BirdLife International 2011a, b).

Albeit this unfavourable status, little is known about the biology of either sandgrouse species, or the possible threats that they face. Their decline is most likely related to changes in land use and landscape structure as a result of agricultural intensification, the expansion of olive groves and irrigated areas, infrastructure development and urbanization (Madroño et al. 2004; Santos and Suárez 2005). It is important to identify which of these factors are primarily affecting the progressively shrinking distribution of Spanish sandgrouse in order to safeguard their conservation.

To date, sandgrouse distribution and habitat requirements have been studied only at local scales (Suárez et al. 1997; Martínez et al. 1998; Martín et al. 2010*a*, *b*; Seoane et al. 2010). However, the distribution of a species is not only determined by local habitat characteristics, but rather by natural and human-induced environmental factors operating at larger scales through history (Ricklefs 1987). Consequently, broad-scale distribution models may help to unravel the factors that affect sandgrouse populations on a larger scale, which in turn can be applied in large-scale conservation programmes to attain more efficient results. Both sandgrouse species are very similar in their ecological requirements, partially sharing their climatic, topographic, trophic and breeding habitat requirements (Herranz and Suárez 1999). They often occur sympatrically and a great part of their distribution areas overlap (Fig. 1), yet there are also broad areas where only one of the two species is found (Herranz and Suárez 1999).

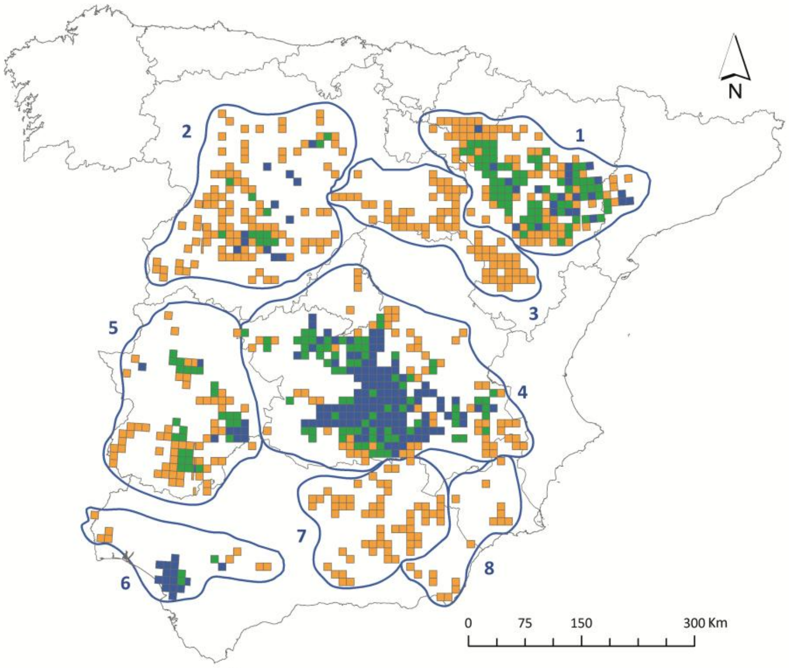


Figure 1. Sandgrouse distribution during the breeding period. *Pterocles alchata* is present in blue squares, *Pterocles orientalis* is present in orange squares, and both species are present in green squares. The main geographical regions are: (1) Ebro Valley, (2) Northern Plateau, (3) Iberian *Páramos*, (4) Southern Plateau, (5) Extremadura, (6) Western Andalusia, (7) Eastern Andalusia and (8) Arid south-east. Adapted from Suárez et al. (2006).

No study has evidently attempted to determine which environmental conditions characterize both areas of overlap and areas where they occur singly at a biogeographical scale, information that could contribute to implementation of coordinated management programmes for both species.

The main objectives of this study were to: (1) identify the factors shaping the current distribution in Spain of the pin-tailed sandgrouse and the black-bellied sandgrouse; (2) estimate the relative importance of climate and topography (abiotic factors), land use, landscape and human pressure (anthropogenic factors) and geographic location (geographical factors) in the occurrence of both species in Spain; (3) determine the independent contribution of each anthropogenic variable to occurrence; and (4) generate habitat suitability maps for both species. These maps, when compared with the current distribution, would serve to identify the areas most suitable for conservation efforts and to pinpoint unsuitable areas that are currently occupied.

Methods

Study area

Mainland Spain is probably the most biogeographically complex country in Europe due to its geology, topography, climate and location between the Eurosiberian and the Mediterranean regions (Font 2000). Environmental conditions vary from the Central Plateau, with a marked contrast between temperate summers and harsh winters, to the Mediterranean lowlands, with hot summers but temperate and rainy winters, and the more humid and colder Eurosiberian northern strip. Vegetation types vary accordingly, including deciduous and coniferous forests, evergreen woodland, tall and dwarf shrublands, and perennial and annual grasslands. Croplands, mainly located on flatlands, also occupy almost 70% of peninsular Spain (Martí and Moral 2004).

Species distribution data

To analyse the current distribution of sandgrouse, we used the best available data, which are the National Breeding Sandgrouse Survey (NBSS), coordinated by the Sociedad Española de Ornitología SEO/BirdLife (Suárez et al. 2006). The census was designed to cover all the 100 km^2 squares where sandgrouse were detected in the Spanish Atlas of Breeding Birds (SABB) (Martí and Moral 2004), while adding additional squares where anecdotal sightings had been recorded in the period between the SAAB and the NBSS. We gathered all georeferenced observations of sandgrouse recorded during the NBSS and overlaid them on the 10 × 10 km grid of Spain. Every 10 × 10 km square containing at least one sandgrouse record (a record could consist of 1–41 individuals) was categorized as a ‘presence’ square. We are confident that the 10 × 10 km resolution is adequate (Dunning et al. 1995) for studying sandgrouse distribution given the home ranges of *c*. 40 km^2 for pin-tailed sandgrouse (Benítez-López et al. 2010*b*) and *c*. 120 km^2 for black-bellied sandgrouse (A. Benítez-López, F. Casas, F. Mougeot, C.A. Martín, J.T. García and J. Viñuela, unpublished data 2007-2013). A smaller scale (for example 1 km^2) would have artificially increased absences.

We compiled both data sources, updating the SAAB information with the NBSS data. Our final dataset consisted of 5312 10 × 10 km squares with presence/absence data for both species (665 squares corresponded to the NBSS data). This information was used to define the main geographical regions where sandgrouse population nuclei were located, which were separated according to topographic and climatic characteristics (Herranz and Suárez 1999; Suárez et al. 2006).

Predictor variables

We modelled the distributions of both species in Spain in relation to large-scale environmental conditions, mainly topographic, climatic, land use, spatial and anthropogenic variables (Table 1). Environmental layers were processed with ArcMap 9.3 (ESRI 1999–2005, http://www.esri.com). Topographic and climatic variables were obtained from source maps at 200 m resolution by calculating the mean value of 200 random points within each 10 × 10 km UTM square (Ninyerola et al. 2005). Land-use variables were obtained from a continuous vector layer that included all habitats present in mainland Spain (SIGPAC, MARM [Sistema de Información Geográfica de Parcelas Agrícolas, Ministerio de Agricultura, Alimentación y Medio Ambiente] 2006) and calculated as the percentage of the area occupied by each land-use category in each square. Additionally, we calculated an index of land-use diversity (DivIndex) using the Shannon function (see Shannon and Weaver 1949), the total number of different patches and the mean patch size per square. Human disturbance variables included human population density in 2006, population growth between 2000 and 2006, total road length and railway length in each square (Table 1) (INE [Instituto Nacional de Estadística] 2001, 2006; IGN [Instituto Geográfico Nacional], 2006).

Table 1. Variables used in the univariate analyses and to model the distribution of pin-tailed sandgrouse and black-bellied sandgrouse. *Variables were not included in the final models to reduce multicollinearity among predictors (see text). Sources: [1]Atlas Climático Digital de la península ibérica (Ninyerola et al. 2005). [2]Spanish Instituto Nacional de Estadística (http://www.ine.es). [3]SIGPAC (Sistema de Información Geográfica de Parcelas Agrícolas, MARM). [4]Spanish Instituto Geográfico Nacional (IGN).

Code	Description
Sp factor	
Spatial variables	
X	Longitude of the centroid of each 10 × 10 km UTM grid
Y	Latitude of the centroid of each 10 × 10 km UTM grid
XY	Latitude × Longitude
X2	Quadratic term of the x-coordinate
Y2	Quadratic term of the y-coordinate
TC factors	
Climatic variables(1)	
AET	Mean annual actual evapotranspiration (mm)*
PET	Mean annual potential evapotranspiration (mm)*
P	Mean annual precipitation (mm)
PSp	Mean precipitation in the spring (mm)*
T	Mean annual temperature (°C)
TJn	Mean temperature in January (°C)*
TJu	Mean temperature in July (°C)
Topographic variables(1)	
A	Mean altitude (m)
AR	Altitude range (maximum altitude – minimum altitude, m)*
S	Mean slope (%)
SR	Slope range (maximum slope – minimum slope, %)*
LULCH factors	
Land use (2)	
Wat	Per cent cover of water reservoirs and rivers
For	Per cent cover of forests
Mix	Per cent cover of mixed forest-shrublands
Shr	Per cent cover of shrublands
Pas	Per cent cover of pasturelands, pastures with some shrubs and meadows
Fru	Per cent cover of fruit groves
Cit	Per cent cover of citrus groves
Oli	Per cent cover of olive groves
Agr	Per cent cover of arable lands
Vin	Per cent cover of vineyards
Urb	Per cent cover of urban areas
Landscape characteristics(2)	
Div	Shannon diversity index
NPa	Total number of patches
Psi	Average patch size (km^2)*
Human disturbance	
Dens06	Population density in 2006 (inhabitants km^{-2})[3]
PGro	(Population density in 2006 – population density in 2000)/population density in 2000 × 100(3)
Road	Total road length per UTM cell (km)[4]
Rail	Total length of railways per UTM cell (km)[4]

We accounted for spatial autocorrelation in our models by including a spatial term of the form $b1x + b2y + b3x^2 + b4xy + b5y^2$ (Legendre 1993). The inclusion of spatial variables in a model can reveal a geographical trend in distribution that does not reflect the spatial structure of the environmental predictor variables (Borcard et al. 1992), and thus could be attributed to historical events or to contagious biotic processes such as migration (Legendre 1993).

Statistical analyses

We characterized squares where species were present and absent by comparing the mean values of the explanatory variables between (1) unoccupied squares, (2) squares occupied by *P. orientalis*, (3) squares occupied by *P. alchata*, and (4) squares occupied by both species (ANOVA). Pairwise comparisons were assessed with Bonferroni post-hoc tests (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC). These exploratory analyses gave us an indication of which predictors could be important at explaining *P. alchata* and *P. orientalis* distributions, and served as a starting point for building multivariate models for each species.

We used generalized linear models (GLMs) (McCullagh and Nelder 1989) with a binomial distribution and logit link to relate the probability of occurrence of each sandgrouse species in each square to environmental variables. We grouped our variables according to three explanatory factors: (1) topography and climate (TC factor), (2) land use, landscape and human disturbance (LULCH factor), and (3) spatial variables (Sp factor); we fitted several logistic models within each factor (Table 1). This procedure enabled us to assess the relative importance of abiotic factors (TC) and spatial structuring of the populations (due to contagious biotic processes and historical evolutionary processes; Sp), compared to anthropogenic variables (LULCH) which can be managed for conservation purposes. All explanatory variables were standardized in order to facilitate the interpretation and comparison of the estimated coefficients in our models. Prior to model building, we avoided multicollinearity among variables within each factor by removing strongly intercorrelated variables (Spearman's coefficient > 0.8) (Legendre 1993; Zuur et al. 2007) and retained those that explained more deviance in univariate logistic models. Models were built starting with the variable that best fitted the data and subsequently adding the rest of the variables. All candidate models were ranked using the corrected Akaike Information Criterion (AIC_c), the Akaike weight and the model fit (percentage of explained deviance) (Burnham and Anderson 2002). We calculated variance inflation factors (VIFs) for each model (package 'car'; Fox and Weisberg 2011; R Development Core Team 2012) and removed the explanatory variables with the highest VIF and those that contributed the least to parsimony (i.e. produced an increase in AIC_c) until all remaining variables had a VIF < 5 (Quinn and Keough 2002; Zuur et al*.* 2007) (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC). The variables included in the best model within each factor were combined to produce a general model for each species (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC). This model was further fine-tuned by removing the variables that explained the least (using a likelihood ratio test) one by one, until we obtained the most parsimonious model (with the lowest AIC_c, highest Akaike weight, highest explained deviance, with VIF < 5 and a lower number of predictors)(Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC).

A 10-fold cross-validation was applied to test the model accuracy. We evaluated the discrimination ability of the final and cross-validated models by estimating the sensitivity, specificity, correct classification rate and Cohen's kappa (Cohen 1960) (package PresenceAbsence; Freeman 2007; R Development Core Team 2012). The classification thresholds were established by maximizing the sum of sensitivity and specificity (0.07 for *P. alchata* and 0.11 for *P. orientalis*) (Liu et al*.* 2005). We also calculated the area under the receiver characteristic curve (ROC, AUC), which is a threshold-independent measure (Fielding and Bell 1997).

Variation partitioning and hierarchical partitioning procedures

Although we tried to maintain multicollinearity below acceptable levels (VIF < 5), we found interactions between TC, LULCH and Sp factors that may result in an overlaid effect in space due to collinearity between them (Borcard et al*.* 1992; Legendre 1993). Therefore, we used variation partitioning procedures to assess both the individual and overlapping contributions of the three factors (Borcard et al*.* 1992; Legendre 1993). Variation partitioning procedures were applied to the final model outputs (the habitat suitability index [HSI]), to account for the variation explained independently by each factor (individual effects) or by two or three factors simultaneously (combined effects), using partial regressions (full description in Hortal et al*.* 2008).

We performed a hierarchical partitioning analysis (package ‘hier.part’; Walsh and Mac Nally 2008; R Development Core Team 2012) including only those variables retained in our general models that could be changed by management policies (LULCH factor). This allowed calculation, for all possible candidate regression models, of the independent and joint contributions of each variable to the total explanatory power of the model (Mac Nally 2002).

The size of the individual effects of each variable (percentage of independent effects) was used as a criterion for ranking and deriving conservation priorities.

Habitat suitability maps and network of suitable areas

We used the most parsimonious models for each species to obtain predicted probability values of occurrence for each square. These probabilities can be considered as a HSI, with high HSI values indicating highly suitable squares. HSI values under the classification thresholds corresponded to unsuitable squares (USS; HSI < 0.07 for *P. alchata* and HSI < 0.11 for *P. orientalis*). Additionally, we divided the whole set of favourable squares for *P. alchata* and *P. orientalis* into three categories. The top 20% of squares with the highest HSI values represented highly suitable squares (HSS), the bottom 20% of the squares with the lowest HSI values were the least suitable squares (LSS), and the rest fell within the intermediate suitability category (ISS). We assessed the percentage of HSS, LSS, ISS and USS currently occupied by sandgrouse in Spain. Also, for each species, we identified highly suitable areas within each geographical region where there were at least two adjacent HSS occupied by sandgrouse, namely a population within a metapopulation in a biogeographical context (Driscoll 2007). Continuous patches of HSS were considered core suitable areas, whereas patches consisting of < 5 HSS or isolated from other suitable areas (distance > maximum movement distances = *c*. 45 km; Casas et al*.* 2012) were considered marginally suitable areas. Unoccupied HSS were also pinpointed to identify areas where sandgrouse populations could potentially become established, or where sandgrouse recently became extinct due to factors not considered by our models or operating at a finer scale. In turn, occupied unsuitable squares were also highlighted since, within a metapopulation framework, they could indicate areas where sandgrouse populations could not be sustained in the long term without the arrival of new individuals; for simplicity we denote these areas as 'sink' areas, although no productivity data are available.

Results

Models combining variables from different factors were more parsimonious than any of the models including variables belonging to a single factor (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC). Three of the candidate models for *P.alchata* had similar weight of evidence, but given the low explanatory power of the variables Cit and Rail, we kept the simplest model to explain and predict sandgrouse distribution (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC). According to the final models, during the breeding period both species are located in flatlands characterized by low annual rainfall, a high cover of arable lands, shrublands and pastures, low land-use diversity and low overall landscape heterogeneity (Table 2).

Table 2. Final models obtained for the probability of occurrence of pin-tailed sandgrouse and black-bellied sandgrouse in peninsular Spain. See Table 1 for explanation of variables. * = <0.05, ** = <0.01, *** = <0.001.

		Pterocles alchata		***Pterocles orientalis***	
Factor	**Variable**	**Estimate**	**VIF**	**Estimate**	**VIF**
	Intercept	-8.11***		-4.47***	
Sp	X	0.50***	2.39	-0.14ns	2.29
	Y				
	X2	-1.31***	3.00	-0.16ns	1.98
	Y2	-0.80***	1.74	-0.29**	1.95
	XY	1.81***	3.39	0.76***	2.34
TC	P	-4.71***	2.13	-3.17***	2.02
	T			-0.32**	2.43
	TJul	1.37***	1.58		
	S	-3.58***	1.73	-0.87***	2.37
LULCH	Wat				
	For			-0.41**	1.61
	Mix				
	Shr	0.71***	2.45	0.51***	2.68
	Pas	0.67***	1.47	0.39***	1.76
	Fru	0.17ns	1.58	0.16*	1.69
	Cit			-2.42*	1.14
	Oli			0.32***	3.22
	Agr	0.55***	3.01	0.53***	3.84
	Vin	0.27***	1.94		
	Urb				
	Div	-0.41***	1.31	-0.20**	1.94
	NPa	-0.49**	1.45	-0.28**	1.66
	PaS				
	Dens06	-1.03*	1.25	-0.82*	1.17
	PopGr	-0.15ns	1.34		
	Road			-0.21**	1.18
	Rail				

Fruit groves were positively but less strongly related to the occurrence of both species. Mean temperature in July was positively related to the probability of occurrence of *P. alchata* but not that of *P. orientalis*. *P. orientalis* avoids areas with a high road density, and both species avoid highly populated areas, particularly those where human population has increased the most in the past five years in the case of *P. alchata.* The main differences between the models of each species regarding land-use variables were the positive effect of vineyards on *P. alchata* and the negative effect of forests on *P. orientalis*. Citrus fruit and olive groves also entered the model for *P. orientalis*, but their relative importance was almost negligible (see results of hierarchical partitioning of the variance). Several spatial variables entered the models of both species indicating that their distribution seems to be spatially structured at our study scale. Thus, the probability of occurrence of both sandgrouse species declines southwards and northwards from the centre of their distribution in Spain, but increases from the south-east towards the north-east (Table 2). *P. alchata* is also more likely to be present towards the east, but avoids areas closer to the coastline.

The combined models for *P. alchata* and *P. orientalis* had good and acceptable model fits, respectively (explained deviance = 48.1% for *P. alchata* and 31.2% for *P. orientalis*). The accuracy of the cross-validated models and of the final combined models was high for both species, indicating a good predictive capacity (Table 3).

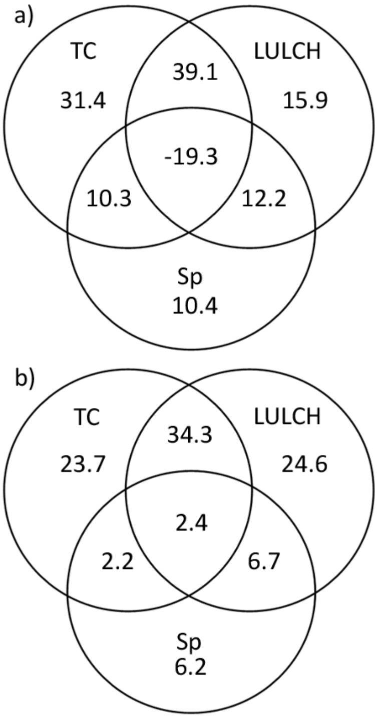
Table 3. Correct classification rate (CCR), sensitivity, specificity, Cohen´s Kappa coefficients and area under curve (AUC) values obtained by comparing the observed distribution with predicted values (HSI) for 10-fold cross-validated (CV) models (mean values and range in brackets) and final models.

Observed distribution	**Model**	**CCR**	**Sensitivity**	**Specificity**	**Kappa**	**AUC**
P .alchata	CV models	0.83 (0.76–0.91)	0.91 (0.86–0.96)	0.82 (0.73–0.91)	0.38 (0.28–0.45)	0.94 (0.90–0.96)
	Final	0.85	0.91	0.84	0.39	0.95
P. orientalis	CV models	0.73 (0.65–0.83)	0.89 (0.81–0.95)	0.71 (0.62–0.82)	0.34 (0.24–0.46)	0.86 (0.79–0.92)
	Final	0.73	0.90	0.71	0.33	0.88

The joint effect of TC (topography and climate) and LUCLH (land use, landscape and human disturbance) variables (39.1%) and the individual effect of TC (31.4%) together accounted for 70% of the total explained variation in the distribution of *P. alchata* (Fig. 2*a*). The individual effects of LULCH also accounted for a further 15.9% of the variation. In the case of *P. orientalis*, TC and LULCH factors jointly explained 34.3 % of the variation, and the individual effects of TC and LULCH factors were 23.7% and 24.6%, respectively (Fig.2*b*).

The spatial factor was more important at explaining the variation in the distribution of *P. alchata* (33% total, 10.4% of individual effects, and 10.3% and 12.2% of joint effects with TC and LULCH, respectively) than that of *P. orientalis* (15% total, 6.2% individual effects, and 2.2% and 6.7% of joint effects with TC and LULCH, respectively) (Fig.2*a*, *b*).

Figure 2. Variation partitioning of HSI into the independent effects of topographic and climatic factors (TC), land use, landscape and human factors (LULCH) and spatial factors (Sp), and their overlaps as percentages for (*a*) *Pterocles alchata* and (*b*) *Pterocles orientalis*. The percentages refer to the total explained deviance of each model.



The hierarchical partitioning analysis indicated that the most important anthropogenic variables explaining sandgrouse distribution were arable lands for both species (explaining independently 40% of the variation for *P. alchata* and 36.3 % for *P. orientalis*), forest cover for *P. orientalis* (27.1%) and vineyards for *P. alchata* (26.4%) (Fig. 3). Less important, but still relevant for both species, were variables related to the heterogeneity of the landscape (land-use diversity or the number of patches of different land uses), land uses with (semi) natural vegetation (pastures and shrublands), human-related variables (human density, road density and population growth) and arboreal crops for *P. orientalis* (Fig. 3).

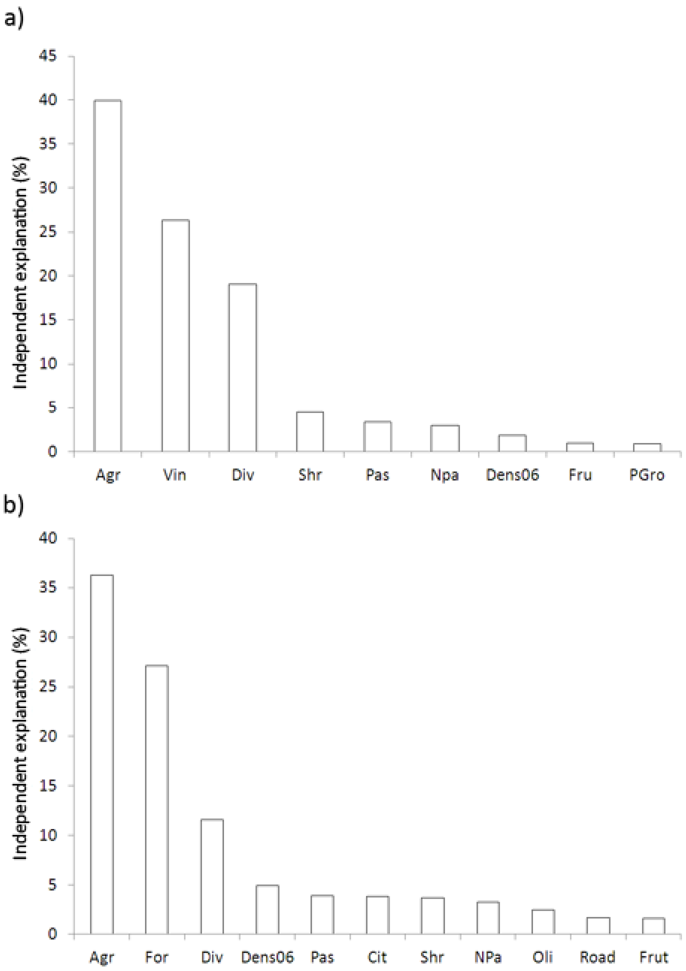


Figure 3. Conservation priorities for (*a*) *Pterocles alchata* and (*b*) *Pterocles orientalis* in peninsular Spain derived from hierarchical partitioning.

A larger number of suitable squares were identified for *P. orientalis* (*n* = 1980) than for *P. alchata* (*n* = 1122), of which 396 squares and 224 squares qualified as highly suitable, respectively (Fig. 4). Among these HSS, 55% were currently occupied by *P. orientalis*, whereas *P. alchata* occupied 71% (Fig. 5). We also identified 32 USS where *P. alchata* was present and 64 USS where *P. orientalis* was currently present.

Core suitable areas for *P. alchata* were identified in the Southern Plateau and the Ebro valley, with two marginally suitable areas in Western Andalusia and Extremadura (Fig. 5a). For *P. orientalis*, the core suitable areas were located in the Ebro valley, the Iberian *Páramos* (plateaux located at high altitude and with low temperature) and the Northern Plateau, with several marginal areas located over the Southern Plateau and Extremadura (Fig. 5b). Unoccupied highly suitable areas (areas where sandgrouse have disappeared and/or where they could establish) were mostly located at the boundaries of currently occupied core areas for both species, and at the edges of some marginal areas in the Southern Plateau, Extremadura and Western Andalusia for *P. orientalis*, and in Extremadura for *P. alchata.*

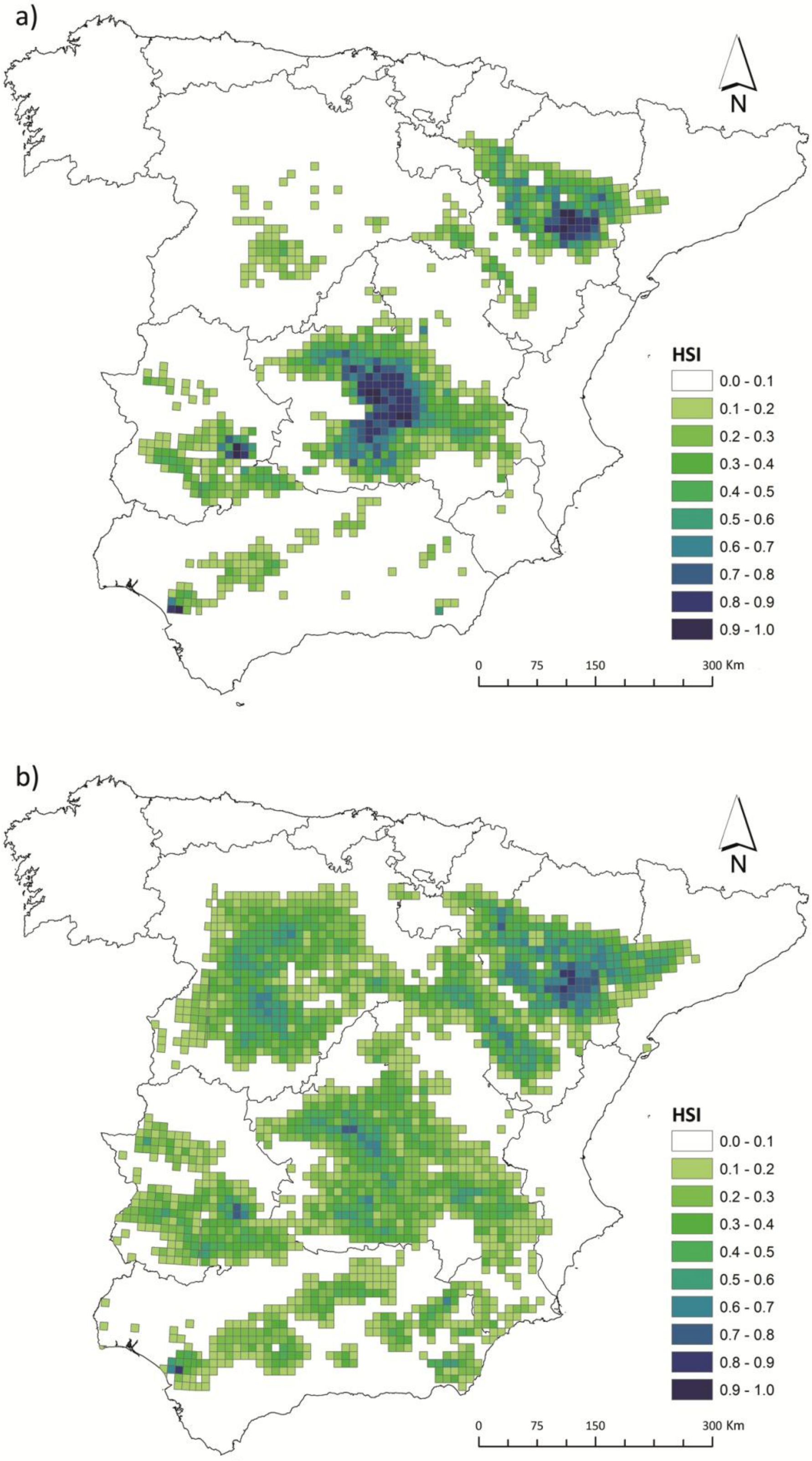


Figure 4. Habitat suitability maps for sandgrouse species (*a*) *Pterocles alchata* and (*b*) *Pterocles orientalis* in Spain.

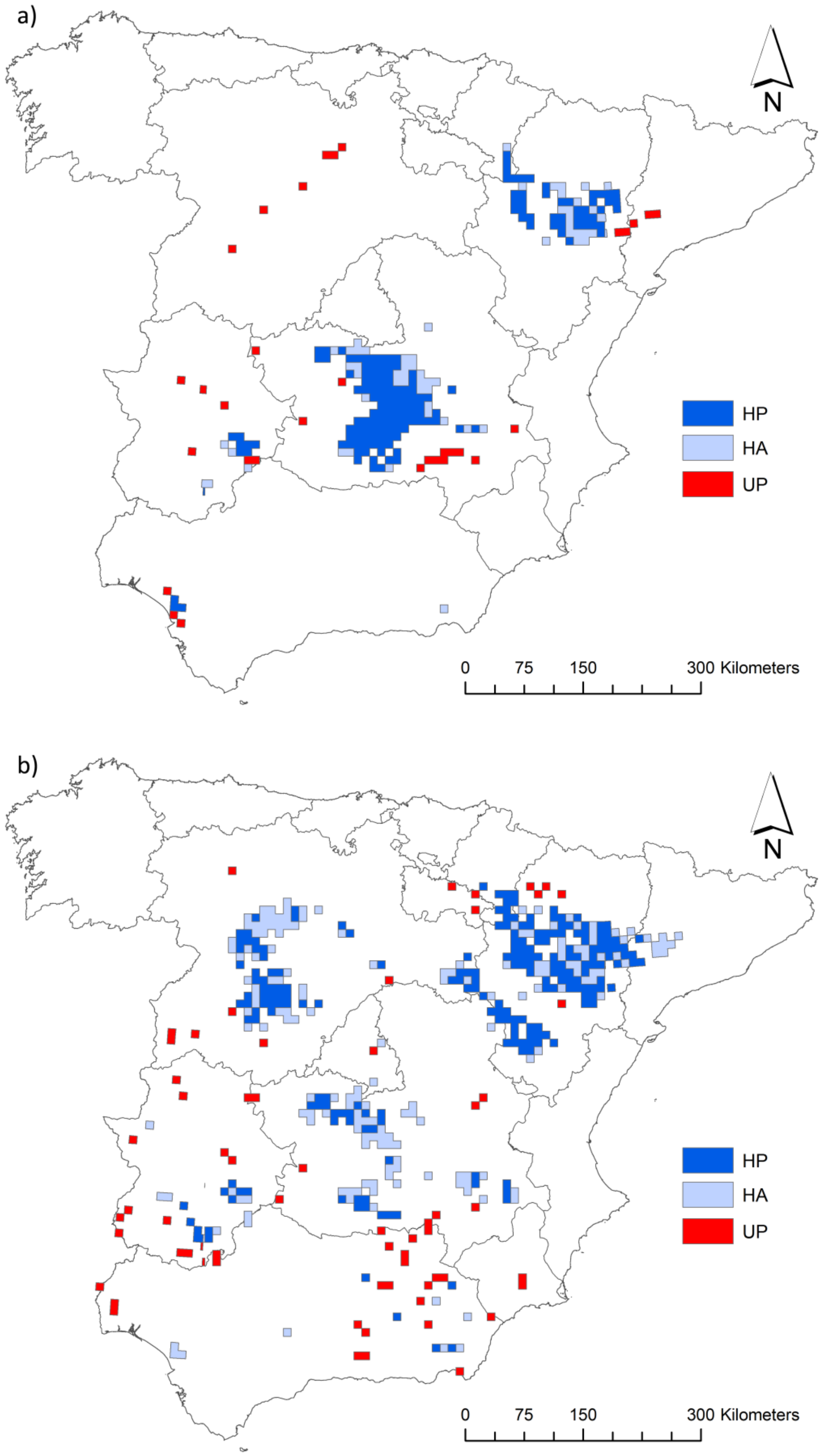


Figure 5. Network of core high suitability areas for (*a*) *Pterocles alchata* and (*b*) *Pterocles orientalis,* indicating where sandgrouse are present (HP) and where sandgrouse are absent (HA), as well as unsuitable areas where sandgrouse are present (UP).

Discussion

Factors determining *Pterocles spp*. distribution

While at a large geographical scale climate and topography are usually the main factors limiting species distributions (Whittaker et al. 2007), our models also identified habitat and anthropogenic factors shaping sandgrouse distribution. For *P. alchata*, the individual effect of topography and climate explained relatively more variation in the probability of occurrence than for *P. orientalis*, for which anthropogenic variables (LULCH) were relatively more important (Fig. 2). This could explain the more restricted distribution of *P. alchata* being more affected by climate. In turn, the relatively large effect of LULCH factors on *P. orientalis* may be, at least partially, explained by the wider range of habitats used (Herranz and Suárez 1999).

Association of both sandgrouse species with flat areas with low annual precipitation concurs with previous studies (Cramp et al. 1985; De Juana 1998), although *P. orientalis* seems to occupy more rugged areas than *P. alchata* (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC; Herranz and Suárez 1999). *P. alchata* was also more intimately linked to hot climate than *P. orientalis* (Table 2; Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC), suggesting that *P. alchata* is more tolerant of high temperatures than *P. orientalis*, and that the latter has more tolerance of low temperatures. Actually, *P. alchata* is typical of meso- and termo-Mediterranean bioclimates (Hinsley et al. 1993), whereas *P. orientalis,* although occurring sympatrically in the meso-Mediterranean region, also occupies the supra-Mediterranean bioclimate typical of *páramos* in Spain and cold Asian desserts (Cramp et al. 1985). The harsh winters typical of the Northern Plateau (and *páramos*) could be hampering *P. alchata* expansion to these areas. A plausible explanation for this geographic segregation driven by the temperature could be a higher cooling capacity of *P. alchata* compared to *P. orientalis,* which allows the former to extend into hotter regions than the latter (Hinsley et al. 1993), whereas *P. orientalis*' larger size probably promotes its spread into areas of lower temperature. This association with climate suggests that sandgrouse might be highly sensitive to variations in climate (Parry 2007), which might provoke a displacement of their distributions, with some populations disappearing and others becoming established in currently unoccupied areas.

TC and LULCH factors jointly explained most of the variation in the distribution of both species, probably because, in Spain, flat arid to semi-arid areas are mostly occupied by arable and/or steppe-like (pastures/shrublands) landscapes (Martí and Moral 2004), which are the habitats preferred by both species (Table 2). It is particularly relevant for conservation and management that, for both species, arable land was the most important variable determining their large-scale distribution (Fig.3), a pattern also observed at local scale (Suárez et al*.* 1997; Herranz and Suárez 1999). Thus, both species are closely associated with habitats intensely managed by humans that may be exposed to rapid changes, mainly due to ongoing rural abandonment in marginal areas and to the implementation of the Common Agricultural Policy (CAP) in the most productive areas (Pain and Pienkowski 1997). The third most important variable explaining the distribution of both species was land-use diversity, which had a negative effect on both species' occurrence (Fig. 3). This suggests that transformation of arable land to other land uses would result in net habitat loss and fragmentation.

Within arable lands, sandgrouse are mainly located on extensive agricultural areas, which, following Spain's economic growth and development, have undergone profound transformations in the last decades. The intensification of agriculture since the 1960s has led to a decline in fallows and legume crops within cereal agricultural systems, resulting in a net loss of important habitats used by both sandgrouse species for nesting and feeding (Herranz and Suárez 1999; Martín et al*.* 2010*b*). Additionally, irrigated crops have expanded enormously, sometimes at the expense of extensive cereal (MAPA [Ministerio de Agricultura, Pesca y Alimentación] 1998), a trend that is changing the traditional agricultural landscape drastically and which has had a negative impact on the distribution of other steppe birds (Brotons et al*.* 2004). Yet, the decline of farmland birds in Spain has not reached the dramatic levels observed in the rest of Europe, mainly because of the late arrival of modern agricultural practices and the relatively recent inclusion of Spain in the EU (Donald et al*.* 2001). The implementation of the CAP has changed this process, since Spain currently receives the second highest proportion of CAP aid payments, and most subsidies have been and are still linked to promotion of intensive farming systems, whereas systems with higher nature value (such as pseudo-steppes and traditional farming systems, and pastures) are omitted, including those within the Natura 2000 network (WWF [World Wildlife Fund] and SEO [Sociedad Española de Ornitología]/BirdLife 2010). At the dawn of the new CAP reform, political effort should be made to secure financial support for environmentally sustainable agriculture compatible with farmland birds (including sandgrouse), and to assure effective implementation of appropriate measures at the national level.

In Spain, *P. alchata* occurrence was also positively related to vineyard cover, in contrast to what has been found locally (Mañosa et al. 1996; Herranz and Suárez 1999; Martín et al. 2010*b*). We can think of three non-exclusive explanations for this. First, factors operating at a local scale do not necessarily apply at larger scales (Ricklefs 1987). Second, our model does not explain all the deviance of the data, implying that there could be variables not considered in our model that influence *P. alchata* distribution (Borcard et al. 1992), and the observed effect of vineyards could be mediated by other unexplained factors. And third, the spatial variables (Sp factor) explain part of the variation in *P. alchata* distribution. The south-east sector of Spain (Southern Plateau) is the main centre for *P. alchata* populations (Figs 1, 4*a*, 5*a*), but also of vast vineyards (650 000 ha), which could lead to the observed positive association with the latter.

Human disturbance variables were negatively related to sandgrouse occurrence, *P. orientalis* seemingly more sensitive to human density than *P. alchata* (Fig. 3). This is not surprising since both species are linked to deserts and isolated areas elsewhere within their global distribution, and urbanization and associated infrastructure development, among other land-use transformations, are important drivers of decline of sandgrouse (Santos and Suárez 2005; Cardoso et al. 2007), other steppe bird populations (Lane et al. 2001; Osborne et al. 2001; Madroño et al. 2004), and of biodiversity in general (Benítez-López et al. 2010*a*).

Network of suitable areas and metapopulation dynamics

One of the strengths of our models was their ability to identify areas with environmental conditions similar to those where the species are known to occur, but which are currently unoccupied. The identified network of core marginally suitable areas and unsuitable currently occupied areas suggests that metapopulation dynamics could be implicated in the distribution of both species. Hence, core suitable areas could be acting as a source of sandgrouse dispersing to unsuitable areas, where sandgrouse are nevertheless present despite suboptimal conditions (Fig. 5*a*, *b*). However, some of the sink areas are located several hundreds of kilometres away from core areas, and recruitment of new individuals by dispersal movements is thus improbable since the magnitude of these movements is commonly limited to *c*. 45 km (Casas et al. 2012). One of the clearest examples is the retreat of *P. alchata* from the Northern Plateau, where it has become rare or has disappeared in the northernmost provinces, and currently occupies several unsuitable squares (Herranz and Suárez 1999; Suárez et al. 2006). In the case of *P. orientalis*, the Northern Plateau is still a core suitable area, yet the species is becoming scarcer also in the northernmost provinces of this area (Suárez et al. 2006). A plausible explanation is that areas near the border of a species' range are usually sink areas with mortality rates higher than breeding rates (Brown and Lomolino 1998). This process could also be taking place in some of the marginal areas and unsuitable occupied areas (Western Andalusia for both species, and arid South-east and Eastern Andalusia for *P. orientalis*).

Unoccupied highly suitable areas were mostly located in the boundaries of core suitable areas (such as the Southern Plateau, Ebro Valley river and Iberian *Páramos*) or in between them, suggesting that they are the reflection of the ongoing decline and disappearance of both sandgrouse species in areas where they were widely distributed in the past (Estrada and Curcó 1991; Manrique and De Juana 1991; Pleguezuelos 1992). Generally, species range contractions are strongly influenced by anthropogenic forces, such as habitat degradation, biocides and introduced species (Channell and Lomolino 2000). Taking into account the association between sandgrouse and agriculture, the range contraction of both sandgrouse species in these areas seems to be related to habitat degradation and loss due to changes in agricultural management. For example, Western Andalusia is one of the agricultural areas in Spain where irrigation has increased most in the last decades (MAPA 2001). In the Northern Plateau, the irrigated area has also notably increased and minimum tillage has expanded substantially (MAGRAMA [Ministerio de Agricultura, Alimentación y Medio Ambiente] 2011). Moreover, recent common vole plagues have induced several vole control campaigns involving massive release of cereal grain treated with rodenticides, which affect several granivorous species in this area (Olea et al*.* 2009).

Conclusions

Since agricultural management is a key factor explaining current sandgrouse distribution in Spain, more detailed information about the relative importance of the multiple recent changes in agricultural management is urgently needed. Thus, these species should be studied in detail at smaller scales, for example comparing areas where contrasts between predicted and observed distributions are indicated by our models. CAP reform will play a major role if the 'greening' proposed by the European Commission is achieved, which would have implications for sandgrouse populations in Spain, and for other farmland and steppe birds. Potential future changes in sandgrouse distribution will probably be directed by the synergistic effects of both climate change and expected land-use transformations at the national level as the result of the new CAP, such as afforestation programmes in marginal low-productivity arable lands and expansion and intensification of permanent crops, or as a result of population growth, urbanization and infrastructure development. In this context, our models help to assess likely shifts in sandgrouse distribution. Conservation plans for sandgrouse should be elaborated from a regional perspective, taking into account the network of core suitable areas we identified when planning the establishment of new Special Protection Areas (SPAs). SPA coverage within the main core areas of these species is remarkably low (Traba et al*.* 2007), particularly in the Southern Plateau (Suárez-Seoane et al*.* 2002). Specific conservation measures should include the maintenance of preferred land uses for sandgrouse (arable lands, pastures and shrublands), and limitation of urban sprawl and road development into protected areas.

Once the specific causes of sandgrouse disappearance have been identified at a smaller scale, as proposed above, local conservation plans to improve the ecological conditions for existing sandgrouse populations or possible reintroduction programmes could be implemented in suitable areas where these species are disappearing or have gone extinct. Ideally, core areas should be expanded and reconnected through previously unoccupied areas that are otherwise suitable, filling the gaps in the current network of core areas. Farmer involvement and complicity, promoted by an appropriately designed CAP and collaboration of conservation bodies, will be crucial.

Acknowledgements

This research was jointly funded by the Dirección General de Investigación (project CGL2008-04282/BOS) and HNV project (MARM). We thank B. Arroyo for useful comments on the manuscript and F. Sánchez for help with data analysis and compilation in ArcGIS 9.3. The English was revised by Sally Bach. This manuscript is dedicated to our beloved Francisco 'Kiko' Suárez, whose previous work on sandgrouse stimulated this research, but who did not live to see this paper completed. We hope to achieve the high standards he exhibited in his science.

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Supplementary material

Species distribution data: explanation of census protocols

The *National Breeding Sandgrouse Survey* (NBSS, Suárez et al. 2006) is the most recent source of information for these sandgrouse species. This survey was coordinated by regional experts and performed by more than 300 professional ornithologists. Each ornithologist was provided with a map of the square (10 × 10 km) to be surveyed, and specific instructions were provided in order to assure there were no differences between censuses performed by different ornithologists (see Annex in Suárez et al. 2006). Sampling focused on *a priori* adequate habitats (pastures, fallows, ploughs, stubbles and low shrub-steppes), according to existing scientific knowledge on habitat requirements (Herranz and Suárez 1999). Every square was surveyed 1–5 times using line transects in a stratified way; sampling effort matched the proportion of adequate habitat within the square. In total, 1736 transects comprising a total length of 5694 km were surveyed. The census was designed to cover all squares where sandgrouse presence had been recorded in the *Spanish Atlas of Breeding Birds* (SABB, Martí and Moral 2004).

Presence/absence data were obtained for 665 10 km × 10 km UTM squares distributed over the main sandgrouse distribution areas. This set of squares covered the areas where sandgrouse had been previously recorded in the NBSS, in previous regional atlases or from anecdotal sightings, and added new squares were sandgrouse presence was suspected. The resolution used must be on a scale relevant to the studied organism, such as its home range (Dunning *et al*. 2005). Since the average breeding home range of *P. alchata* is *c*. 40 km^2 (Benítez-López *et al.* 2010) and that for *P. orientalis* is *c*. 120 km^2 (A. Benítez-López, F. Casas, F. Mougeot, C.A. Martín, J.T. García and J. Viñuela, unpublished data 2007–2013), we assumed that a 10 km × 10 km resolution was adequate for the study of sandgrouse biogeographical patterns.

The second source of information was the SABB (Martí and Moral 2004, p. 100). We used the NBSS to update the presence/absence data recorded in the SABB. The SABB is the most current and detailed source of information for breeding bird ranges in Spain. In this collective work, data were gathered by experienced ornithologists during spring in the period 1998–2001. Our data may thus be regarded as true presence–absence records, since they were all gathered through systematic and standardized surveys that recorded absences (missing in so-called 'presence-only' data). In the analyses that follow, we assumed that the combined data

(1998–2001 and year 2005) indicated the likely distribution patterns of sandgrouse throughout the early 2000s. The final sample size was 5312 UTM squares with presence/absence data for sandgrouse species, with 12.5% of the squares corresponding to the NBSS data, and the rest to SABB data (mostly absences). Pin-tailed sandgrouse was present in 370 UTM squares and black-bellied sandgrouse in 669 UTM squares. We assessed whether there were discrepancies between both sources regarding presence and absence squares and found that 65% and 78.5% of the NBSS squares for *P. orientalis* and *P. alchata*, respectively, matched the presence/absence squares as surveyed during the SABB. Only 4.7% (*P. orientalis*) and 6.0% (*P. alchata*) of the squares surveyed as positive in the NBSS were recorded as negative in the SAAB. The biggest mismatch between both sources occurred in the percentage of absence squares in the NBSS that were recorded as positive in the SABB. However, we believe that, rather than a false absence and given that the NBSS is more recent, this is a reflection of the ongoing disappearance of both species from some squares, especially at the margins of their distribution range (Suárez 2006). This is particularly evident in the case of *P. orientalis*, for which 30.5% of squares recorded as negative in the NBSS were previously positive in the SABB, compared to a percentage of 15.5% in the case of *P. alchata*.

Supplementary material references

Benítez-López A, Martín CA, Casas F, Mougeot F, García JT, Viñuela J (2010b) Áreas de campeo y movimientos estacionales de la ganga ibérica *Pterocles alchata*. In: Casinello J, Castro F (eds) XIII Congreso Nacional y X Iberoamericano de Etología. Ponencias y comunicaciones. Instituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ciudad Real, p 130.

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Table S1. Means and standard deviations of the explanatory variables characterizing areas where sandgrouse are absent (AbsBoth, a), where only *P. orientalis* is present (PresPtori, b), where only *P. alchata* is present (PresPtalc, c) and where both species are present (PresBoth, d). Sample size and letters coding each group of squares appear in brackets.

	AbsBoth (4463,a)		PresPtori (479,b)		PresPtalc (180,c)		PresBoth (190,d)				
Variables	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**F**	**P**	**Bonferroni**
Wat	1.53	2.64	1.42	1.96	1.07	1.59	1.87	3.10	3.26	**0.021**	c < d
Cit	0.39	2.74	0.01	0.14	0.04	0.31	0.00	-	5.15	**0.002**	a > b
For	17.30	18.55	5.14	7.40	3.05	6.00	2.59	3.55	140.72	**<0.001**	a > b, c, d
Fru	1.90	4.57	1.34	3.95	0.60	2.01	1.61	4.69	6.86	**<0.001**	a > c
Oli	4.21	11.81	6.30	15.51	5.02	7.30	4.76	6.66	4.62	**0.003**	a < b
Mix	10.26	14.26	7.04	10.63	3.83	7.86	3.30	6.77	33.46	**<0.001**	a > b, c, d; b > c, d
Shr	22.42	19.13	17.42	14.43	11.78	12.09	18.03	13.96	30.59	**<0.001**	a > b, c, d; c < a, b, d
Pas	5.31	8.97	3.41	6.72	2.56	8.64	1.60	3.73	21.72	**<0.001**	a > b, c, d
Agr	22.91	24.23	49.71	23.94	53.27	20.31	55.75	20.11	349.59	**<0.001**	a < b, c, d; b < d
Vin	1.36	5.25	2.40	7.38	12.44	17.28	5.22	10.14	187.05	**<0.001**	a < b, c, d, c > a, b, c; d > b
Urb	2.02	5.38	0.94	2.05	1.25	2.39	0.93	2.11	9.90	**<0.001**	a > b, d
Rail	1.61	4.10	1.95	4.29	2.54	4.84	2.07	4.17	4.21	**0.006**	c > a
Road	7.98	9.54	7.68	8.48	8.11	8.25	7.51	7.81	0.31	0.820	
Dens06	118.86	538.87	37.38	114.87	44.65	68.48	40.72	76.86	6.08	**<0.001**	a >b
PGro	2.74	13.98	0.20	12.03	4.50	8.13	3.33	10.15	6.52	**<0.001**	b < a, c, d
A	684.11	420.31	710.37	291.85	623.37	247.31	536.32	215.08	10.45	**<0.001**	b > d; a > d
AR	471.72	383.55	225.10	195.44	102.78	94.31	154.16	100.81	160.47	**<0.001**	a > b, c, d; b > c
S	8.26	8.10	2.64	2.64	1.00	1.11	1.57	1.30	166.22	**<0.001**	a > b, c, d
SR	34.31	18.87	20.50	13.39	10.62	9.28	15.42	9.87	228.59	**<0.001**	a > b, c, d; b > c, d
T	13.23	2.88	13.50	2.06	14.47	1.36	14.40	1.15	22.78	**<0.001**	c > a, b; d > a, b
TJn	1.15	2.92	0.74	1.99	1.14	1.66	1.26	1.20	3.43	**0.016**	a > b
TJu	29.86	3.63	31.52	2.03	33.15	1.23	32.65	1.47	116.77	**<0.001**	c > a, b, d; b < c, d
P	724.71	332.62	470.91	85.27	441.49	64.21	434.92	65.11	182.72	**<0.001**	a > b, c, d
PSp	189.43	83.61	131.84	21.58	124.75	14.59	122.99	14.10	150.26	**<0.001**	a > b, c, d
PET	727.18	97.60	739.21	73.79	775.39	48.25	773.10	43.22	30.37	**<0.001**	a > c, d; b < c, d
AET	488.25	92.24	409.95	57.67	402.49	50.04	397.05	48.19	214.85	**<0.001**	a > b, c, d
Div	1.76	0.22	1.64	0.24	1.57	0.24	1.56	0.23	117.11	**<0.001**	a > b, c, d; b > c, d
NPa	5184.19	4903.48	3951.15	2505.45	3519.69	2469.12	3986.05	2428.86	19.89	**<0.001**	a > b, c, d
PSi	0.18	1.55	0.04	0.06	0.07	0.19	0.04	0.03	2.14	0.093	

Table S2. Candidate models for the probability of occurrence of pin-tailed sandgrouse (a) and black-bellied sandgrouse (b) for TC and LULCH factors. The best model (in bold) was the one with the lowest AIC$_c$ (Akaike's information criterion) and highest Akaike weight, and with VIF $_{max}$ <5 (highest variance-inflation factor in the set of explanatory variables for the candidate model). Models were built starting with the variable that explained more deviance of the data, and subsequently adding the variables that contributed the most to the deviance of the model. For models with VIF>5, we dropped the variable that contributed the least to AIC$_c$ and model fit and produced a model with a VIF<5. Details for retaining or not variables are given for each step. Once we added all the variables belonging to each factor, we checked if by adding variables not retained in previous models the AIC$_c$ decreased (i.e.:LULCH model *for P.orientalis*) until no further drop in AIC$_c$ was possible. See Table 1 for variable codes, k is the number of estimated parameters.

a) Pterocles alchata

Sp Model	VIF$_{max}$	Res.Dev.	Exp.Dev.	k	AIC$_c$	Details
X+Y+XY+X2+Y2	**4.97**	**2228.9**	**16.99**	**6**	**2240.92**	**Removing any of the spatial variables result in a model with higher AIC$_c$ (less fit)**

TC Model	VIF$_{max}$	Res.Dev.	Exp.Dev.	k	AIC$_c$	weight
S	n.a.	2134.2	20.52	2	2138.20	0.00
S+P	1.03	1883.2	29.86	3	1889.20	0.00
S+P+Tju	1.2	1739.8	35.21	4	1747.81	0.00
S+P+Tju+T	**3.05**	**1654.5**	**38.38**	**5**	**1664.51**	**1.00**

LULCH Model	VIF$_{max}$	Res.Dev.	Exp.Dev.	k	AIC$_c$	weight	Details
Agr		2312	13.90	2	2316.00	0.00	
Agr+For	1.07	2173.5	19.05	3	2179.50	0.00	
Agr+For+Vin	1.18	2015.9	24.92	4	2023.91	0.00	
Agr+For+Vin+Div	1.3	1911.6	28.81	5	1921.61	0.00	
Agr+For+Vin+Div+Mix	1.52	1911.1	28.83	6	1923.12	0.00	
Agr+For+Vin+Div+Mix+Pas	1.77	1907.5	28.96	7	1921.52	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr	3.14	1862.2	30.65	8	1878.03	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa	3.58	1856.2	30.87	9	1874.23	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa+Dens06	3.89	1853.3	30.98	10	1873.34	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa+Dens06+Cit	3.92	1852.3	31.02	11	1874.35	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa+Dens06+Cit+Urb	4.06	1851	31.06	12	1875.06	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa+Dens06+Cit+Urb+Fru	4.9	1833.8	31.70	13	1859.87	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail	4.98	1829.2	31.88	14	1857.28	0.00	
Agr+For+Vin+Div+Mix+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail+PGro	5.02	1823.3	32.10	15	1853.39	0.02	VIF>5. Mix is dropped to produce a model with VIF<5 and less AIC$_c$
Agr+For+Vin+Div+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail+PGro	3.48	1823.4	32.09	14	1851.48	0.06	

Agr+For+Vin+Div+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail+Pgro+Oli	5.1	1823.1	32.10	15	1853.19	0.03	VIF>5. Oli is dropped to produce a model with VIF<5 and less AIC_c
Agr+For+Vin+Div+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail+Pgro+Road	3.53	1822.6	32.12	15	1852.69	0.03	
Agr+For+Vin+Div+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail+Pgro+Road+Wat	3.71	1818.1	32.29	16	1850.20	0.12	Road is dropped to produce a model with less AIC_c
Agr+For+Vin+Div+Pas+Shr+Npa+Dens06+Cit+Urb+Fru+Rail+Pgro+Wat	3.68	1818.7	32.27	15	1848.79	0.24	Urb is dropped to produce a model with less AIC_c
Agr+For+Vin+Div+Pas+Shr+Npa+Dens06+Cit+Fru+Rail+Pgro+Wat	**3.62**	**1819.2**	**32.25**	**14**	**1847.28**	**0.50**	

COMBINED MODEL	**VIF_{max}**	**Res.Dev.**	**Exp.Dev.**	**k**	**AIC_c**	**weight**	**Details**
X+Y+XY+X2+Y2+S+P+Tju+T+Agr+For+Vin+Div+Pas+Shr+Npa+ Dens06+Cit+Fru+Rail+Pgro+Wat	12.78	1387.40	48.33	23	1433.61	0.02	Model containing the variables included in the best model of each factor.T and Y are dropped to alleviate VIF and produce a model with less AIC_c
X+XY+X2+Y2+S+P+Tju+Agr+For+Vin+Div+Pas+Shr+Npa+ Dens06+Cit+Fru+Rail+Pgro+Wat	3.92	1388.70	48.28	21	1430.87	0.06	
X+XY+X2+Y2+S+P+Tju+Agr+Vin+Div+Pas+Shr+Npa+ Dens06+Cit+Fru+Rail+Pgro+Wat	3.53	1389.30	48.26	20	1429.46	0.13	For is dropped to produce a model with less AIC_c
X+XY+X2+Y2+S+P+Tju+Agr+Vin+Div+Pas+Shr+Npa+ Dens06+Cit+Fru+Rail+Pgro	3.47	1389.90	48.24	19	1428.04	0.25	Wat is dropped to produce a model with less AIC_c
X+XY+X2+Y2+S+P+Tju+Agr+Vin+Div+Pas+Shr+Npa+ Dens06+Cit+Fru+Pgro	3.38	1391.80	48.17	18	1427.93	0.27	Rail is dropped to produce a model with less AIC_c
X+XY+X2+Y2+S+P+Tju+Vin+Div+Pas+Shr+Npa+ Dens06+Fru+Pgro	**3.39**	**1393.80**	**48.09**	**17**	**1427.92**	**0.27**	**Cit is dropped to produce a model with less AIC_c**

b) Pterocles orientalis

Sp Model	**VIF_{max}**	**Res.Dev.**	**Exp.Dev.**	**k**	**AIC_c**	**Details**
X+Y+XY+X2+Y2	**1.46**	**3718.10**	**7.56**	**6**	**3730.08**	**Removing any of the spatial variables result in a model with higher AIC_c (less fit)**

TC Model	**VIF_{max}**	**Res.Dev.**	**Exp.Dev.**	**k**	**AIC_c**	**weight**
P	n.a.	3345.80	16.82	2	3349.80	0.00
S+P	1.00	3158.7	21.47	3	3164.70	0.00
S+P+TJu	1.01	3158.4	21.48	4	3166.41	0.00
S+P+T+TJu	**2.92**	**3068.80**	**23.70**	**5**	**3078.81**	**1.00**

LULCH Model	VIF_{max}	Res.Dev.	Exp.Dev.	k	AIC_c	weight	Details
Agr	n.a.	3444.5	14.36	2	3448.42	0.00	
Agr+For	1.14	3314.7	17.59	3	3320.58	0.00	
Agr+For+Div	1.20	3242.6	19.38	4	3250.45	0.00	
Agr+For+Div+Mix	1.32	3242.6	19.38	5	3252.45	0.00	
Agr+For+Div+Mix+Pas	1.49	3240.9	19.42	6	3252.75	0.00	
Agr+For+Div+Mix+Pas+Dens06	1.58	3202.8	20.37	7	3216.64	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb	1.57	3197.9	20.49	8	3213.73	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb+Npa	1.83	3195.8	20.55	9	3213.63	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb+Npa+Cit	1.81	3177.1	21.01	10	3196.93	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb+Npa+Cit+Shr	2.82	3162.1	21.38	11	3183.92	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb+Npa+Cit+Shr+Vin	3.41	3151.7	21.64	12	3175.51	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro	3.45	3151.6	21.64	13	3177.41	0.00	
Agr+For+Div+Mix+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro+Oli	6.02	3146.5	21.77	14	3174.31	0.00	VIF>5.Dropping Mix we obtain a model with VIF<5 and a significant decrease in AIC_c
Agr+For+Div+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro+Oli	3.39	3146.8	21.76	13	3172.61	0.00	
Agr+For+Div+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro+Oli+Frut	4.02	3117.9	22.48	14	3145.70	0.01	
Agr+For+Div+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro+Oli+Frut+ Rail	4.04	3116.5	22.52	15	3146.30	0.01	
Agr+For+Div+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro+Oli+Frut+ Rail+Road	4.14	3110.4	22.67	16	3142.20	0.05	
Agr+For+Div+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+PGro+Oli+Frut+ Rail+Road+Wat	4.31	3109.4	22.69	17	3143.20	0.03	
Agr+For+Div+Pas+Dens06+Urb+Npa+Cit+Shr+Vin+Oli+Frut+Rail+Road+Wat	4.30	3109.5	22.69	16	3141.30	0.08	PGro is dropped since it produces a model with less AIC_c
Agr+For+Div+Pas+Dens06+Npa+Cit+Shr+Vin+Oli+Frut+Rail+Road+ Wat	4.28	3109.8	22.68	15	3139.60	0.18	Urb is dropped since it produces a model with less AIC_c
Agr+For+Div+Pas+Dens06+Npa+Cit+Shr+Vin+Oli+Frut+Rail+Road	4.10	3110.8	22.66	14	3138.60	0.30	Wat is dropped since it produces a model with less AIC_c
Agr+For+Div+Pas+Dens06+Npa+Cit+Shr+Vin+Oli+Frut+Road	**4.09**	**3112.6**	**22.61**	**13**	**3138.40**	**0.34**	**Rail is dropped since it produces a model with less AIC_c**

COMBINED MODEL	VIF_{max}	Res.Dev.	Exp.Dev.	k	AIC_c	weight	Details
X+Y+XY+X2+Y2+S+P+TJu+T+Agr+Cit+For+Fru+Vin+Div+Pas+Shr+ Npa+Dens06+Road+Oli	14.94	2768.4	31.17	21	2812.23	0.06	
X+XY+X2+Y2+S+P+T+Agr+Cit+For+Fru+Div+Pas+Shr+Npa+Dens06+ Road+Oli	**3.84**	**2768.7**	**31.16**	**19**	**2806.56**	**0.94**	**Tju,Vin and Y are dropped in order to produce a model with VIF<5 and lower AIC_c**

CAPÍTULO 2

Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species

Fotos: François Mougeot

Benítez-López A, Viñuela J, Suárez F, Hervás I, García JT (2014) Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species. Oecologia 176: 193-206.

Abstract

Ascertaining what niche processes allow coexistence between closely-related species is of special interest in ecology. We quantified variations in the environmental niches and densities of two congeneric species, the pin-tailed and the black-bellied sandgrouse (*Pterocles alchata* and *P.orientalis*) in allopatry and sympatry under similar abiotic, habitat and dispersal contexts to understand their coexistence. Using principal component analysis, we defined environmental gradients (niche dimensions) including abiotic, habitat and anthropogenic variables, and calculated niche breadth, position and overlap of both species in sympatry and allopatry. Additionally, sandgrouse density was modelled as a function of the niche dimensions and the density of the other species. We found evidence that each species occupy distinct environmental niches in sympatry and in allopatry. The black-bellied sandgrouse exploits a broader range of environmental conditions (wider niche breadth) while the pin-tailed sandgrouse reaches high densities where conditions seem to match its optimum. In sympatry, both species shift their niches to intermediate positions, indicating the importance of abiotic factors in setting coexistence areas. Environmental conditions determine regional densities of pin-tailed sandgrouse whereas biotic interactions explain the density of the black-bellied sandgrouse in areas with abiotic conditions similarly conducive for both species. Highly suitable areas for the pin-tailed sandgrouse fall beyond the upper thermal limit of the black-bellied sandgrouse, leading to niche segregation and low densities for the latter. Finally, local niche shift and expansion plus possible heterospecific aggregation allows the pin-tailed sandgrouse to thrive in *a priori* less favourable environments. This work provides insight in how different mechanisms allow species coexistence and how species densities vary in sympatry compared to allopatry as a result of environmental filtering and biotic interactions.

Keywords: allopatry, sympatry, co-occurrence, environmental niche, niche breadth, niche position, niche overlap

Introduction

An old yet ongoing challenge for ecologists is ascertaining what factors allow the coexistence between closely related species, which is crucial for understanding the evolutionary and ecological implications of species interactions (Darwin, 1859; Brown, 1984). Factors explaining individual species ranges, and specially those driving the overlap of related species' ranges, are complex, and include abiotic (e.g., temperature and precipitation) and biotic factors (e.g., resource availability, competition, and predation) (MacArthur 1972; Gaston 2003). The study of how species vary in their requirements and tolerance to these factors has greatly advanced due to the continued conceptual development of analytical techniques for quantifying the niche of species (Chase and Leibold 2003; Soberón 2007).

Hutchinson (1957) defined the niche as a multidimensional hypervolume in which a species maintains a viable population. The entire hypervolume under which an organism can potentially exist describes its fundamental niche (abiotic conditions), whereas the portion of the fundamental niche that a species actually occupies due to, in particular, biotic interactions (i.e.: competitors or closely-related species) defines its realized niche. Two niche-based mechanisms that explain species distribution and abundance are the niche-breadth and the niche-position hypotheses (Gaston et al. 1997). The former postulates that species attaining large geographical distributions and occurring at high local densities are capable for that because they occupy a broader range of habitats and exploit diverse environmental conditions and resources (Brown 1984). According to the latter, abundant species use resources that are common in the particular area and time or perform successfully under a certain set of environmental conditions (i.e.: their niche position matches the current prevailing conditions, (Devictor et al. 2010), while rare species utilize locally scarce and restricted resources (Gaston et al. 1997). The two hypotheses are not mutually exclusive (Heino 2005) and although the niche-position hypothesis has widely been supported in the past (Gaston and Blackburn 2000; Gregory and Gaston 2000; Hanski et al. 1993) the niche-breadth hypothesis has recently gained support (Brändle and Brandl 2008; Slatyer et al. 2013) and both may be complementary (i.e.: a species with a broader niche might be more likely to have widespread environmental conditions included within that niche).

Although single-species studies are useful for uncovering potential niche-related mechanisms, virtually all species co-occur with many other species, so the role of species interactions should be incorporated to the study of factors that determine the abundance and distribution of species (Wisz et al. 2013). When two or more closely related species co-occurs at a given time and place, the question arises: how can they coexist? On the one hand, adaptation of co-occurring species to similar abiotic environments can drive species to develop similar ecological preferences and thus, closely related species may compete for ecological resources (García and Arroyo 2005). On the other hand, increased cost of competition for similar resources among co-occurring species can drive competitive exclusion, constraining coexistence of species (MacArthur and Levins 1967). Comparing whether the niche position and niche breadth of a species vary between allopatric and sympatric situations along one or more environmental gradients would provide evidence of interaction (avoidance or aggregation) and niche segregation between closely related species (Chunco et al. 2012; Rannap et al. 2009). Interspecific interactions may affect species density in sympatric sites (Sanza et al. 2012), depending on environmental conditions, or may even induce changes in the ecological niche allowing a species to use in sympatry habitats rarely used in allopatry (i.e.: Martín et al. 2010). Also, conspecific cues might promote the aggregation of individuals at traditionally occupied sites or in areas where they successfully bred in the past (i.e.: allopatric areas) (Osborne et al. 2007), regardless of whether environmental conditions have changed. Hence, biotic factors may also separate habitat suitability from its attractiveness for occupation through both positive and negative interactions affecting species–habitat relationships. Studying how different properties of the niche together shape species' distribution patterns of closely-related species in allopatric and sympatric scenarios is thus of great interest in ecology and conservation biology.

A particularly powerful approach to disentangle the relative role of niche-mechanisms and biotic factors as drivers of co-existence and abundance of closely related species would be assessing niche breadth and position in simpatry and allopatry under similar abiotic, habitat and dispersal context. Here, we use such approach to evaluate different mechanisms by which closely-related species distribute and coexist by assessing large-scale similarities and differences in environmental niches and variations in population densities in sympatric and allopatric scenarios. We use sympatric *Pterocles spp.* (the pin-tailed sandgrouse *P. alchata* and the black-bellied sandgrouse *P. orientalis*) as model species. Sandgrouse are an excellent model system for the investigation of environmental niche similarities and interspecific interactions because species in this family share a relatively narrow range of climatic, topographic and trophic requirements, occupying similar feeding and breeding habitats (Benítez-López et al. 2013; Herranz and Suárez 1999), thus allowing for a clear potential influence of biotic factors more than in other animal groups that have experienced higher niche diversification. Both species are ground-nesting birds associated with open arid habitats, natural steppes and agricultural ‘pseudo-steppes’, and are thus especially exposed to foreseeable land use changes (agricultural intensification)and habitat anthropogenization (Benítez-López et al. 2013). Finally, both sandgrouse species have well developed thermal adaptations (Hinsley et al. 1993), and the abiotic environment (climate) is expected to particularly influence their distribution. Environmental niches are usually defined with climatic gradients or with climatic and habitat gradients (Barnagaud et al. 2012), but current species niches are likely to be influenced by human-mediated processes (Eriksson 2013). We propose using modern analitycal techniques to study the realized environmental niches of congeneric sandgrouse in sympatry and allopatry considering a wide set of environmental variables that include human-related environmental factors, and to assess the importance of the biotic and the abiotic factors in setting the regions of co-occurrence in these closely-related species. Our results might provide valuable indications about the ecological plasticity of co-occurring species towards habitat changes and, thus, about its vulnerability to human land use.

Methods

Study areas

We selected the three main biogeographical areas where both species are distributed in Europe, which are located in Spain. These are the Southern Plateau (Castilla-La Mancha autonomous community, CLM hereafter), the Ebro Valley (VEBR hereafter) and Extremadura (EXT hereafter) (Fig.1) (Benítez-López et al. 2014). These areas are located in the Meso-Mediterranean bioclimatic stage mostly, but the Supra-Mediterranean belt is also found in VEBR (Rivas-Martínez 2004). Average annual temperature ranges from 15.5º to 17ºC and average annual rainfall is 500–600 mm.

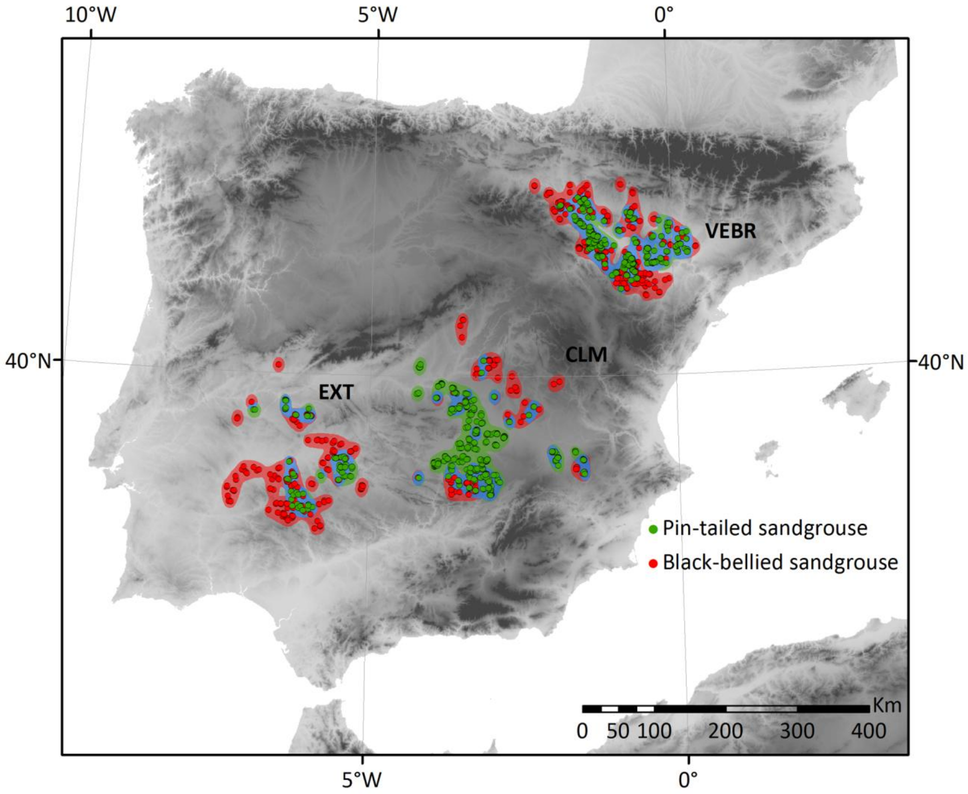

Figure 1. Map of Spain showing sandgrouse distribution over the study areas and occurrence points used for this study. Red: black-bellied sandgrouse; Green: pin-tailed sandgrouse; Blue: Sympatric areas (modified from Benítez-López et al. 2014)

Species and environmental data

We extracted species data from the 2005 *National Breeding Sandgrouse Survey* (NBSS), coordinated by the Sociedad Española de Ornitología (SEO)/BirdLife (Suárez et al. 2006), which is the most recent source of information for sandgrouse species in Europe. The sampling and analysis unit was the UTM 100 km^2 square, and the survey method was the line transect. Sampling focused on *a priori* adequate habitats (pastures, fallows, ploughs, stubbles and low shrub-steppes), according to existing scientific knowledge on habitat requirements (Herranz & Suárez 1999). For each detected bird or flock (hereafter sighting), the distance perpendicular to the observer’s trajectory (line transect) was estimated. Every square was surveyed 1–2 times using line transects (1-5 per square) in a stratified way: sampling effort (cumulative transect length, 1.2-85 km per square) matched the proportion of adequate habitat within the square (Suárez et al. 2006). In total, 1736 transects comprising a total length of 5694 km were surveyed. From all surveyed squares (N=665) we extracted 315 (2874 km of transects) covering the three study regions (see Online resource 1 for further details about the survey).

Sandgrouse density (number of birds per km^2 in each square) was estimated from these data using the cumulative transect length per square to measure survey effort (Suárez et al. 2006) and to estimate surveyed area within a square. Given that detectability of each species could be different due to differences in body size, social behaviour or habitat selection (see Benítez-López et al. 2013), we calculated one value of detectability per species, pooling all sightings from all squares and using the distribution of all sampled distances at which sightings were recorded (Thomas et al. 2006). We used a non-parametric approach to estimate detectability (no *a priori* parametric detection function was fit, i.e.: half normal, hazard rate) assuming that it is maximum (detectability = 1, all birds are counted) in the closest perpendicular distance to the observer and it decreases as the distance from the observer increases (the further the distance the lower the probability of detecting an individual; see Online resource 1 for detailed description of the method and an example). This methodology was specifically developed for steppe bird census data that may be potentially subject to relatively large error in distance estimates obtained in open landscapes (with few reference points) and by multiple observers (Carrascal et al. 2010). The detection distances were right truncated excluding outliers (Buckland et al. 2001); i.e. disregarding the 5% of the longest perpendicular distances from the transect line (>300 m for both species). Detectability was 0.48 for the pin-tailed sandgrouse and 0.39 for the black-bellied sandgrouse and the effective census strip width (ESW = truncation distance x detectability) was 144 m and 118 m at each side of the transect, respectively. The area surveyed in each square was then the transect length (km) x 2 x ESW (km).

Given the variability of transect length per square we tested whether the precision of density estimates varied with survey effort. We defined three survey effort categories: squares with transect lengths below the 25% quartile (< 5.2 km per square) fell in the low survey effort category, and those with lengths over the 75% quartile (9.8 km per square) were allocated to the high survey effort category, with the rest of lengths corresponding to the intermediate survey effort category.

Based on previous information about the ecology of sandgrouse (Benítez-López et al. 2013) we recorded a set of variables (anthropogenic, climatic, topographic, land use, landscape) of potential relevance for explaining sandgrouse environmental requirements (niche breadth and position) and variations in sandgrouse density. The variables were measured using Geographic Information Systems (GIS) and digital cartography from different sources (Table 1; see Benítez-López et al. 2014 for a detailed explanation on how the variables were obtained).

Table 1. Variables used in the Principal Component Analysis. Unstandardized mean ±SD are reported.

Code	Description	Mean ± SD
Climatic variables(1)		
P	Mean anual precipitation (mm)	475.4 ± 82.4
T	Mean annual temperature (ºC)	14.8 ± 1.2
TJn	Mean temperature in January (°C)*	1.6 ± 1.5
TJu	Mean temperature in July (ºC)	33.5 ± 1.2
Topographic variables(1)		
A	Mean altitude (m)	584.3 ± 204.3
S	Mean slope (%)	1.7 ± 1.7
Land use categories(2)		
Wat	Percent cover of water reservoirs and rivers	1.7 ± 3.1
For	Percent cover of forests	3.1 ± 5.0
Mix	Percent cover of mixed forest-shrublands	7.4 ± 12.8
Shr	Percent cover of shrublands	15.0 ± 13.9
Past	Percent cover of pasturelands, pastures with some shrubs and meadows	2.8 ± 5.6
Fru	Percent cover of fruit groves	1.0 ± 3.3
DFru	Percent cover of dry fruit groves	0.4 ± 1.2
Oli	Percent cover of olive groves	6.0 ± 7.2
Agr	Percent cover of arable lands	48.8 ± 21.6
Vin	Percent cover of vineyards	8.3 ± 14.0
Urb	Percent cover of urban areas (cities, towns and villages)	1.8 ± 4.6
Irr	Percent cover of irrigated area	9.9 ± 16.6
Landscape characteristics (2)		
Div	Shannon Diversity Index	1.56 ± 0.24
NPa	Total number of patches	3947.4 ± 2925.5
PaS	Average patch size (km^2)	0.04 ± 0.34
AgrPaS	Average patch size of arable lands (km^2)	0.04 ± 0.05
NAgr	Total number of patches of arable lands	1967.8 ± 1725.8
AgrPerim	Sum of edge length (perimeter) of arable fields	1164.8 ± 725.8
Human disturbance		
High	Total length of highways per UTM square(km) (3)	0.08 ± 0.18
PRoad	Total length of primary roads per UTM square (km) (3)	0.07 ± 0.09
SRoad	Total length of secondary roads per UTM square (km) (3)	0.17 ± 0.15
HRail	Total length of high-speed railways per UTM square (km) (3)	0.01 ± 0.04
Rail	Total length of railways per UTM square (km) (3)	0.03 ± 0.07
Pwr1	Total length of 400 kV-powerlines per UTM square (km) (4)	0.02 ± 0.05
Pwr2	Total length of 220 kV-powerlines per UTM square (km) (4)	0.02 ± 0.04
Pwr3	Total length of 110-150 kV-powerlines per UTM square (km) (4)	0.03 ± 0.06
Pwr4	Total length of low voltage 60-110 kV-powerlines per UTM square (km) (4)	0.05 ± 0.07
PopDens	Population density in 2006 (inhabitants/km^2) (5)	71.9 ± 291.7
PopGro	(Population density in 2006- population density in 2000)/population density in 2000*100(5)	5.9 ±15.9

Sources: (1) Atlas Climático Digital de la Península Ibérica (Ninyerola et al. 2005). (2) SIGPAC (Sistema de Información Geográfica de Parcelas Agrícolas). (3) Spanish Instituto Geográfico Nacional (IGN). (4) Spanish Red Eléctrica Nacional (REE) (5) Spanish Instituto Nacional de Estadística (http://www.ine.es).

Data analyses

To summarize landscape-scale environmental variation, we applied a principal components analysis (PCA) with varimax normalized rotation to reduce the original set of 35 explanatory variables into orthogonalized components (McGarigal et al. 2000). The Principal Components (PC's) were taken as niche dimensions and used as predictors in our models. In the case of habitat data, PC's typically represent overall trends in the habitat, such as major land use and geographical gradients. In the case of climate and topography, PC's represent topographic and climatic gradients. We retained principal components which had eigenvalues > 1 (11 PC's, see results).

For each PC we calculated the niche breadth and niche overlap for squares where only one of the species occurred (allopatric squares) and for squares where the two species co-occurred (sympatric squares) using kernel density estimations (KDE) (Mouillot et al. 2005)(Online Resource 1). This allowed us assessing how each species modify its niche for a certain environmental axis when coexisting with the other species. KDE gives a smooth, flexible, non-parametric curve for a probability density function over the data points, and with the area under the curve equal to one. We used optimal bandwidths to produce the kernel curves (Silverman 1986). For continuous data, such as our PC's, niche overlap based on non-parametric kernel density functions (NO_K) on axis *pc* is calculated as:

$$NO_{K(i,j,PC_{ni})} = 1 - \frac{1}{2}\int |f_{iPC_{ni}}(x) - f_{jPC_{ni}}(x)|\, dx \qquad \text{eqn 1}$$

where f_{iPCni} and f_{jPCni} are the kernel population density functions for species *i* and *j*, respectively, and for the $PC_{ni.}$(adapted from Mouillot et al. 2005).

We generated three kernel curves (representing niche breadth) for each PC (two for allopatric squares and one for sympatric squares) and calculated the overlapped area between them (niche overlap), adapting the script available at Geange et al. (2011) to our data (R Development Core Team 2012). Mean niche overlap was obtained by averaging niche overlap (NO) between allopatric and sympatric squares over each different axis (Mouillot et al. 2005), where PC is the number of axes.

$$NO_{K(i,j)} = \frac{1}{PC}\sum_{pc=1}^{PC} NO_{K(i,j,pc)} \qquad \text{eqn 2}$$

NO is 0 when the two distributions are completely disjoint, and is 1 when they exactly coincide.

Niche comparisons must be done in a way that rules out detecting as different two niches which only differ due to sampling variation (Geange et al. 2011). To differentiate whether species in allopatric and sympatric squares occupied similar or different niches for each PC, we produced null models (see Gotelli 2000). Null models use randomization or permutation tests (1000 permutations) which do not rely on distributional assumptions (Manly 2007). Calculating pseudo-values of the test statistic that would arise if H_0 (no niche differentiation) were true generates the null distribution. This is achieved by permutating species labels over all types of squares. The position of an empirically derived test statistic in relation to the pseudo-values generated by the null model provides the *P*-value for the test (Geange et al. 2011).

We applied Generalized Linear Models (GLM) (McCullagh and Nelder 1989) to relate sandgrouse density to environmental factors of the landscape. Our first approach was to fit GLMs with a Poisson probability distribution with a log link, but there was severe overdispersion in our data (theta= 9.03 for the pin-tailed sandgrouse and 6.39 for the black-bellied sandgrouse for models without interactions, and 134.9 and 52.0, respectively, for models including interactions). Hence, we fitted GLMs with a negative binomial probability distribution (Crawley 2007) with a log link function and surveyed area as an offset, which notably increased the fit (exp. deviance increased 11% for the pin-tailed sandgrouse, and 15% for the black-bellied sandgrouse) and reduced overdispersion (ϕ =1.05 and 1.17, respectively) . First, we tested whether there were differences in species density per region. Second, we assessed the relationship between both species density within each region, using the density of one of the sandgrouse species as a dependent variable, the density of the other sandgrouse species as covariate, region as a factor and the interaction between the covariate and the factor (region). We also tested for differences in the density of each species between allopatric and sympatric squares in each region. Subsequently, we built environmental models using the 11PC's as explanatory variables, region as a factor, and their interactions. This allowed us to assess which factors are important at explaining sandgrouse density, and if their effect differed depending on the region (interaction). If our best global model included interactions, we built models per region, including all PC's and the density of the pin-tailed sandgrouse (DPTS) or of the black-bellied sandgrouse (DBBS) as dependent variables. Model selection was done starting with the most complex model (with interactions), dropping one term at a time and comparing competing nested models by means of likelihood ratio tests (LRT) until reaching the most explanatory model with all terms with $P(\chi^2) < 0.05$ (the one that explained the most deviance) (Zuur et al. 2009). We repeated this procedure until we obtained 8 models, one per species including the whole set of squares (2 global models), and one per species and region (6 regional models).

Statistical analyses were performed using R 2.14 statistical software(R Development Core Team 2012).

Results

No significant differences in sandgrouse density existed between the three categories of survey effort for each region ($F_{4,\ 306}$ = 1.96, P=0.100 for the pin-tailed sandgrouse and $F_{4,\ 306}$ = 0.63, P=0.639 for the black-bellied sandgrouse).Precision did not improve with survey effort: SE_{25th}= 0.67; $SE_{25th\text{-}75th}$ = 0.46 and SE_{75th}= 0.63 for the pin-tailed sandgrouse, and SE_{25th}= 0.37; $SE_{25th\text{-}75th}$ = 0.26 and SE_{75th}= 0.35 for the black-bellied sandgrouse, so all squares (N=315) were included in subsequent analyses.

Globally, the black-bellied sandgrouse was more widely distributed (76% of squares, N=315) than the pin-tailed sandgrouse (59% of squares, N=315). Regionally, in CLM the pin-tailed sandgrouse was present in more squares than the black-bellied sandgrouse (74% vs 54% of squares, respectively, N=112), but in the other two regions the black-bellied sandgrouse occupied notably more squares than the pin-tailed sandgrouse (88% vs 58%, N= 120 in VEBR and 88% vs 39%, N=83 in EXT). The overlap between both species' distributions in the regions considered is 34% (Fig. 1), with the pin-tailed sandgrouse being in sympatry more frequently (58% of squares) than the black-bellied sandgrouse (45% of squares), indicating that the environmental conditions are suitable for the establishment of both species over a large area within the actual range of the pin-tailed sandgrouse. In particular, both species are frequently found in sympatry in the Ebro Valley (46%) whereas the overlap is notably lower in CLM (28%) and EXT (27%, Fig.1).

Niche position, niche breadth and niche overlap in allopatry and sympatry

The PCA resulted in eleven principal components that explain 70.9% of the total variance. The factor loadings, eigenvalues and percentage of variation explained by the PCA are shown in Table OR1 (Online Resource 2) and the interpretation of each axis on basis of the loadings of each variable is given in Table 2.

Table 2. Interpretation of the Principal Components. See Table 1 for explanation of the variables and Online Resource 2(Table OR2) for a full table with loadings, eigenvalues and explained variance of the PCA).

PC	Variables with loadings > 0.4	Variables with loadings < -0.4	Interpretation	Type of factor
PC1	P,T, TJn, Mix, Past, Div	Agr	Gradient running from heterogeneous landscapes with wet and warm climate covered by pastures and mixed forest-shrublands (semi-natural vegetation) towards agricultural landscapes	Abiotic/Land use
PC2	Pwr1, PopGro, Pwr2		Areas that have developed quickly in 2000-2005, with high population growth and density (urban sprawl and infrastructure development)	Anthropogenic
PC3	TJu, T	S, For, DFru, Shr	Hot arid landscapes (Mediterranean climate) vs rugged landscapes with forests, dry fruit groves and shrublands	Abiotic/Land use
PC4	Urb, PopDens, High, SRoad		Highly populated and developed urban areas with linear infrastructures	Anthropogenic
PC5	NPa, Oli	PaS, AgrPas, Agr	Areas with a high number of patches of any land use, high percent cover of olive groves (agricultural mosaic, no land consolidation) vs areas with large patches of any land use and large patches of arable lands (vast extents devoted to agriculture/land consolidation)	Land use
PC6	Vin	AgrPerim, NAgr, Agr	Vineyards vs Arable lands with small field size (traditional arable lands, no land consolidation)	Land use
PC7	Fru, Irr, Div		Irrigated areas with high cover of fruit groves and high land use diversity	Land use
PC8		HRail	Areas with high length of high speed railways	Anthropogenic
PC9	Wat, Shr, TJn, T	A, Vin	Warm lowlands with a high amount of water reservoirs and rivers covered by shrublands (valleys) vs highlands covered by vineyards	Abiotic/Land use
PC10	Pwr4, Rail, PRoad, Pwr2, High		Linear infrastructures outside of urban areas	Anthropogenic
PC11	Pwr3		Areas with high amount of medium to low tension powerlines	Anthropogenic

The principal components PC1 and PC3 were clearly related to abiotic and land use variables whereas anthropogenic variables fell principally within PC2 and PC4. The first principal component (PC1) represented a gradient from natural vegetation (pastures/mixed forest-shrublands) to agricultural landscapes with clear climatic relationships: the more a species tended to be positioned towards natural habitats, the wetter and warmer (Temperate) was its climatic position (Fig 2a).

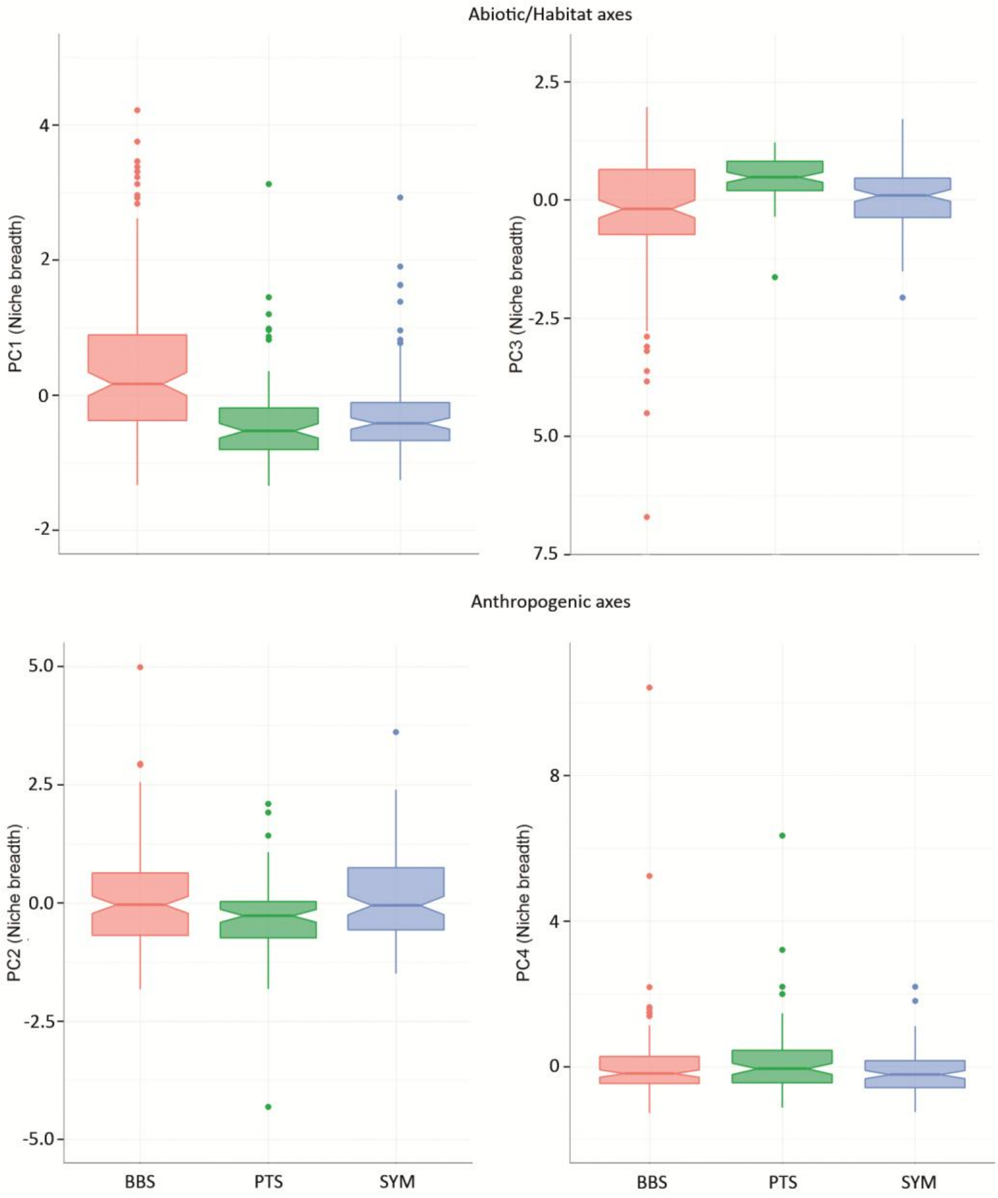

Figure 2. Niche breadth and position of the black-bellied sandgrouse (BBS) and the pin-tailed sandgrouse (PTS) in allopatric sites and in sympatric sites (SYM) along the 4 main PCA axes. a) and b) represent the main abiotic/habitat axes (PC1 and PC3); c) and d) represent the main anthropogenic axes (PC2 and PC4). The box shows the interquartile range (IQR, the 25th and 75th percentiles). Whiskers = 75th percentile + 1.5 * IQR and 25th percentile - 1.5 * IQR. Data beyond the end of the whiskers are outliers and plotted as points. Non-overlapping notches are roughly equivalent to 95% confidence intervals, and therefore provide strong evidence that the medians differ (McGill et al. 1978).

In turn, climate and land use also defined the PC3, with niches associated with rugged landscapes with arboreal vegetation contrasting with the opposite extreme characterized by hot areas (Mediterranean climate) (Fig 2b). Additional land use and climatic variables were retained in principal components with less explained variance (PC5, PC6, PC7 and PC9), while the rest of axes were related to anthropogenic variables (PC8, PC10 and PC11).

When we contrasted the niche positions in PC1 and PC3 between sympatry, allopatry for the black-bellied sandgrouse and allopatry for the pin-tailed sandgrouse, we found significant differences for both PC scores (ANOVA PC1: $F_{2,\ 312}$= 27.58, P< 0.001; PC3: $F_{2,\ 312}$= 13.71, P< 0.001). A Tukey HSD (P<0.05) test revealed that allopatric black-bellied sandgrouse sites are substantially wetter and warmer and positioned along the gradient towards more natural habitats than sympatric and pin-tailed sandgrouse sites. In turn, allopatric pin-tailed sandgrouse sites appeared more similar to sympatric sites (PC1, Fig. 2a), which was further confirmed by the niche overlap analyses (Table 3). Also, pin-tailed sandgrouse sites are characterized by a hotter climate, particularly in the summer, than black-bellied sandgrouse sites, which seem to be more tolerant to rugged landscapes with arboreal vegetation, whereas sympatric sites occupy an intermediate position (PC3, Tukey HSD test: P<0.05, Fig. 2b). Thus, niche overlap was higher between allopatric and sympatric sites than between allopatric sites (Table 3). Niche breadth was substantially wider for allopatric black-bellied sandgrouse for both PC's, whereas the pin-tailed sandgrouse's niche was narrower, particularly for PC3.

As seen, both species shifted their niches in sympatric sites, but the black-bellied sandgrouse also narrowed it for both PC's. As a result, climatic and habitat niches (PC1, PC3) differ both in their position and in their breadth between allopatric pin-tailed sandgrouse, allopatric black-bellied sandgrouse and sympatric sites (Fig. 3).

Regarding the anthropogenic axes (PC2 and PC4), there were significant differences between allopatric and sympatric sites for PC2 (ANOVA PC2: $F_{2,\ 312}$= 5.16, P= 0.006) but not for PC4 (ANOVA PC4: $F_{2,\ 312}$= 2.39, P= 0.093), with high niche overlap between the three situations (Table 3). In the case of PC2, allopatric pin-tailed sandgrouse sites were significantly different from allopatric black-bellied sandgrouse and from sympatric sites (Tukey HSD test: P<0.05), with niche overlaps (NO) of 0.76 and 0.77, respectively, whereas no statistical differences were found between black-bellied sandgrouse in allopatric sites and in sympatric sites (NO=0.93, Table 3).

Table 3. Niche overlap between sympatric (SYM) and allopatric squares (PTS: pin-tailed sandgrouse and BBS: black-bellied sandgrouse) for 11 environmental axes defining their main distribution areas in Spain. Niche overlap was calculated for the three regions and for each region. Statistically different niches, as identified by null model tests, are indicated in bold (P < 0.05).

	ALL REGIONS			**CLM**			**VEBR**			**EXT**		
	SYM/PTS	SYM/BBS	PTS/BBS	SYM/PTS	SYM/BBS	PTS/BBS	SYM/PTS	SYM/BBS	PTS/BBS	SYM/PTS	SYM/BBS	PTS/BBS
PC1	0.86	**0.63**	**0.58**	0.79	**0.60**	**0.59**	0.72	**0.69**	**0.54**	0.76	0.70	0.77
PC2	**0.77**	0.93	**0.76**	0.90	0.77	**0.73**	**0.66**	0.88	**0.67**	0.62	0.86	0.69
PC3	**0.70**	**0.76**	**0.54**	0.80	**0.48**	**0.32**	0.68	**0.66**	**0.48**	0.86	**0.64**	0.74
PC4	0.87	0.92	0.90	0.74	0.80	0.83	0.78	0.86	0.71	0.63	0.76	0.79
PC5	0.92	0.92	0.91	0.84	**0.60**	**0.67**	**0.60**	0.83	**0.53**	0.68	0.87	0.64
PC6	**0.78**	0.88	0.85	**0.70**	0.85	**0.74**	0.87	**0.75**	0.80	0.78	0.76	0.67
PC7	0.87	0.88	0.93	**0.69**	0.88	**0.75**	0.90	0.86	0.84	0.63	**0.56**	0.65
PC8	0.83	0.91	0.87	0.89	0.81	0.84	0.87	0.82	0.74	0.83	0.81	0.82
PC9	**0.69**	0.90	**0.68**	0.79	0.80	0.75	0.88	0.87	0.84	0.78	**0.60**	0.70
PC10	0.90	0.87	0.93	0.82	0.85	**0.72**	0.82	0.77	0.80	0.91	0.76	0.74
PC11	0.85	**0.76**	**0.78**	0.78	**0.64**	**0.54**	**0.59**	**0.66**	**0.51**	0.88	**0.64**	0.60
Mean	**0.82**	**0.85**	**0.79**	**0.79**	**0.73**	**0.68**	0.76	**0.79**	**0.68**	0.76	**0.72**	0.71
(SD)	**(0.08)**	**(0.09)**	**(0.14)**	**(0.07)**	**(0.13)**	**(0.15)**	(0.12)	**(0.09)**	**(0.14)**	(0.11)	**(0.10)**	(0.07)

The combination of both PC's in multispace reflects that both species avoid areas of high human pressure, evidenced through high human population density, urban areas and major transport infrastructures (positive values of PC4), but they still seem to tolerate areas where human population is growing and energy infrastructures are expanding (positive values of PC2) (Fig. 3).

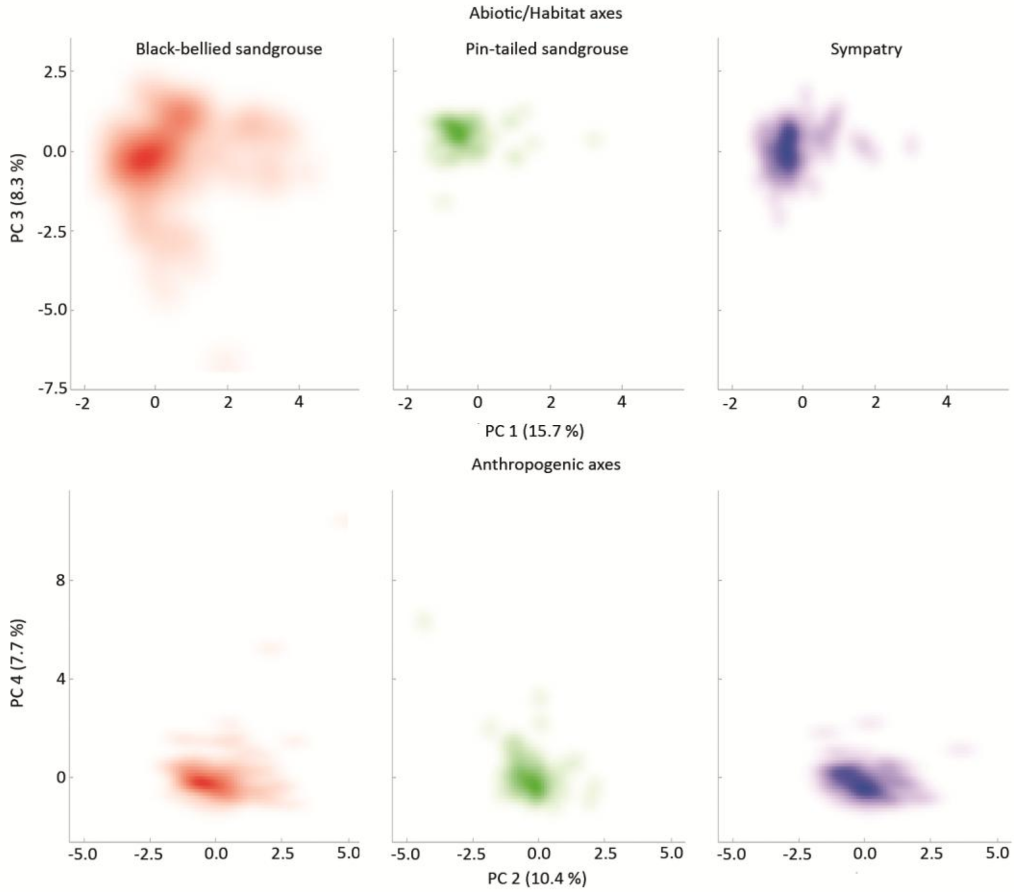

Figure 3. Niche of the black-bellied sandgrouse and the pin-tailed sandgrouse in allopatry and sympatry along the PC1 and PC3 (Habitat and abiotic niche) and along the PC2 and PC4 (anthropogenic niche). Colour shading shows the density of occurrences of the species by square.

Population density and regional niche variation

Density of both species greatly differed among the three regions considered (DPTS: $F_{2, 312}$= 13.49, P < 0.001; DBBS: $F_{2, 312}$= 14.04, P < 0.001; Fig 4). DPTS was significantly higher in CLM (Mean num. sandgrouse/km^2 ± SE: 5.72 ± 0.73) than in EXT (1.69 ± 0.35; Tukey HSD test, P < 0.001) and in VEBR (3.10 ± 0.39; Tukey HSD test, P < 0.001), but similar in the last two regions (Tukey HSD test, P = 0.178; Fig. 4a).

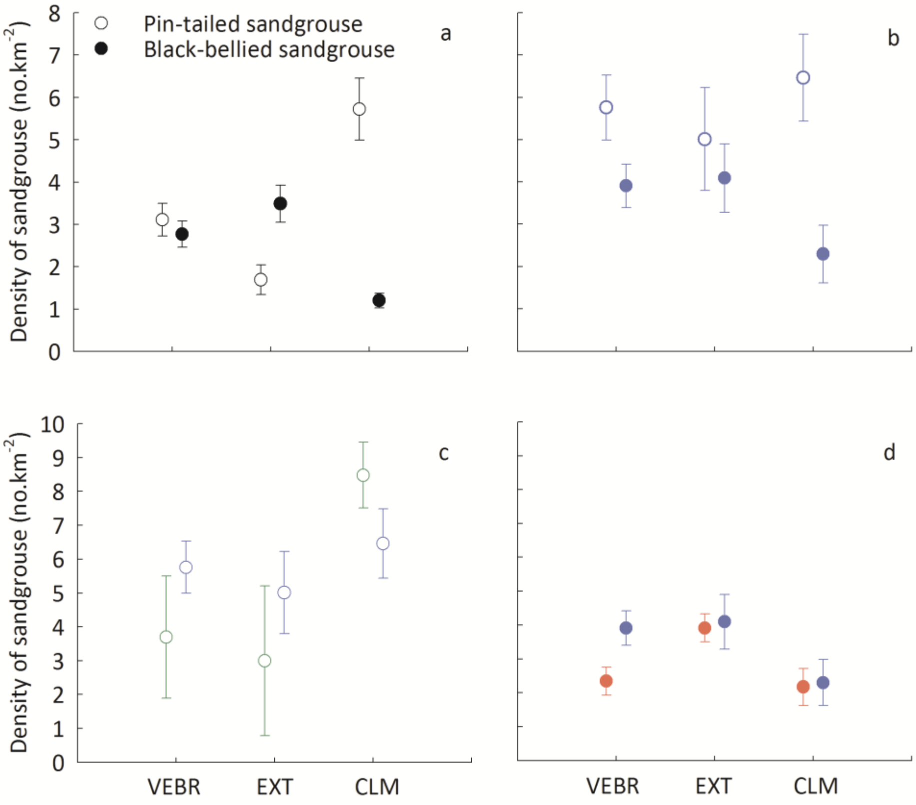

Figure 4. Density (mean ± SE) of the pin-tailed sandgrouse (open circles) and of the black-bellied sandgrouse (filled circles) in each region for (a) all sites (black), for (b) sympatric sites (blue) (c) for pin-tailed sandgrouse in allopatric (green) and sympatric sites(blue) and (d) for black-bellied sandgrouse in allopatric (red) and sympatric sites (blue)

On the contrary, in CLM, DBBS was significantly lower (1.20 ± 0.17) than in EXT (3.49 ± 0.44, Tukey HSD test, $P < 0.001$) and VEBR (2.77 ± 0.31, Tukey HSD test, $P < 0.001$), being similar in these two last regions (Tukey HSD test, $P = 0.239$; Fig. 4a). The pin-tailed sandgrouse was more abundant than the black-bellied sandgrouse in CLM, whereas the latter was more abundant in EXT than the former (Fig. 4a). When considering only sympatric sites, the density of the pin-tailed sandgrouse was higher than the density of the black-bellied sandgrouse in CLM and in VEBR (Fig. 4b).

There were no differences in sandgrouse densities between sympatric and allopatric sites (DPTS: $F_{2,179} = 2.00$, $P=0.138$; DBBS: $F_{2,232} = 1.25$, $P = 0.287$), although in CLM the DPTS tended to be higher in allopatric sites (8.48 ± 0.87) than in sympatric ones (6.46 ± 1.13, Fig. 4c); and in VEBR, where DBBS was higher in sympatric than in allopatric sites (Fig. 4d). Actually, the densities of both species were negatively related in CLM (slope ± SE: -0.20 ± 0.09, $P=0.026$) but positively, although not significantly, in VEBR (0.07 ± 0.04, $P = 0.108$).

Niche space occupied by the two species also varied regionally (Fig. 5, Table 3), with variations in niche positions and niche breadth along some environmental and anthropogenic axes and between sympatric and allopatric sites.

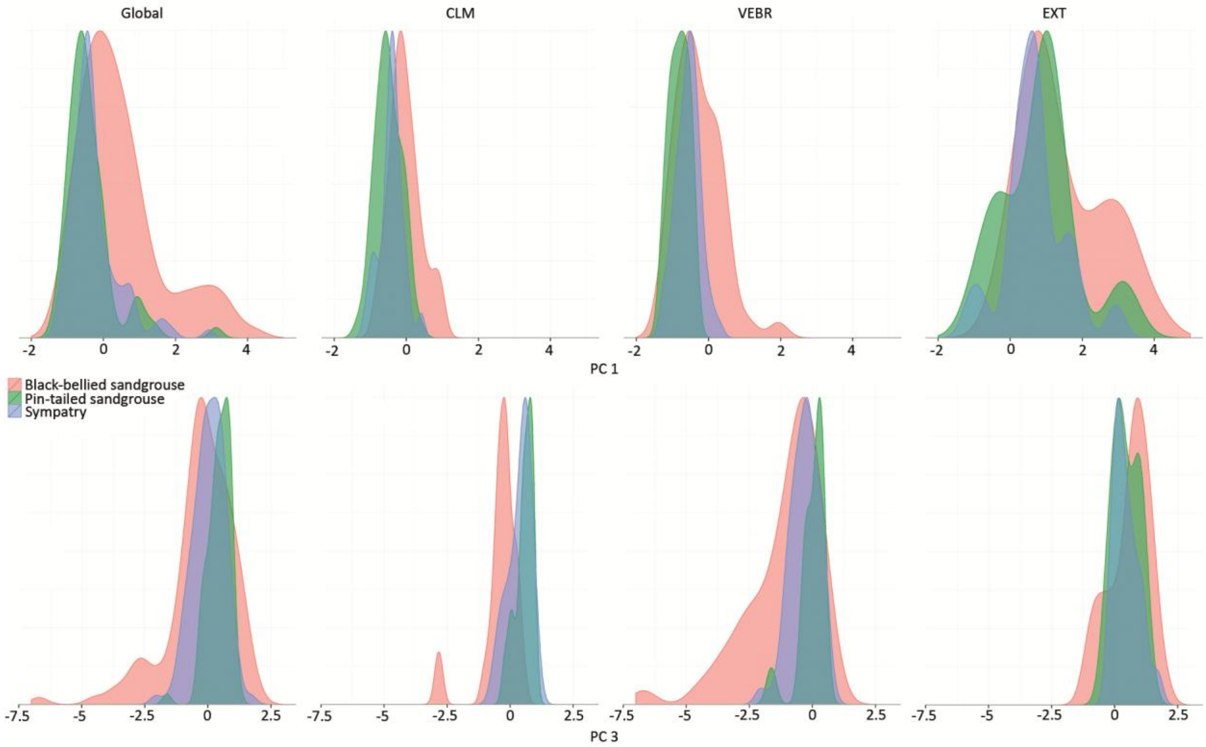

Figure 5. Niche breadth (represented by a kernel density plot) along the PC1 and PC3 for sympatric squares and allopatric squares of the pin-tailed sandgrouse and of the black-bellied sandgrouse. Niche breadth is shown for all regions (global) and for each region

In CLM, where the relationship between the densities of the two species is negative, both species seem to occupy a narrower niche for the main environmental gradients (PC1 and PC3, Fig. 5) than globally, reflecting the more restricted range of environmental conditions in this region. Also, the black-bellied sandgrouse niche is clearly positioned towards the opposite side of sympatric and allopatric pin-tailed sandgrouse sites. As a result, niche similarity for the main environmental axes between allopatric black-bellied sandgrouse and allopatric pin-tailed sandgrouse is minimum (Table 3). In this region, the slight niche overlap observed between sympatric and allopatric black-bellied sandgrouse sites suggests that the black-bellied sandgrouse shifted its niche when in sympatry (Table 3, Fig. 5). On the contrary, both species seem to expand their environmental niches in EXT region, which are not only broader but also positioned towards positive values of the PC1 (natural habitat with temperate climate) (Fig. 5). Also, there is a substantial overlap between the niche spaces occupied by both species, both in sympatry and allopatry. Finally, in VEBR region, where the densities of the two species are positively related, niche overlap is low among allopatric black-bellied sandgrouse and allopatric pin-tailed sandgrouse sites, and both species shift their niches when in sympatry, achieving higher densities than in allopatric sites (Fig. 4).

The importance of environmental and anthropogenic factors

The best global models for the densities of the pin-tailed sandgrouse and of the black-bellied sandgrouse explained 29.6% and 24.5% of the deviance, respectively. There were significant interactions between some environmental factors (PC´s) and region for both species, indicating that the effect of those factors on density differed between the three regions (Online Resource 2, Table OR2 and OR3). In general, DPTS was mostly explained by the interaction PC3 x region ($\chi^2 = 32.18$, $P < 0.001$) and PC1 ($\chi^2 = 26.08$, $P < 0.001$). In turn, DBBS was mostly explained by the interactions PC7 x region ($\chi^2 = 21.10$, $P < 0.001$), followed by PC10 x region ($\chi^2 = 13.21$, $P = 0.001$), being slightly more explanatory than the rest. Given the strong effect of the interactions, we further explored the relationship between sandgrouse density and environmental factors within each region.

The best regional models for the pin-tailed sandgrouse and the black-bellied sandgrouse explained 40.9% and 24.3% (CLM), 21.6% and 13.9% (EXT) and 19.6% and 10.5% (VEBR) of the deviance, respectively (Table 4). Interestingly, the most explanatory principal components in each region differed per species and, if the same component entered the model for both species, it had a different sign (i.e.: PC5 in EXT), except for the anthropogenic gradients PC4 in EXT and PC10 in CLM (Table 4). Thus, in CLM and VEBR the highest densities of the pin-tailed sandgrouse were associated with hot arid flatlands with low cover of forests, dry fruit groves and shrublands (PC3, Table 4), whereas no significant relationship was found for the black-bellied sandgrouse. In turn, in CLM, DBBS was mostly influenced by the PC7 (low densities in heterogeneous areas under irrigation, covered by fruit groves), by the PC10 (negatively related with high levels of lineal infrastructures).

Table 4. Overview of the factors explaining the density of the pin-tailed sandgrouse (PTS) and the black-bellied sandgrouse (BBS) in each region. The estimates ± SE for the explanatory factors and the % of deviance explained by each model are given. Values in bold denote the factors that explained the most deviance in the model according to likelihood ratio tests (LRT). DPTS and DBBS are the density of the pin-tailed sandgrouse and of the black-bellied sandgrouse, included as covariates in the models.

	CLM				**VEBR**				**EXT**			
PC	**PTS**		**BBS**		**PTS**		**BBS**		**PTS**		**BBS**	
	Estim. ± SE	**LRT (*P*(χ^2)**	**Estim. ± SE**	**LRT (*P*(χ^2)**	**Estim. ± SE**	**LRT (*P*(χ^2)**	**Estim. ± SE**	**LRT (*P*(χ^2)**	**Estim. ± SE**	**LRT (*P*(χ^2)**	**Estim. ± SE**	**LRT (*P*(χ^2)**
Int.	0.04 ± 0.23		-0.09 ± 0.22		1.21 ± 0.20		0.72 ± 0.12		-0.24 ± 0.26		1.22 ± 0.10	
PC1	-1.01 ± 0.33	8.79 (0.003)										
PC2	**- 0.50 ± 0.14**	**13.31 (<0.001)**										
PC3	**1.40 ± 0.28**	**24.13 (<0.001)**			**1.08 ± 0.18**	**25.31 (<0.001)**						
PC4			-0.33 ± 0.12	6.37 (0.012)					0.95 ± 0.40	6.38 (0.012)	**0.44 ± 0.18**	**6.64 (0.010)**
PC5			-0.38 ± 0.16	6.00 (0.014)			0.23 ± 0.11	4.01 (0.045)	-0.56 ± 0.19	6.67 (0.010)	**0.22 ± 0.09**	**5.60 (0.018)**
PC6												
PC7			**-1.01 ±0.26**	**14.47 (<0.001)**					**-1.38 ± 0.30**	**16.65 (<0.001)**		
PC8												
PC9												
PC10	-0.31 ± 0.13	5.34 (0.021)	**-0.56 ± 0.18**	**11.11 (0.001)**								
PC11	**0.54 ± 0.13**	**12.32 (<0.001)**										
DPTS			-0.05 ± 0.03	6.30 (0.012)			**0.06 ± 0.02**	**12.78 (<0.001)**				
DBBS	-0.19 ± 0.07	7.12 (<0.008)			0.08 ± 0.04	8.30 (0.004)						
%Tot. Exp. Dev	40.9%		24.3%		19.6%		10.5%		21.6%		13.9%	

Also, the negative relationship between sandgrouse densities sustained even when controlling for the environmental conditions. In VEBR, DBBS was mostly explained by DPTS, but in this case, such as in the models without environmental gradients, the relationship was positive. In the case of EXT, DPTS was the highest in areas with low irrigation, low cover of fruit groves and low land use diversity (PC7) and DBBS was positively associated with urban areas, human population density and linear infrastructures (PC4) and agricultural mosaics with olive groves interspersed among different land uses PC5).

Discussion

Our analysis of the ecological niches of two closely-related sandgrouse species based on the most informative climatic and anthropogenic variables across their principal distribution areas has allowed us to evaluate different mechanisms by which closely-related species distribute and coexist. The examination of the position of both species in multivariate ecological space reveals that they occupy distinct realized environmental niches in sympatry and in allopatry, particularly for the main environmental gradients comprising climatic and habitat variables (natural vs agricultural). Thus, the black-bellied sandgrouse preferably occupies wet sites that are exposed to warmer winter temperatures, characterized by heterogeneous landscapes ranging from pasturelands to agrarian substrates. In turn, the pin-tailed sandgrouse distributed preferably over flat agricultural landscapes with high temperatures, which seemingly represent the upper thermal limit of its counterpart. Additionally, the black-bellied sandgrouse is more widely distributed than the pin-tailed sandgrouse, which in turn is more abundant at certain locations. Our niche comparisons considered only two related species across a small region within their whole geographical range and thus should not be overgeneralized. However, such a restriction did not hamper our ability to test several alternative explanations when exploring the niche-related hypotheses.

Several non-mutually exclusive mechanisms may explain sandgrouse distribution and population density, including variations in niche breadth and niche position, and interspecific relationships. A wider niche breadth allows the black-bellied sandgrouse to exploit a wide range of environmental conditions and it is thus distributed more widely, being abundant in some localities (niche-breadth hypothesis) (Gaston and Lawton 1990; Hanski et al. 1993; Slatyer et al. 2013). Evolutionary and ecological processes including past niche shifts have possibly been involved in widening the habitat and climatic tolerance of this species. Black-bellied sandgrouse's larger size, home range and dispersal distances (authors, unpublished data) has probably allowed this species to reach and colonize areas which were inaccessible for the smaller-sized pin-tailed sandgrouse, settling in new environments, either because they were part of the fundamental niche (ecological process) or because an actual shift in both realized and fundamental niches occurred (evolutionary process) (Eriksson 2013). The more restricted distribution of the pin-tailed sandgrouse seems thus to be associated to its narrower niche breadth, and it is consistent with the idea that, based on energetic reasons, smaller species should require less space to maintain viable populations (Brown 1995). Given the broader niche breadth of the black-bellied sandgrouse, both species co-occur frequently within the pin-tailed sandgrouse's geographic range (58% of sympatric sites within its range). Sympatric sites are positioned at intermediate climates and habitats (relative to allopatry), suggesting that the abiotic environment is the primary factor mediating co-occurrence between sandgrouse and the main driver of both species' range, such as for other species (Swenson 2006; Walls 2009).

Ecological niche differences between allopatry and sympatry along several niche axes are further corroborated at regional level, and are reflected in the results of the regional density models. Environmental niches differ substantially between allopatric sites in two regions (CLM and VEBR), but are similar in the other region (EXT). Interestingly, in the two regions where allopatric sites differ the most the relationships between the densities of both species are opposite and their distributions differ (Fig. 1, 4). Additionally, the most explanatory principal components in each region differ per species or have different signs. The density of the pin-tailed sandgrouse is highly influenced by habitat and climatic gradients, whereas black-bellied sandgrouse's density is particularly influenced by habitat gradients and, overall, by the density of its congeneric. Furthermore, the density of both species is higher in regions where their distribution is wider, supporting the positive regional distribution-density relationship (Heino 2005).

The black-bellied sandgrouse attains the highest densities both in allopatry and sympatry in EXT, which are similar to densities in sympatric sites in VEBR. This suggests that environmental conditions in EXT are the most adequate for this species, and that in areas where the environment is less optimum (VEBR) the interaction with the other congeneric species may foster the black-bellied sandgrouse's performance (in terms of abundance). Indeed the main factor explaining the density of the black-bellied sandgrouse in this region is the density of its counterpart. Additionally, the environment in sympatry tends to be more similar to allopatric pin-tailed sandgrouse than to allopatric black-bellied sandgrouse, which is further consistent with the idea that association with the pin-tailed sandgrouse may facilitate the abundance of the black-bellied sandgrouse in this region. Thus, although abiotic conditions primarily set the regions of co-occurrence, biotic interactions should not be neglected. The more generalist and less abundant black-bellied sandgrouse may be using the presence of the more specialist and more abundant pin-tailed sandgrouse as a heterospecific cue to inform about the availability of suitable habitats and mutually beneficial resources at a finer scale (availability of feeding grounds, water points, shelter from predators…) (i.e.: Sridhar et al. 2009; Martín et al. 2010) for establishment of new populations (sandgrouse are nomadic and partial migrants Benítez-López et al. 2010; Casas et al. 2012). Given the low deviance of the model when accounting only for large-scale environmental variables, it seems reasonable that the density of the black-bellied sandgrouse may be further explained by fine-grained variables in this region. A more detailed study at a finer scale would help us elucidate whether behavioural patterns are facilitating the coexistence and performance of the black-bellied sandgrouse in least adequate environments, or it is just a consequence of the local convergence of ecological conditions.

Although intuitively the niche breadth hypothesis may explain the narrower niche breadth and more restricted distribution of pin-tailed sandgrouse, the niche-position hypothesis should not be disregarded as it seems to fit the density-distribution relationship equally, at least in CLM. In this region, which is the core area of the distribution and holds a continuous extent of highly suitable sites (Benítez-López et al. 2013), the pin-tailed sandgrouse holds the highest densities both in sympatry and in allopatry (i.e.: “abundant centre” distribution hypothesis, Brown 1984); and it is more widely distributed than in the other regions, yet keeping a narrow niche. Therefore, it seems that its niche position matches the environmental conditions in this region, fostering its abundance. Indeed, constant environmental conditions during a species lifetime favour species with high level of Grinnellian specialization (Levins 1968). Additionally, the density of the pin-tailed sandgrouse is higher in allopatric squares than in sympatric squares and both species densities are negatively related. This relationship is not fully supported statistically when analysing only sympatric squares, so one could think that this might be an artefact derived of pin-tailed sandgrouse’s wider distribution in this region (the black-bellied sandgrouse is absent in more squares than the pin-tailed sandgrouse). Following this idea, a similar pattern should arise in VEBR where the distribution of the black-bellied sandgrouse is wider and there are more squares where the density of the pin-tailed sandgrouse is zero, however, the opposite occurs. Thus, in CLM, the presence of the pin-tailed sandgrouse does not attract the black-bellied sandgrouse, probably because the environmental conditions in the pin-tailed sandgrouse allopatric sites fall beyond the environmental limits of the black-bellied sandgrouse (most likely, thermal limits; Benítez-López et al. 2013; Hinsley et al. 1993)). Hence, the negative relationship between both species' densities in CLM appears to be driven by dissimilar environmental requirements, leading to partial niche segregation. Additionally, conspecific interactions might be involved in the process of habitat occupancy, with individuals of the pin-tailed sandgrouse aggregating in squares with specific environmental conditions, resulting in higher densities in allopatry.

Both species seem to expand their environmental niches in EXT region, which are not only broader but also positioned towards positive values of the PC1 (natural habitat with temperate climate). Actually, this is the region where the environmental conditions are the most different compared to the other regions, with more availability of natural habitats (Online Resource 1, Table OR4). As stated before, the performance of the generalist black-bellied sandgrouse is the highest in this region, seemingly because, within it wide niche, the environmental conditions in this region match better its requirements. In turn, the pin-tailed sandgrouse appears to thrive in these environments by niche shifts and variations in niche breadth, such as other specialists (see Devictor et al. 2010), and by partial association with the black-bellied sandgrouse in sites with less natural habitat (agriculture).

Both sandgrouse species are positioned on the negative end within the 'anthropogenic niches', avoiding densely populated urban areas and major transport infrastructures, and partially tolerating areas of increasing growth of human population and development of energy infrastructures (corresponding with Spanish rural areas). One of the novelties of this work is the inclusion of the human dimension within the species niche. Species niches are usually defined in terms of climate (climatic niche) or habitat (habitat niche), or both (Barnagaud et al. 2012). It can be argued that the habitat niche already considers partly the anthropogenic influence (most current landscapes have been shaped by humans; i.e.: cultural landscapes, Eriksson 2013), however, if we are to define contemporary species niches, the anthropogenic dimension should be included formally given the widespread modification of the environment as a result of human activities. This will allow us to predict more accurately species response to global change (climate change plus land use change, including urban sprawl and infrastructure development).

The blending of ecological niche modelling, abundance modelling and species interactions can guide greater insight into the factors that affect species co-occurrence and has great potential for application to multi-species bird conservation programs.Our results display a clear example of how different mechanisms act synergically to allow the coexistence of closely-related species. Thus, although at large scale abiotic factors seem to mediate areas of co-occurrence between sympatric species, biotic interactions should not be disregarded, and can even become more important than the former in some cases (Chunco et al. 2012). In view of our results, we may conclude that the niche-breadth hypothesis seems to fit the black-bellied sandgrouse distribution and the pin-tailed sandgrouse distribution globally, whereas the niche-position hypothesis explains why both species attains high densities in regions with optimum environmental conditions, achieving wide regional distributions if such conditions are widespread. Finally, biotic interactions may play a role in the achievement of higher densities of the black-bellied sandgrouse when environmental conditions are neither optimum for any of the two sandgrouse, but similarly conducive. In this sense, we recommend the inclusion of biotic interactions in species distribution models which will most likely improve the predictions of responses of interacting species to climate and land use change in allopatric and sympatric scenarios.

Acknowledgements

Financial support was provided by the Dirección General de Investigación (project CGL2008-04282/BOS) and HNV project (Spanish Ministry of Rural and Marine Environment). SEO/Birdlife provided data from sandgrouse national census. Ana Benítez-López was supported by the 2012-BIN-4462 research grant conceded by the UCLM. We thank Fidel Sánchez for his help at some stages during the process of data compilation and analyses in ArcGIS 9.3.

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Supplementary material

Online Resource 1. Detailed description of the methods.

Species and environmental data

We extracted species data from the 2005 *National Breeding Sandgrouse Survey* (NBSS), coordinated by the Sociedad Española de Ornitología (SEO)/BirdLife (Suárez et al. 2006), which is the most recent source of information for sandgrouse species in Europe. This survey was supervised by regional experts and performed during the sandgrouse breeding period (25th May to 31st June) by more than 300 trained and experienced ornithologists. The sampling and analysis unit was the UTM 100 km^2 square, and the survey method was the line transect. Each ornithologist was provided with a map of the square (10 × 10 km^2) to be surveyed, and specific instructions in order to assure there were no differences between censuses performed by different ornithologists (see Annex in Suárez et al. 2006). The starting point of line transects was randomly determined, but the protocol indicated that sampling effort should be focused on habitats *a priori* favourable for sandgrouse (open areas, avoiding forests), according to existing scientific knowledge on habitat requirements (Herranz and Suárez 1999). The transects were carried out on windless, rainless days, walking cross country or following little–used dirt tracks at a low speed (1–3 km/h approximately), in the 4 hours after dawn and the 2.5 hours before dusk. For each detected bird or flock (hereafter sighting), the distance perpendicular to the observer's trajectory (line transect) was estimated. Distances were not truncated in the field. Line transects and sightings were georeferenced to avoid transect overlaps. Every square was surveyed 1–2 times (different days or daytimes) using line transects (1-5 per square) in a stratified way: sampling effort (cumulative transect length) matched the proportion of adequate habitat within the square. In total, 1736 transects comprising a total length of 5694 km were surveyed. From all surveyed squares (N=665) we extracted 315 (2874 km of transects) covering the three study regions (see Benítez-López et al. 2013 and Suárez et al. 2006 for further details about the survey).

Given the high variability in transect length, the fact that transects were not repeated and that many of them were spatially contiguous, the cumulative transect length per square was used to measure survey effort (Suárez et al. 2006) and to estimate the surveyed area within a square. We calculated the density of the species in each square (expressed in birds per km^2) assuming that the detectability of the individuals did not differ among squares. This is a plausible assumption, given that these birds are exclusive of open habitats, where detectability should not be highly variable (see recommendations in Bibby et al. 1998). Given that detectability of each species could be different due to differences in body size, social behaviour or habitat selection (see Benítez-López et al. 2013), we calculated one value of detectability per species, pooling all sightings from all squares and using the distribution of all sampled distances at which sightings were recorded (Thomas et al. 2006). We used sightings to estimate the loss of detectability instead of number of birds to avoid pseudorreplication. Detectability was estimated with a non-parametric approach (no *a priori* parametric function was fit, i.e.: half normal, hazard rate) assuming that it is maximum (detectability = 1, all birds are counted) in the closest perpendicular distance to the observer and it decreases as the distance from the observer increases (the further the distance the lower the probability of detecting an individual) (Bibby et al. 1998). This methodology was specifically developed for steppe bird census data that may be potentially subject to relatively large error in distance estimates obtained in open landscapes (with few reference points) and by multiple observers (Carrascal et al. 2010). The detection distances were right truncated excluding outliers (Buckland et al. 2001); i.e. disregarding the 5% of the longest perpendicular distances from the transect line, which, in our case, were those beyond 300 m for both species. We built histograms with all observations distributed at same-sized distance intervals (i.e.: 50 m interval, 0-50, 50-100-100-150,150-200,200-250,200-300 and >300 m) and annotated the number of sightings for each species in each interval. Then, all sightings were summed up and divided by the expected number of sightings we would have obtained if the detectability was maximum, i.e.: the number of sightings obtained in the first distance interval (0-50m) (Järvinen and Väisänen 1975), which gave us the detectability. Then we calculated the effective census strip width multiplying the truncation distance of 300 m by the calculated detectability) (see example below).

Estimation of detectability for the pin-tailed sandgrouse using data from the National Breeding Sandgrouse Survey of 2005 (NBSS) and a non-parametric approach.

Distances (m)	<50	50-100	100-150	150-200	200-250	250-300	>300
Observed sightings	265	247	89	99	21	42	52
Used for calculation	265	247	89	99	21	42	discarded
Expected sightings	265	265	265	265	265	265	
Detection Probability	1.00	0.93	0.34	0.37	0.08	0.16	

Truncation distance: 300 m
Detectability: (265+247+89+99+21+42)/(265x6)= 763/1590 = 0.48
Effective strip width (ESW): 300 m x 0.48 = 144 m at each side of the observer
Surveyed area: transect length (km) x 2 strips x 0.144 km (ESW)

Detectability was 0.48 for the pin-tailed sandgrouse and 0.39 for the black-bellied sandgrouse and thus the ESW was 144 m and 118 m at each side of the transect, respectively. The area surveyed in each square was then the transect length (km) x 2 x ESW (km).

The transect length varied per square (1.2-85 km per square, depending on the suitability of sandgrouse habitats within a square, i.e.: forests, high cereal crops and tall shrublands were avoided (Suárez et al. 2006), therefore we considered three categories to assess whether the precision of density estimates varied with survey effort. Squares with transect lengths below the 25% quartile (< 5.2 km per square) fell in the low survey effort category, and those with lengths over the 75% quartile (9.8 km per square) were allocated to the high survey effort category, with the rest of lengths corresponding to the intermediate survey effort category.

Kernel density estimation and niche overlap (extracted partially from Mouillot et al. 2005)

For each PC we calculated the niche breadth and niche overlap for squares where only one of the species occurred (allopatric squares) and for squares where the two species co-occurred (sympatric squares) using kernel density estimations (KDE) (Mouillot et al. 2005). This allowed us assessing how each species modify (or not) its niche for a certain environmental axis when coexisting with the other species. The KDE is non-parametric, and can be used when the distribution of the trait (for resources) or environmental gradient (i.e. its density function) is unknown. These estimates are based on Stine and Heyse (2001)’s work, replacing the overall unknown density function by a set of normal density functions (Fig. OR1).

Given *n* data from a sample of a continuous trait *X*: $x_1, x_2, \ldots, x_n$, the kernel density is:

$$f_h(x) = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{h}K\left(\frac{x - X_i}{h}\right) \qquad (1)$$

The non-parametric estimator of the density is calculated with the standard normal density function *K*, named kernel:

$$K\left(\frac{x - X_i}{h}\right) = \frac{e^{-\left(\frac{x - X_i}{h}\right)^2 \big/ 2}}{\sqrt{2\pi}} \qquad (2)$$

These kernels are centred on each data point and integrate to 1.0. Each kernel is divided by n to estimate the total kernel density (Equation 1) so that each area is 1/n and the area under the population density function is 1.0. *h* is the bandwidth which controls the smoothness of the estimator.

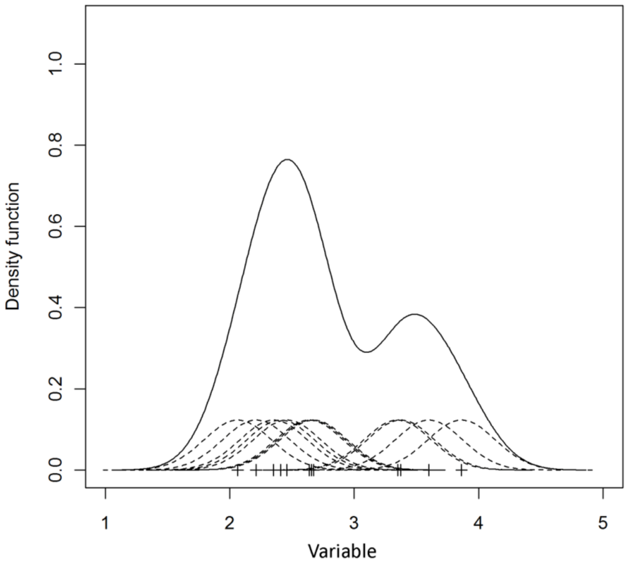

Figure OR1. Kernel density estimate for the distribution of a data set with 12 values. The population density is the sum of twelve kernel normal distributions for each observed data. (adapted from Tarn Duong, 2001).

Density estimation by the kernel method gives a smooth, flexible, non-parametric curve for a probability density function over the data points, and with the area under the curve equal to one. KDE allow modelling niche overlap from continuous data independently of the underlying distribution of the data. Kernel bandwidth was based on the standard deviation of the data set and the population size when applying normal kernel density to normal data (optimal bandwidth) (Silverman 1986). For continuous data, such as our PC's, niche overlap based on nonparametric kernel density functions (NO_K) on axis *pc* is calculated as:

$$NO_{K(i,j,pc_{ni})} = 1 - \frac{1}{2}\int | f_{ipc_{ni}}(x) - f_{jpc_{ni}}(x) | \, dx \qquad (3)$$

where $f_{ipc_{ni}}$ and $f_{jpc_{ni}}$ are the kernel population density functions for species *i* and *j*, respectively, and for the $pc_{ni.}$(adapted from Mouillot et al. 2005).

We produced three kernel curves (representing niche breadth) for each PC (two for allopatric squares and one for sympatric squares) and calculated the overlapped area between them (niche overlap), adapting the script provided by Geange et al. (2011) to our data (R Development Core Team 2012)). Mean niche overlap was obtained by averaging niche overlap

(NO) between allopatric and sympatric squares over each different axis (Mouillot et al. 2005) (eqn 4), where PC is the number of axes.

$$NO_{K(i,j)} = \frac{1}{PC}\sum_{pc=1}^{PC} NO_{K(i,j,pc)} \qquad (4)$$

NO is 0 when the two distributions are completely disjoint, and is 1 when they exactly coincide.

Permutation tests (extracted from Geange et al. 2011)

To rule out detecting as different two niches that only differ due to sampling variation, niche comparisons between two species must be done statistically to determine whether the same probability distribution describes the niche of two (or more) species, or whether there is evidence of some difference. On any axis *t*, species *i* has n_i readings $\{x_{i1};\ x_{i2};\ \dots\ x_{ini}\}$, which are realizations of the random variable X_{it}; similarly, species *j* has n_j readings $\{x_{j1};\ x_{j2};\ \dots\ x_{jnj}\}$,from the random variable X_{jt}. The observed readings are used to estimate the parameters and hence the probability structure of each distribution; however, even if the random variables X_{it} and X_{jt} are the same, sampling variation will almost certainly cause the sampled data values to differ, giving $NO_{ijt} < 1$. The question of interest is whether NO_{ijt} is sufficiently <1 to provide evidence of niche differentiation. The same argument applies to the combined *NO* measure, averaged over all the axes.

Because the assumptions of equal variance and normality are unlikely to be met, the use of null models and their associated permutation tests have been advocated (Gotelli 2000; Gotelli and Graves 1996). Null models use randomization or permutation tests which do not rely on distributional assumptions (Manly 2007). Calculating pseudo-values of the test statistic that would arise if H_o (no niche differentiation) were true generates the null distribution. This is achieved by permutating species labels over all species (i.e., average niche overlap over all species; in our case we permutated squares labels). The justification is that if all the species in question occupy the same niche (i.e.: allopatric and sympatric squares are the same), the actual labelling of each species is irrelevant. The position of the value of the data-based test statistic (*NO*) in relation to the pseudo-values provides the *P*-value for the test with a number of decimals according to the number of permutations (i.e.: 1000 permutations provide a *P*-value with 3 decimals).

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Online Resource 2

Table OR1. Factor loadings and eigenvalues resulting from the Principal Component Analysis (PCA) for 35 variables measured in 315 10x10 km squares. Loadings > 0.4 or < -0.4 are in bold.

Variable	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9	PC 10	PC 11
PopDens	-0.080	0.340	0.001	**0.722**	-0.064	0.049	-0.004	-0.296	0.036	-0.011	-0.007
PopGro	-0.140	**0.437**	-0.026	0.180	-0.022	0.104	0.274	-0.094	-0.382	0.014	0.315
A	-0.135	-0.282	-0.190	0.195	0.019	-0.030	-0.317	0.251	**-0.660**	-0.204	0.092
S	0.223	-0.072	**-0.763**	-0.081	0.232	0.103	-0.142	-0.077	0.072	-0.078	-0.047
P	**0.764**	-0.132	-0.113	0.033	-0.091	0.099	-0.142	0.245	0.053	-0.096	-0.142
T	**0.509**	0.021	**0.650**	-0.090	-0.009	0.255	-0.049	-0.083	**0.415**	0.073	0.018
TJn	**0.606**	0.158	0.390	-0.128	-0.015	0.190	0.006	-0.068	**0.518**	0.142	-0.034
TJu	0.329	-0.224	**0.719**	0.047	0.004	0.282	-0.225	0.017	-0.003	-0.106	0.096
High	-0.085	0.308	0.086	**0.499**	-0.043	0.050	0.170	-0.063	-0.217	**0.415**	0.127
Proad	0.020	0.224	-0.039	0.347	0.184	-0.012	0.101	-0.141	0.132	**0.456**	0.068
SRoad	0.062	-0.289	0.116	**0.687**	0.209	-0.052	0.011	0.269	-0.029	0.053	-0.073
HRail	-0.116	-0.019	-0.008	0.093	-0.050	-0.045	0.108	**-0.761**	-0.013	0.029	-0.043
Rail	0.059	-0.202	0.000	0.197	0.060	-0.147	-0.024	-0.261	-0.088	**0.669**	0.088
Pwr1	0.029	**0.693**	-0.008	0.060	0.017	-0.279	-0.111	0.089	0.023	0.041	-0.158
Pwr2	-0.123	**0.431**	-0.041	0.206	0.063	-0.079	0.029	-0.058	0.181	**0.427**	0.034
Pwr3	-0.030	-0.094	0.170	0.038	-0.171	-0.052	-0.001	0.055	-0.019	0.177	**0.760**
Pwr4	-0.128	0.110	0.055	0.034	0.072	0.006	0.072	0.240	-0.050	**0.768**	0.051
NAgr	-0.132	0.163	-0.128	0.079	0.354	**-0.786**	0.064	-0.029	-0.002	0.114	0.102
AgrPaS	0.150	-0.045	0.207	-0.084	**-0.601**	0.295	-0.071	0.141	0.173	-0.099	0.252
AgrPerim	-0.218	0.137	0.017	0.022	0.176	**-0.879**	-0.034	-0.034	-0.080	0.034	0.043
Vin	-0.230	0.093	0.280	0.107	0.324	**0.432**	0.063	0.254	**-0.441**	0.046	0.131
Urb	-0.017	0.058	0.048	**0.834**	0.089	-0.060	0.057	-0.041	-0.022	0.291	0.052
Irr	-0.333	-0.100	0.112	0.033	-0.168	-0.057	**0.664**	0.045	0.074	0.316	-0.161
Wat	0.043	-0.086	0.013	0.185	-0.120	0.060	0.123	0.288	**0.659**	-0.142	0.034
For	0.177	-0.089	**-0.697**	-0.015	-0.112	0.098	-0.069	-0.041	-0.104	-0.016	-0.223
DFru	-0.108	0.160	**-0.553**	-0.129	0.282	-0.077	0.266	0.190	0.098	0.030	0.219
Fru	-0.061	0.002	-0.057	-0.026	0.278	0.063	**0.674**	-0.208	0.168	-0.066	0.063
Oli	0.108	-0.122	0.309	0.041	**0.638**	0.233	-0.347	0.091	-0.117	-0.020	-0.062
Mix	**0.795**	-0.070	-0.084	-0.078	-0.082	0.148	-0.014	-0.081	-0.049	-0.029	-0.070
Shr	-0.074	0.043	**-0.423**	-0.142	-0.008	0.147	-0.331	-0.295	**0.527**	-0.116	0.306
Past	**0.703**	0.038	0.092	0.008	-0.128	0.052	0.059	0.085	0.110	-0.070	0.089
Agr	**-0.424**	-0.027	0.293	-0.101	-0.376	**-0.566**	0.144	0.089	-0.141	0.049	-0.217
Div	**0.434**	0.018	-0.070	0.262	-0.016	-0.089	**0.644**	0.028	-0.122	0.049	0.075
PaS	0.214	-0.010	0.047	-0.090	**-0.757**	0.245	-0.082	-0.011	0.083	-0.046	0.189
NPa	-0.083	0.038	-0.145	0.045	**0.842**	-0.100	0.122	0.089	0.053	0.132	0.089
Eigenvalue	5.5	3.7	2.9	2.7	2.1	1.7	1.6	1.3	1.2	1.1	1.0
%Cum. Explained Variance	15.7	26.1	34.4	42.1	48.3	53.2	57.9	61.5	64.8	68.0	70.9

Table OR2. Results of likelihood ratio tests (LRT) for our global models explaining sandgrouse density. Initial models included all Principal Components (PC), the factor region, and all possible two-way interactions. Dropped terms (in italic) were removed sequentially and models refitted.

a) Pin-tailed sandgrouse

Variable	**Df**	**LRT**	***P*** **(χ^2)**
PC1	1	26.08	<0.001
PC11	1	12.43	<0.001
PC2:region	2	12.47	0.002
PC3:region	2	32.18	<0.001
NULL	314		
- PC4:region	*2*	*0.00*	*1.000**
- PC10:region	*2*	*0.00*	*1.000**
- PC8:region	*2*	*0.13*	*0.937*
-PC10	*1*	*0.08*	*0.777*
-PC4	*1*	*3.39*	*0.066*
-PC8	*1*	*3.30*	*0.069*
-PC5:region	*2*	*5.31*	*0.070*
-PC5	*1*	*0.18*	*0.668*
-PC11:region	*2*	*3.92*	*0.141*
-PC9:region	*2*	*4.13*	*0.127*
-PC7:region	*2*	*2.73*	*0.255*
-PC7	*1*	*0.01*	*0.933*
-PC1:region	*2*	*2.80*	*0.247*
-PC9	*1*	*3.28*	*0.070*
-PC6:region	*2*	*3.73*	*0.155*
-PC6	*1*	*0.26*	*0.613*

* algorithm did not converge

b) Black-bellied sandgrouse

Variable	**Df**	**LRT**	***P*** **(χ^2)**
PC1:region	2	9.57	0.008
PC4:region	2	9.62	0.008
PC5:region	2	10.29	0.006
PC7:region	2	21.10	<0.001
PC10:region	2	13.21	0.001
NULL	314		
-PC11:region	*2*	*0.01*	*0.994*
-PC3:region	*2*	*0.37*	*0.830*
-PC8:region	*2*	*0.32*	*0.854*
-PC6:region	*2*	*0.93*	*0.630*
-PC6	*1*	*0.07*	*0.791*
-PC3	*1*	*0.08*	*0.777*
-PC9:region	*2*	*2.27*	*0.321*
-PC9	*1*	*0.25*	*0.619*
-PC2:region	*2*	*1.91*	*0.384*
-PC2	*1*	*0.00*	*0.972*
-PC11	*1*	*0.87*	*0.350*
-PC8	*1*	*1.71*	*0.191*

Table OR3. Best models for the pin-tailed sandgrouse and the black-bellied sandgrouse, for all regions (global models). PCs in bold explained most of the deviance of the model.

a) Pin-tailed sandgrouse (three regions; region as a factor)

Variable	Estimate	SE	Z	*P*
Intercept	0.414	0.190	2.172	0.030
regionEXT	1.403	0.388	3.614	0.000
regionVEBR	0.617	0.253	2.440	0.015
PC1	-0.841	0.157	-5.367	0.000
PC2	-0.371	0.153	-2.424	0.015
PC3	1.508	0.308	4.901	0.000
PC11	0.381	0.090	4.227	0.000
regionEXT:PC2	1.096	0.298	3.678	0.000
regionVEBR:PC2	0.437	0.207	2.112	0.035
regionEXT:PC3	-2.765	0.426	-6.486	0.000
regionVEBR:PC3	-0.473	0.357	-1.325	0.185

Theta=0.509
Null Deviance: 453.5
Residual Deviance: 319.2
Exp. Deviance: 29.6%

b) Black-bellied sandgrouse (three regions; region as a factor)

Variable	Estimate	SE	Z	P
Intercept	-0.09	0.18	-0.48	0.63
PC1	0.77	0.29	2.65	0.01
regionEXT	**1.48**	**0.27**	**5.59**	**0.00**
regionVEBR	**0.80**	**0.24**	**3.33**	**0.00**
PC4	-0.30	0.10	-2.87	0.00
PC5	-0.30	0.13	-2.24	0.02
PC7	-0.99	0.22	-4.55	0.00
PC10	-0.56	0.16	-3.57	0.00
PC1:regionEXT	**-0.89**	**0.31**	**-2.84**	**0.00**
PC1:regionVEBR	**-1.06**	**0.36**	**-2.93**	**0.00**
regionEXT:PC4	0.69	0.24	2.90	0.00
regionVEBR:PC4	0.06	0.18	0.34	0.74
regionEXT:PC5	0.53	0.17	3.09	0.00
regionVEBR:PC5	0.50	0.19	2.61	0.01
regionEXT:PC7	**1.18**	**0.27**	**4.36**	**0.00**
regionVEBR:PC7	**1.07**	**0.24**	**4.55**	**0.00**
regionEXT:PC10	**0.67**	**0.23**	**2.89**	**0.00**
regionVEBR:PC10	**0.56**	**0.18**	**3.10**	**0.00**

Theta: 1.06
Null Deviance: 458.4
Residual Deviance: 346.1
Exp.Deviance: 24.5%

Table OR4. Mean values, SD and range of the 11 environmental axes for the three regions (total) and per region.

Region	VEBR	EXT	CLM	Total
N	120	83	112	315
PC1	-0.48±0.51	1.18±1.14	-0.36±0.42	0.00±1.00
	(-1.33-1.94)	(-1.11-4.22)	(-1.33-0.93)	(-1.33-4.22)
PC2	0.28±1.01	-0.02±0.78	-0.29±1.06	0.00±1.00
	(-1.59-3.61)	(-1.49-1.79)	(-4.31-4.99)	(-4.31-4.99)
PC3	-0.61±1.13	0.54±0.69	0.26±0.64	0.00±1.00
	(-6.70-0.74)	(-1.11-1.97)	(-2.88-1.05)	(-6.70-1.97)
PC4	-0.28±0.72	-0.12±0.56	0.39±1.34	0.00±1.00
	(-1.28-3.21)	(-1.09-1.81)	(-0.68-10.42)	(-1.28-10.42)
PC5	0.07±0.83	-0.07±1.20	-0.02±1.01	0.00±1.00
	(-1.46-2.65)	(-3.04-2.94)	(-2.61-2.30)	(-3.04-2.94)
PC6	-0.31±0.99	0.39±0.92	0.05±0.97	0.00±1.00
	(-3.59-1.79)	(-1.51-3.04)	(-2.45-2.56)	(-3.59-3.04)
PC7	0.38±1.22	-0.25±0.86	-0.22±0.66	0.00±1.00
	(-1.71-5.60)	(-2.68-2.10)	(-1.82-1.30)	(-2.68-5.60)
PC8	-0.27±1.35	0.10±0.64	0.21±0.67	0.00±1.00
	(-5.36-2.50)	(-1.07-2.13)	(-2.62-1.93)	(-5.36-2.50)
PC9	0.38±0.65	0.59±1.06	-0.85±0.64	0.00±1.00
	(-1.69-2.90)	(-1.16-5.50)	(-3.55-1.11)	(-3.55-5.50)
PC10	0.18±1.14	0.01±0.74	-0.20±0.98	0.00±1.00
	(-1.82-5.08)	(-1.68-2.22)	(-2.24-4.02)	(-2.24-5.08)
PC11	-0.12±1.04	-0.08±1.07	0.18±0.89	0.00±1.00
	(-2.66-5.26)	(-6.56-3.36)	(-1.22-3.58)	(-2.66-5.26)

CAPÍTULO 3

Integrating landscape, land use and microhabitat preferences of threatened sympatric steppe species for informing conservation needs

Foto: Ana Benítez

Benítez-López A, Viñuela J, Suárez F, Hervás I, García JT. Integrating landscape, land use and microhabitat preferences of threatened sympatric steppe species for informing conservation needs (en preparación).

Abstract

Habitat selection is an inherently scale-sensitive process in which detected selection patterns frequently depend on the scale of analysis employed. Here we used a multi-scale approach and variation partitioning to identify how the distributions of two sympatric steppe bird species, the pin-tailed sandgrouse (PTS) and black-bellied sandgrouse (BBS) are shaped by differential habitat selection at varying spatial scales. We focused on preferences at the landscape (broad), land use (intermediate) and microhabitat (fine) scales, and the influence of human infrastructures (as possible sources of disturbance). The pure effect of land use gradients explained the greatest variation in PTS occurrence, but there was cross-scale interdependence between the immediate lower and upper scales, and synergies between the three scales, highlighting the importance of integrating habitat scales in a single modelling framework. Landscape factors better explained BBS occurrence, which exhibited a broader habitat tolerance but lesser human tolerance than the PTS. Both species selected larger fields within their preferred land uses (ploughs for both species and fallows for the PTS) distant from houses and tracks and from infrastructures (PTS). Thus, the process of habitat selection was also modulated by human disturbance. At microhabitat scale, PTS selected locations within ploughs with greater green vegetation cover and insect abundance, and within fallows with lower dry vegetation cover and height but greater stone cover. These fine-scale habitat selection patterns might reflect a trade-off between camouflage (vegetation and stone cover for concealment) and visibility (for predator detection and escape). The strong preference of both species for ploughs and fallows highlights the importance of maintaining traditional agricultural practices for sandgrouse conservation. Ongoing (illegal) urbanization trends into protected areas and infrastructure development should be also limited. Multi-scale models offer an important tool for identifying scale-specific factors determining species distributions and for setting conservation requirements at appropriate levels in order to guide regional and local-level conservation efforts.

Keywords: *Pterocles alchata, Pterocles orientalis,* multi-scale habitat selection, distribution models, sympatry, conservation, human disturbance, infrastructure

Introduction

Habitat selection is at the core of ecology and a crucial component determining species distribution and abundance. It constitutes an important axis of a species' ecological niche (Rosenzweig 1981), and is a hierarchical process in which the detected selection patterns frequently depend on the scale of analysis employed (Levin 1992). Habitat selection levels range from the macro-habitat scale, defined as the area in which an organism performs most of its biological activities (Morris 1987), to the microhabitat scale, a term that refers to the structural characteristics of the locations that are actually perceived and selected by an organism (Morales et al. 2008). Understanding habitat selection is more crucial than ever since habitat loss is the primary driver of species imperilment and extinction (Sala et al. 2000) and habitat protection is frequently incorporated into endangered species recovery planning and legislation.

Habitat association modelling is a common method for understanding non-random selection of a given habitat. Explanatory fine-grained models built with direct, biologically relevant predictors allow understanding basic species-habitat relationships (Mackey and Lindenmayer 2001). However, habitat selection at fine-grained scale may be modulated by habitat selection at scales above, existing a cross-scale interdependence and hierarchy that explain species distribution and requirements (Traba et al. 2013). Because ecosystems or populations cannot be described adequately at a single scale and because the effect of environmental variables is scale-dependent (Levin 1992), multi-scale rather than single-scale approaches are increasingly gaining popularity to characterize habitat use patterns (e.g.: Mateo-Tomás and Olea 2009; Razgour et al. 2011), but remain however remarkably uncommon in ecology (Du Toit 2010; Sandel and Smith 2009).

Multi-scale studies may be especially informative for species with overlapping areas of co-occurrence, and can allow a better understanding of niche segregation and species coexistence (Indermaur et al. 2009). Thus, similar species co-occurring at coarse geographical scale may show a spatial segregation at smaller spatial scales, following landscape features, land use selection or at the microhabitat scale, often related to fine scale partitioning of habitat selection and vegetation structure (Traba et al. 2013). In this context, differential habitat selection is a key process that stabilizes the coexistence of species (MacArthur and Levins 1967). However this approach has rarely been used to assess differentiation among closely-related species sharing similar habitat types.

In this work we illustrate how a multi-scale, top-down modelling approach can aid in identifying effective conservation measures for endangered sympatric species, through the identification and ranking of ecological and anthropogenic factors determining their distribution at varying spatial scales. We use the congeneric pin-tailed sandgrouse (*Pterocles alchata*) and the black-bellied sandgrouse (*P. orientalis*) as model species, and analysed the influence of landscape features, land use availability and microhabitat variables on their distribution, with the aim of identifying local – but generalizable – habitat and conservation requirements.

The pin-tailed and the black-bellied sandgrouse (hereafter PTS and BBS, respectively) are sympatric in ca. 34% of their European distribution and share a relatively narrow range of climatic, topographic and trophic requirements, occupying similar feeding and breeding habitats (Benítez-López et al. 2014a; Benítez-López et al. 2014b; Herranz and Suárez 1999). Both species are ground-nesting birds associated with open arid habitats, natural steppes and agricultural ‘pseudo-steppes’, which are increasingly humanized and are especially exposed to foreseeable land use changes through agricultural intensification (Benítez-López et al. 2014a). Large-scale niche segregation related with differential thermal and habitat preferences have been recently described (Benítez-López et al. 2014b), as well as their distribution at large geographical, landscape and microhabitat scales (Martín et al. 2014). However, these previous works failed to integrate scale-specific explanatory factors into a multi-scale modelling framework. Additionally, we focus here on intermediate (landscape, land use configuration) and microhabitat scales (i.e. within sandgrouse home ranges), and gauge whether there are differential habitat selection regarding landscape and land use preferences. Also, we take a step forward by assessing microhabitat features within preferred land uses, with the aim of providing more accurate conservation and management recommendations. Specifically, we studied sandgrouse’s land use preferences based on observation points as compared to random points. Second, we defined environmental gradients at three separate spatial scales: landscape (ca. 100km^2), land use (100 m) and microhabitat (1m^2), including human-related variables. We built scale-specific habitat models, which were subsequently integrated into a multi-scale habitat model to extract the main environmental and anthropogenic factors explaining sandgrouse distribution, and we highlight similarities and differences between both species. Third, we assessed specific microhabitat requirements within preferred land uses (only for the more abundant PTS). Finally, we highlight the usefulness of a multi-scale approach i) to assess habitat partitioning for sympatric species, ii) to pinpoint how human activities (agrarian practices, infrastructure and urbanization development) influence their distribution at different spatial scales, and iii) to provide sound recommendations for sandgrouse conservation.

Methods

Study area

Fieldwork was conducted in late May-mid June during three consecutive breeding seasons (2009-2011) in the pseudo-steppes of the Special Protected Area (SPA) "Área esteparia del Campo de Calatrava" (89.8 km^2, 38º 54'N, 3º 55'W, Castilla-La Mancha, Spain). This SPA is located within the largest extent of continuous distribution of pin-tailed sandgrouse in Europe, but where black-bellied sandgrouse are less frequent and abundant (Benítez-López et al. 2014a; Benítez-López et al. 2014b) (Figure 1).

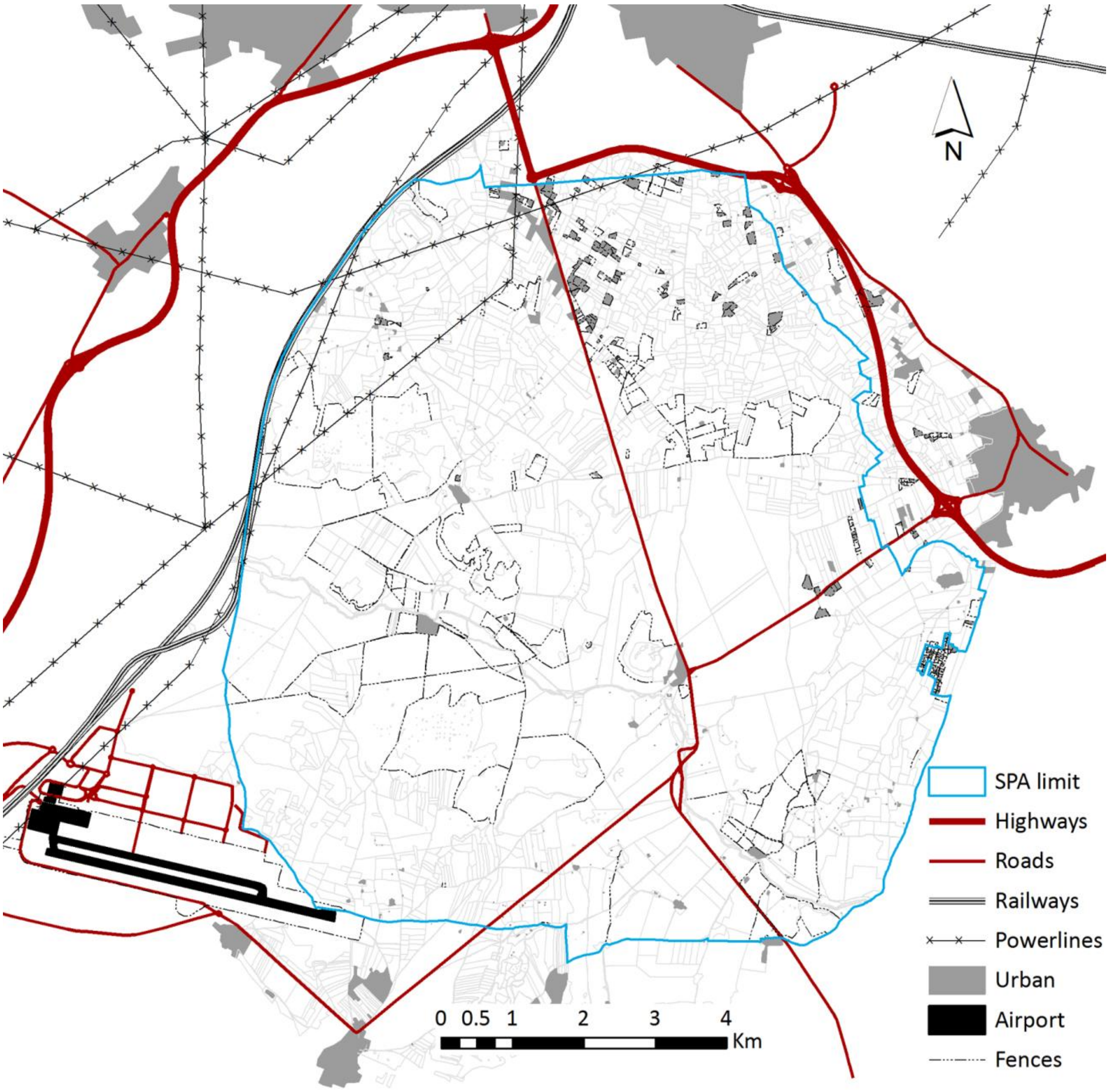

Figure 1. Map of the study area showing the main landscape features and distribution of agrarian fields.

This area is under a Mediterranean climate with annual mean precipitations around 550 mm, and consists of a flat to slightly undulated landscape (590–685 m a.s.l.) encompassing mosaics of different agrarian substrates (Table 1).

Table 1. Main land use types in the study area and their relative surface across years. Land uses were mapped during the last week of May, just before surveys.

Substrate	Code	Description	Proportion (%) 2009	Proportion (%) 2010	Proportion (%) 2011
Crops					
Cereal	CE	crops of barley, oats or wheat	48.33	44.58	48.38
Stubble	ST	recently harvested cereal or legume fields	0.03	0.07	0.00
Fallow	FA	unploughed cereal fields harvested in the previous year; cereal fields ploughed > 1 and < 2 years ago and with dense herbaceous coverage (>20%)	8.52	10.63	9.17
Old Fallows	OF	Fallows > 2 years old and set aside	3.28	3.39	3.56
Plough	PL	ploughed fields, mostly without vegetation (<20% weed vegetation cover). When they had developed a significant herbaceous vegetation cover (>20%) they were classified as fallow land	15.09	16.12	12.65
Legume	LE	crops of *Vicia spp.* or *Pisum sativum*	4.64	3.05	6.49
Pastureland	PA	fields of short scrubland and pastureland	5.37	5.36	5.37
Olive and fruit groves	AR	Arboreal crops	5.31	5.36	5.35
Intensive vineyards	VI	Vineyards with metal structures	4.90	4.45	4.59
Traditional vineyards	VT	Vineyards grown in a traditional way	1.38	1.24	0.92
Others	OT	vegetation of rivers and streams, piles of stones, maize, unproductive land, unregistered	1.74	4.35	2.06
Urban	UR	Villages, farms and recreational houses	1.41	1.41	1.46

Land uses within the SPA were updated every year during the last week of May using a digital map with detailed field boundaries created upon geo-referenced aerial photographs at 0.25-m pixel resolution). Extensive dry cereal croplands and ploughed lands constitute >50% of the surface, with a varying cover of fallows of different ages, leguminous crops and interspersed patches of olive groves, vineyards and fruit tree orchards. Pasturelands are also present but in a low percentage. Cereals are harvested between mid-June and early July. This farming system is complemented with extensive sheep grazing in stubbles, fallows and small areas of short scrubland and pastureland. The SPA is surrounded by several major infrastructures (i.e. highways, airport, high-speed railway, power lines…) and traversed by three main roads (see Figure 1). The SPA is a hotspot area for steppe birds (Traba et al. 2007) and holds a population of ca. 200 breeding and ca. 1000 wintering PTS and of ca. 20 breeding and ca. 100 wintering BBS (Hervás and Suárez 2007).

Species occurrence data

Surveys were conducted during the first week of June, in the middle of sandgrouse breeding seasons of 2009, 2010 and 2011. The survey method (line transects) followed the recommendations of the National Breeding Sandgrouse Survey (Suárez et al. 2006). Line transects of variable length were set out over the study area aided by the land use map of the study area. The starting points of these transects were randomly selected, but sampling focused on *a priori* adequate habitats (pastures, fallows, ploughs, stubbles...) (Suárez et al. 2006), covering bands 200 m wide at each side and each band separated from the other by 300 m, which is within the detection distance for sandgrouse (detectabilities of 0.48 and 0.39, with effective interval distances of 144 m and 118 m at each side of the transect, for PTS and BBS, respectively, Benítez-López et al. 2014b). Non-preferred habitats were not traversed, but were included within the transect strip (vineyards, olive groves and cereals). Surveys were performed simultaneously by 6-8 observers in 2-3 days over contiguous sub-areas in a given day, to minimize double-counting. Each line transect was surveyed by independent and experienced observers walking cross-country at approximately constant speed (1-3 km/h) in dry, windless weather conditions during the first 3–4 hours of daylight. The position of all sandgrouse observed on the ground was mapped and geo-referenced using a GPS receiver. Although observers made efforts to avoid double counting during surveys, we also compared the number, location, flight direction and times of recorded observations and kept for analysis only those observations for which we were confident that they were not sampled twice. We cumulated a total of 327643 m (average: 109214 m/year) along 423 transects (average: 141 transects/year), sampling 70.5% of the study area.

Landscape, land use and microhabitat data

Landscape, land use and microhabitat preferences were studied comparing the characteristics of locations used by PTS and BBS to available random locations. The random locations (N= 150) were generated automatically according to land use availability (stratified sampling) over geo-referenced cartography of the study area using ArcGIS 9.3 (ESRI, 1999-2005). Due to logistic or climatic constraints, we sampled a subset of 140-149 random locations each year (see below). At each location point (used vs. random), we measured a range of variables (see Table S1) that were considered *a priori* relevant to explain the distribution of sandgrouse at landscape, land use and microhabitat levels (Table S1). In the hierarchical process of habitat selection, animals first place home ranges within a larger area and subsequently use patches within home ranges (Johnson 1980). Average home ranges are ca. 40km^2 and ca. 120km^2 for PTS and BBS, respectively (Benítez-López et al. 2010b) (authors, unpublished data), thus we could reasonably assume that locations of sandgrouse individuals within the SPA (ca. 100 km^2) belonged to individuals that placed their home ranges in this protected area, and then selected certain land uses by first taking into account the spatial configuration of the landscape. Thus, our broader scale of analysis was defined by the structure of the SPA landscape, which would roughly correspond to the second-order of selection (Johnson 1980). We described it by a set landscape variables that were static across study years (Table S1). Our intermediate scale of analysis was defined by the availability of land uses for exploitation (third-order of selection), which further determines resource availability and conditions at smaller spatial scales (fourth-order of selection, Johnson 1980) (i.e. microhabitat scale and vegetation structure). Hence we measured land use and microhabitat variables, which vary dynamically (seasonally and annually) due to climate variation between years and the agricultural practices.

Landscape variables were extracted from digital cartography (see Table S1 for sources). Land uses were mapped in the field prior the surveys and incorporated in a GIS. Microhabitat variables were also measured in the field. The landscape variables consisted of the spatial coordinates (longitude X, latitude Y, XY, X^2, Y^2, i.e.: to control for spatial autocorrelation (Legendre 1993), topographic variables (altitude and slope), the field size (size of agrarian field units) and variables related to landscape humanization (minimum distance to highways, roads, railways, powerlines, towns, airport, tracks, farm and recreational houses -hereafter houses-).

For land uses, we extracted the land use type for each location point (sandgrouse or random) using our digital cartography and estimated the % cover of each land use type within a radius of 100 m. We used this radius, because it roughly corresponds to the average flight initiation distance of PTS (ca. 95 m, Martín et al. 2010) and BBS (ca. 135 m, authors, unpublished data) in the study area. Furthermore, we deemed habitat selection within this radius (100 m) as a compromise between fulfilling sandgrouse habitat requirements for normal activities (feeding, resting, potential breeding site…) and minimizing predation or disturbance (in case of humans) risk (i.e.: compromise between risk and rewards, (Brown 1992; Mayor et al. 2009).

Microhabitat features were recorded in the field shortly after the survey (from afternoon until dusk in the same day of the survey, and within 3-5 days after the survey). At each location point (sandgrouse or random, GPS error: 3-5 m), three microhabitat sampling points (1x1 m quadrats) were systematically defined: a central quadrat, located at the sandgrouse observation point or at the random point UTM coordinates, and two other quadrats placed 10 m north and south of the central quadrat point, all three quadrats located within the same field to characterize that particular land use. We measured microhabitat variables at each quadrat, and used the average measures from the three quadrats to characterize sandgrouse and random locations. The measured variables included: vegetation height (VH, in cm, five measures per quadrat), furrow depth (FD, in cm, three measures per quadrat) and number of insects (NI, count of insects within the quadrat during 30 seconds). Additionally, we took perpendicular photographs (1.5 m height from the ground) of the quadrats. These photographs were later analysed by the same observer (to avoid potential observer bias) who quantified the following: green vegetation cover (GVC, in %), dry vegetation cover (DVC, in %), bare ground cover (BGC, in %), cover of large stones (> 10 cm, LSC, in %) and of small stones (2-10 cm, SSC, in %) per quadrat.

Throughout the study, we sampled a total of 198 locations used by PTS (61 in 2009, 79 in 2010 and 58 in 2011), 10 locations used by BBS (2 in 2009, 5 in 2010 and 3 in 2011) and 429 random locations (148 in 2009, 140 in 2010 and 149 in 2011). In order to increase sample size for BBS, we added an extra 19 locations from the same area and study period, which were obtained during annual spring censuses (conducted late April-early May; 10 locations) and during a radiotracking study of BBS (Benítez-López et al. 2011; Casas et al. 2014); 9 additional locations from May). For these additional BBS locations we had information on all landscape and land use variables, but not on microhabitat characteristics.

Data analyses

Land use selection

We analyzed for each species separately the selection pattern of land use within the agricultural mosaic by comparing the frequency of sandgrouse observations with the availability of the different land use types in the SPA (frequency of random locations) using the Manly's selection index (design I in package adehabitatHS, Manly et al. 2003; R Development CoreTeam 2012). The Manly index ranges from infinity (all observations within the habitat type) to 0 (0 = no observations within the habitat; 1 = use according to availability) and tests the selection/avoidance under the null hypothesis that animals use the habitat in proportion to availability (Log-likelihood χ^2 test). P-values were compared with a Bonferroni-corrected α level of 0.05/11 = 0.0045 (11 being the number of land use types, all those described in Table 1 except "Urban" which is not used by sandgrouse).

Principal Component Analyses

We carried out three separate Principal Component Analyses with Varimax normalized rotation (McGarigal et al. 2000) for 1) landscape variables (spatial, topographic and anthropogenic), 2) land use proportions and 3) microhabitat variables, in order to reduce the original set of variables into orthogonal gradients. This allowed us to assess the range of variability among sandgrouse and random locations. We retained Principal Components that had eigenvalues > 1, which were used as predictors in subsequent models (see below).

Multi-scale habitat models

We built habitat models to relate the occurrence of sandgrouse to landscape, land use and microhabitat gradients using Generalized Linear Models (GLMs) with a binomial error and logit link. We built five sets of scale-specific models, three for the PTS (landscape, land use and microhabitat variables) and two for the BBS (landscape and land use variables). For each set, we initially considered both the linear and quadratic term of each variable included. We selected the best models within each set (see below) and used the best explanatory landscape, land use and microhabitat factors to subsequently build a global multi-scale model. We tested for collinearity amongst explanatory variables used in the global models using variance inflation factors (VIF). Model selection for scale-specific and multi-scale models was done starting with the most complex model, dropping one term at a time and comparing competing nested models by means of likelihood ratio tests (LRT) until reaching the most explanatory model with all terms with $P(\chi^2) < 0.05$ (Zuur et al. 2009).

We additionally used variation partitioning procedures to assess the relative importance of landscape, land use and microhabitat gradients at explaining PTS and BBS occurrence. Variation partitioning is a quantitative method in which the variation in a dependent variable can be separated into independent components reflecting the relative importance of different groups of explanatory variables (factors) and their joint effects. This allowed us to specify how much of the variation of the final model was explained by the pure effect of each factor, i.e. not affected by collinearity with other factors in the model, and which proportion was attributable to their shared effect (Borcard et al. 1992; Legendre 1993). The sum of the amounts of variation explained by each factor group and by the combined effects usually may differ from the total amount explained by the whole global model, mainly due to the interactions between factors and the subsequently overlaid effects (Borcard et al. 1992). Positive values in the shared variability of factors indicate collinear variation, whereas negative values indicate probable synergistic effects (i.e. a function of the two factors together is able to explain more than the sum of the separate functions of these two factors; (Legendre and Legendre 1998) (see Supplementary Material for further explanations).

We also tested whether within the preferred land uses of the PTS (ploughs and fallows, see results obtained with Manly's index) we could detect microhabitat features that determined why the PTS selected certain ploughs or fallows over other available ones. We previously tested whether microhabitat gradients (vegetation cover and height) varied differed between years for ploughs and fallows (variation could occur because of differences between years in climate or agricultural practices). However, no significant differences were found (all P-values >0.05) indicating that microhabitats gradients were overall similar during the three study years.

Results

Land use preferences: Manly's selectivity index

At the land use level, habitat use significantly differed from habitat availability for PTS (χ^2 = 459.53, P < 0.001, df=10) and BBS (χ^2 = 103.75, P < 0.001, df = 10). The PTS selected positively ploughs and fallows, but avoided cereal crops, traditional and intensive vineyards, arboreal crops and old fallows, and other habitats (Figure 2). Stubbles, pastures and legumes were used according to their availability (P > 0.0045). The BBS selected positively ploughs, tended to select legumes and fallows (the small sample size and large confidence intervals does not exclude that these were used according to availability), but avoided the rest of land use types (P > 0.0045; Figure 2).

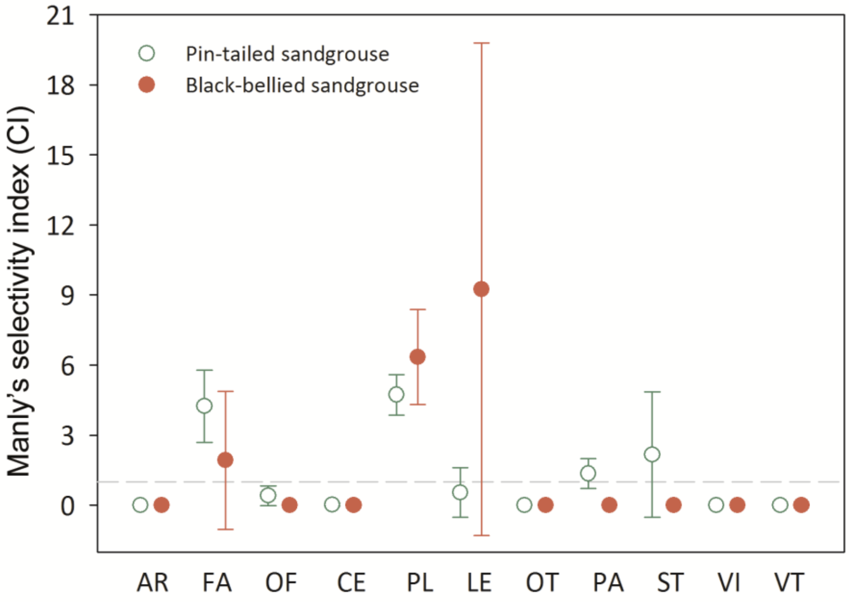

Figure 2. Manly's selectivity index (± CI) for each land use type (x-axis). Values range from 0 (complete avoidance) to infinity (maximum preference). An index of 1 indicates that the habitat is used according to availability. Confidence intervals overlapping the dashed baseline (1) indicate non-significant habitat selection (P> 0.0045). Land use types and codes are described in Table 1.

Principal Component Analyses

The PCAs at landscape, land use and microhabitat scale resulted in five, eight and three principal components explaining 79.9%, 73.5% and 73.3 % of the total variance, respectively. The factor loadings, eigenvalues and percentage of variation explained by each PCA are shown in Tables S2, S3 and S4 (Supplementary material) and the description of each axis on basis of the loadings of each variable is given in Table 2. At landscape level, the principal components (LC1-LC5) represented geographic, topographic and human disturbance gradients. In the case of land use data, LU1, LU2 and LU3 characterized a gradient of human disturbance (presence of houses and farms, and abandoned fallow fields), a gradient of increasing cover of pastures,

3and a gradient from cultivated cereal fields to uncultivated ploughs. The rest of components represented the major land uses in the area, with associations between arboreal crops and minor land uses, and between intensive and traditional vineyards. Finally, in the case of microhabitat data, the gradients represented vegetation structure and micro-topographic characteristics of the fields.

Table 2. Description of gradients resulting of the PCA's for landscape, land use and microhabitat variables. For ease of interpretation the PC's have been coded as LC's, LU's and MH's to distinguish between the three levels of analysis.

Principal component	Negative loadings (< -0.4)	Positive loadings (> 0.4)	Description
Landscape			
LC1	Y, Y2, Alt, DistWat, DistAirpor	DistHigh, DistPower, DistRail	**N-S** gradient from points at higher **altitude distant from water** and from the **airport** (north) to points distant from **highways, railways** and **powerlines** (south)
LC2	DistRoad	X, X2,XY, DistRail, DistPower, DistAirpor	**W-E** gradient (with a slight SW-NE drift) from points distant from **roads** (west) to points distant from **railways, powerlines and the airport** (east)
LC3	Field size, DistTrack, DistHouse		Gradient from points located in **large fields** and distant to **tracks and houses** to points with opposite characteristics.
LC4	DistRoad	Alt, DistFence	Gradient from points at **high altitude** and distant from **fences** to points distant from **roads**
LC5	Slo, DistTown		Gradient from points with **steep slopes** (hills) and distant from **town**s and **villages**
Land use			
LU1	OF, UR, DIV		Gradient from points surrounded by a larger cover of **old fallows,** recreational and farm **houses** and **high diversity of land uses** to points with opposite characteristics.
LU2	PA		Gradient from points surrounded by a larger cover of **pastures** to points with opposite characteristics.
LU3	PL	CE	Gradient from points surrounded by a larger cover of **cultivated cereal crops** to points surrounded by a larger cover of **uncultivated ploughs**
LU4	AR, OT		Gradient from points surrounded by a larger cover of **arboreal crops** and **minor land uses** (riparian vegetation, stone piles…) to points with opposite characteristics
LU5	FA		Gradient from points surrounded by a larger cover of **fallows** to points with opposite characteristics.
LU6	VE, VT		Gradient from points surrounded by a larger cover of **intensive and traditional vineyards** to points with opposite characteristics.
LU7	ST		Gradient from points surrounded by a larger cover of **stubbles** to points with opposite characteristics.
LU8	LE		Gradient from points surrounded by a larger cover of **legumes** to points with opposite characteristics.
Microhabitat			
MH1	DVC, VH	BG, FD	Gradient characterizing points with greater **bare ground cover** and **furrow depth** vs points with greater **dry vegetation cover** and **higher vegetation height**
MH2	GVC, NI		Gradient characterizing points with greater **green vegetation cover** and **number of insects** vs points with opposite characteristics
MH3	LSC, SSC		Gradient characterizing points with greater cover of **large and small stones** vs points with opposite characteristics

See Table 1 for land use codes. Landscape codes: X, Y, XY, X^2, Y2: Spatial coordinates, Alt: Altitude, Slo: Slope, DistHigh: Distance to closest highway, DistPower: Distance to closest powerline, DistRoads: Distance to closest road, DistAirpor: Distance to closest airport, DistRail: Distance to closest railway, DistWat: Distance to closes water point, DistTrack: Distance to closest track, DistTown: Distance to closest town. Microhabitat codes: BGC: Bare ground cover, FD: Furrow depth, DVC: Dry vegetation cover, VH: Vegetation height, GVC: Green vegetation cover, NI: Number of insects, LSC: Large stones cover, SSC: Small stones cover.

Habitat models for the pin-tailed sandgrouse

Scale-specific habitat models

At landscape scale, the best model for PTS occurrence included the linear and quadratic terms of LC1 ($\chi^2 = 8.63$, $P = 0.013$), LC2 ($\chi^2 = 42.88$, $P < 0.001$) and LC3 ($\chi^2 = 23.59$, $P < 0.001$), and the linear term LC5 ($\chi^2 = 5.79$, $P = 0.016$) as significant explanatory factors, and explained 9.6% of the deviance. As for the level of land uses, the best model included the linear terms LU1 ($\chi^2 = 18.72$, $P < 0.001$), LU4 ($\chi^2 = 62.42$, $P < 0.001$) and LU6 ($\chi^2 = 70.42$, $P < 0.001$); and the linear and quadratic terms of LU3 ($\chi^2 = 136.02$, $P < 0.001$) and of LU5 ($\chi^2 = 39.81$, $P < 0.001$), explaining 37.1% of the deviance. Finally, at microhabitat scale, the best model explained 12.4% of the deviance and included the linear and quadratic terms of MH1 ($\chi^2 = 75.78$, $P < 0.001$) and of MH3 ($\chi^2 = 8.96$, $P < 0.001$) (Table S5). All these parameters were retained and integrated into the global multi-scale model for which model selection was applied again.

Multi-scale habitat models

In the multi-scale model, VIF's ranged between 1.5 and 3.2, below the recommended level of 5 (Zuur et al. 2007)), so there was low collinearity between our factors. From all retained variables, we dropped LU1 and LC5 based on LRT ($\chi^2 = 2.34$, $P = 0.126$ and $\chi^2 = 2.72$, $P = 0.099$).

Table 3. Results of the multi-scale model selection explaining the presence of the pin-tailed sandgrouse and of the black-bellied sandgrouse. Estimates for microhabitat gradients are not available for the black-bellied sandgrouse.

	Pin-tailed sandgrouse				**Black-bellied sandgrouse**			
Variable	**Estimate**	**SE**	**Z**	**P**	**Estimate**	**SE**	**Z**	**P**
Intercept	-2.19	0.24	-9.05	<0.001	-4.78	0.83	-5.76	<0.001
Landscape								
LC2	-20.10	4.17	-4.82	<0.001				
$LC2^2$	-12.32	4.10	-3.01	0.003				
LC3	-12.21	3.33	-3.66	<0.001	-1.39	0.22	-6.45	<0.001
$LC3^2$	-6.92	3.11	-2.22	0.026				
Land use								
LU2					3.70	1.67	2.21	0.027
LU3	-19.94	5.33	-3.74	<0.001	-1.07	0.26	-4.03	<0.001
$LU3^2$	-19.32	5.00	-3.86	<0.001				
LU4	1.54	0.31	4.99	<0.001				
LU5	-14.59	3.25	-4.49	<0.001	-0.68	0.27	-2.48	0.013
$LU5^2$	-13.77	3.44	-4.00	<0.001				
LU6	1.69	0.37	4.61	<0.001				
LU8					-0.50	0.16	-3.07	0.002
Microhabitat								
MH1	29.94	5.06	5.92	<0.001	n.a.	n.a.	n.a.	n.a.
$MH1^2$	-15.86	3.75	-4.22	<0.001	n.a.	n.a.	n.a.	n.a.
MH3	-0.60	0.15	-4.11	<0.001	n.a.	n.a.	n.a.	n.a.

The resulting model still had non-significant parameters with P values > 0.05, so we further fine-tuned the model by dropping all the non-significant terms (linear and quadratic terms of LC1and quadratic term of MH3). The final global multi-scale model explained 47.3%, of the deviance (Table 3), thus more % of deviance than each scale-specific model separately. Variation partitioning indicated that the pure effects of land use variables explained the larger part of the variation (Figure 3). Additionally, the joint effect of the land use and landscape, and of the land use and microhabitat, explained a further 22.1% and 21.8% of the total variation, respectively (Figure 3a). For PTS, the negative value for the joint effect of the three types of factors indicated the presence of synergistic effects (i.e. a function of the three factors together explained more than the sum of the separate functions of these three factors).

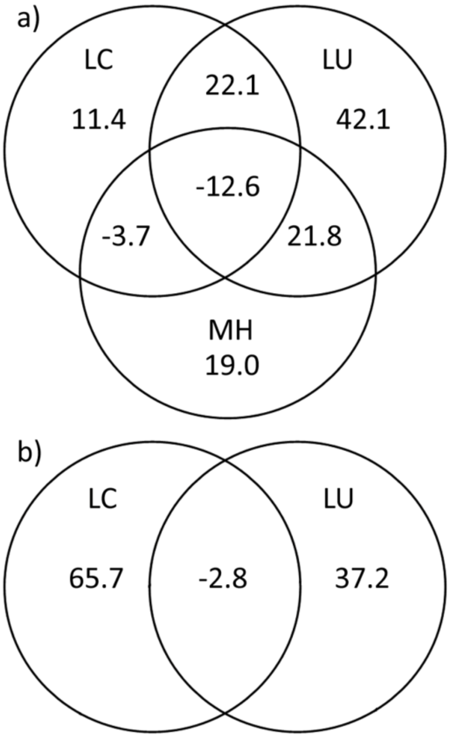

Figure 3. Variation partitioning to determine the different contributions of (a) landscape (LC), land use (LU) and microhabitat gradients (MH) in the occurrence of the pin-tailed sandgrouse and of (b) landscape and land use in the occurrence of the black-bellied sandgrouse. Positive values in the shared variability of factors indicate collinear variation, whereas negative values indicate probable synergistic effects (i.e. a function of the two or three factors together is able to explain more than the sum of the separate functions of these factors; see (Legendre and Legendre 1998).

At landscape level, PTS occurrence was a quadratic function of LC2 and of LC3 (Table 3). PTS occurrence was lower nearer roads, but higher at closer-intermediate distances from the rail track, power lines and airport along a West-East gradient (LC2, see Fig. S1 in Supplementary material). PTS occurrence was also higher in larger fields more distant from houses and tracks (LC3, Figure 4).

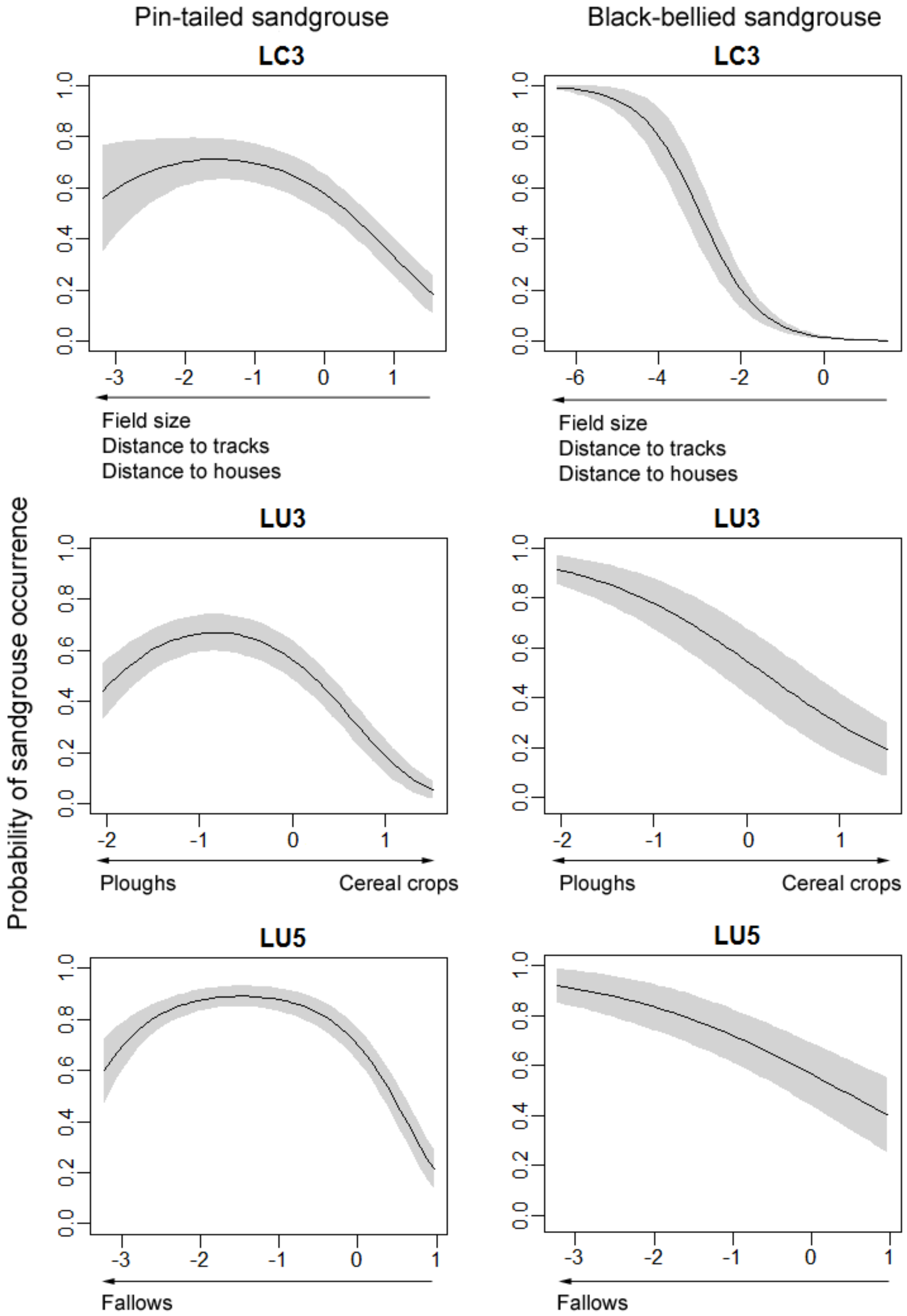

Figure 4. Probability of occurrence of the pin-tailed and the black-bellied sandgrouse along landscape (LC3) and land use (LU3, LU5) gradients that entered the model for both species. Grey shades denote SE at both sides of the predicted curves. Predicted responses are plotted by varying one predictor while holding the other predictors constant at median values; except for LU3 and LU5 for the black-bellied sandgrouse, that were plotted for LC3=-3 which is the value at which the probability of presence becomes 0.5. Values of LC3 >-3 resulted in extremely low predicted values for LU3 and LU5 gradients. Note also that for LC<-3 there are no Random observations (see range for the PTS plot), indicating the extreme selection of BBS for the largest fields. Values of individual variables below the x-axis increase following the direction of the arrows (and decrease in the opposite direction).

At the land use level, PTS occurrence was positively associated with increasing but intermediate-high cover of ploughs (LU3) and fallows (LU5) (Figure 4), and with decreasing cover of vineyards (LU6), cereals (LU3) and arboreal crops (LU4) (Table 3, Figure S1). Finally, at the microhabitat level, PTS selected fields with intermediate levels of dry vegetation cover and vegetation height, and with greater cover of big and small stones (but see results within preferred land uses) (Table 3, Figure S1).

Habitat models for black-bellied sandgrouse

Scale-specific habitat models

At landscape scale, the best model included only the linear term LC3 ($\chi^2 = 64.47$, $P < 0.001$), and explained 29.8% of the deviance. At land use level, our best model included the linear terms LU2 ($\chi^2 = 12.56$, $P < 0.001$), LU3 ($\chi^2 = 20.90$, $P < 0.001$) and LU8 ($\chi^2 = 12.58$, $P < 0.001$), and the quadratic term of LU5 ($\chi^2 = 40.39$, $P < 0.001$), and explained 26.5% of the deviance (Table S5). These parameters were integrated into the global multi-scale model and model selection was applied again.

Multi-scale habitat models

When we included landscape and land use factors in a global multi-scale model, all parameters were significant according to LRT. However, VIF values indicated collinearity with two explanatory variables, LU2 and LU5 (VIF_{LU2} 7.2 and $VIF_{LU5\ (q)} = 6.28$), which was solved by dropping the quadratic term of LU5. The best global model explained 47.5% of the deviance (Table 3). Variation partitioning indicated that the pure effects of landscape variables explained the largest part of the variation (Figure 3b). Although all factors in the final model were significant (Table 3), the most important factor was LC3 ($\chi^2 = 67.32$, $P < 0.001$), which described a clear a tendency for BBS to occupy larger fields away from houses and tracks (Figure 4). The relationships between BBS occurrence and the land use factors were only evident when the LC3 gradient was below -3 (large fields isolated from houses and tracks, Figure 4; see Figure S1 for medium sized fields).

Microhabitat selection by the pin-tailed sandgrouse in preferred land uses

According to the Manly's selectivity index, PTS selected preferably two land use types within the study area: ploughs and fallows (54% and 23% of locations, respectively, Figure 2). We further evaluated microhabitat selection within these two preferred land uses. For ploughs, PTS selected those with greater cover of green vegetation and insect abundance (MH2: slope ± SE: -1.11 ± 0.51, Z= -2.18, P = 0.029; Figure 4a). For fallows, pin-tailed sandgrouse selected those with lower dry vegetation cover, with lower vegetation height, greater bare ground cover and furrow depth (MH1: 1.35 ± 0.50, Z= 2.69, P= 0.007, Figure 4b) and with greater large and small stone cover (MH3: -11.28 ± 3.23, Z= -3.49, P < 0.001, $MH3^2$: -5.35 ± 2.68, Z=-2.00, P =0.046, Figure 4c).

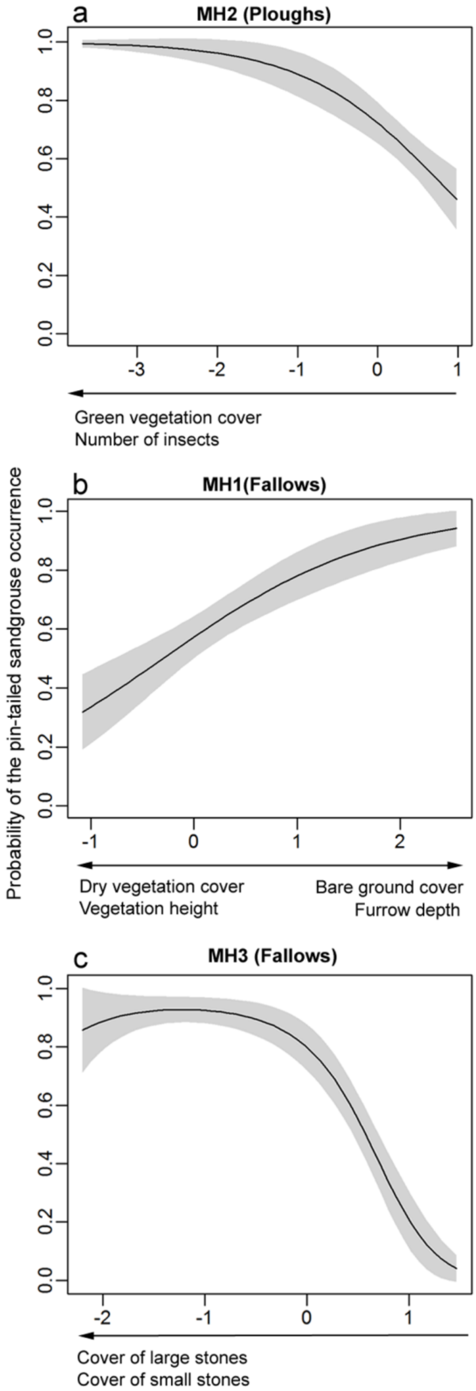

Figure 4. Relationships between the probability of the pin-tailed sandgrouse in (a) ploughs along the MH2 gradient, and in (b) fallows along MH1 and (c) MH3 gradients. Grey shades denote SE at both sides of the predicted curves. Values of individual variables below the x-axis increase following the direction of the arrows (and decrease in the opposite direction).

Discussion

Scale-specific vs multi-scale models

This study investigated the application of species distribution modelling to predicting patterns of multi-scale habitat selection, from landscape to microhabitat scales, using *a priori* biologically meaningful ecological variables for the specific model scale and application. Using single-scale approaches or pseudo multi-scale approaches (studies with models built at several scales but that do not integrate scale-specific factors in single multi-scale model, e.g.: Martín et al. 2014; Martínez et al. 2003) provide useful information about habitat preferences and factors determining the distribution of a species at different scales separately. However, given the hierarchical nature of habitat selection these approaches are neglecting potential cross-scale influence in the distribution and space use of organisms. Furthermore, factors relevant at a specific scale, when integrated into a single multi-scale framework, may become less important (i.e., their amount of explained deviance may be better explained by other factors from another scale, e.g.: LC1 and LC5 in PTS model) or their relationship with occurrence may change or appeared as mediated by other factors (e.g. $MH3^2$ in PTS model), thus precluding our understanding of species-habitat relationships. Additionally, once integrated in a single multi-scale model, variation partitioning allows identifying the relative importance of each scale and of combinations of scales, taking into account interrelations among all scales considered. In the case of PTS occurrence, land use gradients alone explained the highest amount of variation, thus indicating that the intermediate scale (land use availability and configuration) is the most important. However, there is also a high amount of variation explained by the combined effect of two factors. Specifically, the high positive values between the intermediate scale (land use) and landscape and microhabitat scales, respectively, indicate some degree of association between both pairs of scales, with effects being overlaid and varying collinearly (Borcard et al. 1992). It also reflects that the amount of interdependence between the intermediate and the broader scales, and the intermediate and finer scales is higher than between the broader and finer scales, as expected given that habitat selection at a lower spatial scale is conditional upon the subsequent higher order spatial scale, and viceversa (Hutto 1985). Additionally, the negative added value for the joint effects of landscape, land use and microhabitat gradients indicate that synergistic effects between the three scales are acting to explain sandgrouse occurrence, that is, the three factors together explain more than the sum of each factor separately. When only scale-specific models are considered, inter-scale associations and synergies are impossible to grasp. The use of multi-scale modelling is therefore crucial to evaluate the relative importance of factors at each scale of analysis and to set relevant conservation goals at different spatial scales.

Differential habitat selection and human tolerance between sympatric sandgrouse

We extracted patterns of differential habitat selection according to landscape and land use features for two similar co-occurring species. Our starting point was a scenario of high suitability at regional scale for one species (PTS), whereas for the other species (BBS) environmental conditions were far from optimal (Benítez-López et al. 2014a; Benítez-López et al. 2014b). The broader environmental (climatic and habitat) tolerance of BBS nevertheless allowed its presence in the study area. This was reflected in the frequency of observations for each species: PTS was much more widespread and frequent in the SPA during the breeding season than the BBS, for which fewer observations were recorded. Given the low suitability of this area for breeding BBS, our conclusions about its habitat preferences, although relevant, should be considered with caution since they are not representative of an optimal area for this species, in contrast with the PTS.

The process of habitat selection is a complex process during which individual behavioural choices are driven by decreasing scales of complexity. Species do not choose a given habitat independently of its surroundings, particularly in anthropogenic landscapes where the human dimension is pervasive. Thus, human disturbance (infrastructures and houses) may preclude fields with preferred land uses from being used, i.e.: wildlife usually avoid preferred land uses that are closer to urban areas, houses or major infrastructures (Benítez-López et al. 2010a). In this sense, multi-scale approaches are also useful to identify how species distributions are shaped by habitat preferences and modulated by human disturbance. Despite our small sample size for BBS, similarities and differences with the PTS regarding habitat preferences and their response to human disturbance could be extracted. In the PTS, land use variables were the most important explanatory factors, followed by microhabitat variables and landscape variables. The PTS distribute hierarchically, selecting adequate habitats (ploughs and fallows), surrounded by a determined cover of land uses (avoiding arboreal crops and vineyards), which are sufficiently isolated from human disturbance and infrastructures, and with a suitable vegetation structure and stone cover. For the BBS, the clearest relationship was found for a landscape factor (avoidance of houses and tracks and selection of larger fields), with the relationships with land use variables being less strong. It is particularly interesting that the relationships between BBS occurrence and land use gradients only became relevant in sufficiently large fields isolated from houses and tracks (Figure 3). This could indicate that: a) human disturbance is modulating BBS distribution more strongly than land use preferences, or at least is mediating the choice of fields to settle; and b) BBS has a broader habitat tolerance and less human tolerance than PTS, a pattern already described at larger regional scales (Benítez-López et al. 2014a; Benítez-López et al. 2014b), and at landscape scale (Herranz and Suárez 1999; Martín et al. 2014). Although both sandgrouse preferred large-sized fields distant from houses and tracks (see also Martín et al. 2014), this response was much more pronounced for the BBS, further supporting the idea that BBS is more sensitive to human disturbance. The BBS is less conspicuous and more discrete in its behaviour than the PTS, has greater flight initiation distances and rarely calls when flushed (authors, unpublished data). This more discrete behaviour may have evolved as response to a lesser tolerance to disturbances. Indeed, the BBS was never observed in the northern side of the SPA, where urbanization and recreational houses (some illegal, Hervás and Suárez 2007) are pervasive, where PTS have been recorded (occasional observation and even a couple of nests; authors, unpublished results). This differential sensitivity to human disturbance suggests that an increasing advance of illegal urbanization would have more impacts on the already scarce BBS than on the PTS.

Both species selected preferably ploughs and fallows (especially PTS) and avoided cereal crops. Despite these similar land use preferences, mixed-species flocks have never been recorded, and both species were very rarely observed in the same field. This suggests that large-scale sympatry (Benítez-López et al. 2014b) does not necessarily translate into local-scale association. Possible explanations for segregation at local scale may be related to the above mentioned differential tolerance to human disturbance (BBS in larger isolated fields than PTS), microhabitat features (which we were unable to evaluate for BBS, but see Martín et al. 2014) or simply interspecific agonistic behaviours (or a combination of the three). We have provided some evidence for the first explanation, whereas for the second, spatial segregation could be driven by the abundance of large stones in fields occupied by the BBS, but not by the PTS, which prefers fields with low roughness (Martín et al. 2014). In contrast, we have found a clear association of PTS with stone coverage, depending on dry vegetation cover and height. In our area, both sandgrouse may differentially select fields depending on stone coverage, although further research would be necessary to gain more insight into microhabitat segregation between both species.

Microhabitat preferences: camouflage-visibility trade-offs

Microhabitat selection, which could only be evaluated for the PTS, typically reflects relationships with the most direct predictors of the biology of a species, that is, habitat selection for feeding, resting, roosting and, during the breeding season, nesting. Microhabitat gradients were modulated within preferred land uses (ploughs and fallows). Among ploughs, which typically have no or low vegetation, the PTS selected those with greater green vegetation cover (i.e.: crop weeds and ruderals) and number of insects. In turn, among fallows, normally characterized by greater dry vegetation cover and height, the PTS selected those with more bare ground cover, and greater cover of large and small stones. Predation is the most important cause of mortality in this area (Benítez-López et al. submitted), thus a strong selection pressure may drive microhabitat selection of PTS, which may be explained by trade-offs between camouflage and visibility in order to reduce conspicuousness (the PTS relies on its cryptic plumage and freezes when threatened) while simultaneously allowing an early predator detection and rapid escape. Fallows are widely used for nesting (authors, unpublished data; De Borbón et al. 1999), and thus maximizing chances of nest success (which is extremely low in this species, De Borbón et al. 1999; Mougeot et al. 2014) may drive the process of nest placement. Sandgrouse observed during the breeding survey in fallows are likely searching for optimal sites for nesting, and may prefer fallows with lower dry vegetation cover and height (i.e. more visibility) and with more stones for a better concealment of clutches (Lloyd et al. 2000; Znari et al. 2008) as well as for self camouflage, which would reduce predation risk for the nest contents or chicks, while maintaining a good visibility for vigilance and quick escape (see also Magaña et al. 2010). In turn, ploughs with greater green vegetation cover (probably due to low management intensity) may provide enough visibility but also shelter for resting (i.e.: cooler microclimatic conditions in ploughs with green vegetation compared to fully bare ground ploughs), while being an alternative source of weed seeds and green matter, both main components of the diet of the PTS (Herranz and Suárez 1999) and insects, whose importance on the diet of adult sandgrouse and, especially, of sandgrouse chicks (see similar examples in *Alectoris rufa, Lagopus scoticus*, Park et al. 2001) is yet unknown and deserves further investigation. Given than this time of year (early June), cereal crops (whose seeds are the most important dietary component in summer, Herranz and Suárez 1999) are yet to be harvested, and unavailable for feeding due to their vegetation structure (high vegetation and low visibility), PTS could be selecting ploughs, among other reasons, as alternative feeding ground.

Implications for conservation

This study highlighted the usefulness of multi-scale models for identifying hierarchically scale-specific factors determining species distribution, habitat preferences and influence of human disturbance. They also offer novel insights about conservation requirements at several levels that can guide regional and local-level conservation management strategies. At landscape scale, our results highlight the need for an environmental-sound and scientifically based design of infrastructures, and limitation in terms of urbanization within protected areas and biodiversity hotspots. Given the importance of ploughs and fallows for sandgrouse and for other steppe species (e.g*.: Tetrax tetrax*, Martinez 1994, *Otis tarda,* Magaña et al. 2010) traditional two-year rotations should be maintained. Reductions in the frequency and intensity of ploughing would also be beneficial, allowing the development of weeds that may be used for feeding. Fallows should also be left unmanaged during the breeding season since they are widely used as nesting habitat, and agricultural practices could result in nest destruction. Finally, the spread of arboreal crops and vineyards could be also detrimental for the conservation of sandgrouse. In this framework, the Common Agricultural Policy (CAP), seems to be the major driving force determining the future of sandgrouse populations at large national scale (Benítez-López et al. 2014a) and at local scale (this study, Suárez et al. 1997), and the future of other farmland species of conservation concern.

Acknowledgements

Many people helped with the surveys and microhabitat measurements, and we particularly thank Fidel, Iván García and Jesús Carrasco for their efforts. This study is a contribution to the CGL2008-04282/BOS project funded by the Spanish Ministry of Science. A. Benítez-López was supported by the CGL2008-04282/BOS project and by the 2012-BIN-4462 research grant conceded by the UCLM.

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Supplementary material

Table S1. Description of variables used in the Principal Component Analyses at different scales. Variables were measured at random and sandgrouse observation points.

Variable	Description
Landscape [1,2,3]	
Field size	Field size (km^2)
X	X coordinate
Y	Y coordinate
X^2	Quadratic term of the X coordinate
Y^2	Quadratic term of the Y coordinate
XY	Interaction term between X and Y coordinates
Alt	Altitude (m)
Slo	Slope (%)
DistFence	Minimum distance to fences (m)
DistTown	Minimum distance to towns (m)
DistWat	Minimum distante to water reservoirs and rivers (m)
DistHigh	Minimum distance to highways (m)
DistRoad	Minimum distance to roads (m)
DistTrack	Minimum distante to tracks (m)
DistRail	Minimum distance to railways (m)
DistPower	Minimum distance to powerlines (m)
DistHouse	Minimum distante to recreational and farmhouses (m)
DistAirpor	Minimum distance to the airport (m)
Land uses [1,4]	
FA	Percent cover of fallows around a 100-m radius
OF	Percent cover of old fallows around a 100-m radius
CE	Percent cover of cereals around a 100-m radius
ST	Percent cover of stubbles around a 100-m radius
UR	Percent cover of urban land (houses) around a 100-m radius
AR	Percent cover of arboreal crops around a 100-m radius
PL	Percent cover of ploughs around a 100-m radius
LE	Percent cover of legumes around a 100-m radius
PA	Percent cover of pastures around a 100-m radius
VI	Percent cover of intensive vineyards around a 100-m radius
VT	Percent cover of traditional vineyards around a 100-m radius
OT	Percent cover of other land uses (see table 1) around a 100-m radius
DIV	Shannon Diversity Index
Microhabitat [4]	
DVC	Percent cover of dry vegetation in 1x1 m quadrats
GVC	Percent cover of green vegetation in 1x1 m quadrats
LSC	Percent cover of large stones (>10 cm) in 1x1 m quadrats
SSC	Percent cover of small stones (2-10 cm) in 1x1 m quadrats
BGC	Percent cover of bare ground in 1x1 m quadrats
VH	Mean vegetation height (cm)
FD	Depth of furrows (cm, roughness)
NI	Number of insects (num/30'')

Sources: (1) SIGPAC (Sistema de Información Geográfica de Parcelas Agrícolas). (2) Spanish Instituto Geográfico Nacional (IGN). (3) Spanish Red Eléctrica Nacional (REE) (4) Fieldwork

Table S2. Results of the Principal Component Analysis performed on landscape variables featuring sandgrouse and random locations within the SPA (N= 656). For ease of interpretation the PC's have been recoded as LC's. Loadings >0.4 are in bold.

Variable	LC1	LC2	LC3	LC4	LC5
Field size	0.08	0.02	**-0.72**	-0.16	0.24
X	-0.13	**0.98**	0.07	0.07	0.09
Y	**-0.97**	0.01	0.08	-0.09	0.03
X^2	-0.13	**0.98**	0.07	0.07	0.09
Y^2	**-0.97**	0.01	0.08	-0.09	0.03
XY	-0.24	**0.96**	0.08	0.06	0.09
Alt	**-0.56**	0.03	0.04	**0.56**	-0.13
Slo	0.11	-0.08	-0.06	0.03	**-0.87**
DistFence	0.18	0.06	-0.19	**0.79**	0.08
DistTown	0.38	-0.20	-0.12	-0.33	**-0.54**
DistWat	**-0.88**	0.24	0.18	0.17	0.24
DistHigh	**0.77**	-0.01	0.03	0.02	-0.16
DistRoad	-0.06	**-0.47**	-0.26	**-0.57**	-0.07
DistTrack	0.07	-0.03	**-0.71**	0.18	-0.12
DistRail	**0.44**	**0.87**	0.01	0.17	0.04
DistPower	**0.80**	**0.55**	-0.05	0.09	-0.05
DistHouse	0.06	-0.18	**-0.66**	0.01	-0.24
DistAirpor	**-0.80**	**0.54**	0.13	-0.03	0.08
Eigenvalue	6.00	4.60	1.56	1.29	1.04
% Exp. Variance	32.87	25.35	8.25	7.29	6.14

Table S3. Results of the Principal Component Analysis performed on land use variables featuring sandgrouse and random locations within the SPA (N=656). For ease of interpretation the PC's have been recoded as LU's. Loadings >0.4 are in bold. See Table 1 for abbreviations**.**

Variable	LU1	LU2	LU3	LU4	LU5	LU6	LU7	LU8
FA	0.07	0.06	0.05	0.08	**-0.98**	0.07	-0.02	0.03
OF	**-0.74**	-0.06	0.04	0.03	0.04	0.07	0.05	0.03
CE	0.17	0.38	**0.72**	0.25	0.32	0.29	-0.16	0.12
ST	0.04	0.04	0.00	-0.05	0.02	0.01	**0.93**	0.00
UR	**-0.74**	0.02	0.01	0.06	0.08	-0.03	0.01	0.04
AR	0.09	0.03	-0.02	**-0.75**	0.04	0.01	0.03	-0.06
PL	0.13	0.25	**-0.87**	0.21	0.24	0.19	-0.09	0.09
LE	0.02	0.03	0.01	0.05	0.02	0.04	-0.01	**-0.99**
PA	0.05	**-0.97**	0.05	0.06	0.06	0.08	-0.05	0.04
VI	0.12	0.04	0.01	-0.16	0.09	**-0.75**	-0.21	0.02
VT	-0.09	0.03	0.02	0.25	-0.02	**-0.65**	0.20	0.02
OT	-0.09	0.00	0.06	**-0.61**	0.02	0.03	0.01	0.09
DIV	**-0.55**	0.15	-0.07	-0.27	-0.19	-0.05	-0.21	-0.14
Eigenvalue	1.55	1.31	1.27	1.16	1.14	1.09	1.03	1.01
% Exp. Variance	11.94	10.05	9.75	8.95	8.80	8.36	7.92	7.76

Table S4. Results of the Principal Component Analysis performed on microhabitat variables featuring sandgrouse and random locations within the SPA (N=637). For ease of interpretation the PC's have been recoded as MH's. DVC: Dry vegetation cover, GVC: green vegetation cover, LSC: relative cover of large stones, SSC: relative cover of small stones, BGC: bare ground cover, VH: vegetation height, FD: depth of furrows, NI: number of insects

Variable	**MH1**	**MH2**	**MH3**
DVC	**-0.88**	0.21	0.31
GVC	-0.09	**-0.83**	0.17
LSC	0.02	0.01	**-0.86**
SSC	0.33	0.12	**-0.75**
BGC	**0.89**	0.19	0.23
VH	**-0.79**	-0.14	0.35
FD	**0.71**	0.22	-0.19
NI	-0.09	**-0.73**	-0.04
Eigenvalue	3.32	1.29	1.26
% Exp. Variance	41.48	16.11	15.71

Table S5. Results of the model selection explaining the presence of the pin-tailed sandgrouse and of the black-bellied sandgrouse separately at landscape, land use and microhabitat levels. *variables that were included in the best global multiscale models after model selection.

	Pin-tailed sandgrouse					**Black-bellied sandgrouse**				
Variable	**Estimate**	**SE**	**Z**	**P**		**Estimate**	**SE**	**Z**	**P**	
Landscape										
Intercept	-0.94	0.10	-9.32	<0.001		-3.36	0.28	-11.82	<0.001	
LC1	-5.53	2.52	-2.20	0.028						
LC1^2	-6.28	2.89	-2.17	0.030						
LC2	-13.56	2.75	-4.93	<0.001	*					
LC2^2	-13.28	3.04	-4.37	<0.001	*					
LC3	-9.18	2.54	-3.61	<0.001	*	-1.15	0.17	-6.97	<0.001	*
LC3^2	-8.39	2.42	-3.46	0.001	*					
LC4										
LC5	0.27	0.11	2.33	0.020						
Land use										
Intercept	-1.77	0.21	-8.42	<0.001		-5.01	0.98	-5.11	<0.001	
LU1	0.65	0.18	3.60	0.000						
LU2						4.79	1.90	2.52	0.012	*
LU3	-33.73	4.11	-8.21	<0.001	*	-1.08	0.26	-4.15	<0.001	*
LU3^2	-24.12	4.45	-5.42	<0.001	*					
LU4	1.64	0.31	5.23	<0.001	*					
LU5	-14.71	2.82	-5.22	<0.001	*	-11.04	4.60	-2.40	0.016	*
LU5^2	-14.92	3.20	-4.66	<0.001	*	25.48	7.25	3.51	<0.001	
LU6	1.56	0.38	4.08	<0.001	*					
LU7										
LU8						-0.57	0.16	-3.49	<0.001	*
Microhabitat										
Intercept	-0.98	0.10	-9.39	<0.001		n.a.	n.a.	n.a.	n.a.	
MH1	21.19	2.84	7.46	<0.001	*	n.a.	n.a.	n.a.	n.a.	
MH1^2	-11.12	3.09	-3.60	<0.001	*	n.a.	n.a.	n.a.	n.a.	
MH3	-4.54	2.55	-1.78	0.076	*	n.a.	n.a.	n.a.	n.a.	
MH3^2	-6.15	2.47	-2.49	0.013		n.a.	n.a.	n.a.	n.a.	

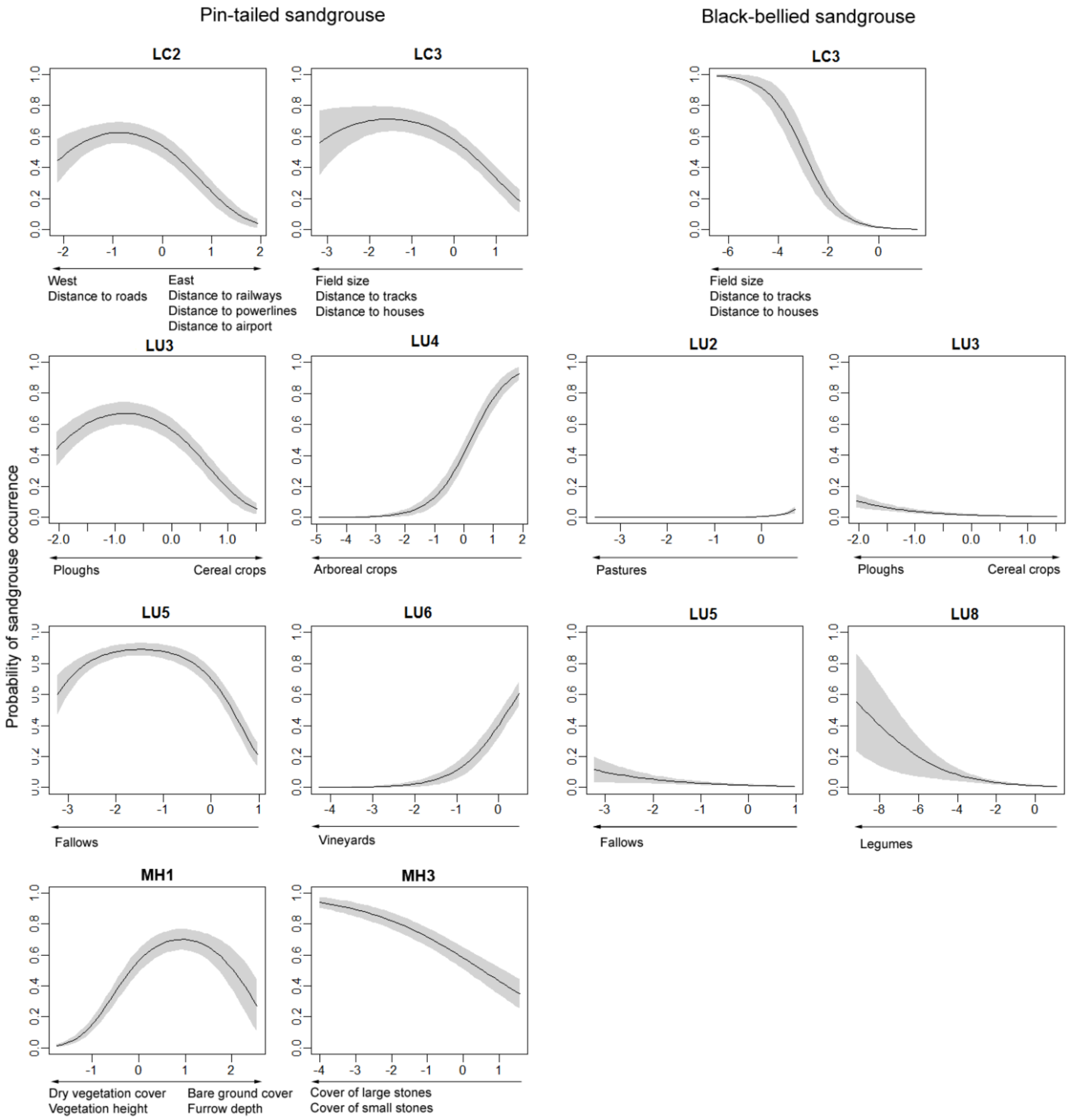

Figure S1. Probability of occurrence of the pin-tailed and the black-bellied sandgrouse along landscape, land use and microhabitat gradients (results from global models). Grey shades denote SE at both sides of the predicted curves. Predicted responses are plotted by varying one predictor while holding the other predictors constant at median values. Note the low probability of occurrence of black-bellied sandgrouse in the relationships with land use gradients when using the median value of LC3 (the most important predictor) for plotting. Values of individual variables below the x-axis increase following the direction of the arrows (and decrease in the opposite direction).

Variation Partitioning Analysis

We obtained the total amount of variation by modeling sandgrouse occurrence with the three groups of factors (LC+LU+MH). Afterwards, we modelled the landscape and land use variables simultaneously to obtain the amount of variation explained by both factor groups together (LC+LU); in a similar way, we determined the amounts of variation explained by environment and individual together (LC+MH), and by population and individual factors together (LU+MH). Then, the proportion of the variation explained exclusively by the landscape (lc) was obtained with the following subtraction: (LC+LU+MH) − (LU+MH). The proportions explained exclusively by population factors (lu) and by individual factors (mh) were obtained in a similar way. The amount of variation attributable exclusively to the interaction (or simultaneous influence) of landscape and land use factors (lclu) was obtained with the subtraction (LC+LU+MH) – MH – lc − lu. The amount of variation attributable exclusively to the interactions between environmental and individual factors (lcmh) and between population and individual factors (lumh) was calculated in a similar way. Finally, the amount attributable to the interactions between all three factors (lclumh) was obtained with the subtraction (LC+LU+MH) – lc – lu – mh – lclu – lcmh − lumh. Therefore, we provided a value for each part of variation explained and knew how much corresponded to its pure effect and how much to interactions between groups of factors (see also (Alzaga et al. 2009; Carrete et al. 2007; Real et al. 2003). A similar (although simpler) procedure was used for the partition of the two factors included in the model for black-bellied sandgrouse.

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CAPÍTULO 4

Development and application of capture methods for sandgrouse and assessment of short-term effects

Foto: Hans Hut

CAPÍTULO 4A

An improved night-lighting technique for the selective capture of sandgrouse and other steppe birds

Foto: Hans Hut

Benítez-López A, Mougeot F, Martín CA, Casas F, Calero-Riestra M, García JT, Viñuela J (2011) An improved night-lighting technique for the selective capture of sandgrouse and other steppe birds. Eur. J. Wildl. Res. 57: 389-393.

Abstract

The night-lighting technique is routinely used to catch birds. We improved this technique using a thermal-infrared camera to catch steppe birds such as sandgrouse. Target birds were located by an observer using the thermal camera, and approached and dazzled by another observer carrying a spotlight attached to a helmet and a hand-held net, together with a play-back noise to camouflage the footsteps of the observer. Using this improved technique, we caught on average 1.1 individuals per 3h capture session (*N*=81), and a total of 92 sandgrouse in 2007-2010 (86 pin-tailed sandgrouse *Pterocles alchata* and 6 black-bellied sandgrouse *Pterocles orientalis*). Capture rate and success were negatively influenced by moonlight (lowest during full moon nights). Our night-lighting technique is a highly selective and harmless method to capture sandgrouse, and can be used for other small/medium-sized open-land birds or mammals.

Keywords: capture; thermal infrared camera; night-lighting; sandgrouse; trapping technique

Introduction

A wide variety of capture methods have been used in avian field studies, depending on the characteristics of the target species, the capture period or the habitat (Bub 1991). The night-lighting technique consists in using a powerful light to locate (usually by light-reflection from the bird's eyes) and dazzle birds at night, and to approach and catch them with a hand-held net. This technique have proved highly effective for many species (e.g. red grouse: Hudson 1986; woodcocks: Duriez et al. 2005; nightjars: Forero et al. 2001), several aquatic species and owls (Hernandez et al. 2006; King et al. 1994; Labisky 1959) and is selective, allowing targeting certain species and individuals (Bub 1991; King et al. 1994; Labisky 1959). Furthermore, catching diurnal birds at night (a time of low physiological activity) might reduce the stress suffered during the capture and handling, which is especially important in the case of sensitive species (Ponjoan et al. 2008). However, this technique can be time-demanding when roosts need to be located in advance, or when birds are difficult to find (small size, cryptic plumage, eyes poorly reflecting the spotlight).

Here we report on an improved night-lighting technique that allows to selectively capture pin-tailed and black-bellied sandgrouse (*Pterocles alchata* and *P. orientalis*) in order to study their breeding ecology and movements (e.g. Martín et al. 2010a; b); and we also give recommendations for the optimal use of our methodology.

Materials and methods

Fieldwork was conducted in July 2007-May 2010 in different areas of Spain: Campo de Calatrava and Carrión de Calatrava in Ciudad Real province, Carrizales y Sotos de Aranjuez in Madrid province, and Bardenas Reales Natural Park, in Navarra. These areas were covered by agro-steppes, natural steppes and/or ploughed fields or barren areas with low vegetation cover. Captures were performed at night avoiding bad weather conditions (rain, mist, strong winds) to minimize the risk of hypothermia and stress for birds. Birds were located before dusk in order to determine where they roost. Two persons were needed to guarantee both capture efficiency and bird safety during handling.

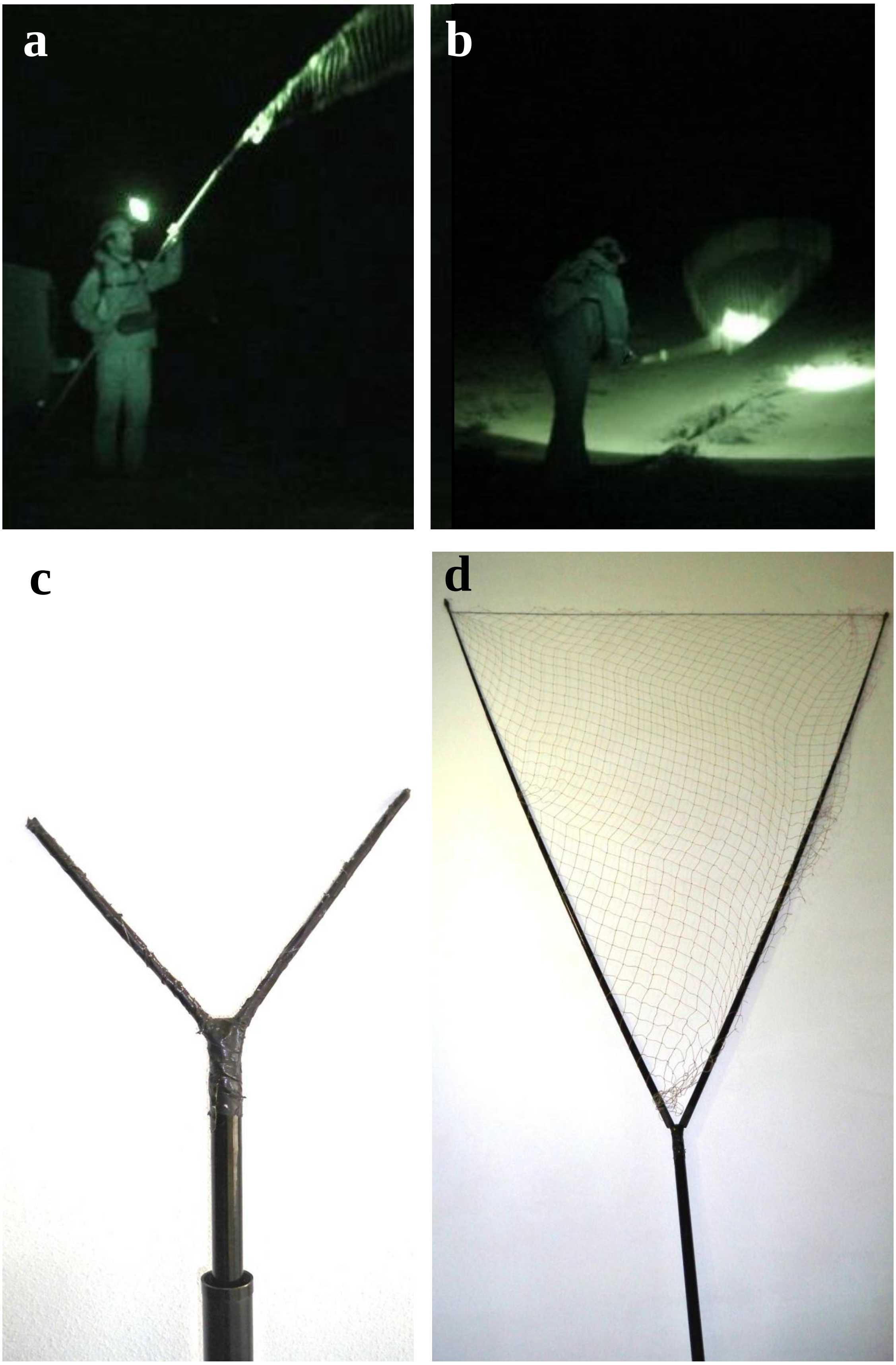

Figure 1. a) Image of a researcher carrying the large hand-nest attached to the telescopic pole and the helmet with a fitted spotlight used for trapping sandgrouses (photo taken by Faena); b) image of a researcher performing a capture attempt; c) detail of the V-shaped piece attached to the telescopic pole d) net assembled to the pole using the V-shaped piece.

One person carried a thermal infrared camera (Panatec, Madrid, Spain), the other carried the catching equipment, which consisted of: 1) a hand-held net (2.5 x 2.5 m, 3-5 cm 3-ply netting mesh) fitted to a telescopic pole (2.5 - 5 m length, diameter: 5 cm) built in lightweight materials (carbon fibre) and dark- coloured (Fig.1a, c, d); 2) a plastic helmet fitted with a strong halogen spotlight (50 watts); 3) a backpack containing the battery (12V-12AH) for the spotlight; and 4) a tape player to broadcast a recording of a tractor´s engine sound when approaching target birds. Captures started at least one hour (winter) or two (summer) after the sunset when the temperature dropped sufficiently to optimize the use of the thermal infrared camera, and lasted until the battery of the thermal infrared camera was over (c. 3 hours). Birds were first located in darkness using the thermal infrared camera by scanning and looking for birds in the field where the roosting birds were previously located. With this camera, the shape of sandgrouse was easily recognizable from a distance of c. 100 m in fields with no or low vegetation (Fig. 2a,b). The camera detects the amount of infrared radiation that each object's emits according to its temperature (the greater the temperature contrast between object / surroundings, the brighter the object; Fig 2a,b,c). The system works in total darkness, but open space between the object and the camera is essential to get infrared radiation. Thus, bird detection is possible in open areas with no or short vegetation (for sandgrouse, on bare grounds, ploughs or one-year fallows). Once a target individual was located with the camera, the bird was pinpointed to the second observer who approached and dazzled it with the spotlight while playing the tape-recorded noise to camouflage footsteps ´noise. When the individual was close enough (c.3-4m), the net was rapidly swung downward over the bird to capture it (Fig. 1b, 2d).

To assess the efficiency of our method we recorded capture success (1= one or more birds captured/session, 0= unsuccessful session), and capture rate (number of birds captured/session, each session lasting c. 3h.; *N*=81 sessions). We also recorded the number of attempts/session and number of birds captured/ attempt for 26 out of the 81 sessions (an attempt was performed when an observer managed to approach an individual and swing the net over). We recorded several variables (season, moon phase, and wind speed) that could affect capture success and capture rate (moonlight might influence awareness and intruder´s detection; wind might reduce the noise of an approaching intruder). Moonlight was coded as 0 (new moon ± 3 days, or moon absent or hidden by clouds), 1 (increasing or decreasing half moon phase ± 3 days, moon present and not obscured by clouds) or 2 (full moon phase ± 3 days, moon present and not obscured).

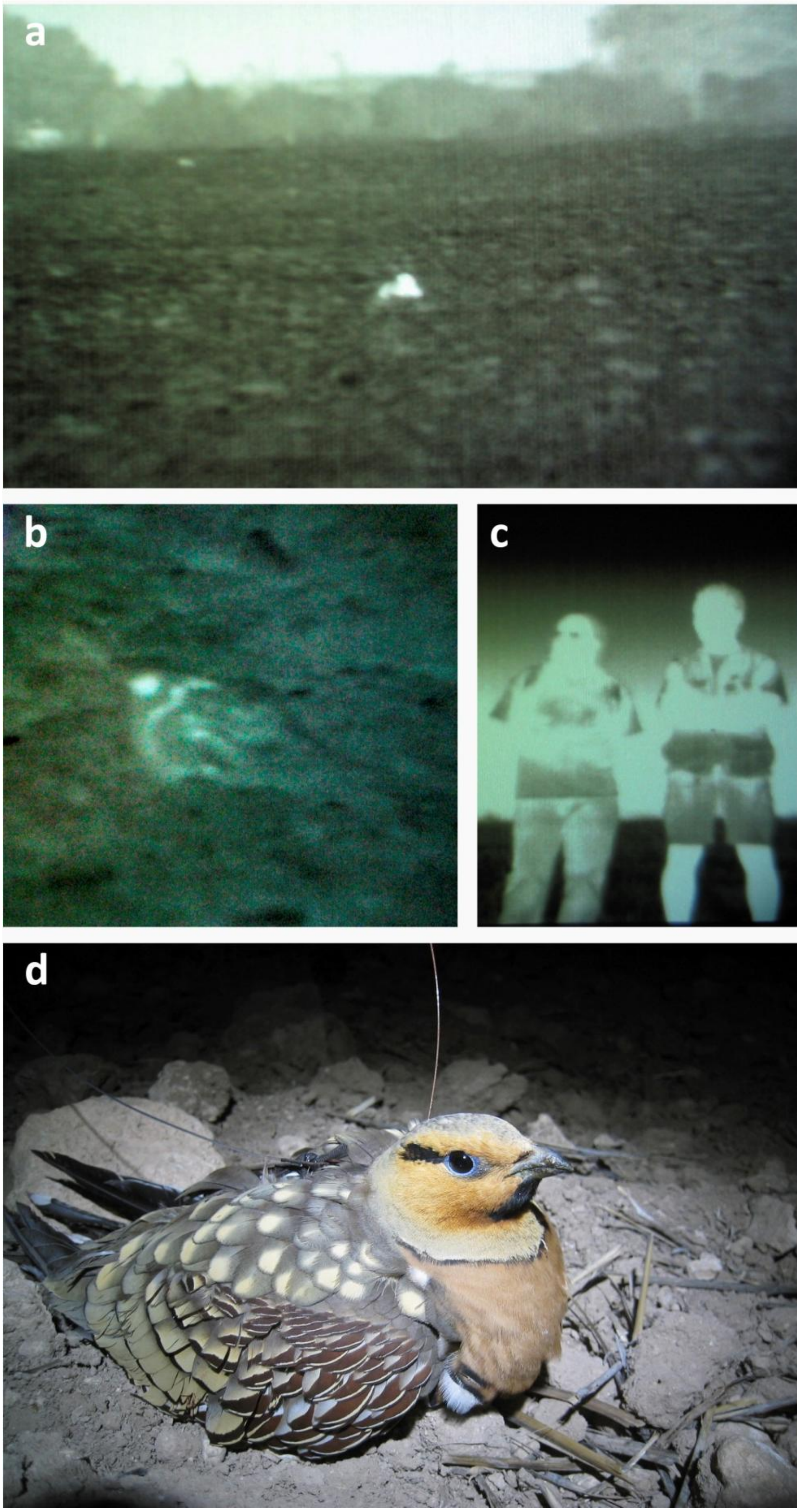

Figure 2. a) Image of sandgrouse in a ploughed field viewed through the thermal infrared camera (distance of c. 100m); b) close up view of a pin-tailed sandgrouse through the thermal infrared camera (distance c. 10 m); c) a pair of researchers as viewed through the thermal infrared camera; d) male pin-tailed sandgrouse prior to release (photos taken by F. Mougeot).

Average wind speed was recorded as a continuous variable (in km/h, MARM 2010), and season as categorical variable: pre-breeding (March/May), breeding (June/mid-August), post-breeding (mid-August/September) and winter (October/February). We tested the effect of these variables on the capture success (binomial distribution) and the capture rate (Poisson distribution) using GLMs and the function “step” / backward direction in R 2.10 (R Development Core Team 2009) to select the best model out of our candidate models (the model with the lowest AIC_c or Second-order Akaike Information Criterion). Akaike weights were calculated to determine the probability that each model in the candidate set is the “best” model as an inference (Burnham and Anderson, 2002). We calculated the importance weight for each variable included in our candidate models to determine their relative importance in predicting capture success or rate (Burnham and Anderson, 2002).

Results

We captured 92 sandgrouse (86 pin-tailed sandgrouse: 50 males, 33 females and 3 juveniles and 6 black-bellied sandgrouse: 4 males and 2 juveniles). Most captures were performed during winter (*N*=34) and pre-breeding (*N*=34) periods, followed by post-breeding (*N*=17) and breeding (*N*=7) periods. Birds were always apparently calm when captured and flew upon release. No individual died when captured or handled. On average, 1.14 individuals (range 0-4) were captured per session (*N*=81), out of 2.08 attempts per session (range 1-4, *N*=26).

The models containing moonlight, or moonlight + wind best explained capture success (Table 1), the former being 2.76 times more likely to be the best explanation for capture success than the latter.

Table 1. Results of Generalized Linear Models testing for the effects of moonlight (MOON), wind speed (WIND) and season on capture success and capture rate.

Variable	**Model**	**AICc**	***K***	**Δ_iAICc**	**w_i**	**% Dev.**
Capture success	**MOON**	**110.85**	**3**	**0.00**	**0.69**	**2.73**
	MOON+WIND	**112.66**	**4**	**0.38**	**0.25**	**2.9**
	MOON+WIND+SEASON	115.53	5	1.11	0.05	5.81
	MOON+WIND+SEASON+MOON*WIND	118.51	6	3.12	0.01	6.75
Capture rate	**MOON**	**226.31**	**3**	**0.00**	**0.72**	**7.94**
	MOON+WIND	**228.30**	**4**	**1.88**	**0.24**	**7.94**
	MOON+WIND+MOON*WIND	231.77	5	4.23	0.04	8.46
	MOON+WIND+SEASON+MOON*WIND	235.85	6	8.32	0.00	10.31

Capture success and capture rate were fitted to models using binomial and Poisson error distributions, respectively; AICc = Second-order Akaike Information Criterion; *K* = No. of estimated parameters; Δ_iAICc = difference between the model AICc and the lowest AICc for the model set; w_i = Akaike weight (relative likelihood of each model: the smaller the weight the less plausible the model); % Dev.= Percentage of deviance explained by the model ((Null Deviance-Residual Deviance)/Null Deviance*100)

The same held for capture rate (Table 1) with the moonlight model being 3 times more likely to explain capture success than the moonlight + wind model. The variable moonlight turned out to be 3.23[1] and 3.57[2] times more plausible than wind speed for explaining capture success and capture rate, respectively. Both capture success (mean ± SE: 0.70±0.09) and capture rate (1.50 ± 0.21, *N*=30) were greater in dark overcast nights and in half moon nights (success: 0.62 ± 0.08; rate: 1.05 ± 0.18, *N*=37) than in clear moonlit nights (success: 0.43 ± 0.14; rate: 0.57 ± 0.23, *N*=14). Wind speed had a slight, negligible negative effect on capture success (effect size ± SE= -0.014 ± 0.031) and rate (-0.001 ± 0.014).

Discussion

The improved night-lighting technique presented here was highly successful for capturing sandgrouse. Greater effectiveness was achieved in "dark", overcast nights with no or little moonlight (i.e. new moon or cloudy increasing/decreasing moon phase) and in light wind conditions. However, our models explained little of the variation in capture rate or success (see deviances in Table 1), so other factors, not considered here such as habitat type, equipment (length of the pole, size of the net, intensity of spotlight), observer's experience or simply chance, are likely to also explain success. We did not record habitats where capture attempts were successful or not, but our experience suggest that attempts on ploughs might be more successful because we are better able to detect birds with the thermal camera without vegetation, and because walking on substrates with dry vegetation generates more noise. We also noticed that using a longer pole, a larger net and more powerful spotlight may enhance success.

Other causes of failure easy to avoid through practice and experience are: a) failing to properly dazzle the target individual (spotlight not always aimed at the bird when approaching), b) failing to detect a bird closer than the target individual, which flushes before the target bird, causing other birds to flush, c) lighting the net when swung downwards, allowing the target bird to see it before capture, d) dropping the net too far / close from the bird or failing to locate the bird with the spotlight from a very close distance.

The primary advantages of this improved trapping technique are that it allows the selective capture of individuals of diurnal species, with low injury rate and reduced capture stress. This

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[1] Model for capture success: Importance weight for moonlight= 1; Importance weight for wind speed = 0.31

[2] Model for capture rate:Importance weight for moonlight= 1; Importance weight for wind speed = 0.28

technique also allowed us to catch other birds such as red-legged partridges *Alectoris rufa* (Casas et al. 2009), stone curlews *Burhinus oedicnemus*, or passerines (larks), and even mammals (juvenile Iberian hares *Lepus granatensis*). Thus, its applicability goes beyond capturing sandgrouse and it can be easily adapted for capturing other open-land birds and mammals.

Acknowledgements

We thank A. Urmeneta, S. González, Faena, C. Ponce, C. Bravo, F. Alda, S. Luna and A. Mateo for their help during fieldwork, owners for allowing us to work in their properties, and the Regional governments for capture permits. Funding came from the Dirección General de Investigación (projects CGL2007-66322/BOS and CGL2008-04282/BOS), Consejería de Educación y Ciencia de Castilla-La Mancha (projects PAI08-0171-9582 and PAC06-137) and Bardenas Reales Natural Park (project CTR09-0268).

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CAPÍTULO 4B

Assessing the short-term effects of capture, handling and tagging of sandgrouse

Foto: François Mougeot

Casas F, **Benítez-López A,** García JT, Martín CA, Viñuela J, Mougeot F (2014) Assessing the short-term effects of capture, handling and tagging of sandgrouse. Ibis (in press).

Abstract

Capturing and marking free-living birds permits the study of important aspects of their biology, but may have undesirable detrimental effects. Bird welfare should be a primary concern, so it is crucial to evaluate and minimise any adverse effects of procedures used. In this study, we assess short-term effects associated with the capture, handling and tagging with backpack-mounted transmitters of Pin-tailed and Black-bellied Sandgrouse, two steppe birds of conservation concern. We show a significantly higher mortality (15%) during the first week after capture than during the following weeks (< 2.5%) of Pin-tailed Sandgrouse, but no significant temporal mortality pattern in Black-bellied Sandgrouse. In Pin-tailed Sandgrouse, mortality rate during the first week increased with increasing relative radio-transmitter and harness weight regardless the season, and with handling time during the breeding season. We did not find significant differences in mortality rate between study areas, type of tag, sexes, ages or an effect of restraint time. These results suggest the use of lighter transmitters (< 3% of the bird´s weight) and a reduction of handling time (< 20 minutes), particularly during the breeding season. These recommendations would help to reduce the mortality risk associated with the capture, handling and tagging of these vulnerable species.

Keywords: capture method, mortality, *Pteroclidae*, radio-tracking, radio-transmitters, steppe birds, survival, telemetry.

Introduction

Many capture methods have been used in avian field studies, depending on the characteristics of the target species (Bub 1995, Gill et al. 2001, Kenward 2001, Sutherland et al. 2004). Capture, handling and attachment of devices to wild animals allows direct study of important aspects of bird biology such as morphology, physiology, behaviour and ecology, and the collection of samples for genetic or biochemical analyses (Ropert-Coudert and Wilson 2005). This information can deliver novel insights applicable to management and conservation policies (White and Garrott 1990, Sutherland et al. 2004).

Nevertheless, capturing, handling and marking wild birds have associated risks, which might cause higher mortality, nest abandonment, behaviour alterations or worsening of physical condition (Murray and Fuller 2000, Kenward 2001, Barron et al. 2010, Dennis and Shah 2012). Most fieldworkers claim that capture, handling and tagging effects are negligible, or that the associated mortality risks are compensated by the benefits derived from the application of the research results to the conservation of the studied species (Wilson and McMahon 2006), but potential negative effects still have to be assessed, and bird welfare should be a primary concern (Cox and Afton 1998, Ponjoan et al. 2008). There is much variation in species' responses to different catching and tagging techniques, and it is important to evaluate and reduce risks (Wilson and McMahon 2006, Spotswood et al. 2012), particularly in species of conservation concern.

One of the main side-effects of capturing and handling animals is capture myopathy (Höfle et al. 2004, Marco et al. 2006, Mulcahy et al. 2011). Capture myopathy is characterized by damage to muscle tissues caused by strenuous and vigorous use of the large appendicular muscles during trapping, pursuit, capture, restraint or transport (Williams and Thorne 1996). As a consequence, captured birds exhibit impaired mobility and coordination after release, a risk that can be reduced if handling and restraint times are kept to a minimum (Ponjoan et al. 2008, Ruder et al. 2012). Although in some cases birds may recover normal mobility shortly after capture, in others the behavioural alterations associated with capture and handling (Nicholson et al. 2000, Ponjoan et al. 2008) may affect mobility and flight reaction from predators during the days after their release, thus hampering escape ability and increasing predation risk.

Animals may be tagged with rings or tags, and these devices may have deleterious effects on bird behaviour and fitness (e.g. Ropert-Coudert et al. 2000, Zuberogoitia et al. 2012, Trefry et al. 2013). Radio-tracking, for example, is often the only way to collect data on habitat use and selection, behaviour and survival in wary, elusive or cryptic animals (Kenward 2001). Yet, when birds are captured for radio-tracking, the transmitter may affect bird survival either because the additional weight increases energetic expenditure (standard protocols recommend < 5% of the weight of the animal, Kenward 2001) or by altering behaviour, perhaps even injuring the birds when they try to remove the radio-transmitter and attachment (Höfle et al. 2004).

In this study, we assessed the effects associated with capture, handling and tagging with backpack-mounted transmitters of free-living Pin-tailed and Black-bellied Sandgrouse *Pterocles alchata* and *P. orientalis*. Both species are characteristic of steppes and open-land agricultural pseudo-steppes, and occur in low intensity, non-irrigated agro-ecosystems (De Juana 1997, Suárez et al. 2006, Benítez-López et al. 2014). They show cryptic behaviour and plumage which make them difficult to locate, observe and study. Although sandgrouse are currently classified as “Least Concern” worldwide, both Pin-tailed and Black-bellied Sandgrouse have ‘Unfavourable Conservation Status’ at European level (BirdLife International 2004). Spain hosts ca. 90 and 25% of the estimated European populations of Pin-tailed and Black-bellied Sandgrouse, respectively (Suárez et al. 2006, Birdlife International 2013a, b), where both species have a “Vulnerable” conservation status (Suárez and Herranz 2004a, b). Despite this conservation concern, scientific knowledge of both species is scarce. This is in part due to their elusive behaviour and sensitivity to human disturbance (Mougeot et al. 2014), but also because of the difficulty of catching and tagging these birds without negative impacts. Previous attempts to capture and tag Pin-tailed Sandgrouse with cannon nets produced high short-term mortality (two of seven birds died and a further three lost the radio-transmitter during the first week after capture) and low long-term monitoring success (just one individual) (Gil 2007). This prompted abandonment of this capture and tagging method, and development of a new one (capture at night with a hand-held net and a strong spotlight when birds are roosting; see Benítez-López et al. 2011 and below for further details) that allowed a much greater proportion of tagged sandgrouse to be successfully monitored (15 birds, Martín et al. 2010a, b).

In this paper, our main aim is to test whether sandgrouse were affected by capture, handling and tagging involved in research and conservation projects using the above methods, focusing on short-term mortality. Our second aim is to evaluate which factors explain the probability of sandgrouse mortality after capture, and subsequently give recommendations to reduce the impact of these field techniques on these sensitive steppe birds. We considered two main types of factors: 1) factors that can be controlled for, such as the timing of captures (e.g. during the breeding or the non-breeding season), handling time, type of tag and weight of the transmitter fitted to captured sandgrouse (specifically the transmitter and harness weight, relative to the bird´s weight); 2) factors that may be more difficult to control for, such as the age and the sex of the bird captured, or its weight and body condition.

Methods

Study areas

We conducted fieldwork in Spain, in two different regions of the Southern Central Plateau (central Spain, hereafter SCP) and Bardenas Reales (northern Spain, hereafter BR). In SCP we captured sandgrouse in three populations: Campo de Calatrava (core area; 38º 54’N, 3º 55’W, Ciudad Real province, 89.8 km^2), Carrión de Calatrava (39º 01’N, 3º 49’W, Ciudad Real province, 66.3 km^2) and Aranjuez (40º 02’N, 3º 36’W, Madrid province, 149.8 km^2). Campo de Calatrava and Aranjuez are included within the European Union Special Protection Areas (SPA) 157 (Área esteparia del Campo de Calatrava) and 119 (Carrizales y sotos de Aranjuez), respectively. The Bardenas Reales, with an area of 418.5 km^2, is located in SE Navarra province (42º 08’N, 1º 26’W), in the middle of the Ebro Valley depression. This area is a protected Natural Park and a Biosphere Reserve.

Field procedures

All birds were captured using the method described in Benítez-López et al. (2011). Briefly, captures were performed at night with the aid of a thermal camera, with birds then dazzled with a powerful spotlight and captured with a large hand-held net. Between August 2007 and December 2012, we captured and tagged 128 Pin-tailed Sandgrouse (91 in SCP and 37 in BR) and 13 Black-bellied Sandgrouse (8 in SCP and 5 in BR). We also captured six young birds that were not tagged because they were not fully grown or in family coveys. At capture, we recorded the exact position by GPS, the species (Pin-tailed or Black-bellied Sandgrouse), and kept the bird in a bag to take it back to a car where it was subsequently processed. For each capture, we recorded the restraint time (RT, in min) as the time elapsed between capture and handling (i.e. the time spent by the bird in a bag between capture and the start of handling), and handling time (HT, in min.) as the time spent handling the bird until it was released. These two time measures could have different implications in terms of adverse effects. Handling time depended on the number of samples and measures taken per bird and on the time spent fitting the tag, while restraint time depended on the distance between capture and processing sites, as well as how many birds were caught simultaneously (usually one, but sometimes up to four). Therefore, an effect of restraint time on short-term mortality would imply a reduction in distance between capture and processing sites and in the number of birds caught simultaneously, while an effect of handling time would imply a reduction in the number of samples and measures taken or gaining experience in processing and tagging. During handling, we noted the sex and age of each bird (based on plumage characteristics; see De Juana 1997, Blasco-Zumeta & Heinze 2013). We weighed each bird (with an electronic balance; nearest 0.1 g), and took several biometric measurements (at least tarsus and wing length). We also took a blood sample for genetic analyses (~50 µl), and four photographs for plumage characterisation. Finally, we fitted the birds with a backpack-mounted transmitter, and released them at the capture site. Throughout the six years of study, we used different types of tags. Pin-tailed Sandgrouse (mean weight: 342.1 g, range 260-415 g, *n* = 128) were tagged with TW3 radio-transmitters of 11.0, 9.9, 7.5 or 7.0 g (*n* = 118; Biotrack, UK) or Solar PTT satellite-transmitters of 12.0 or 9.5 g (*n* = 10; Microwave Telemetry, USA). Black-bellied Sandgrouse (mean weight: 493.7 g, range 404-581 g, *n* = 13), which are heavier than Pin-tailed Sandgrouse, were tagged with TW3 radio-transmitters of 16.5 or 16.0 g (*n*= 9; Biotrack, UK) or with Solar PTT satellite-transmitters of 12.0 or 9.5 g (*n* = 4; Microwave Telemetry, USA). The different transmitter weights reflect the fact that we preferred lighter transmitters as these became available (see also results). Radio-transmitters had between 0.8 and 1.8 years of battery life, and an average signal detection range of 1-3 km on flat land (depending on the tag model) and up to 6 km from elevated points. Backpack-mounted transmitters were attached by passing the loops of a Teflon harness (average weight 1 g) attached to the tag around and over each wing, positioning the tag on the upper back of the bird. Each end of the loop was fastened with a double knot sealed with Superglue.

For all tagged birds, the weight of the transmitter plus harness relative to the weight of the bird (RTW hereafter) ranged between 2.1 and 4.4% for Pin-tailed sandgrouse, and between 2.2 and 4.2% for Black-bellied Sandgrouse (Fig. 1). RTW was thus below the *a priori* recommended upper limit of 5% of the bird weight (Kenward 2001).

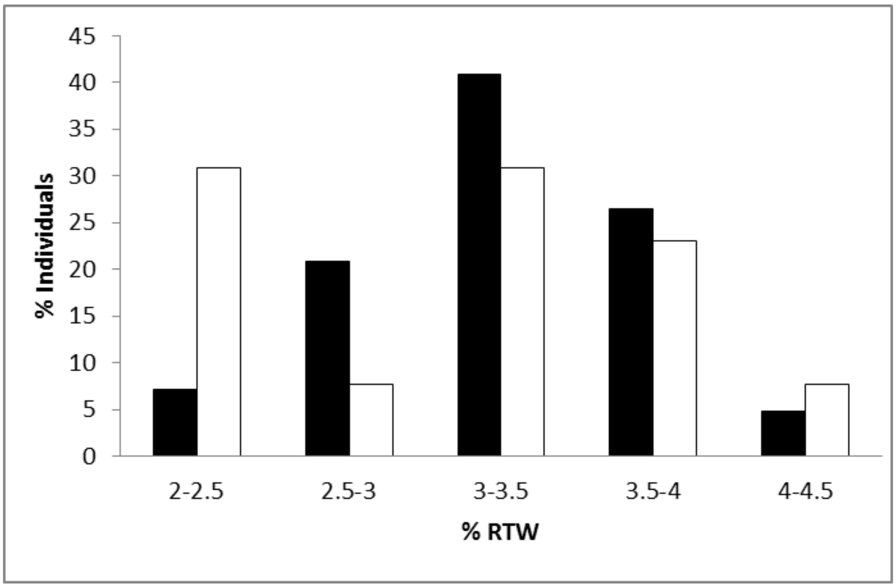

Figure 1. Frequency distribution (% individuals) of the RTW (in %) used for tagging Pin-tailed (black) and Black-bellied Sandgrouse (white).

Radio-tagged birds were subsequently located using Biotrack Sika telemetry receivers connected to a three-element directional YAGI antenna at least once per week by visual observations or using triangulations (see Martín *et al.* 2010a, b), and satellite-tagged birds using the Argos satellite system, selecting the most accurate Location Class (LC) per day (e.g. Terraube *et al.* 2011). We used periodic flights (1-2 flights/year) in small aeroplanes with attached directional antennae to relocate radio-tagged birds that dispersed outside the range usually covered by ground tracking (ca. 140-210 km^2 in SCP and ca. 250 km^2 in BR). When the signal of a satellite transmitter was erratic or lost, we located the birds using a Yaesu VR-500 receiver connected to a 4-element Yagi antenna (Biotrack). We recorded for each bird observation: 1) date, 2) hour, 3) geographical position (with a Garmin eTrex Vista Cx GPS, nearest 3 - 4 m), 4) survival (dead or alive), and 5) mortality cause when possible.

Data treatment and analyses

All analyses were performed with Statistica 7.1 (StatSoft, 2005) and R 2.13.1 (R Development Core Team 2011). In order to evaluate short-term deleterious effects related to capture, handling and tagging (CHT hereafter), we calculated the proportion of tagged birds that were alive each week during the first eight weeks after capture, and used a Fisher exact test (two tailed) to assess weekly differences in the proportion of birds that died after CHT (Ho: mortality rate during week$_x$ = mortality rate during week$_y$), assuming that a weekly mortality rate higher than expected naturally during this period would likely be associated to CHT. Two birds tagged with radio-transmitters and one with satellite-transmitter were excluded from this and subsequent analyses, because the signal was lost before eight weeks after capture (unknown fate). We also investigated between-species differences in factors that can be controlled for (RT, HT and RTW) using Student t-tests. When a bird was found dead, we tried to determine cause of mortality by visual inspection of the remains and a necropsy. The latter was possible in three cases during the study period, and no clear macroscopic lesions associated with capture myopathy were found (but microscopic lesions and levels of creatine kinase were not analysed, Höfle et al. 2004). In all other cases, the birds had been predated, and remains were too few to determine whether capture myopathy occurred before predation. Additionally, sometimes it was uncertain whether the bird had been predated or had a different cause of death and had been scavenged.

To evaluate the factors explaining mortality after CHT, we analysed variation in the probability that a Pin-tailed Sandgrouse died during the first week after capture (the week for which the observed proportion of deaths was higher than expected; see results, hereafter referred as "CHT mortality"). The sample size of Black-bellied Sandgrouse was too small for a similar analysis. We initially considered as explanatory variables, factors that can be controlled for (type of tag, RT, HT and RTW) and factors that are more difficult to control for during captures (sex, age and body condition). We used body mass and tarsus length (better correlated with body mass than wing length, tarsus length: $r = 0.454$, $P < 0.001$, wing length: $r = 0.427$, $P < 0.001$) to calculate a scaled mass index as a measure of body condition (Peig and Green 2009, 2010). Scaling relationship between body mass and tarsus length was different by sex ($P < 0.05$), but not by age ($P > 0.1$), thus the scaled mass index was calculated individually for males and females separately (Peig and Green 2010). We explored collinearity among explanatory variables using Spearman correlation coefficients. Pairs of variables that were highly correlated ($P < 0.05$) were considered as estimates of a single underlying factor. In such cases, we chose only the variable with highest biological meaning for posterior analyses. We selected % RTW instead of capture order (sequentially allocated to each bird following the order of capture, 1 = first bird caught and tagged; 125 = last; as a surrogate for capture and tagging experience over the study period) or body condition (scaled mass index). We did so because both were correlated with RTW ($r_s = -0.69$, $P < 0.05$, and $r_s = -0.37$, $P < 0.05$, respectively) and because the interpretation of the variable % RTW have more practical relevance in terms of deciding whether a sandgrouse of a given weight should or should not be tagged with a transmitter of a given weight.

The probability of CHT mortality was fitted to a Generalized Linear Mixed Model (GLMM) with binomial error distribution and a logit link function, with the factor “year” (6 levels) included as a random effect (lme4 package in R). The initial model included the following explanatory variables: sex, age, season (2 levels: breeding = April-September; non-breeding = October-March; De Borbón *et al.* 1999), type of tag (2 levels: satellite and radio transmitters), study area (2 levels: SCP and BR), RT, HT, RTW (in %). Interactions formed by two variables with biological sense were also tested (sex × season, sex × RT, sex × HT, season × RT and season × HT). Non-significant ($P > 0.10$) terms were removed sequentially using a backward stepwise procedure (drop1 function in R). Pin-tailed Sandgrouse tagged with satellite-transmitters ($n = 9$) were included initially although satellite tags were preferably fitted to heavier birds, which were mostly males (eight of ten birds and, within the males, the heaviest birds). We tested for differences in body condition (scaled mass index) between birds tagged with radio or satellite transmitters and seasons using ANOVAs.

Results

Short-term deleterious effects of CHT on sandgrouse

Throughout the study period, we had no case of mortality during capture, handling and tagging procedures for either species. For Pin-tailed Sandgrouse, we found a significantly higher percentage of mortality during the first week after capture (15%; $P < 0.01$) than during the following seven weeks when weekly mortality never exceeded 2.5% (average of 1.7% during the weeks 2-8 after capture, Fig. 2a). In the small sample of Black-bellied Sandgrouse, we found no significant differences in weekly percentage mortality during the eight weeks after capture (Fig. 2b), with an average weekly mortality of 1.9%.

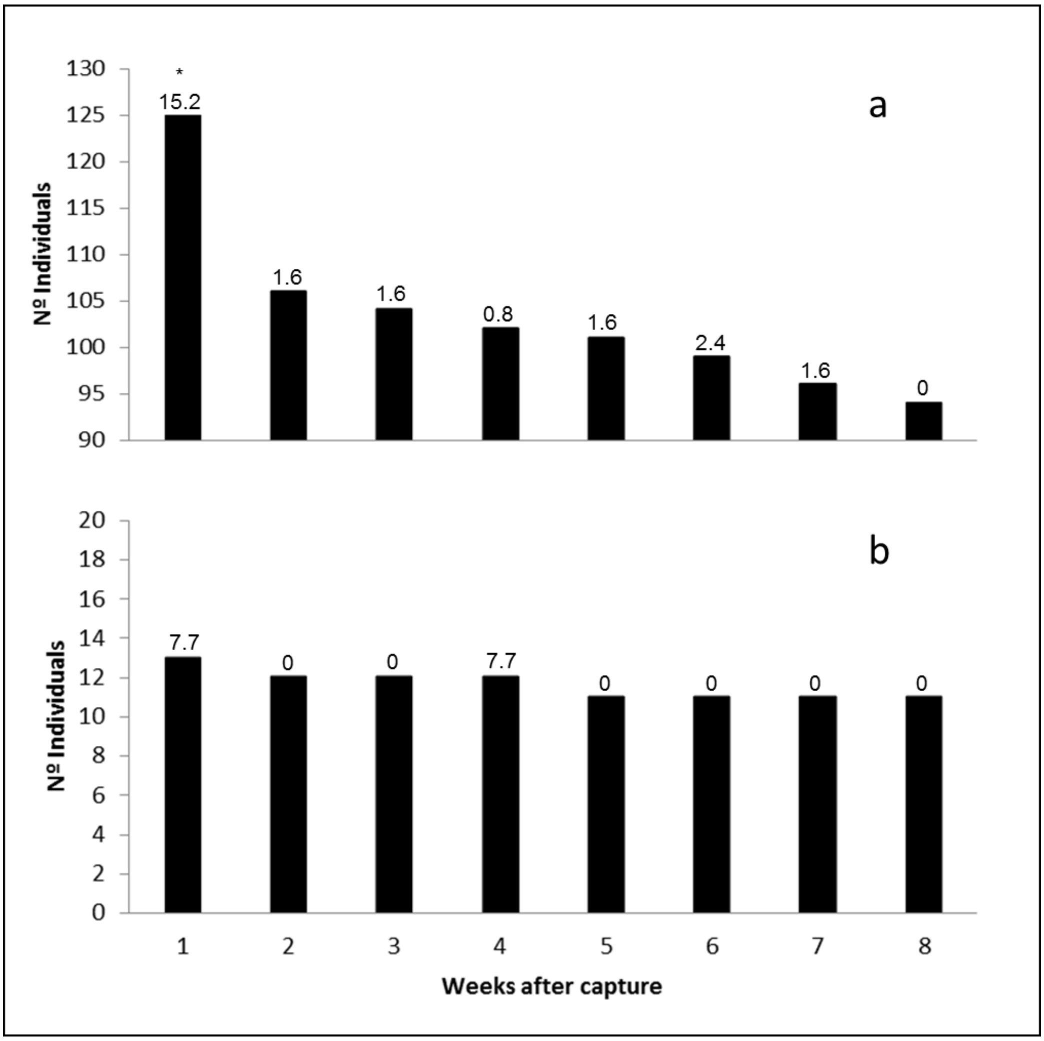

Figure 2. Weekly total number of captured and tagged Pin-tailed (a) and Black-bellied Sandgrouse (b) alive at the beginning of each week during the first eight weeks after capture (*n* = 125 and 13 for Pin-tailed and Black-bellied Sandgrouse, respectively). Numbers above bars refer to weekly % mortality rates. Fisher exact p test (two tailed) indicated a significantly (* $P < 0.05$) higher mortality in week 1 as compared with each of the other weeks for Pin-tailed Sandgrouse.

Differences between species

Neither restraint time (RT: t = 0.81, *P* = 0.42; mean ± se: 12.8 ± 1.0 and 11.2 ± 3.1 min. in Pin-tailed and Black-bellied Sandgrouse) nor handling time (HT: t = -0.6, *P* = 0.55; 17.6 ± 0.4 and 18.4 ± 1.3 min.) differed between species. Moreover, although tags fitted to Black-bellied Sandgrouse (14.1 ± 0.8 g) were heavier than those fitted to Pin-tailed Sandgrouse (10.1 ± 0.1 g; t = -6.62, *P* < 0.001), RTW did not differ between species (t = 1.23, *P* = 0.22; RTW of 3.3% ± 0.1 and 3.1% ± 0.2 in Pin-tailed and Black-bellied Sandgrouse, respectively). All four satellite-tagged Black-bellied Sandgrouse survived during the first week after capture, but two of nine Pin-tailed Sandgrouse tagged with satellite transmitter died.

Factors explaining CHT mortality in Pin-tailed Sandgrouse

CHT mortality rate increased with RTW, notably when it exceeded 3% of the bird weight (Table 1, Fig. 3). We also found that CHT mortality varied with handling time, depending on season (Table 1; significant season x HT interaction). CHT mortality increased with HT during the breeding season (Wald = 4.29, estimate = 0.14, $P = 0.038$), but not during the non-breeding season (Wald = 0.53, estimate = -0.08, $P = 0.464$). CHT mortality averaged 16.2% ± 3.7 ($n = 37$) during the non-breeding season and 13.9% ± 3.5 ($n = 79$) during the breeding season (main effect: Z = 0.29, $P = 0.77$). We did not find significant differences in CHT mortality between study areas, type of tag, sexes, ages or an effect of RT (Table 1). Body condition did not differ significantly between seasons ($F_{1,123} = 0.26$, $P = 0.61$) or birds tagged with different type of transmitter ($F_{1,123} = 1.85$, $P = 0.18$).

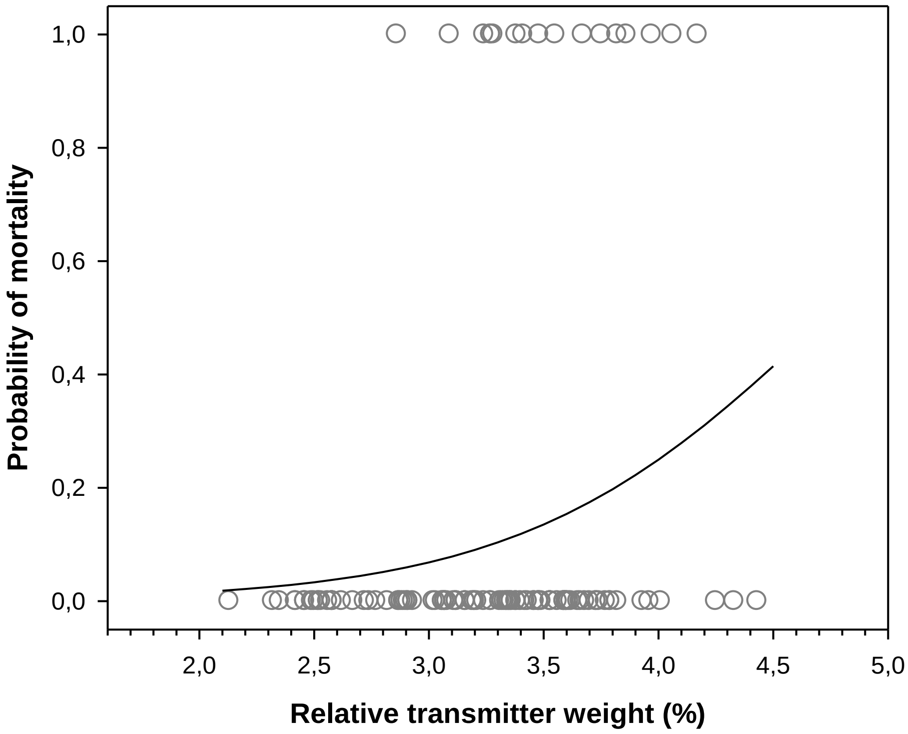

Figure 3. Predicted probability of mortality during the first week after capture depending on relative transmitter weight, as % of tagged bird weight (solid line, $n = 116$; tagged Pin-tailed Sandgrouse). The white dots show the raw data.

Table 1. Results of the Generalized Linear Mixed Models explaining variation in the probability that a captured and tagged Pin-tailed Sandgrouse died during the first week after catching. Mixed models included the factor 'Year' as a random effect. Significant variables are highlighted in bold. RTW = relative transmitter weight (in % of bird´s weight), HT = handling time duration and RT = restraint time.

Variables retained in final model	**Variables removed from initial model**	**Estimate**	**SE**	**Z Value**	***P***
Intercept		**-9.18**	**2.43**	**-3.77**	**0.000**
Season (= non-breeding)		**5.06**	**2.34**	**2.16**	**0.031**
HT		0.12	0.07	1.57	0.116
RTW		**1.51**	**0.61**	**2.46**	**0.014**
Season x HT		**-0.25**	**0.13**	**-2.00**	**0.045**
	Age	-1.72	1.16	-1.48	0.139
	Sex	0.15	0.55	0.43	0.668
	Sex x Season	-1.67	1.16	0.28	0.778
	Zone	0.55	0.71	0.77	0.443
	Type of tag	0.54	0.99	0.55	0.582
	RT	0.01	0.02	0.42	0.675
	Sex x RT	-0.07	0.05	-1.33	0.184
	Sex x HT	-0.18	0.17	-1.05	0.294
	Season x RT	-0.03	0.07	-0.41	0.679

Discussion

Our results show that capture, handling and backpack-mounted transmitter tagging was associated with especially high mortality of Pin-tailed Sandgrouse (15%) during the first week after capture. This mortality rate was significantly higher than that observed during the following seven weeks after the first week of capture (average 1.7% per week). From our tagged birds, we estimated an average weekly mortality of 1% throughout the year (Authors, unpubl. data), similar to that observed during the weeks 2-8 after capture. To the best of our knowledge, there is no available information on mortality rates of untagged Pin-tailed Sandgrouse, but these observations suggest that mortality is most problematic during the first week after capture, and not necessarily afterwards. Our mortality rate during the first week after capture was high, but nevertheless lower than that found in a previous study in northern Spain in which sandgrouse were caught using cannon nets when attending drinking sites during daytime (28.6%; Gil 2007). This difference might be due to the higher direct mortality and stress associated with capture by cannon net (Gil 2007, Ponjoan et al. 2008) and to the heavier radio-transmitter (15 g) used by Gil (2007). In addition, differences in the timing of captures (day vs night) may be influential if interventions are less stressful to the birds at night (Hinsley 1992). Although with our data it was not possible to evaluate separately the effect of the capture method and of the transmitter weight on short-term mortality, our results suggest that a) our method is safer for capturing Pin-tailed and Black-bellied Sandgrouse and b) that the use of lighter transmitters and the reduction of handling times, particularly during the breeding season, can help to reduce short-term mortality in Pin-tailed Sandgrouse.

CHT mortality in Pin-tailed Sandgrouse was higher than in other medium-sized species, such as Little Bustard *Tetrax tetrax* (6.6%; Ponjoan et al. 2008), but lower than Red-legged Partridge *Alectoris rufa* (30.4% of juvenile mortality, Höfle et al. 2004) or Pileated Woodpecker *Dryocopus pileatus* (36.4%, Ruder et al. 2012). Differences between species responses to capture and handling can be related to body mass, sex, age, capture method, handling and restraint time, or even environmental factors (Nicholson et al. 2000, Ponjoan et al. 2008, Spotswood et al. 2012). We caught and tagged few Black-bellied Sandgrouse, as compared with Pin-tailed Sandgrouse, and thus we should consider our CHT mortality estimates in Black-bellied Sandgrouse cautiously due to the limited sample size. However, handling (RT and HT) and the relative transmitter weight did not differ between study species, suggesting that Black-bellied Sandgrouse may be less sensitive to CHT than Pin-tailed Sandgrouse. We did not measure stress levels (e.g. intensity of breathing and heart rate or circulating corticosterone levels), but we noticed during captures that Pin-tailed Sandgrouse seemed to experience more stress during handling (e.g. higher frequency of wingbeats, heart beats and gaping during handling, pers. obs.). Stress responses can vary between species (Cockrem 2007), thus both species might differ in their stress responses to the same capture method and handling procedures.

Factors difficult to control for during capture of Pin-tailed Sandgrouse appeared overall of lesser importance for explaining CHT mortality risk compared to factors that can be controlled for. This gives scope for adjusting procedures when undertaking captures of Pin-tailed Sandgrouse in order to reduce CHT mortality risk. Among the modifiable factors, handling time and relative radio-transmitter weight appeared to affect CHT mortality. Reducing handling times can reduce the probability of adverse effects, as found in other studies (Nicholson et al. 2000, Ponjoan et al. 2008, Buttler et al. 2011, Ruder et al. 2012). A significant reduction in handling time could change the outcome of a project from being unsuccessful to being successful. For example, Ruder et al. (2012) had a large initial mortality (36.4%) associated with capture, but when they reduced handling time considerably (from c. 56 minutes to less than 30 minutes), no more birds died after capture. Samples and measures collected during handling can have different effects on bird welfare (e.g. blood sampling can reduce survival; Brown and Brown 2009). In our study, we took blood samples and the same measurements from almost all captured birds (>90%) and therefore we could not tease apart the effects of each specific procedure. Longer handling time were associated with increased CHT mortality during the breeding season only, when constraints due to reproduction (e.g. Mougeot et al. 2014) may add to the induced stress during handling. Reducing handling time may thus reduce the risk of CHT mortality, especially during breeding season. In addition, we did not find significant effects of restraint time on CHT mortality, suggesting that keeping birds in bags for longer until the start of processing did not cause additional stress.

According to standard transmitter tagging protocols, backpack-mounted transmitters should weigh < 5% of the weight of the animal (Kenward 2001), in order to avoid behavioural alterations in the animal that could compromise welfare and survival. Nevertheless, this upper limit has been considered overestimated (Irvine et al. 2007), and it should be carefully evaluated for each species. Our results show that in Pin-tailed Sandgrouse, this upper limit should be reduced at least to 3% of the bird´s weight (Fig. 3). This result could partially indicate that birds in worse condition could suffer higher CHT mortality, since body condition was negatively correlated with RTW.

Through the study years (2007-2012) we were able to use progressively lighter transmitters, so RTW decreased (year effect: $F_{1,123} = 82.33$, $P < 0.001$, slope ± SE: -0.633 ± 0.070), and handling time fell with experience ($F_{1,123} = 28.44$, $P < 0.001$, slope ± SE: -0.433 ± 0.081). These modifications in our capture protocol were adopted as a result of our personal observations and experience, and both influenced sandgrouse CHT mortality. Regarding satellite transmitters, we fitted only a few satellites tags in this study. Despite the limited sample size, our results did not show differences in CHT mortality between birds tagged with satellite- or radio-transmitters on Pin-tailed Sandgrouse. Although these observations should be treated with caution due to the small sample sizes, we suggest that similar recommendations (in terms of RTW and HT) should be followed in order to reduce CHT mortality in birds tagged with satellite-transmitters.

Overall, our results highlight the importance of reducing transmitter weight and handling time, especially during the breeding season. RTW should be under 3% and HT should not exceed 20 minutes. These specific constraints may not apply to Black-bellied Sandgrouse, but with such small sample sizes we make the same recommendations for this species based on current knowledge. Experience in handling and tagging is important in order to reduce HT and can be achieved by previous training on captive birds before attempting the CHT of wild-birds. Capture protocols should be improved and assessed in all studied species, particularly for species that have never been captured before or that are of conservation concern. Adaptive review and modification of procedures is important to minimize adverse effects associated with CHT of wild animals. Additionally, removing tags whenever signs of adverse effects are noted or after the required data have been collected should be considered especially, in species of conservation concern (Casper 2009). In species with a low recapture rate, such as our study species, harnesses could be designed with weak links so that the tags would fall off the birds once the battery has run out (e.g. Kesler 2011). In any case, this should be tested on captive birds before implementing on wild birds. A better understanding of the factors involved can greatly help researchers to select the most appropriate capture method and types of transmitter in order to minimize risks for the studied species.

Acknowledgements

We thank M. Calero-Riestra, S. González, A. Urmeneta, J. Terraube, X. Piñeiro, JL. Guzmán-García, F. Alda, S. Luna, A. Mateo, Faena, C. Bravo and C. Ponce for their help during fieldwork. We also thank to the owners for allowing us to work on their properties. We also thank Jeremy Wilson and two anonymous reviewers for helping us to improve the manuscript. All appropriate ethics and birds capture and handling approvals were obtained previously (References: SVSI/avp_10_006_aut; DGAPyB/SB/avp 11_186_aut, CMADRCLM_14_07_2007, OAENCLM_05_12_2008, LPE/jav 10/560233_9/08, GNDDRMA-SCB_18_09_2009, GNDDRIEMA_704), according to standards of BOU's Ethical Policy. F. Casas was supported by a JAE-Doc contract funded by CSIC and the European Social Fund (ESF) and by the Steppe-Ahead project funded by FGCSIC. Funding came from the Dirección General de Investigación (projects CGL2007-66322/BOS and CGL2008-04282/BOS), Consejería de Educación y Ciencia de Castilla-La Mancha (projects PAI08-0171-9582 and PAC06-137) and Bardenas Reales Biosphere Reserve (projects UCTR09-0268, UCTR110053 and UCTR120308).

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CAPÍTULO 5

Individual traits and life history strategies influence survival: the case of the threatened pin-tailed sandgrouse (*Pterocles alchata*)

Benítez-López A, Casas F, Mougeot F, García JT, Martín CA, Tatin L, Wolff A, Viñuela J. Individual traits and life history strategies influence survival: the case of the pin-tailed sandgrouse (*Pterocles alchata*). Biol. Conserv. (enviado 24/10/2014)

Abstract

Survival and the underlying causes of mortality are key demographic parameters for understanding animal population dynamics and identifying conservation needs. Here we use a large data set of radio-tagged wild pin-tailed sandgrouse (*Pterocles alchata*) to examine temporal and spatial variations in the survival of this endangered steppe-bird, and evaluate the influence of individual and life-history traits (age, sex, size, movements and reproduction) on survival. Adult and juvenile annual survival were similar and averaged 0.60-0.61. Survival rate tended to be lower towards the northern margin of the European distribution. In the core distribution area (central Spain) mortality was more frequent during the non-breeding season due to higher predation rates. Survival rate was slightly higher in males than females, which may explain male skewed population sex-ratios. Sedentary birds had lower survival than birds using different areas for breeding and wintering, indicating that movement could be an adaptive strategy increasing fitness. Predation was the main cause of mortality, but illegal hunting was also recorded, indicating a need for stricter law enforcement and regulation plans within protected areas. Sandgrouse can be characterized by a relatively slow life history (medium-high adult survival and low reproductive rate), but with lower survival rates than reported for other sympatric steppe birds. Management and conservation efforts should focus on maintaining a high adult survival within protected areas (i.e. hunting regulation and predator control). Sandgrouse mobility, which positively influenced survival, should also be taken into account in conservation plans, especially when considering the size and connectivity of protected areas.

Keywords: pin-tailed sandgrouse, movements, life history traits, illegal hunting, mortality, predation

Highlights

- Using a large data set of radio-tagged pin-tailed sandgrouse, we report on survival and mortality causes.
- Juveniles and adults had similar survival rates.
- Survival was lower during the non-breeding season in core distribution areas.
- Predation was a main cause of mortality, but illegal hunting was also recorded.
- Sedentary birds had lower survival than mobile birds and annual movements likely increase fitness.
- Scaling up conservation efforts from a local to a regional perspective is advisable

Introduction

Survival and the underlying causes of mortality are crucial for understanding animal population dynamics and identifying conservation needs (Newton 1998). In birds, there is usually extensive and detailed information on reproductive parameters, but information on survival is often crucially lacking, particularly for non-passerine and non-temperate species (but see Tarwater et al. 2011). This is most likely due to the difficulty of estimating this key demographic parameter, which requires captures, individual marking and monitoring through mark-recapture or mark- tracking methods that are costly and time-demanding.

Factors influencing survival are often complex, as it may vary through time, space and among individuals (Newton 1998). Determining the precise timing and location of mortality events, such as seasons and areas of low survival is key to identifying ecological causes of variation in population growth rate and hence for effective assessments of population viability and conservation needs (Gould and Nichols 1998; Reid et al. 2011). The actual timing of mortality is critical for understanding both ecological and evolutionary processes affecting populations as different constraints may operate in each season (Newton 1998). Mortality may increase as a result of investment in reproduction (Reznick 1985; Williams 1966), harsh environmental conditions (Robinson et al. 2007; Van Balen 1980), resource limitation, or any combination of these. Although much has been published on annual survival rates in birds, there is a dearth of information on the timing of mortality (but see Robinson et al. 2010). Often, multiple sources of mortality (predation, hunting, disease...) contribute to observed survival rates, and each of these may differentially influence population dynamics (Schaub and Pradel 2004). To better understand population dynamics and conservation needs, it is thus crucial to know the relative importance of specific mortality causes as well as their variation over time.

Survival is also determined by individual traits, such as age (Clobert et al. 1988), sex (Post and Gotmark 2006), size (Murphy 1985), and by life-history strategies. Within a life history context (Roff 2002; Stearns 1992), there is a trade-off between investment in reproduction and survival, in order to not risk future reproduction and thereby maximize fitness (Clutton-Brock 1991). Fitness is ultimately determined by an individual´s ability to survive and reproduce, and animal movements, whether exploratory or triggered by low resource availability (Bennetts and Kitchens 2000), can influence both (Parker and Stuart 1976). Resident individuals may be better able to locate available resources (food, refuge, roosting sites, breeding habitat…), avoid predators and resist competitive intrusion (Pärt 1995). However, when environments are characterised by unpredictable variations in the abundance of key resources, the advantages of leaving may outweigh the advantages of staying (Wiens 1976), and movements to better breeding or wintering habitats may result in increased fitness (Dingle and Drake 2007; Lloyd et al. 2001b). Movements (regardless the temporal or spatial scale) are implicitly recognized as an adaptation driven by the transitory availability and changing location of resources (Dingle and Drake 2007).

Adult survival (which can increase population size by reproduction) and juvenile survival (recruitment) are two central demographic parameters for evaluating population stability, and differences among these may drive life-history evolution (Reznick et al. 1990). Higher first-year and adult survival characterize species with ‘‘slow’’ life histories i.e. with low fecundity or delayed reproduction, apparently owing to high costs of breeding early (McNamara et al. 2008; Ricklefs 2000; Stearns 1992). In these “slow” species, offspring with higher pre-reproductive survival contribute more to their parent’s lifetime reproductive success, and are thus of higher relative value (Ricklefs 2010). A high reproductive investment, defined as the additional risk that adults accept to care for their entire brood (Tarwater et al. 2011), is usually assigned to ensure a high survival rate of a small number of offspring (Ricklefs 1977; Ricklefs 2010).

We investigated survival and mortality causes in the endangered pin-tailed sandgrouse (*Pterocles alchata*), with the goal of examining these attributes within the framework of species imperilment. Pin-tailed sandgrouse is an interesting species model from an ecological and evolutionary perspective. Their small clutch size (2-3 eggs), low reproductive success (Herranz and Suárez 1999; Mougeot et al. 2014) and relatively high longevity (up to more than 10 years in captivity, De Juana et al. 1997) suggest a slow life-history for this species, but survival estimates are needed to confirm so. Sandgrouse are also characterized by facultative annual movements ranging from nomadic behaviour to migration, with the use of different areas for wintering and breeding (De Juana et al. 1997; Lloyd et al. 2001b), which may influence survival.

Insights into the extrinsic and intrinsic factors influencing survival and mortality causes are currently lacking for any sandgrouse species (*Pteroclidae*; De Juana et al. 1997). In this study, we provide the first detailed estimates of survival rates for adult and juvenile pin-tailed sandgrouse, a species of conservation concern in Europe and Vulnerable in Spain (BirdLife International 2004; Madroño et al. 2004), where populations are declining and the distribution is progressively shrinking (Figure 1). We then examine temporal (seasonal) and geographical (population) variations in sandgrouse survival rates, and evaluate whether individual traits (size, sex) and life history strategies (movement and reproduction) influence survival. Finally we assess the timing and possible causes of mortality.

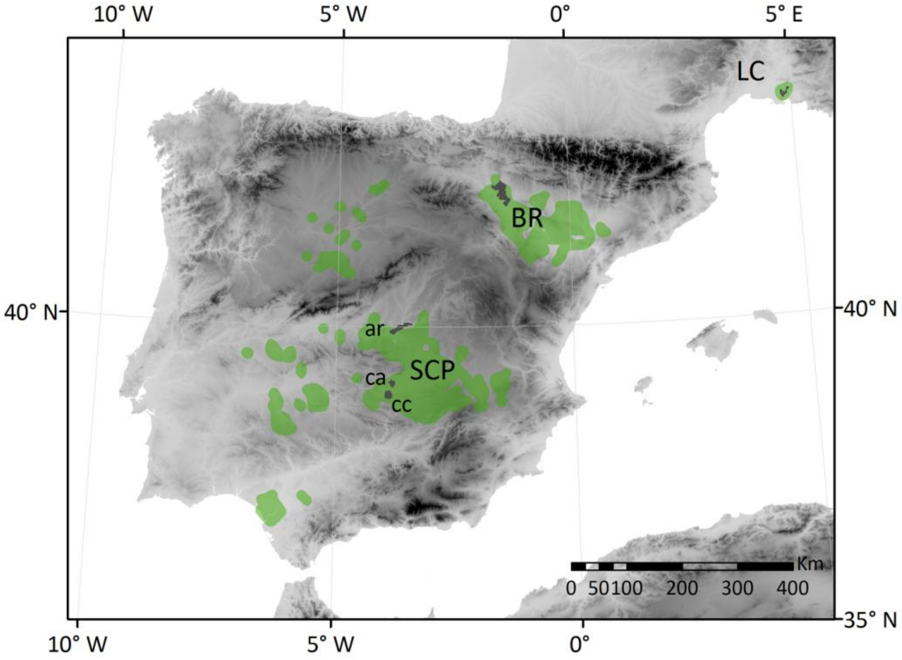

Figure 1. European distribution map of the pin-tailed sandgrouse (adapted from Benítez-López et al. 2014a) and location of study areas (SCP: Southern Central Plateau, comprising SPA Campo de Calatrava (cc), Carrión (ca) and SPA Carrizales y Sotos de Aranjuez (ar); BR: Bardenas Reales Natural Park; LC: Reserve Naturelle Nationale La Crau).

Methodology

Study areas

Fieldwork was conducted in 2007-2012 in Spain (Southern Central Plateau-SCP, central Spain; and Bardenas Reales-BR, N Spain) and in France (La Crau-LC, SE France; Figure 1). The SCP area is included in a wide homogeneous region with high pin-tailed sandgrouse population density (Benítez-López et al. 2014a; Benítez-López et al. 2014b). Sandgrouse were captured in the Special Protection Area (SPA) “Área esteparia del Campo de Calatrava” (cc, 89.8 km^2), Carrión de Calatrava (ca, 66.3 km^2) and SPA “Carrizales y Sotos de Aranjuez” (ar, 149.8 km^2). The BR area (418.5 km^2), is a protected Natural Park and a Biosphere Reserve, and it includes two SPA’s. LC area is a 600-km^2 alluvial plain, where only 17% of the original steppe habitat remains (102 km^2) after development of irrigated agriculture, and is protected as a SPA and Natural Reserve. LC holds the only pin-tailed sandgrouse population in France, representing the northern limit of its global range together with the breeding population of Kazakhstan (BirdLife International 2004). All study areas were characterized by agro-steppes, natural steppes and/or ploughed fields or barren areas with low vegetation cover.

Field procedures

Sandgrouse were captured at night using a thermal camera and a large hand-held net (see Benítez-López et al. 2011 for details). Between 2007 and 2012, we captured and tagged 138 pin-tailed sandgrouse (91 in SCP, 37 in BR and 10 in LC; Table A1, Appendix). Birds were weighed, measured (wing chord and tarsus-length) and blood sampled (see Casas et al. in press for details), tagged with TW3 backpack-mounted radio transmitters (N = 128; Biotrack, UK) or with Solar PTT satellite transmitters (N = 10; Microwave Telemetry, USA) and then released at the capture site. Sex and age (juvenile: bird born during the previous breeding season, i.e.: < 1 year old; adult: bird > 1 year old) was determined from plumage (Blasco-Zumeta and Heinze 2013; De Juana et al. 1997). The weight of the transmitter plus harness averaged 2.1-4.4% of the bird´s weight (< 5 % limit, Kenward 2001, see also Casas et al. in press). We located radio-tagged birds at least once a week using Biotrack Sika telemetry receivers connected to a three-element directional YAGI antenna, or the Argos satellite system for satellite-tagged birds. When radio-tagged birds dispersed outside the range covered by ground tracking (ca. 140 km^2 in SCP-cc, 70 km^2 in SCP-ca and ca. 250 km^2 in BR), we performed flight searches (1-2 flights/year) using a small airplane with attached directional antennae. For each located bird, we recorded the date, geographical position (with Garmin GPS), status (dead or alive) and mortality cause, when possible.

Data treatment and analyses

We excluded all individuals that died within the 7 days post-release due to mortality associated with the capture, handling and tagging process (N= 22, Casas et al. in press), and thus used a study population of 116 pin-tailed sandgrouse (108 radio-tags and 8 satellite-tags, Table A1).

Survival rates

We estimated monthly, seasonal and annual survival rates for adults and juveniles using known-fate models in Program MARK 7.1 (White and Burnham 1999). Satellite-tagged birds (N= 8) were excluded from our survival analyses to avoid bias in the parameter estimates derived from a different monitoring method. Also, we did not use the adults from La Crau (N=5) for our survival analyses because the small sample size did not allow for comparison between areas (see Model set 1 below), but used the two juveniles to maximize sample size in the analyses of juvenile survival. Satellite-tagged birds and adults captured at La Crau were nonetheless used for examining timing and causes of mortality (Table A1).

Although sandgrouse were monitored continually (1-6 times per week), we pooled the tracking data into 12 monthly intervals per year, beginning in May and ending in April (most captures were in May), and we allowed a staggered entry. Thus, the encounter history file included 12 × 1-month live/dead entries per sandgrouse for each year they were monitored. Because several sandgrouse were monitored for more than one year (until battery exhaustion), 'pin-tailed sandgrouse-years' (PTS-years) determined sample size (see Waldron et al. 2013 for a similar methodological approach). Birds were censored (i.e. their fate was unknown) when the transmitter battery ran out (battery life ~ 0.8-1.8 years) or when not located within a month interval.

We examined how factors that could potentially affect survival rate, such as study area and individual and life-history traits (sex, size, reproduction and movements) influence pin-tailed sandgrouse survival. We distinguished between candidate models using relative changes in the small-sample version of Akaike's Information Criterion (AIC_c) and associated model weights (w_i), which are a measure of support for a model relative to the other models in the candidate set (Burnham and Anderson 2002). We calculated parameter coefficients (β) along with their 95% confidence intervals and considered covariate effects to be meaningful when confidence intervals did not overlap zero. We averaged parameter estimates across supported candidate models ($\Delta AIC_c \leq 2.00$) to account for model uncertainty and used weighted-average parameter estimates (based on AIC_c weights) with unconditional standard errors. Models containing uninformative parameters were removed from the candidate set (Arnold 2010). We estimated the relative importance of each variable comparing the sum of AIC_c weights across supported models where each variable appeared.

Adult survival

We estimated survival rates from 93 adult pin-tailed sandgrouse (65 in SCP; 26 in BR; 52 males and 41 females). The final encounter history file consisted of 139 adult PTS-years (89 in SCP and 50 in BR; and 60 for males and females, respectively).

We first evaluated the effects of study area (SCP, BR), month, sex and size (PC1 score of tarsus and wing length, calculated by sex and age) on sandgrouse survival across the 6-year study period (Model set 1). We also grouped months into two seasons according to sandgrouse breeding biology, and built several models including the variable season plus the additive and interactive effects of study area, size and sex (Table A2). The period May-Oct encompasses the breeding season, with the first clutches being laid in May, and the last ones in September (authors, unpublished data). The period of parental care lasts up to 8 weeks after hatching (Herranz and Suárez 1999). During this season, flocks are smaller, temperatures are warmer and days are longer. The other season (non-breeding) includes the fall, winter and early spring. During this season sandgrouse aggregate in large flocks, the weather becomes harsher (frosts) and days are shorter. Additionally, hunting activities and agrarian practices are widespread between Nov-Feb.

Juvenile survival

Juvenile encounter histories consisted of 12 monthly intervals beginning 1 Oct and ending 30th Sept of the following year. We estimated survival rates for 12 juvenile pin-tailed sandgrouse (9 in SCP, 2 in LC and 1 in BR; 9 males and 3 females, N=12 PTS-years). We tested the effects of season and sex on juvenile survival, but not the effect of study area, due to sample size limitations.

Movements, reproduction and adult survival

Accurate data on movements and reproduction were available for three years (2010-2012), so we built another set of candidate models to assess their effects on adult male and female survival (Model set 2, N = 65 PTS-years, 35 and 30 for males and females, respectively). We tested whether survival was influenced by reproduction using two classes, namely birds that attempted to breed (regardless of their breeding success) vs. those that did not. During a given breeding season, we considered a tagged bird as breeder whenever we (a) found its nest, (b) located it with chicks or (c) repeatedly observed it with a mate throughout the breeding season, and occasionally alone at a daytime period when its mate should be on incubation duty (males incubate at night and females during the day; Mougeot et al. 2014). Otherwise, tagged birds were considered as non-breeders. Birds that were captured and tagged right after the breeding season and did not survive the non-breeding season were removed from these analyses because we could not determine their breeding status (1 male and 5 females).

Pin-tailed sandgrouse space use is highly variable, with some individuals keeping a restricted home range throughout the year, and others performing medium-long distance movements (max. distance recorded was 65 km, authors unpublished data) and using different areas for breeding and wintering (Benítez-López et al. 2010; Casas et al. 2012). We tested whether survival differed between birds with low mobility (i.e. clearly sedentary) or high mobility (likely using separate breeding and wintering areas). We performed these analyses for two study areas, SCP (cc and ca) and BR. We considered as high-mobility birds (HM) those birds that abandoned the study area for > 30 days during the breeding or the non-breeding season, and were relocated upon their return to the study area after this absence (N=19) or in the new area by aerial tracking (N=18). Else, birds were categorized as low-mobility birds (LM, N=28). The 30-day time interval was based on our sampling frequencies (see Bennetts and Kitchens 2000). We tracked birds 3.6 (1-6) days a week during the breeding season, and 1.5 (1-6) days a week during the non-breeding season. Thus, we were reasonably certain to have located all birds present within our study areas (and adjacent areas) at monthly intervals. Birds that completely disappeared and were never relocated before the end of an annual cycle or the exhaustion time of the transmitter battery were left out of these analyses (unknown fate). We recorded the timing of movements (pre-breeding or post-breeding) and tested whether there were differences between study areas.

Causes of mortality

We used apparent causes of mortality to examine temporal patterns of sandgrouse survival. Whenever possible, we tried to determine the exact mortality cause through a necropsy (N=3). In most cases, however, the degree of decomposition of the carcass or the lack of sufficient remains left by predators did not allow a precise determination of the cause of death through a necropsy, and was assessed from a visual inspection of the remains in the field. We classified causes of mortality into natural (predation) and human-induced. We considered that a bird was predated when we found the carcass partly devoured (usually with the head and breast missing) and the transmitter was damaged (Teflon harness bitten and/or antenna bended). The most frequent predators were carnivores and raptors. We assigned the cause of the death to carnivores when birds were found buried, or with signs of biting on the body or harness and cut feathers, or when we found carnivore faeces next to the corpse; and to raptors when we observed a faecal splash or plucked (non-cut) feathers spread around the corpse (Thirgood et al. 1995). Unfortunately, in some cases we were not able to distinguish unambiguously between predated and scavenged sandgrouse and, therefore, we used the term predated (which is, to our experience, more likely to occur in our study species).

Human-induced mortality causes were related to hunting activities, and corresponded to the following cases: (a) bird shot, with shot holes clearly visible on the body; (b) transmitter found intact without any bird remains and without damage to the antenna or the harness (no signs of bite). In some cases the harness was removed or cut with a knife. We tested for differences in the frequency of human-induced and natural mortalities according to season, sex, age and study area using one-tailed Fisher’s exact tests.

Results

Adult survival

When assessing our first set of candidate models, we realized that the individual covariate body size had no effect on survival (i.e.: all models that included this variable had a $\Delta AIC_c > 2$, and 95% C.I. for body size overlapped zero; Table A2). In addition, removing size from our set of candidate models allowed us to eliminate overdispersion (variance inflation factor, $\hat{c} = 1.80$, calculated as the observed residual deviance/df, (White and Burnham 1999). Our global model with study area, month and sex had a $\hat{c} = 0.86$, so no adjustment for overdispersion was necessary. Models including monthly variation (S_{month} and $S_{area+month}$) revealed seasonal variations in monthly survival rates, with lower survival towards the second half of the breeding season (Aug-Sep), a marked drop in survival between Nov-Dec and another in February (Figure 2a). However, models including seasonal variation instead of monthly variation received much more support since the number of estimated parameters was sensibly less. Overall, seven candidate models received support ($\Delta AIC_c \leq 2$) after removing models containing uninformative parameters (Arnold 2010) (Table 1, Table A3).

Table 1. Supported ($\Delta AIC_c \leq 2.00$) known-fate survival models, ranked in order of support, for adult pin-tailed sandgrouse. Survival was modelled as a function of month, season, study area and sex (i.e., Model Set 1). ΔAIC_c = the difference between the model with the lowest AIC_c score and the present model, w_{adj} = adjusted model weights, Likelihood = model likelihood, and K = number of parameters.

Model	AIC_c	ΔAIC_c	w_{adj}	Likelihood	*K*	Deviance
S(area+sex+season+area*season)	236.86	0.00	0.23	1.00	5	34.77
S(sex+season)	237.28	0.41	0.18	0.81	3	39.23
S(area+season+area*season)	237.69	0.83	0.15	0.66	4	37.62
S(area+sex+season)	238.16	1.29	0.12	0.52	4	38.09
S(season)	238.20	1.33	0.12	0.51	2	42.17
S(sex+season+sex*season)	238.25	1.39	0.11	0.50	4	38.18
S(area+season)	238.75	1.89	0.09	0.39	3	40.70

Season was the most important variable explaining variation in adult survival (cumulative weight, cum. *w*= 0.97), followed by sex (cum. *w* =0.77) and study area (cum. *w* =0.72). Season was also the only variable with a clear effect on survival (β_{season}= 1.00 ± 0.40, i.e.: 95% confidence intervals did not overlap zero, Table A4), with higher survival rates during the breeding than the non-breeding season. This effect was more obvious in SCP than in BR due to apparently lower breeding survival in BR (interaction area*season, Table A4, Figure 2b). Beta coefficients for sex indicated that survival was marginally higher for males than females (β_{sex}= 0.66 ± 0.39, 95% C.I. =-0.11 – 1.43 in top model), being the non-breeding season more critical for females than for males (interaction sex*season) (Table A4). Annual survival varied from

0.50 ± 0.12 for females in BR to 0.69 ± 0.08 for males in SCP (Figure 2c), based on derived estimates averaged across supported models ($\Delta AIC_c \leq 2$).

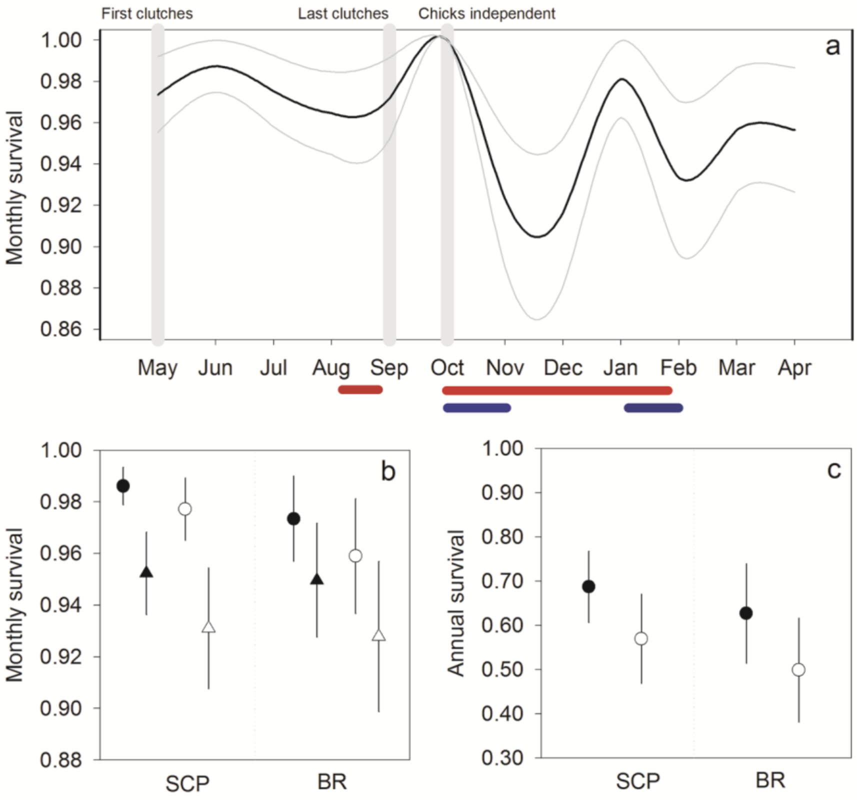

Figure 2. Estimates of monthly and annual survival for adult pin-tailed sandgrouse (Model set 1). **a**) Monthly variation in survival according to the model S_{month} (black smoothed line; grey smoothed lines represent SE). The breeding period (May-Oct) begins with the laying of the first clutches and ends when the last hatched chicks are independent (Oct). Hunting period: red bars; cereal sowing events: Blue bars; **b**) Monthly survival estimates (±SE) according to sex (males: filled symbols; females: open symbols), season (breeding: circles; non-breeding: triangles) and study area (SCP and BR); **c**) Annual survival estimates (±SE) according to sex (males: filled circles; females: open circles) and study area. Estimates in (b) and (c) are based on model-averaged estimates across supported models ($\Delta AIC_c \leq 2.00$)

Juvenile survival

As with adults, body size was initially considered, but removed from the set of candidate models because it turned out to be an uninformative parameter (Arnold 2010), and because its removal considerably reduced overdispersion ($\hat{c}$ dropping from 3.6 to 0.62).

For juvenile survival rate, only the model with constant survival (no temporal variation or individual covariates) was supported ($\Delta AIC_c \leq 2$; $w_i = 0.52$), with $S_{(season)}$ and $S_{(sex)}$ having ΔAIC_c just over 2 (Table 2). The examination of beta covariates for sex and season indicated that the effect of these covariates was not relevant (confidence intervals included zero). Juvenile annual survival rate was estimated at 0.61 ± 0.15 ($S_{(.)}$).

Table 2. Candidate known-fate survival models for juvenile pin-tailed sandgrouse, ranked in order of support. ΔAIC_c = the difference between the model with the lowest AIC_c score and the present model, *w* = model weights, Likelihood = model likelihood, and *K* = number of parameters**.**

Model	AICc	ΔAIC_c	*w*	Likelihood	*K*	Deviance
S(.)	35.55	0.00	0.52	1.00	1	13.20
S(season)	37.58	2.03	0.19	0.36	2	13.15
S(sex)	37.61	2.06	0.18	0.37	2	13.18

Movements, reproduction and adult survival

93.3% and 62.9% of adult female and male sandgrouse were breeders, and 50.0% and 62.9% were categorized as high mobility (HM) birds, respectively (N=65). In BR, 50% of sandgrouse performed movements (N=22), all of them after the breeding season, whereas in SCP 60.5% of sandgrouse moved away (N=43), mostly before the breeding season (76.9%, Fisher's exact P, one tailed, P <0.001). Six candidate models received support ($\Delta QAIC_c \leq 2$, Table 3, Table A5), all of them including movement, which was the most important variable (w_{adj} = 1.00), followed by sex and season (w_{adj} = 0.45 and 0.42, respectively).

Table 3. Supported ($\Delta AIC_c \leq 2.00$) known-fate survival models, ranked in order of support, for analyses examining adult pin-tailed sandgrouse survival as a function of sex, season, movement and reproduction (i.e., Model Set 2). ΔAIC_c = the difference between the model with the lowest AIC_c score and the present model, w_{adj} = adjusted model weights, Likelihood = model likelihood, and K = number of parameters.

Model	AIC_c	ΔAIC_c	w_{adj}	Likelihood	*K*	Deviance
S(mov)	153.92	0.00	0.26	1.00	2	51.51
S(sex+mov)	154.40	0.48	0.21	0.79	3	49.97
S(mov+season)	154.80	0.88	0.17	0.64	3	50.36
S(sex+mov+season)	155.33	1.42	0.13	0.49	4	48.87
S(mov+season+mov*season)	155.45	1.53	0.12	0.47	4	48.98
S(sex+mov+sex*mov)	155.62	1.70	0.11	0.43	4	49.15

Movement was the only variable included in the best model and the only one with a clear positive effect on survival ($\beta_{movement}$= 1.15 ± 0.51, 95% C.I. =0.15 – 2.15 in best model, Table A6): HM birds had higher monthly survival than LM birds (Figure 3). Monthly survival rate was higher during the breeding season compared to the non-breeding season, but 95% C.I. overlapped zero, and the effect was almost undistinguishable (Table A6, Figure 3a). Also, monthly survival was slightly higher for males than for females, although not significantly (Table A6, Figure 3a). Annual survival was overall higher for HM birds compared to LM birds, for both males and females (Figure 3b).

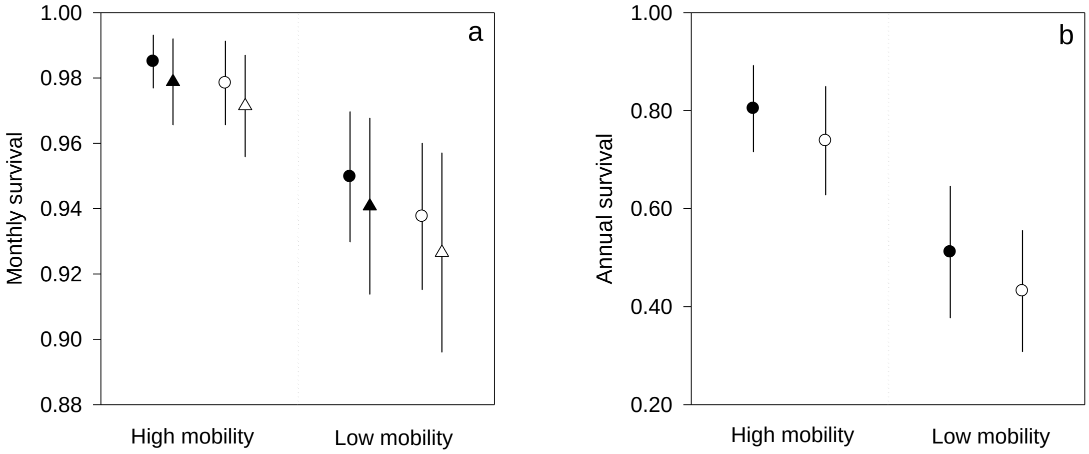

Figure 3. Mean (±SE) monthly and annual adult survival rates based on model-averaged estimates across supported models ($\Delta AIC_c \leq 2.00$) testing the effects of movements and reproduction (i.e. Model set 2). **a**) Monthly survival according to movement (low vs. high mobility), sex (males: filled symbols; females: open symbols) and season (breeding: circles; non-breeding: triangles); **b**) Annual survival according to movement (low vs. high mobility) and sex (males: filled circles; females: open circles).

Causes of mortality

We recorded mortality in 42 (36.2%) of the 116 tagged pin-tailed sandgrouse, mostly during the non-breeding season (69.0%; Table A1). Mortality cause was unknown for 9.5 % of cases, but was attributed to predation in 73.8% of cases and to human-caused mortality in 16.7% of cases (illegal hunting, 5 in SCP, 1 in BR and 1 in LC). Predation tended to be more frequent during the non-breeding season (50.0%, N= 42) than the breeding-season (23.8%, N=42, Fisher's exact P= 0.015). Human-caused mortalities occurred during both the breeding (7.1%, N = 42) and non-breeding seasons (9.5%, N = 42). We found no differences in the frequency of human-caused and natural mortalities between sexes, ages or study areas. Predation tended to be more frequent during the non-breeding season (80%) than during the breeding season in SCP, (20%; N=15), but not in BR (50% vs 50%, N=14; Fisher's exact P=0.095). Predation was slightly more frequent during the breeding than the non-breeding season in females (6 out of 13) than in males (3 out of 14; Fisher's exact P, one tailed =0.171). Carnivores were the main predator in SCP (71.4 vs 28.6% for raptors, N=14), whereas the reverse occurred in BR (31 vs 69%, N=13; Fisher's exact P= 0.041).

Discussion

Adult survival contributes more to population growth in long-lived species, whereas juvenile survival is more determinant for population persistence in short-lived species (Clark and Martin 2007). In the pin-tailed sandgrouse, we found similar survival rates for adults and juveniles, although estimates for the latter should be considered cautiously due to the smaller sample size. Overall annual adult survival found in this study (0.5-0.6 in females and 0.6-0.7 in males) would be among mid to high values for birds of temperate latitudes, and slightly higher than those expected for sandgrouse body size (Jimenez et al. 2014). This places pin-tailed sandgrouse towards the “slow” end of the slow-fast continuum that organizes life-history variation (Martin 1996; McNamara et al. 2008), similar to other south-temperate species (Lloyd et al. 2014).

Adult survival was lower during the non-breeding season, particularly in SCP. The clearest drop in survival occurred in Nov-Dec, when environmental conditions become harsher (lower ambient temperatures, first frosts) and the daylight and time for foraging decrease while the need to maintain fat reserves to overcome winter temperatures is exacerbated, particularly for a warm thermal-adapted species (Hinsley et al. 1993). Another lesser drop in survival occurred in late winter / early spring. Interestingly, these two periods of reduced survival correspond to the autumn and late winter cereal sowing seasons in Spanish farmlands (for long-cycle and short-cycle winter cereal cultivation, respectively). Recent studies have highlighted that the widespread use of treated seeds (seeds coated with fungicides or insecticides) is a main threat to farmland birds (López-Antia et al. 2013; Mineau et al. 2013). Treated seed ingestion has lethal to sub-lethal toxic effects (reduced condition and immunity, López-Antia et al. 2013; López-Antia et al. in press). Granivorous sandgrouse may be particularly exposed to pesticide coated seeds during cereal sowing practices, when treated seeds are more readily available in recently sowed ploughed fields, a threat that would deserve further investigation. Additionally, human leisure activities such as hunting (Oct-Feb), which is ubiquitous in SCP, may be another important source of disturbance that negatively affects wintering pin-tailed sandgrouse (causing more frequent flights, altered habitat use and increased stress hormone levels after hunting days; Casas et al., in prep). Finally, from October on, sandgrouse aggregate in large flocks for feeding and for roosting (Martín et al. 2010), which may attract predators (i.e.: carnivores), and would explain the larger predation rate in the non-breeding period. Sub-lethal effects derived from the intake of coated seeds, stress-inducing human disturbances, worsened weather conditions, and a reduced time for feeding, may be acting synergistically, reducing sandgrouse condition and ability to escape from predators, and hence contributing to the observed reduced survival during the non-breeding season.

One of the most interesting outcomes of this work is related to the effect of movement on sandgrouse survival. Regardless of season or sex, individuals with high mobility had consistently higher survival than sedentary individuals. Sandgrouse nomadic movements are extensively described in strictly arid landscapes (deserts), and may be prompted by climatic events (rainfall) and subsequent increases food availability (Lloyd et al. 2001a; Van Niekerk 2012). Although European agricultural areas might look *a priori* more resourceful than deserts, they are characterized by a patchy distribution of resources, where high mobility may be an asset. Moreover, agrarian practices drive seasonal changes in land use that profoundly alter the location and availability of key resources along the year. Food availability is thus likely unpredictable in these environments, being locally abundant and accessible for a limited amount of time, particularly after the summer and coinciding with the onset of the non-breeding season and the aggregation of sandgrouse in large-sized flocks (Martín et al. 2010a), when most fields are ploughed and prepared for sowing. By contrast, at the beginning of sandgrouse breeding season, suitable habitat availability is much more limited (the landscape is dominated by un-preferred cereal fields, with fewer ploughed fields and fallows, Martín et al., 2010b). During the breeding season, breeders may better cope by moving to other areas, a pattern that was mostly found in the more agricultural and humanized area (SCP). During the non-breeding season, sandgrouse may be using their gregarious behaviour for socially communicating the location of patches with high food availability (i.e. fallow fields or recently sown legume crop fields), which might trigger the movement of flocks of varying size to other areas outside individual home ranges. Alternatively, in the northern population of BR, where all recorded movements occurred after the breeding season, major harsh climatic events (frosts and blizzards, authors, personal observation) may set off movements to southern warmer locations (Casas et al. 2012). The actual mechanisms behind sandgrouse movements remain unresolved, but mobility was associated with increased survival and can be thus regarded as an advantageous strategy (Dingle and Drake 2007).

Reproductive investment in pin-tailed sandgrouse spans for ca. 90 days, with chicks being dependent up to 8 weeks after hatching (Herranz and Suárez 1999). This high reproductive investment, along with the high energetic costs of breeding in arid environments (Mougeot et al. 2014) and the high risk (i.e. predation) induced by prolonged parental care could be affecting adult survival. The drop in survival towards the second half of the breeding season suggests this could be the case, with females having slightly lower survival (2.4% less monthly survival) than males. Although both sexes invest in parental care and take turns to incubate the clutch (Herranz and Suárez 1999; Mougeot et al. 2014), sandgrouse females have the extra cost of producing eggs (see Tinbergen and Dietz 1994; Ward 1972). Also, the incubation timing may be crucial, as females incubate during the day and males at night, and cooling the eggs may be more costly than warming them in arid environments (Mougeot et al. 2014). To meet energy demands, females need to forage intensively, and while males may use all day to forage, females can only do so during short periods after switching incubation turns, i.e. around dawn or dusk (Hinsley and Ferns 1994; Mougeot et al. 2014), reducing the time spent vigilant (Dukas and Kamil 2000; Lima and Dill 1990) and becoming more vulnerable to predation. Additionally, during egg production and incubation, females also gain weight, which may affect their response to predators (Veasey et al. 2000; Witter et al. 1994). Indeed, we found higher predation rates for females during the breeding season albeit both sexes share incubation duties.

Differences in survival between sexes may have affect population structure, in particular adult sex ratios (ASR). Skewed adult sex-ratios (ASR) in birds are caused by lower survival of the rarer sex, generally the female (Donald 2007; Székely et al. 2014). Documented ASR's are male-skewed in pin-tailed sandgrouse (0.64, Herranz and Suárez 1999), and in other sandgrouse species (Tarboton et al. 1999). Although no ASR estimates are available for our study populations (except for La Crau: 0.59 in 2012 and 0.57 in 2013 during counts at water points), our capture rate (that presumably should not be sex-biased) produced a slightly male-skewed ASR (0.58). The higher proportion of breeders among females (93.3%) compared to males (62.9%) is also consistent with a male-skewed ASR ("surplus" males unable to find a mate). Male-skewed ASR has been related to higher female reproductive effort, leading to lower female survival (Bennett and Owens 2002), an assertion in concordance with our findings. Male-skewed ASR's are often found in threatened species (Donald 2007), and extinction risk is predicted to increase more rapidly with increasingly male-skewed ASR, as reported, among others, in the sympatric little bustard *Tetrax tetrax* (Morales et al. 2005). Overall, although more accurate information about ASR in pin-tailed sandgrouse is necessary, sex-biased mortality should be carefully considered for population viability and for the species conservation.

We did not find marked differences in survival between areas, survival tended to be higher in SCP (a core area within sandgrouse European distribution; (Benítez-López et al. 2014a) than in BR or LC, both located in the NW edge of the global distribution (Table A1). The small sample size in the latter area did not allow to accurately estimating survival, and future works should clarify this in isolated, peripheral populations. Differential predator identity was found between areas, being carnivores the main predators in SCP, and raptors in BR. BR is characterized by a more natural landscape with a more diverse and abundant raptor community, whereas SCP is a more humanized landscape near villages, with increasing urbanization and relatively low-intensity of predator control, where domestic (cats *Felix catus* and dogs *Canis familiaris*) or wild carnivores are relatively common (foxes *Vulpes vulpes)*(Casas and Viñuela 2010).

Another cause of concern is the observed mortality presumably due to hunting activities. Sandgrouse hunting is not allowed in Spain since the 1980s, but illegal hunting still represents a conservation threat for the pin-tailed sandgrouse, as well as its counterpart, the black-bellied sandgrouse (Madroño et al. 2004). More efforts should be made to prevent these illegal actions, especially for species of conservation concern, such as sandgrouse.

Conclusions

This study provides the first estimates of survival for any species of sandgrouse. Sandgrouse adult survival is comparatively lower than that of other sympatric steppe birds of larger body size and similar clutch size (*Otis tarda*: 0.87 for males, 0.93 for females, Lane and Alonso 2001; *Tetrax tetrax*: 0.80, Morales et al. 2005). Survival data are crucial for demographic modelling and population viability analyses, although in the case of sandgrouse, additional data would be necessary on productivity, which seems to be extremely low and thus another important limiting factor (Herranz and Suárez 1999; Mougeot et al. 2014). This would greatly contribute to improve our knowledge on conservation needs and management priorities in order to improve the current status of these and other threatened steppe-birds (e.g. Bretagnolle et al. 2011; Morales et al. 2005; Newton 1998). This study highlights the necessity of moving beyond obtaining mere survival estimates and plausible causes of mortality of threatened species, and including information on the ecology and traits that drive species life-history variation in order to enhance our ecological understanding of population dynamics of endangered species, with the final goal of designing efficient conservation measures. Specific conservation measures include the monitoring of potential predators (particularly generalists attracted by human encroachment) by annual surveys in areas that hold important sandgrouse populations (i.e.: protected steppe areas) and implementing predator control measures where necessary. These measures may in turn result beneficial for other farmland species which are associated to open habitats (*Otis tarda*, *Tetrax tetrax*, etc…) (Estrada et al. submitted). Finally, sandgrouse mobility should be considered in conservation plans, particularly in light of the species' longevity, since sandgrouse may readily redistribute at the landscape scale in unprotected areas after harsh climatic or stress-inducing events or low resource availability. Scaling up the protection level from local to a regional perspective would be advisable.

Acknowledgements

We thank I. García-Egea, J. Carrasco and S. González for their help during fieldwork. We also thank the owners for allowing us to work in their properties. All appropriate ethics and birds capture and handling approvals were obtained previously (References: SVSI/avp_10_006_aut; DGAPyB/SB/avp424 11_186_aut, CMADRCLM_14_07_2007, OAENCLM_05_12_2008, LPE/jav10/560233_9/08, GNDDRMA-SCB_18_09_2009). A. Benítez-López was supported by the CGL2008-04282/BOS project funded by Dirección General de Investigación and by the 2012-BIN-4462 research grant conceded by the UCLM. F. Casas was supported by a JAE-Doc contract funded by CSIC and the European Social Fund (ESF). Financial support was provided by the Dirección General de Investigación (projects CGL2007-429 66322/BOS and CGL2008-04282/BOS), Consejería de Educación y Ciencia de Castilla-La Mancha (projects PAI08-0171-9582 and PAC06-137), Bardenas Reales Biosphere Reserve (projects UCTR09-0268, UCTR110053 and UCTR120308) and Direction Régionale de l'Ecologie, de l'Aménagement et du Logement de Provence-Alpes-Côte d'Azur.

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Appendix

Table A1. Sample sizes for tagged birds, survival analyses with Mark and for assessment of mortality causes. Number of tagged pin-tailed sandgrouse with radio or satellite transmitters, the number discarded due to capture, handling and tagging mortality (CHT mortality, Casas et al. in press), the number used for survival analyses in MARK, and for assessing mortality causes. Number of dead sandgrouse and timing of mortality are also shown. Data are presented by study area, sex and age.

	SCP	**BR**	**LC**	**Total**	**Ad-Males**	**Ad-Females**	**Total Adults**	**Juv-Males**	**Juv-Females**	**Total Juveniles**	**Total Males**	**Total Females**
N. Tagged	91	37	10	138	71	52	123	11	4	15	82	56
Radio-transmitter	88	30	10	128	64	50	114	10	4	14	74	54
Satellite-transmitter	3	7	0	10	7	2	9	1	0	1	8	2
CHT mortality	15	4	3	22	12	8	20	1	1	2	13	9
N. used for assessment of mortality causes	76	33	7	116	59	44	103	10	3	13	69	47
N. used for MARK analyses	74	27	2	103	52	41	93	9	3	12	61	44
N. Dead	20	17	5	42	18	19	37	4	1	5	22	20
N. Dead -Breeding season	6	7	0	13	4	8	12	1	0	1	5	8
N. Dead -Non-Breeding season	14	10	2	26	14	11	25	3	1	4	17	12
% Dead (Num. Dead/Num. Tagged x 100)	26.3	51.5	71.4	36.2	30.5	43.2	35.9	40.0	33.3	38.5	31.9	42.6

Table A2. Model-selection results for the effects of month, season, area, sex and body size on adult sandgrouse survival. S_{global} (in italic) includes all variables and 2-way interactions. Size had no effect on survival (95% C.I. largely overlapped zero) was thus removed from the set, reducing overdispersion ($\hat{c}$ dropped from 1.8 to 0.8. See Table A3). ΔAICc = the difference between the model with the lowest AICc score and the present model, w = model weights, Likelihood = model likelihood, and K = number of parameters.

Model	**AIC_c**	**ΔAIC_c**	***w***	**Likelihood**	***K***	**Deviance**
S(area + sex + season + area x season)	237.01	0.00	0.18	1.00	5	226.93
S(sex + season)	237.44	0.43	0.15	0.81	3	231.41
S(area + sex + season + area x season + sex x season)	238.11	1.10	0.11	0.58	6	226.00
S(season)	238.32	1.31	0.10	0.52	2	234.30
S(area + sex + season)	238.37	1.36	0.09	0.51	4	230.32
S(sex + season + sex x season)	238.39	1.38	0.09	0.50	4	230.34
S(area + season)	238.91	1.90	0.07	0.39	3	232.88
S(area + sex + season + sex x season)	239.24	2.23	0.06	0.33	5	229.16
S(area + sex + area x sex + season)	239.57	2.56	0.05	0.28	5	229.50
S(area + sex + season + area x sex + area x season +sex x season)	239.69	2.68	0.05	0.26	7	225.55
S(sex)	241.99	4.98	0.02	0.08	2	237.98
S(area + sex)	242.77	5.76	0.01	0.06	3	236.74
S(.)	242.86	5.86	0.01	0.05	1	240.86
S(area)	243.37	6.36	0.01	0.04	2	239.35
S(area + sex + area x sex)	243.78	6.78	0.01	0.03	4	235.73
S(size)	244.84	7.83	0.00	0.02	2	240.82
S(month)	251.11	14.11	0.00	0.00	12	226.70
S(area + month)	251.45	14.45	0.00	0.00	13	224.98
S(area + sex + area x sex + month)	251.84	14.83	0.00	0.00	15	221.21
S(area + sex + area x sex + month + size)	253.93	16.92	0.00	0.00	16	221.21
S(area + sex + area x sex + month + size + area x size)	254.72	17.71	0.00	0.00	17	219.91
S(area + sex + area x sex +month + size + area x size + sex x size)	*256.52*	*19.51*	*0.00*	*0.00*	*18*	*219.61*

Table A3. Model-selection results for the effects of month, season, area and sex on adult sandgrouse survival. S_{global} (in italic) includes monthly variation and the 2-way interaction between area*sex. Models with $\Delta AIC_c < 2$ were considered for inference (in bold). Models 4 and 5 were discarded because they had one extra uninformative parameter (Arnold, 2010). ΔAIC_c = the difference between the model with the lowest AIC_c score and the present model, *w* = model weights, Likelihood = model likelihood, and *K* = number of parameters.

Model	**AIC_c**	**ΔAIC_c**	***w***	**Likelihood**	***K***	**Deviance**
S(area + sex + season + area x season)	**236.86**	**0.00**	**0.14**	**1.00**	**5**	**34.77**
S(sex + season)	**237.28**	**0.41**	**0.11**	**0.81**	**3**	**39.23**
S(area + season + area x season)	**237.69**	**0.83**	**0.09**	**0.66**	**4**	**37.62**
S(area + sex + season + area x season + sex x season)	237.98	1.12	0.08	0.57	6	33.86
S(area + sex + season + area x sex + area x season)	237.99	1.13	0.08	0.57	6	33.87
S(area + sex + season)	**238.16**	**1.29**	**0.07**	**0.52**	**4**	**38.09**
S(season)	**238.20**	**1.33**	**0.07**	**0.51**	**2**	**42.17**
S(sex + season + sex x season)	**238.25**	**1.39**	**0.07**	**0.50**	**4**	**38.18**
S(area + season)	**238.75**	**1.89**	**0.05**	**0.39**	**3**	**40.70**
S(area + sex + season + area x season + sex x season + area x sex x season)	238.91	2.05	0.05	0.36	7	32.75
S(area + sex + season + sex x season)	239.05	2.19	0.05	0.33	5	36.96
S(area x sex + season)	239.33	2.47	0.04	0.29	5	37.23
S(area x sex + season + area x season + sex x season)	239.54	2.68	0.04	0.26	7	33.38
S(area x sex + season + area x season + sex x season + area x sex x season)	240.95	4.09	0.02	0.13	8	32.75
S(sex)	241.89	5.03	0.01	0.08	2	45.86
S(.)	242.79	5.93	0.01	0.05	1	48.77
S(area)	243.27	6.40	0.01	0.04	2	47.24
S(sex + month)	250.07	13.21	0.00	0.00	13	31.58
S(area + sex + month)	250.69	13.83	0.00	0.00	14	30.12
S(month)	251.08	14.21	0.00	0.00	12	34.65
S(area + month)	251.40	14.54	0.00	0.00	13	32.90
S(area x sex + month)	251.75	14.89	0.00	0.00	15	29.10

Table A4. Coefficients from supported (i.e., $\Delta QAIC_c \leq 2.00$) known-fate survival models. Survival was modelled as constant (.) and as a function of area (SCP versus BR), body size (size, finally removed from the set, see methods), sex, and over time (monthly variation and 2-season = breeding versus non-breeding season). Models are listed in order of support according to Akaike's Information Criterion adjusted for small sample size (AIC_c). Confidence intervals (95%) are represented by LCI (lower) and UCI (upper).

Model	**Parameter**	***β***	**SE**	**LCI**	**UCI**
S(area + sex + season + area x season)	Intercept	2.57	0.48	1.63	3.52
	area	-0.16	0.55	-1.23	0.91
	sex	0.66	0.39	-0.11	1.43
	season	0.13	0.62	-1.10	1.35
	area x season	1.52	0.85	-0.15	3.19
S(sex + season)	Intercept	2.46	0.30	1.87	3.04
	sex	0.67	0.39	-0.10	1.43
	season	1.01	0.40	0.22	1.80
S(area + season + area x season)	Intercept	2.86	0.46	1.96	3.76
	area	-0.08	0.54	-1.14	0.98
	season	0.16	0.62	-1.05	1.38
	area x season	1.46	0.85	-0.21	3.12
S(area +sex + season)	Intercept	2.19	0.38	1.46	2.93
	area	0.43	0.40	-0.35	1.22
	sex	0.63	0.39	-0.14	1.40
	season	1.00	0.40	0.21	1.79
S(season)	Intercept	2.80	0.24	2.32	3.28
	season	1.00	0.40	0.22	1.79
S(sex + season + sex x season)	Intercept	2.60	0.35	1.92	3.28
	sex	0.37	0.49	-0.58	1.32
	season	0.67	0.52	-0.35	1.68
	sex x season	0.85	0.85	-0.81	2.52
S(area + season)	Intercept	2.48	0.34	1.80	3.15
	area	0.49	0.40	-0.29	1.27
	season	1.00	0.40	0.21	1.79

Table A5. Model-selection results for the effects of season, sex, movements (mov) and reproduction (rep) on adult sandgrouse survival. S_{global} (in italic) includes seasonal variation and biologically plausible 2-way interactions. Models with $\Delta \mathrm{AIC}_c < 2$ were considered for inference (in bold). $\Delta \mathrm{AIC}_c$ = the difference between the model with the lowest AIC_c score and the present model, *w* = model weights, Likelihood = model likelihood, and *K* = number of parameters. N= 34 models.

Model	**AIC_c**	**$\Delta \mathrm{AIC}_c$**	***w***	**Likelihood**	***K***	**Deviance**
S(mov)	**153.92**	**0.00**	**0.15**	**1.00**	**2**	**51.51**
S(sex + mov)	**154.40**	**0.48**	**0.12**	**0.79**	**3**	**49.97**
S(mov + season)	**154.80**	**0.88**	**0.10**	**0.64**	**3**	**50.36**
S(sex + mov+season)	**155.33**	**1.42**	**0.07**	**0.49**	**4**	**48.87**
S(mov + season + mov x season)	**155.45**	**1.53**	**0.07**	**0.47**	**4**	**48.98**
S(sex + mov + sex x mov)	**155.62**	**1.70**	**0.06**	**0.43**	**4**	**49.15**
S(rep + mov)	155.94	2.02	0.05	0.36	3	51.51
S(sex + rep + mov)	155.97	2.05	0.05	0.36	4	49.50
S(sex + rep + mov + season)	156.92	3.00	0.03	0.22	5	48.41
S(sex)	156.98	3.06	0.03	0.22	2	54.57
S(.)	157.39	3.47	0.03	0.18	1	57.00
S(sex + rep + mov + season + mov x season)	157.57	3.65	0.02	0.16	6	47.02
S(sex + rep + mov + mov x rep)	157.71	3.79	0.02	0.15	5	49.21
S(sex + season)	158.08	4.17	0.02	0.12	3	53.65
S(sex + rep + mov + season + sex x season)	158.09	4.17	0.02	0.12	6	47.54
S(sex + rep + mov + season + sex x repro)	158.23	4.31	0.02	0.12	6	47.68
S(sex + rep)	158.42	4.50	0.02	0.11	3	53.99
S(season)	158.47	4.55	0.02	0.10	2	56.06
S(sex + rep + mov + season + rep x mov)	158.64	4.72	0.01	0.09	6	48.09
S(sex + rep + mov + season + rep x season)	158.90	4.98	0.01	0.08	6	48.34
S(sex + season + sex x season)	159.32	5.40	0.01	0.07	4	52.86
S(sex + rep + mov + season + sex x season + sex x rep)	159.38	5.46	0.01	0.07	7	46.77
S(rep)	159.40	5.48	0.01	0.06	2	56.99
S(sex + rep + mov + season + sex x rep + mov x rep)	159.51	5.59	0.01	0.06	7	46.90
S(sex + rep + mov + season + sex x season + sex x mov + mov x season)	159.74	5.82	0.01	0.05	8	45.06
S(sex + rep + mov + season + sex x season + mov x rep)	159.82	5.91	0.01	0.05	7	47.22
S(sex + rep + sex x rep)	160.29	6.37	0.01	0.04	4	53.82
S(sex + rep + mov + season + sex x season + sex x rep + mov x rep)	160.73	6.81	0.00	0.03	8	46.05
S(sex + rep + mov + season + sex x season + sex x rep + sex x mov + mov x season)	161.28	7.37	0.00	0.03	9	44.54
S(rep + season + rep x season)	162.46	8.55	0.00	0.01	4	56.00
S(sex + rep + mov + season + sex x season +sex x rep + mov x rep+ rep x season)	162.80	8.88	0.00	0.01	9	46.05
S(sex + rep + mov + season + sex x season + sex x rep + mov x rep + sex x mov + mov x season)	162.99	9.07	0.00	0.01	10	44.16
S(sex + rep + mov + season + sex x season + sex x rep + mov x rep +rep x season + sex x mov)	164.55	10.63	0.00	0.00	10	45.72
S(sex + rep + mov + season + sex x season + sex x rep + mov x rep + rep x season + sex x mov + mov x season)	165.08	11.16	0.00	0.00	11	44.16

Table A6. Coefficients from supported (i.e., $\Delta QAIC_c \leq 2.00$) known-fate survival models assessing the effect of sex, season, movements (mov) and reproduction (rep, not in set of best models) on adult pin-tailed sandgrouse survival. Models are listed in order of support according to Akaike's Information Criterion adjusted for small sample size (AIC_c). Confidence intervals (95%) are represented by LCI (lower) and UCI (upper).

Model	**Parameter**	***β***	**SE**	**LCI**	**UCI**
S(mov)	Intercept	2.76	0.30	2.17	3.34
	mov	1.15	0.51	0.15	2.15
S(sex + mov)	Intercept	2.50	0.35	1.82	3.18
	sex	0.61	0.50	-0.37	1.59
	mov	1.06	0.51	0.06	2.07
S(mov + season)	Intercept	2.42	0.41	1.62	3.23
	mov	1.17	0.51	0.17	2.17
	season	0.53	0.49	-0.43	1.49
S(sex + mov + season)	Intercept	2.18	0.45	1.30	3.05
	sex	0.60	0.50	-0.38	1.58
	mov	1.09	0.51	0.08	2.10
	season	0.52	0.49	-0.44	1.48
S(mov + season + mov x season)	Intercept	2.69	0.52	1.68	3.70
	mov	0.56	0.73	-0.87	1.98
	season	0.10	0.63	-1.14	1.34
	mov x season	1.23	1.08	-0.88	3.35
S(sex + mov + sex x mov)	Intercept	2.63	0.39	1.86	3.40
	sex	0.28	0.60	-0.90	1.47
	mov	0.69	0.64	-0.57	1.94
	sex x mov	0.95	1.06	-1.14	3.03

Síntesis

En esta Tesis **se ha investigado cómo determinadas especies propias de los agrosistemas responden a los cambios ecológicos provocados por las alteraciones derivadas del desarrollo humano.** Hemos utilizado para ello dos especies de aves simpátricas: la ganga ibérica (*Pterocles alchata*) y la ganga ortega (*Pterocles orientalis*), especies cuyo origen está asociado a medios desérticos y semi-desérticos pero que en el contexto europeo se distribuyen por paisajes eminentemente agrarios y, por tanto, sometidos a un alto grado de humanización.

En este apartado se pretenden destacar los resultados más relevantes de cada uno de los capítulos presentados, sin entrar en demasiados aspectos relativos a la discusión de los mismos, ya que esa tarea ya ha sido realizada de manera independiente en cada uno de los capítulos que componen esta Tesis.

1. Factores que determinan la distribución, abundancia y selección de hábitat de especies de medios humanizados

A gran escala, los factores abióticos deberían ser los principales determinantes de la distribución de una especie (Whittaker et al. 2007) y de su nicho ecológico (Soberón 2007), pero en un mundo cada vez más humanizado, como es el caso del continente Europeo, los factores antrópicos adquieren una importancia cada vez mayor, modificando profundamente los hábitats y la biodiversidad que estos sustentan (Eriksson 2013). De esta forma, aunque los factores abióticos (precipitación, temperatura y topografía), explican en gran parte la distribución de Pteróclidos en Europa (capítulo 1), es sin duda el proceso expansivo de la agricultura (que en la actualidad supone la mitad de la superficie europea) ocurrido durante los últimos milenios, el que ha debido permitir una notable expansión del área de distribución de estas y otras especies esteparias y ligadas a medios agrarios en nuestro continente.

Durante muchos años la distribución y coexistencia de la ganga ibérica y la ganga ortega ha sido un misterio para muchos autores (Herranz y Suárez 1999 y referencias incluidas), lo cual no es de extrañar tratándose de especies originarias de ecosistemas áridos pobres y simples, con estructuras anatómicas e historias de vida muy similares (De Juana 1997), y en las que, por tanto, la diversificación de nicho podría estar limitada. Nuestros resultados confirman que la temperatura, como factor abiótico principal, parece mediar en parte la partición de nicho de ambas especies a gran escala (capítulo 2). Así, la ganga ibérica pertenecería preferentemente a los pisos termo- y mesomediterraneo, mientras que la ganga ortega sería más típica de los pisos meso- y supramediterraneo, coexistiendo ambas especies de forma general en el piso intermedio –mesomediterráneo–, y parcialmente en los otros pisos (capítulo 1 y 2). Aunque ambas especies muestran preferencia por los medios agrarios (áreas cerealistas), la ganga ortega muestra preferencia por una mayor variedad de hábitats a nivel global (mayor amplitud de nicho) que la ganga ibérica, lo que le permite a su vez tener un rango de distribución más amplio (capítulo 1 y 2), siendo la primera en este sentido más generalista que la segunda (hipótesis de amplitud de nicho). De esta forma, a gran escala podemos decir que la ganga ibérica está asociada en mayor medida a pasajes eminentemente agrarios y paisajísticamente homogéneos, mientras que la ganga ortega selecciona paisajes con mayor heterogeneidad de usos (tierras arables, pastos, matorral), y que ambas coexisten en ambientes intermedios entre los dos extremos de este gradiente de hábitats, aunque hay intrigantes desplazamientos aparentes del nicho óptimo en ambas especies que podrían estar explicados por factores como la atracción heteroespecífica (capítulo 2). Por tanto, tanto el clima como el hábitat determinan la coexistencia de ambas especies a gran escala, pero posiblemente las interacciones etológicas interespecíficas también cumplan un papel importante. En condiciones óptimas (alta temperatura media anual, alta temperatura en julio, y alta cobertura de tierras arables) la ganga ibérica alcanza las mayores densidades y área de distribución a nivel regional (meseta sur), que es, a su vez, el principal núcleo de distribución de esta especie en Europa (capítulo 1), sugiriendo que la hipótesis de posición de nicho actúa a escala regional. Sin embargo, en regiones con condiciones ambientales intermedias, encontramos evidencia de que las interacciones bióticas, que suelen adquirir más relevancia a escalas más pequeñas (Soberón 2007), podrían ser determinantes para explicar la densidad de la ganga ortega (capítulo 2). Intentamos aproximarnos a este tipo de interacciones y al estudio de la selección de hábitat diferencial de ambas especies a escala local (capítulo 3), pero dado que nuestra principal área de estudio estaba localizada en la meseta sur, donde la densidad de ganga ortega es muy baja, sólo el segundo de los objetivos pudo ser evaluado (selección de hábitat diferencial).

El hecho de que la ganga ibérica tenga unas preferencias de hábitat más estrictas que la ganga ortega sugiere que los profundos cambios en la gestión agraria del último milenio pueden haber influido de manera más negativa en la ganga ibérica que en la ganga ortega. De hecho, la ganga ibérica ha desaparecido en las últimas décadas de las regiones donde más hectáreas de cereal de secano han sido transformadas a regadío (meseta norte y valle del Guadalquivir, capítulo 1), dando lugar en la actualidad a una red de núcleos poblacionales que, en el caso de la ganga ibérica, está menos interconectada espacialmente (núcleos principales y marginales más distantes, ver definición en capítulo 1) que en el caso de la de la ganga ortega (capítulo 1).

2. Impacto directo de desarrollo humano y transformación del paisaje

Los sistemas agrarios se caracterizan por ser ambientes altamente dinámicos donde un mismo tipo de cultivo o sistema de producción, como por ejemplo el cultivo de cereal, puede dar lugar a paisajes muy diferentes a lo largo del año. Esto hace que un mismo cultivo pueda ser percibido como un hábitat adecuado o no por una determinada especie dependiendo de la época del año y de sus requerimientos ecológicos (Cardador et al. 2014). En las últimas décadas la intensificación de la agricultura ha supuesto la modificación de las prácticas tradicionales, abandonándose el ciclo habitual de siembra (cereal-rastrojo-barbecho o cereal-rastrojo/labrado-barbecho), y sustituyéndose por siembras directas (y aplicación de mayor cantidad de pesticidas) en las cuales el campo nunca es dejado en barbecho o es labrado. Dado que ambas especies de Pteróclidos tienden a evitar el cereal cuando está crecido (Abril-Mayo-principios de Junio) (capítulo 3, Martín et al. 2010b), y seleccionan positivamente los labrados y barbechos, este tipo de manejo (siembra directa) supone una pérdida neta de hábitat para ambas especies tanto durante el periodo no reproductor (los rastrojos son usados como sustrato para alimentación durante el periodo invernal en asociación con sisones (*Tetrax tetrax*, Martín et al. 2010a) como durante el periodo reproductor (los labrados y los barbechos pueden ser usados como refugio, alimentación de semillas de plantas ruderales, y lugar de nidificación para cría, capítulo 3). Es, además, precisamente al principio del periodo reproductor cuando registramos la mayoría de movimientos en la zona protegida del Campo de Calatrava (capítulo 5), por lo que estos movimientos pueden haber sido en parte iniciados como una posible adaptación a las variaciones espacio-temporales en las condiciones locales (ver Cody 1985; Roshier et al. 2008), es decir, a la menor disponibilidad de hábitats. El cereal en este periodo (Abril-Mayo-principios de Junio) todavía no ha sido cosechado, pero ya está crecido, lo que unido a la menor disponibilidad de barbechos y labrados generalizada en los últimos años, bien por siembra directa o intensificación, y la evitación de parcelas agrícolas en la proximidad de viviendas e infraestructuras (capítulo 3), supone una reducción notable de la superficie disponible de hábitat para momentos clave del ciclo anual. En definitiva, la capacidad de carga del medio agrario para estas especies podría variar en función de la gestión agraria y los requerimientos específicos en cada fase del ciclo anual, de forma que zonas idóneas para invernada pueden no serlo para reproducción y viceversa (ver Hervás y Suárez 2007; Martín et al. 2010b). Aunque el mecanismo preciso que impulsa estos movimientos no está totalmente claro, hemos visto que estas decisiones individuales repercuten positivamente en la supervivencia a nivel individual y poblacional (capítulo 5), y nuestra hipótesis es que podrían estar motivados por la búsqueda de mejores hábitats de cría y alimentación.

Además de la gestión agraria, otros cambios en el uso del suelo derivados del crecimiento poblacional humano, el desarrollo urbanístico y el desarrollo de infraestructuras tienen una influencia claramente negativa en la distribución y abundancia de las gangas (capítulos 1,2 y 3). A nivel local, nuestros resultados muestran la influencia clara de las actividades humanas en la distribución de ambas especies (evitan casas y caminos, utilizan parcelas en zonas intermedias entre varias infraestructuras, etc), siendo la ganga ortega quizá más sensible a estas perturbaciones que la ganga ibérica, un patrón que se repite a escalas mayores (capítulo 1 y 2). Este es un claro ejemplo de que algunos procesos que actúan a escala local pueden ser observados a escalas regionales.

Estos resultados tienen importantes implicaciones para la conservación de los dos Pteróclidos: El hecho de que a escala nacional y regional ambas especies estén asociadas a medios agrarios (capítulos 1 y 2), la gestión humana a nivel de paisaje (urbanización progresiva del medio, construcción de infraestructuras, actividad cinegética) y de usos del suelo (manejo de sustratos agrarios) puede estar resultando perniciosa para estas especies (capítulo 3), resultando en un desacoplamiento entre las predicciones de los modelos a gran escala y la situación real a escala local, que puede explicar en parte la existencia de áreas en teoría altamente adecuadas que están actualmente desocupadas (capítulo 1, Figura 5). Por ejemplo, grandes zonas de tierras arables que teóricamente deberían estar ocupadas por ambas especies, sobre todo por la ganga ibérica (meseta norte, capítulo 1), no lo están quizá porque la gestión agraria es mucho más intensiva (menor índice de barbecho, no rotación de cultivos, siembras directas) (Suárez et al. 1997) en estas zonas que en otras (meseta sur). Por otro lado, nuestros resultados sugieren que la intensificación agraria parece afectar más a las poblaciones de ganga ibérica, mientras que la ganga ortega parece ser más sensible a los procesos de urbanización y desarrollo de infraestructuras.

3. Supervivencia y causas de mortalidad en paisajes humanizados: impactos indirectos

La supervivencia de ganga ibérica fue ligeramente mayor en las poblaciones de la meseta sur, respecto a poblaciones localizadas hacia el margen norte de su distribución europea, particularmente la población francesa de La Crau. Esta es una población cerrada y que además parece tener una tasa de endogamia mayor a las de las poblaciones peninsulares españolas (García y Calero-Riestra, datos no publicados), sugiriendo la posible existencia de efectos Allee (Allee 1932), que deberían ser más profundamente investigados. De hecho, poblaciones situadas cerca del límite del rango de distribución de una especie suelen ser tener tasas de mortalidad mayores que las tasas de reproducción y reclutamiento (Brown y Lomolino 1998), es decir, con crecimiento poblacional negativo (zonas "sumidero").

Por otra parte, en poblaciones de la meseta sur (que podría considerarse una zona "fuente" en un contexto de metapoblación a gran escala), la supervivencia de ganga ibérica se caracteriza por una acusada estacionalidad, siento el periodo no reproductor (otoño-invierno), el más crítico para este parámetro demográfico. Creemos que varios factores indirectos asociados a actividades humanas pueden estar afectando de manera sinérgica a la supervivencia de la especie. De una parte, el alto grado de desarrollo humano en zonas rurales de la meseta sur (capítulo 1 y 3) sugiere que la densidad de depredadores generalistas en estas zonas podría ser particularmente alta respecto a zonas menos humanizadas (Bino et al. 2010; Fedriani et al. 2001), como el Parque Natural de Bardenas Reales. De hecho, la principal causa de mortalidad en la meseta sur es la depredación por carnívoros, mientras que en Bardenas Reales es la depredación por rapaces. El alto grado de gregarismo de esta especie a partir de otoño y durante todo el invierno (Martín et al. 2010a), con la formación de dormideros de varios miles de individuos, puede estar atrayendo a depredadores generalistas (observación personal) que pueden estar ejerciendo una presión mayor en esta especie si otras presas alternativas en su dieta escasean (ej: perdiz roja *Alectoris rufa* o conejo común *Oryctolagus cuniculus*, con densidades moderadas por enfermedades, sobrecaza o problemas relacionados con la actividad agraria). Adicionalmente, la actividad cinegética, además del impacto directo de la caza ilegal o accidental (capítulo 5), podría estar induciendo alteraciones en el comportamiento de la ganga ibérica, y estrés fisiológico, lo cual podría repercutir en la condición física (Casas et al, en preparación). Esto podría traducirse en una mayor ingesta de semillas en un menor espacio de tiempo (por acortamiento de los días) para crear reservas necesarias para el invierno. Muchas de estas semillas puede ser semillas tratadas químicamente o semillas blindadas, cuyo uso se ha extendido como parte del proceso de intensificación agraria. Estas semillas blindadas, incluso a bajas dosis, producen efectos letales y subletales (López-Antia et al. 2013), por lo que puede estar afectando a la condición física de los individuos de ganga ibérica. Aunque todos estos procesos deben ser investigados más profundamente, otros autores han sugerido que los cambios introducidos por el hombre en los medios agrarios pueden haber creado un medio en el que las dinámicas poblaciones sean más sensibles a la depredación, y por tanto ambos procesos (alteración de los usos del suelo y depredación) pueden estar teniendo un efecto sinérgico y negativo en las poblaciones de ganga ibérica asociadas a medios agrarios humanizados, al igual que en otras aves de medios agrarios (Evans 2004) .

4. Reflexión breve sobre el pasado y futuro de los Pteróclidos ibéricos y aves de medios agrarios

Las dos especies de gangas, al igual que gran parte de la comunidad actual de aves de medios agrarios, colonizaron Europa desde las estepas asiáticas y los semi-desiertos del Mediterráneo siguiendo la el proceso expansivo de la agricultura (hace 7000-10000 años)(Donald et al. 2006). Ambas especies han evolucionado en medios desérticos, con poca o nula presencia humana, y baja presión de depredadores. Es bien sabido que los procesos de extinción ocurren de manera más frecuente cuando aparecen nuevas amenazas ajenas a la experiencia evolutiva de las especies, o cuando ocurren a una tasa superior a la capacidad de adaptación y plasticidad ecológica de las mismas (Brook et al. 2008). El desarrollo socioeconómico en España, aunque tardío respecto al resto de Europa, con los consiguientes procesos de intensificación agraria, urbanización y desarrollo de infraestructuras, puede estar ocurriendo a una velocidad superior a la capacidad adaptativa de estas especies, lo que puede tener consecuencias irreversibles. Es especialmente paradójico que el mismo proceso (actividad agraria) que permitió la expansión de los Pteróclidos ibéricos y otras aves de medios agrarios por Europa, sea el mismo que quizá esté expulsándolas en la actualidad de este continente. Queda en nuestras manos, y en especial en los escenarios políticos Europeo y nacionales, pues, revertir la actual situación para la biodiversidad de los sistemas agrícolas europeos.

5. Futuras líneas de investigación

- El conocimiento actual del comportamiento reproductor de las dos especies peninsulares de gangas es en general reducido, hecho al que sin duda ha contribuido la dificultad de encontrar, y por tanto estudiar, sus nidos y pollos (De Borbón y Barros 1999; De Borbón et al. 1999). Durante el trabajo de campo de esta Tesis Doctoral se han obtenido datos sobre el uso de hábitat de nidificación, éxito reproductivo, fenología de la reproducción y comportamiento durante la incubación de ambos parentales para la ganga ibérica (Mougeot et al. 2014), con observaciones muy anecdóticas para la ganga ortega. En este proceso, la captura y marcaje para seguimiento individual ha sido clave. Sin embargo, la muestra total de nidos o eventos de reproducción (pollos, familias, comportamiento de individuos marcados) es heterogénea y espaciada a lo largo del periodo 2003-2014 (N=105), siendo 2010 y 2011 los años con mayor muestra (N=59). Por tanto, con los datos actuales no es posible evaluar con fiabilidad la variabilidad anual en los parámetros reproductivos, que es altamente dependiente del clima y otros factores, y las conclusiones obtenidas con estos datos (ej: fenología de puesta), aunque útiles, serán bastante generales. Se ha comprobado que hay algunas parejas monógamas a lo largo de al menos dos estaciones de cría, y que no se separan a lo largo del ciclo anual, pero se desconoce en qué proporción. Se desconoce el grado de fidelidad que presentan estas especies a la zona de cría (aunque hemos constatado nidos de la misma hembra en dos estaciones de cría separados por un máximo de 1 km), la distribución espacial de los nidos y los factores que determinan la selección del lugar de nidificación. Varios de estos aspectos pueden ser estudiados con la muestra actual, pero un esfuerzo intenso con suficientes recursos humanos y logísticos sería necesario durante al menos dos temporadas más de cría, para resolver muchos de los interrogantes en la biología de la reproducción de estas especies.

- Actualmente sabemos que determinados sustratos agrarios son particularmente usados por ambas especies, fundamentalmente labrados y barbechos (y en menor medida leguminosas y pastizales), y creemos que la disponibilidad de alimento puede ser un recurso crucial para la selección de estos medios. El conocimiento actual sobre la dieta de las dos especies es prácticamente inexistente, por lo que, dado el estricto granivorismo de los Pteróclidos, estudios detallados sobre este aspecto crucial de su ecología serían necesarios. Mediante la identificación del tipo y abundancia de semillas de las que se alimenta cada especie, respecto a la disponibilidad en el medio, se podrían identificar sus requerimientos tróficos, importantes para entender el uso de distintos sustratos agrarios y para entender el efecto que algunas prácticas agrarias (siembra directa, mayor frecuencia de laboreo, aplicación de agroquímicos) está teniendo en la disponibilidad de alimento y por tanto distribución de ambas especies. Desde un punto de vista más ecológico, podríamos determinar si existe segregación de nicho trófico entre ambas especies. A su vez, interesaría determinar la presencia (o no) y abundancia de semillas blindadas en el buche de ejemplares de individuos vivos y muertos para poder establecer algún tipo de relación causal que nos permita explicar si efectivamente los Pteróclidos ibéricos están ingiriendo semillas blindadas, y los efectos que esta ingesta pueden estar teniendo en la supervivencia invernal en la ganga ibérica a nivel individual y poblacional.

- Un aspecto que no ha quedado del todo claro en esta Tesis Doctoral es el grado de interacción entre ambas especies a escala local, y la comparación de estas interacciones a distintas escalas. Dado que los resultados del capítulo 2 indican que la densidad de ganga ortega puede estar altamente relacionada con la de ganga ibérica (aunque no al contrario) en regiones con alta simpatría entre ambas especies (valle del Ebro), sugerimos la posible existencia de interacciones entre ambas especies a nivel local. Este tipo de interacciones, que pretendíamos tratar en el capítulo 3, son aún desconocidas. En principio, según nuestras observaciones, parece que ambas especies se evitan a nivel de parcela, pero desconocemos si la ganga ortega puede estar utilizando a la ganga ibérica, de carácter más gregario, para localizar áreas con hábitats idóneos. Teniendo en cuenta que la primera prefiere una mayor variedad de hábitats que la segunda, parece razonable que un área adecuada (en cuanto a disponibilidad de hábitat) para la ganga ibérica también lo sea, en principio, para la ganga ortega, si el paisaje no es estrictamente agrario y el clima lo permite (ver capítulos 1 y 2), lo cual parece cumplirse en el Valle del Ebro. Por tanto, sería interesante plantear un estudio similar al del capítulo 3, pero incluyendo adicionalmente variables explicativas tipo atracción conespecífica y heteroespecífica, en esta región donde el grado de simpatría entre ambas especies es alto, y las densidades relativas son similares.

- Sería recomendable la captura, marcaje y seguimiento de un mayor número de ejemplares juveniles para mejorar la precisión de las estimas de supervivencia juvenil obtenidas para la ganga ibérica, y para poder evaluar, si es posible, diferencias espaciales y temporales en estas estimas. Este parámetro es de vital importancia para poder luego modelizar la persistencia de poblaciones y el posible riesgo de extinción mediante análisis de viabilidad poblacional. Para estos modelos serían necesarias además las estimas de éxito reproductivo mencionadas en la primera línea de investigación sugerida.

- Dada la escasez de datos para la ganga ortega, sería interesante establecer un programa de captura, marcaje y seguimiento de más ejemplares de esta especie para obtener parámetros demográficos claves como éxito reproductivo y reclutamiento o supervivencia adulta y juvenil, además de posibles causas de mortalidad. Por otro lado, el seguimiento sería particularmente útil para estimar áreas de campeo estacionales y movimientos de ganga ortega, y establecer diferentes áreas de cría e invernada para esta especie.

- Teniendo en cuenta que la depredación es la principal causa aparente de mortalidad de la ganga ibérica, harían falta estudios más detallados sobre impacto real de depredadores generalistas en ambas especies de ganga. Es sabido que además que el éxito reproductivo es bajo en ambas especies (De Borbón et al. 1999; Mougeot et al. 2014), y gran parte se debe a la depredación de nidos y pollos (datos no publicados), tal y como en otras especies de esteparias que crían en el suelo (Yanes y Suárez 1996), aunque el impacto real e identidad de los potenciales depredadores es difícil de constatar. Más estudios en este sentido son necesarios dado que este bajo éxito reproductivo parece ser un factor limitante (junto a una supervivencia no excesivamente alta en el caso de la ganga ibérica) para las poblaciones de Pteróclidos ibéricos.

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Conclusiones

1. Los factores abióticos y de origen antrópico explican la distribución de Pteróclidos ibéricos a gran escala. Ambas especies están asociadas a llanuras de carácter árido, siendo la ganga ibérica de carácter más termófilo que la ganga ortega. La cobertura de tierras arables es la variable antrópica más importante que determina su distribución, sin descartar el efecto negativo de infraestructuras y el desarrollo urbanístico. Así, la Política Agraria Común (PAC) se convierte en un agente vital que afecta de manera directa a la distribución y abundancia de ambas especies, y a su evolución en el tiempo.

2. Los requerimientos de hábitat de la ganga ortega a gran escala son menos estrictos que los de la ganga ibérica, un patrón que también parece repetirse a escala local. Como consecuencia, la red de núcleos poblacionales centrales y marginales identificados por nuestros modelos varía para cada especie. Esta red parece ir restringiéndose de forma paulatina por cambios derivados de la intensificación agraria y otros cambios en los usos del suelo. Futuros cambios en la distribución de ambas especies vendrán dados por efectos sinérgicos entre el cambio climático, la implementación de las nueva PAC y el crecimiento poblacional y el desarrollo urbanístico e infraestructural.

3. La ganga ibérica y la ganga ortega ocupan distintos nichos ecológicos en simpatría y en alopatría. En simpatría los nichos de ambas especies ocupan posiciones intermedias respecto a condiciones alopátricas, indicando la importancia de los factores abióticos a la hora de determinar áreas de coexistencia. Las condiciones ambientales (factores abióticos) explican las densidades regionales de la ganga ibérica mientras que las interacciones bióticas explican las de la ganga ortega en regiones con condiciones ambientales adecuadas e intermedias al óptimo de ambas especies.

4. La hipótesis de amplitud de nicho parece explicar la distribución global (en la península ibérica) de ambas especies. La ganga ortega tiene un nicho más amplio que le permite explotar una mayor variedad de condiciones ambientales (climáticas, topográficas y tipo de hábitats), al contrario que la ganga ibérica, con un nicho más estrecho y distribución más restringida. Sin embargo, la hipótesis de posición de nicho puede explicar por qué ambas especies (sobre todo la ganga ibérica) alcanzan altas

densidades en regiones donde las condiciones ambientales son óptimas, logrando distribuciones amplias si estas condiciones están ampliamente distribuidas a su vez.

5. Determinadas actividades humanas en el medio afectan de manera negativa la distribución y abundancia de ambas especies a escala nacional, regional y local, siendo la ganga ortega más sensible a las perturbaciones de origen humano que la ganga ibérica. A escala local, la estructura del paisaje, los usos del suelo y las preferencias de microhábitat explican de manera conjunta e integrada la distribución de la ganga ibérica mejor que por separado. La selección de hábitat a escala local en ambas especies es modulada por las perturbaciones humanas: un sustrato a priori adecuado puede ser rechazado dependiendo su proximidad a infraestructuras, caminos, casas y asentamientos humanos. La actual tasa de crecimiento poblacional, desarrollo urbanístico e intensificación agraria parece estar ocurriendo a un ritmo superior a la plasticidad ecológica y capacidad adaptativa de ambas especies.

6. La selección de hábitat a escala local indica que los labrados y barbechos son los sustratos agrarios más usados durante el periodo reproductor por ambas especies, mientras que los cultivos de cereal son evitados. Además, la ganga ibérica parece seleccionar estos sustratos atendiendo a recursos críticos: refugio, alimentación o lugar de nidificación, con suficiente visibilidad para escapar de depredadores. El mantenimiento de la rotación tradicional (cereal-barbecho de uno o dos años) en estos medios, y la reducción del laboreo de estos sustratos durante el periodo reproductor podrían beneficiar a las dos especies de Pteróclidos.

7. Nuestra técnica de captura con cámara térmica, foco y red es suficientemente efectiva y no dañina para la ganga ibérica y la ganga ortega comparada con procedimientos anteriores, y ha resultado tremendamente eficaz para abordar estudios de marcaje y seguimiento, y posterior obtención de parámetros demográficos cruciales. La ganga ibérica es más sensible a la captura y marcaje que la ganga ortega. Recomendamos el uso de emisores más pequeños que el umbral normalmente recomendado (< 3% del peso del individuo vs 5% habitual) y un tiempo de manejo que no supere los 20 minutos, particularmente en capturas realizadas durante el periodo reproductor.

8. Las tasas de supervivencia de adultos y juveniles de ganga ibérica son similares, aunque menores que las de otras especies de aves esteparias simpátricas. Los movimientos estacionales pueden jugar un papel muy importante en la supervivencia de los individuos y en la dinámica poblacional de esta especie. Además de una estrategia dirigida a la declaración de espacios protegidos, deberían desarrollarse medidas de gestión horizontales que abarquen todo el territorio (dentro y fuera de los espacios protegidos).

9. La estación no reproductora (invierno) es la más crítica para la ganga ibérica en cuanto a mortalidad. Nuestros resultados indican que la depredación es la principal causa de mortalidad en ganga ibérica, tanto por carnívoros en áreas fuertemente humanizadas de la meseta sur, como por rapaces en poblaciones periféricas con menor presencia humana (Bardenas Reales). Se considera necesario conocer hasta qué punto son naturales dichas tasas de depredación, pudiendo reflejar no tanto condiciones naturales sino ser el resultado del incremento artificial de ciertos depredadores (zorros, búhos) por la acción directa o indirecta del hombre, en cuyo caso sería deseable evaluar la posibilidad de un cierto control de la densidad de depredadores en zonas de protección o ante situaciones de conservación críticas.

10. Es necesario exigir una mayor vigilancia de la actividad cinegética en áreas protegidas, impidiendo toda caza fuera de la legalidad. Asimismo, sería recomendable el establecimiento de zonas de reserva, con criterios de conservación y fomento de las poblaciones de aves esteparias existentes, en cotos de caza privados dentro de ZEPAS declaradas como tales por la importancia de este grupo de especies.

Agradecimientos

Esta aventura empezó oficialmente en Mayo del 2009, pero en realidad comenzó mucho antes, en Diciembre de 2008, en mi primera reunión con mis posibles futuros directores. Llegué de Holanda, país del orden, de la organización a nivel máximo, de la cuadratura, de la reunión fijada en el calendario con varios días e incluso semanas... y me topé con el caos y la entropía, con la copa de Navidad del IREC, con gente etílicamente indispuesta pero que me recibieron con el máximo cariño posible, con mucho calorcito y que enseguida me hicieron sentirme parte de la casa (de hecho me llevé un polo del IREC sin haber firmado nada). La reunión hubo que repetirla varios días más tarde, y por fin pude conocer a Txuso y Javi en condiciones más sobrias. A ellos sin duda tengo que agradecerles que mi vida diera un giro radical, que hoy por fin pueda estar poniendo punto y final a una Tesis que no es sólo mía, si no que es muy vuestra también. Os agradezco enormemente que confiarais en mí viniendo de fuera, sin conocerme de nada, sin yo apenas saber ni lo qué era una ganga, sin haber cogido unos binoculares en años. No entiendo que se os pasaría por la cabeza cuando se os presentó una tía que quería dejar un curro bien pagado, en un sitio donde le ofrecían hacer la Tesis, para venirse a La Mancha (tierra hostil y acogedora a partes iguales) a un país que acababa de entrar en una crisis que aún nos dura, y en unas condiciones menos competitivas económicamente. Pensaríais que estaba lo suficientemente zumbada para encajar bien en vuestro equipo, pero esto en ese momento sólo lo sabíais vosotros, yo sólo me di cuenta meses más adelante, y ya era tarde para huir ☺. Os agradezco que aparte de las discusiones y reuniones de Tesis ("momento cigarro"), me hayáis abierto las puertas de vuestras casas y me hayáis hecho sentir siempre con la suficiente confianza y comodidad para discutir otros temas más personales. Os agradezco vuestra paciencia durante mis periodos de desvarío y desconcierto existencial, sin nunca exigirme cuentas. Os agradezco que en realidad, más que directores, seáis amigos. En fin, que sois unos cracks, caiga quien caiga.

Javi se ha encargado de que nunca me faltase de nada, nunca ha puesto pegas para soltar la pasta para dietas, coches, reponer GPS rotos y perdidos, y ha hecho todo lo posible para sacarme contratos y becas de la nada. Te agradezco que, incluso siendo Director del IREC durante los dos primeros años de mi Tesis, siempre hayas estado dispuesto para venir a campo cuando nadie más podía, a rescatarme por la noche en un camino perdido entre rastrojos tras perder las llaves del coche, a censar bajo un calor del infierno y encontrar el único nido que han labrado durante la Tesis (Dr. Katastroff), a revisarme los capítulos y responderme a intempestivas horas cuando iba de culo, a acogerme en tu hogar y alimentarme en momentos de crisis. Tu input científico quizá haya sido menos intenso o continuado en el tiempo que el de Txuso, por tu ausencia o por la mía, pero ha sido el justo y el necesario, peleas sobre zorros y viñedos incluidas, y creo que has sabido sobre todo poner el contrapunto a mi otro director. Tanto contrapunto que creo que sólo 1 de cada 100 veces Txuso y tú coincidís en una interpretación de resultados, pero creo que después de 5 años me voy a doctorar también en tirar por la calle de "en medio" y hacer lo que al final una considera lo más razonable. Gracias por quitarme el conservacionismo a collejas y hacerme mejor ecóloga.

A **Txuso**, gracias por retarme, por ponerte borde, por darme caña para que espabilase, por no ponerme las cosas fáciles, desde el principio hasta al final, por criticar mis métodos, mis resultados, mis interpretaciones, mis discusiones, por insistir tanto en que me olvidase del "detallito" e intentase explicar los resultados en un contexto más global, una y otra vez, una y otra vez, yo soy cabezona, pero tú lo eres más, para muestra, un botón:
"Yo este paper lo veo, claramente: a) para enfocar por lo metodológico -y olvidarse del ***detallito-*** o para b) enfocarlo por el lado conservación -y olvidarse del ***detallito***- Lo mejor sería combinar ambos enfoques en la discusión y darle al ***detallito*** su espacio justo". En definitiva, gracias por empujarme a pensar de manera más crítica, por hacerme mejor investigadora. Al final hasta se te coge cariño...

Mis **padres**, "er Dani y la Teo", me han dado la vida, y eso ya lo es todo. Pero yo seguramente no sería lo que soy, no me habría dedicado a la ecología y la conservación, si ellos no me hubieran llevado fin de semana sí y fin de semana no al CAMPO. Esto era una ley no escrita en nuestra familia, y yo nunca me la planteé, nunca fui consciente de la impronta que me dejaría su amor por la naturaleza, su pasión por perderse por un encinar adehesado o un monte escarpado. Gracias por vuestro apoyo incondicional, gracias por haberme dejado decidir siempre sin cuestionar qué "era lo mejor para mí". Mi hermana **Blanca** seguirá chinchándome hasta el fin de los tiempos y más allá repitiéndome que yo lo que estudio en realidad son perdices, que me deje de rollos. No puedo estar más orgullosa de ella no podría haber tenido una hermana mejor, con esa capacidad de trabajo, con esa generosidad, con ese amor que me profesa, con esa manera que tenemos de entendernos y reírnos de nuestros propios pegos y chorradas. Seguiré escribiéndote y llamándote cuando estés dormida, yo en cambio espero tu llamada de camino a la academia para entretenerte el viaje ;)

No sé cuántos compañeros de despacho diferentes he tenido en estos últimos años, pero si ha habido una constante en todo este periodo esa es **María.** Calerito me guió en mi primer día en el IREC (literalmente), y ahora se encarga de que no caiga enferma en mis últimos momentos de Tesis. Hemos reído y hemos llorado, ha habido largos periodos de ausencias pero sé que siempre puedo contar contigo para lo que necesite, y espero que al contrario también. Ánimo que ya queda poco para que seáis tres, después de eso lo de la Tesis será un camino de rosas.

Aldita se me fue pronto a hacer las Américas, previo paso por Panamá, pero con él y María compartí diez mil conversaciones escatológicas y alguna que otra sobre ciencia. Se me fue mi compi de Rock Band, pero nos reencontraremos de gira, o quizá firmemos un paper juntos, todo es posible. Miss u, Alda.

François y Bea no son mis directores, pero han estado ahí para resolver cualquier duda que me haya surgido, y para echarme una mano con lo que fuese cuando Txuso y Javi estaban de Topillos. Vuestro hogar en Picón me dio cobijo en momentos complicados, y nunca podré estar lo suficientemente agradecida por vuestro cariño, vuestra generosidad y por lo fácil que hacéis las cosas a los demás. François me ha regalado una portada preciosa, largas noches de capturas muy productivas tanto en número de gangas como en número de risas, y sobre todo sé que tengo su amistad. Siempre se dice de Bea que es como una madre, que acoge a todos y a todos cuida, yo diría que es más que eso, es un pedazo de mujer y una gran científica.

Al equipo de **Gangosos** en conjunto**: Txuso, Javi, François, Fabi y Carlos.** Soy la única chica pero creo que hemos sabido acoplarnos bien. **Fabiancito,** contigo quizá es con quien mejor me entiendo por edad y momento vital y científico, aunque me queda mucho para llegar a tu punto. Gracias también a tus padres **Fabi y Julia** por esas cenitas estupendas precaptura, y a ti por tu inmensa ayuda, por nuestras charlas skype, por los viajecitos a Arguedas escuchando Onda Melodía, por echar una mano en campo cuando ha hecho falta. La siguiente en el desierto omaní**. Carlos** me enseñó a hacer radioseguimiento, a usar un GPS, y me enseñó los cerros clave para “trackear” gangas. Gracias por tu apoyo en los primeros años de Tesis, sobre todo, y por tu contribución en la distancia a los artículos que han ido saliendo.

A la gente de la Comunidad de Bardenas Reales, por darnos la oportunidad de trabajar durante 2-3 años allí y ofrecernos siempre las mejores comodidades. En concreto, gracias a **Alejandro y** a **Sergio.** Gran parte de mi Tesis depende de vuestro trabajo**.**

Cuando a mitad de Tesis mi vida se rompió en pedacitos **Conchi** apareció para recogerlos y ayudarme a pegarlos poquito a poco. Ambas comenzamos en el IREC en la misma semana, y yo creo que hasta me odió brevemente por mi impertinencia con ese mal genio boquerón que gasta. No fue hasta hace 2 años que descubrí el gran corazón que llevas en ese pecho moreno (marrón?) malagueño. Gracias por aportar cordura, amor y sensatez cuando más hundida estaba. Te echo de menos cada día que pasa, y sin duda los lunes no son lo mismo sin compartir la comida de Mariquina y Teo. Te quiero, amiga.

De las tres patas del banco, **Víctor** sigue ahí. Amigo, eres el tío más interesante, gracioso y sensible que me he cruzado en los últimos años. Gracias por todos los ratitos compartidos, cañitas, transectos y estaciones de escucha. Eres un grande en todos los sentidos. PRRRRRRRR!!!! 

Anna, as you said, “sin ti esta aventura no hubiera empezado”. Thanks for supporting me all these years, thanks for being my partner and my friend for such a long period, and, specially, for still being my friend. I would not have had the strength to pursue my dreams without you, and for that I will always be grateful. I definitely shared too much with you to sum it up in few lines. Harstikke bedankt, Dr. Van Spanje.

A la gente de la administración y biblio del IREC, porque en algún momento os habéis encargado del infierno burocrático de mis dietas, pedidos, papeles de Tesis y todo lo que ha ido surgiendo. **Arturo, Juan Carlos, Lucía, Carolina, Jorge Yepes, Jorge Ladero, Almudena, Ana Aparicio...** muchas gracias. También a nuestros ex vigilantes, en especial **Vicente** que me ayudó tela con los coches.

A mis compis de **Villapaciencia,** los que se han ido, los que quedan y los que han llegado recientemente: **Chipi, Chai, Anza, Iván y Mer.** Todos sois especiales en vuestro ser. Habéis sido un gran pilar en mi vida ciudarrealeña, puede que haya habido temporadas más ausentes que otras, pero en cuanto aparcaba el Cadillac rosa ahí estabais para recibirme con los brazos abiertos. Iván además me aguantó como jefa (Foxy) todo un verano, y me temo que le toca aguantarme como amiga el resto de su vida.

Merce, flamenquita, tú apareciste de la nada para acompañarme en mi último año de Tesis. Sé la paciencia que has debido de tener en muchos momentos, has aguantado neuras, bajones, y estreses como nadie. Me quedo con todos los grandes momentos, y con tu cariño, con nuestras largas conversaciones y nuestras escapadas. Estoy deseando descubrir lo que nos deparará el futuro. A ti, también, gracias (también por enseñarme a distinguir tientos, soleás y alegrías).

Jesús Carrasco fue mi compañero de andanzas en el verano de 2010. Gracias por currar como un loco y siempre con esa buena disposición a pesar de las largas jornadas bajo el sol abrasador manchego. No está "pagao", nene, te portaste como un campeón. **Xurxo** ha sido crucial para sacar adelante mucho trabajo de campo, tanto de censos, como de capturas, como de plantillas de vegetación. Con **María Santoro** aprendí a sangrar aves, en concreto las perdices de su DEA. Pero tengo que sobre todo agradecerle su gran sonrisa y buena disposición, aunque me traiga a Carla menos de lo que yo quisiera. **Fidel** sobrevivió al campo manchego el verano de 2009, y me ayudó muchísimo con ArcGIS al principio de mi Tesis. Algunos alumnos de prácticas metieron datos como posesos en el PC, o echaron una mano en campo, en particular **Arturo** y sobre todo **Andrés** han sido vitales para que esta Tesis no se haya demorado más.

A **Kiko** e **Isra**, que me proporcionaron los datos del Censo Nacional. Me encantaría que Kiko pudiese ver todo lo que hemos aprendido sobre las gangas, estoy segura de que su input científico habría mejorado notablemente los artículos que componen esta Tesis. Isra me ayudó con los mapitas de usos del suelo, con ArcGIS, con los censos, con explicarme las características de la ZEPA,...vamos, con mi aterrizaje en la zona de estudio.

La gente de La Comuna, ex comuneros ya: **Elena (Chapa), Raspa, Loren, Eli, David...** gracias por esos pequeños ratitos de descanso de Tesis. Elena y Raspa siempre tienen una sonrisa en la boca; Loren también, pero maligna; Eli es un sol y David es vasco ☺, para bien y para mal (sobre todo para bien).

A **Julián Garde** porque siempre está disponible para resolver dudas, y es el tío más eficiente que conozco.

Marcianitoooooossss!!!! (**Tiri, Elena, Ana Fliki, Tula, Marce, Ángel, Sergio, Rodri, Giuli, Rafiky**...) Creo que he tenido la suerte de cruzarme con lo mejorcito que ha dado el terreno manchego. Gracias por las cañas, las barbacoas, las paellas, las noches de feria, los festivales cancelados (Pacientón 2015?) y los no cancelados (cumples y despedidas). Prometo divulgar el saludo manchego por todos los rincones de la Tierra...”QuéeeEEEEEEeeeee?” (leer con entonación culiparda).

A todo el mundo que alguno vez participó en unos censos de ganga, una noche de capturas o una jornada de radioseguimiento, un big thank you!

A las chicas del Miguelturreño, porque me han ayudado a descargar tensiones acumuladas después de 8 horas empantallada.

El grupo de hortelanos son **Jesús Caro, Marisa, Alba, Jesús Martínez**. Ellos han dado (aún más) vida a Villapaciencia, y a mi estancia en el IREC. **Jesusito** me ha sacado con la bici, **Marisa** me ha dado de comer pucherazos de madre, **Albita** me ha salvado el culo en el último minuto, y me ha esponsorizado los cafés mañaneros; y con **Jesús M.** he compartido divagaciones científicas y personales. Pero eso es lo de menos, lo de más es lo querida que me hacen sentir. Un besoteee!

A mis amigos de Holanda, en particular a **Addy**. Dr. van Dijk, ik ga ook promeveren!!! Zullen we dus een paar bier drinken? Bedankt voor jouw vriendschap!

Laura se ha encargado de sosegar mi ánimo, de cuidarme mucho y respetar mis tiempos en los últimos tres meses de mi Tesis. Gracias por compartir tu música, tus inquietudes y tu cariño, y por esos filtritos en las fotos de los capítulos. Tengo mucha suerte, sólo puedo decir eso y que... eres muy guay!

AMIGAS, unders de toda la vida y rescatadas en los últimos tiempos, gracias por estar ahí SIEMPRE, en Madrid, en Utrecht, en Hue, en Ciudad Real, en Picón y donde sea que vayan mis pasos, sé que iréis a ver a vuestra amiga la descastada hasta el último pueblo de mala muerte donde acabe. **Elena, Rocío, Almu, Clara, Carmen, Julia, Chose, Isa...** Me siento muy afortunada de teneros en mi vida durante tantos años ya, de haberme hecho adulta con vosotras, de haber crecido y haberme convertido en lo que soy, desde la infancia, hasta la adolescencia, juventud y ahora “adolestreinta”, ¡porque a espíritu joven no nos gana ni dios!

A mi gran familia en general, tíos, primos y sobrinos de nueva hornada, tanto **Chaparros** como **Benítez**. A los que están y a los que ya no están, porque llevan toda la vida cuidándome y amándome incondicionalmente, y porque a todos nos une de alguna forma el cortijo de “La

Vera de los Julios” y el de “Los Almadenes”; los torreznos, las bellotas, los pedos de lobo, los paseos al Pozo Los Arcos o los partidos de fútbol en la era. ¡Os quiero!

Al resto de compis (y ex compis e investigadores) del IREC, con algunos compartí despacho, con otros simplemente unas risas, algún viaje de campo, alguna comilona... con otros incluso compartí casa: **Cat, Julien, Fernando Aparicio, Jota, Dolo, Rafa M., Ana Romero, Javitxa, Dani Topillos...** y varias personas más que fijo olvido.

Es difícil después de tanto tiempo no dejarse a alguien atrás, seguramente lo haya hecho y lo siento en el alma, pero una se va haciendo mayor y la memoria empieza a fallar. A ellos/as también un gran gracias.