Selección del hábitat en el escribano palustre iberoriental, estructura genética y tendencia poblacional: aplicaciones para su conservación

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Doctorando

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Imagen de portada: Macho de escribano palustre iberoriental, marcando territorio desde la inflorescencia de una masiega, en el Parque Nacional de las Tablas de Daimiel.

Tesis presentada por Pablo Vera García para optar al grado de Doctor en Biología por la Universitat de València.

Firmado: Pablo Vera García

Tesis dirigida por los doctores

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Firmado: Juan Salvador Monrós González	Firmado: Eduardo Jorge Belda Pérez

A Carmen,

a Marina y Candela,

y a mis padres

Resumen

La pérdida de hábitats, fragmentación del paisaje y en consecuencia la pérdida de conectividad ha sido un proceso especialmente intenso y negativo en los humedales de las regiones mediterráneas a lo largo de los dos últimos siglos, llevando a algunas de las especies más íntimamente ligadas a ellos a aumentar su aislamiento y ver empeorado su estado de conservación. El escribano palustre (*Emberiza schoeniclus*) es una de estas especies. Se trata de un ave paseriforme de distribución paleártica que no se encuentra amenazada a nivel mundial, aunque sí lo están algunas subespecies, como es el escribano palustre iberoriental (*E. s. witherbyi*), que se reproduce en varios humedales del interior de la península Ibérica y costa mediterránea española, francesa y marroquí. La última estima del tamaño de población en España corresponde a 2015 (122-136 parejas distribuidas en 9 humedales). Por tanto, conocer y entender la estructura de sus poblaciones, sus requerimientos de hábitat y cómo éstos influyen en su declive, objetivos de esta tesis, son cuestiones críticas para definir las estrategias y actuaciones que requiere para abordar su conservación de una manera urgente.

Los resultados obtenidos sugieren que las poblaciones de escribano palustre iberoriental no muestran signos de una reducción de su variación genética a pesar de los bajos tamaños poblacionales efectivos, aunque sí de un aislamiento entre sus poblaciones, probablemente como respuesta a la existencia de un mayor flujo génico debido a la baja conectividad entre humedales que habita. En el momento del estudio ninguna población mostró efectos de haber sufrido un cuello de botella. De acuerdo a los resultados, se propuso distinguir tres unidades de gestión: Delta del Ebro, Castilla La Mancha y Mallorca. Los datos disponibles de censos permitieron estimar su tasa de crecimiento anual entre 2002-2005 y 2005-2015, poniendo de manifiesto su declive y la falta de reclutamiento de nuevas poblaciones durante el periodo más reciente. La proyección de las tendencias futuras evidenció una probabilidad muy alta de sufrir aún mayores declives o incluso su extinción a medio plazo. De manera complementaria, en un estudio preliminar para hacer un seguimiento de su población reproductora en las Tablas de Daimiel, evidenció un claro declive en la ocupación de los territorios.

A través del análisis de los requerimientos de hábitat a escala paisajística y de sus territorios encontramos que su ocurrencia es independiente del tamaño del humedal y se encuentra relacionada con la cobertura de parches mixtos de carrizo y enea (menor en humedales ocupados), cobertura de parches de juncos con carrizo, y perímetro de parches

mixtos de carrizo y juncos (mayor en humedales ocupados). Las formaciones de enea y carrizo pueden ser utilizadas como indicadores de condiciones de inundación fluctuante favorables para el desarrollo de las formaciones de juncos y carrizo en distintos grados de dominancia y para aumentar las oportunidades de alimentación tanto de los adultos como de los volantones. La coherencia a distintas escalas espaciales refleja que la probabilidad de ocurrencia de escribano palustre iberoriental en un humedal se encuentra determinada por la disponibilidad de hábitat para establecer los territorios. De manera complementaria, mediante el análisis de imágenes satélite se pudo comprobar cómo en el Marjal de Pego-Oliva, de manera acoplada al declive de la especie hasta su desaparición, se produjo una reducción significativa de los hábitats preferidos y un aumento de los hábitats menos adecuados precisamente en aquellas zonas donde los machos establecían sus territorios. De acuerdo a estos resultados, resulta urgente elaborar y poner en marcha los planes de recuperación de la especie y los planes de gestión de los humedales en los que habita (todos ellos pertenecientes a la Red Natura 2000) para preservar todas las poblaciones que aún se mantienen y su diversidad genética.

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Introducción

La especie

El escribano palustre (*Emberiza schoeniclus*) es un ave paseriforme que presenta una amplia distribución paleártica, extendiéndose sus áreas de reproducción desde la península Ibérica hasta China (Copete y Christie, 2017). A lo largo de su extensa área de distribución, el escribano palustre se reproduce de forma localizada en ambientes asociados al agua, desde la vegetación palustre encharcada de grandes humedales hasta pequeños carrizales fragmentados en matrices agrícolas, siendo más notable su querencia por humedales hacia el sur de esta área de distribución. Durante el invierno en España se encuentra asociado a ambientes abiertos, especialmente de naturaleza acuática, como riberas, humedales y embalses con vegetación palustre, junto con cultivos de regadío o inundación, evitando ambientes arbóreos y secos (Vera y Monrós, 2012).

Fruto de la variación de su tamaño, color del plumaje y morfología del pico, se han descrito 20 subespecies (Copete y Christie, 2017). De éstas, cuatro de ellas se distribuyen en el Mediterráneo occidental: el escribano palustre norteño (*Emberiza schoeniclus schoeniclus*), que se reproduce en Europa continental e islas británicas e inverna en el sur de Europa y norte de África, siendo el de mayor tamaño, mayor longitud alar y pico más bajo y corto; el escribano palustre italiano (*E. s. intermedia*), reproductor en Italia, mayoritariamente sedentario y con un pico alto y fuerte; el escribano palustre iberoriental (*E. s. witherbyi*), sedentario, que se reproduce de forma puntual en humedales del interior de la península Ibérica, y costa mediterránea española y francesa, así como la vertiente atlántica de Marruecos, es el que presenta un plumaje de color ligeramente más apagado y un pico alto; y el escribano palustre iberoccidental (*E. s. lusitanica*), reproductor en humedales de la cornisa cantábrica y atlántica de la península Ibérica, sedentario, el más pequeño, y coloración más oscura. Conocer con precisión las relaciones taxonómicas entre estas especies es fundamental de cara a poder otorgar un estatus correcto y establecer normativas de gestión y conservación integradas en las herramientas legislativas de protección de la biodiversidad.

La especie no se encuentra amenazada a nivel mundial y por ello no está incluida en la Lista Roja de la UICN (IUCN, 2016), pero sí lo están las poblaciones de algunos países. De esta manera aparece en la "Birds of Conservation Concern Red List" y en el Apéndice II de la Convención de Berna. En Inglaterra se encuentra protegida por el "Wildlife and Countryside Act 1981" (Battern et al., 1990). Sin embargo, las poblaciones de algunos países europeos se encuentran sufriendo un declive poblacional marcado (Bufield y Van Bommel, 2004; Voříšek et al., 2010), entre ellos España (Atienza, 2006; Monrós et al., 2017). Diversos estudios han relacionado este declive directamente con la pérdida y alteración del hábitat tanto durante la época de reproducción como la invernada (Siriwardena et al., 2000; Brickle y Peach 2004; Surmacki 2004; Orłowsky 2005; Voříšek et al., 2010).

En el caso del escribano palustre iberoriental, las últimas estimas fiables del tamaño de población en España corresponden a los años 2005 y 2015. La estima de 2005, realizada en el marco del I Censo Nacional de la especie, reflejó un tamaño poblacional de entre 250 y 360 parejas, concentrándose su mayoría en los humedales de Castilla-La-Mancha (Atienza, 2006). En 2015, en el marco del II Censo Nacional de la especie, y repitiéndose el censo en todas las localidades en las que se detectó la especie en 2005 y, prácticamente, en todas las muestreadas con censo negativo en ese mismo año, refleja un tamaño poblacional de 122-136 parejas, afectando la mayor reducción precisamente a la población reproductora en Castilla-La Mancha (Monrós et al., 2017).

La tendencia negativa de esta subespecie y su área de distribución en 2005, menor de 500 km^2, fueron los motivos por los cuales la especie fue considerada como “En Peligro” en el Libro Rojo de las Aves de España (Atienza y Copete, 2004) de acuerdo a los criterios de la Unión Internacional para la Conservación de la Naturaleza. Sin embargo, la revisión del estado de conservación de la subespecie atendiendo a los mismos criterios con la información del censo nacional de 2015 la calificaría como “En Peligro Crítico” (9 localidades, con una superficie de ocupación total menor de 10 km^2, unido a la reducción de su área de distribución, de ocupación, de calidad del hábitat, de localidades y de individuos, criterio B2b (i,ii,iii,iv,v)), y por tanto considerándose que se enfrenta a un riesgo extremadamente alto de extinción en estado silvestre. En el Catálogo Nacional de Especies Amenazadas (Real Decreto 139/2011) aparece catalogada como “En Peligro de Extinción”, categoría otorgada a aquellos taxones o poblaciones cuya supervivencia es poco probable si los factores causales de su actual situación siguen actuando. En la misma situación legal se encuentra la subespecie *lusitanica* (escribano palustre iberoccidental), restringida a la parte oriental de la cornisa cantábrica y a algunos humedales del norte de Portugal.

Este marco legal y el estatus de protección que presenta la subespecie requiere de la preservación de los hábitats y ambientes en los que se encuentra, especialmente de aquellos utilizados por ella en un momento tan crítico como es la época de cría, y la reducción de la presión de sus amenazas ligadas a la degradación de los humedales, la predación y la intensificación agrícola. De forma complementaria, esta catalogación debe ser traspuesta a las normativas de cada autonomía en que el escribano palustre iberoriental se encuentra presente, y, una vez recogida la especie en los catálogos de especies amenazadas a nivel regional, acometerse la redacción de planes de recuperación. A pesar de la preocupante y delicada situación de las poblaciones ibéricas ya detectada en 2005, las comunidad autónomas de

Madrid, Castilla-La Mancha, Navarra, Cataluña y Baleares no han elaborado dicho plan de recuperación, siendo la Comunidad Valenciana la única autonomía que ha redactado un borrador de documento técnico al respecto, en 2016.

Por otro lado, siendo un ave ligada estrechamente a humedales y estando todas las localidades de reproducción incluidas en la Red Natura 2000, sus requerimientos de hábitat deben ser contemplados en la redacción tanto de los Planes de Gestión de estos espacios como de aquellos en los que se ha extinguido recientemente, de forma que puedan ser recogidos y contemplados en los Planes de Cuenca que abarquen estos espacios.

Las preferencias y uso de hábitat

Los humedales mediterráneos, a pesar de su gran importancia por el valor conservacionista de su fauna y flora, se han visto fuertemente alterados a lo largo de los dos últimos siglos. Las principales presiones que han sufrido han sido la desecación (Fernández-Alés, 1992), pérdida de calidad del agua y del suelo (Zalidis et al., 2002) y la reducción de la conectividad debido a la homogeneización del paisaje (Gallego-Fernández et al., 1999). En consecuencia, las aves ligadas a los humedales son, junto con las aves agrícolas, el grupo de aves que sufre una mayor amenaza por la pérdida y degradación de su hábitat (Butchart et al., 2004; Dudgeon et al., 2006). En estos ecosistemas dinámicos, el hábitat utilizado por distintas especies amenazadas puede sufrir grandes cambios interanuales en la estructura y composición de la vegetación predominante en el ecosistema a causa del viento, fuego o cambios en el régimen hídrico (White et al., 2007), cambios que influyen directamente en la disponibilidad de alimento y selección de lugares de nidificación. Por ello, el conocimiento de la distribución y de las características del hábitat que influyen en la ocurrencia de las especies es una cuestión esencial en los estudios dirigidos a establecer las actuaciones destinadas a mejorar el estado de conservación de una especie.

Las aproximaciones multiescala a la selección y preferencias de hábitat suponen una herramienta importante para entender cuáles son los factores que influyen en su ocurrencia y de qué manera lo hacen (Hall y Mannan, 1999; Luck, 2002, Pickett y Siriwardena, 2011). Los estudios a escala paisajística tienen como gran utilidad la posibilidad de generar modelos de idoneidad de hábitat a partir de capas de sistemas de información geográfica (SIG), fotografía aérea o satélite (Guisan y Zimmermann, 2000). Estos modelos permiten determinar espacialmente las áreas más idóneas para realizar prácticas de gestión y conservación, y establecer áreas y prácticas prioritarias (Store y Jokimäki, 2003; Gibson et al., 2004). Tradicionalmente estos estudios se han realizado mediante el uso de información disponible mediante SIG. Estas variables disponibles mediante SIG y otros análisis análogos pueden actuar como variables causales y ayudar a identificar relaciones de hábitat (Guisan y Zimmermann, 2000; Gibson et al., 2004; Brambilla et al., 2009), e incluso aportar información aplicable para determinar el tamaño, forma y grado de fragmentación adecuados para el diseño de restauración de humedales (Harrison y Bruna, 1999; Pasinelli et al., 2008, Benassi et al., 2009). Pero debido al elevado coste de tiempo y presupuesto que implica el mapeo detallado de la composición y estructura de la vegetación, raramente tienen la resolución espacial y detalle necesarios para describir preferencias de hábitat a escala de territorio. Sin embargo, el análisis de las preferencias de vegetación a escala de territorio resulta fundamental para entender de qué manera trabajan las fuerzas de selección para que las aves escojan territorios con cierta disponibilidad de alimento, lugares seguros para establecer sus nidos reduciendo el riesgo de predación y lugares con perchas para cantar, especialmente en ambientes heterogéneos (Neto, 2006; Pasinelli y Schiegg, 2006; Pasinelli et al., 2008, Menz et al., 2009). Así, resulta imprescindible combinar los estudios sobre selección de hábitat realizados en varias escalas, en la medida en que la preferencia por ciertos tipos, estructura o composición de hábitats pueden estar influenciados por factores que afectan de manera diferente dependiendo de la escala (Söderströn y Pärt, 2000; Brambilla et al., 2009).

Debido al dinamismo de los humedales, el estudio de los hábitats de las especies que viven en ellos puede ser realmente complejo (Mialon, 2005). Por esta razón, se están desarrollando rápidamente nuevos procedimientos, basados en las nuevas tecnologías de mapeo, para el seguimiento y planificación de los documentos técnicos de conservación de estos ecosistemas (Kerr y Ostrovsky, 2003; Davranche et al., 2009; Poulin et al., 2010), incluso a escala de territorio (Leyequien et al., 2007; Keith et al., 2009). Todos estos nuevos procedimientos comparten la necesidad de un trabajo de campo previo e intenso que permita entrenar los métodos de identificación de variables de composición y estructura de la vegetación. Por lo tanto, el uso de fotografía y satélite suponen unas herramientas de alto interés que permiten combinar campañas de trabajo de campo con el seguimiento continuado de las variables de vegetación, así como extrapolar a años anteriores y entender las tendencias y dinámicas recientes de las especies. De esta forma, el análisis de la variación de hábitat disponible a diferentes escalas tanto espaciales como geográficas, permite generar una información que complementa a la de las tendencias de las especies amenazadas, ayudando a entender los factores que influyen en éstas, así como mitigarlos y revertirlos.

La estructura de las poblaciones

Conocer y entender la estructura de las poblaciones es una cuestión fundamental para definir las estrategias y actuaciones de gestión de la biodiversidad y, de manera más crítica, en aquellas especies de interés conservacionista. A nivel aplicado, esto se traduce en la necesidad de adquirir la capacidad de definir las unidades de gestión de las poblaciones e identificar los parámetros demográficos y los factores del medio biótico que influyen en mayor medida en la viabilidad de la población o en su capacidad de recuperación.

Esta información es especialmente importante en aquellas especies que se distribuyen y ocupan el espacio de una manera parcheada en una matriz paisajística heterogénea o en ambientes fragmentados (de manera natural o derivada de la acción humana) (Opdam et al., 1994; Akçakaya et al., 2007; Van Teeffelen et al., 2012). Desde la segunda mitad del s. XX, procesos que afectan a las comunidades a escala paisajística, como la pérdida de calidad del hábitat y su consiguiente fragmentación en la matriz paisajística, han conducido a numerosas especies de aves, mamíferos, invertebrados, parásitos, etc., a sufrir extinciones y experimentar situaciones dramáticas (Reed, 2004). De hecho, la pérdida de hábitat y sus efectos a escala paisajística son considerados como una de las causas más relevantes de extinción de especies (Butchart et al., 2010) a través del cambio en la dinámica de las poblaciones (Fahrig, 2003; Wiegand et al., 2005). Este proceso ha sido especialmente intenso y negativo en los humedales de las regiones mediterráneas (Silva et al., 2007; Valiela y Fox, 2008) y ha llevado a las especies más íntimamente ligadas a ellos a aumentar su aislamiento y ver empeorado su estado de conservación (Cuttelod et al., 2008).

De forma general, se conoce como metapoblación al conjunto dinámico de las poblaciones de una especie que se estructuran espacialmente discretas en un área geográfica y que intercambian individuos mediante procesos de dispersión activos o pasivos (Akçakaya et al., 2007). Desde los primeros modelos propuestos por Levins en 1969, el conocimiento y modelización de la dinámica de las metapoblaciones han tenido un papel cada vez más relevante en la ecología aplicada a la conservación de las especies, aumentando la complejidad de los planteamientos gracias al alcance de una mayor precisión en la definición y estima de los parámetros que intervienen en esta dinámica y al uso de nuevas tecnologías (Hanski, 1998). Su concepto y enfoque resultan fundamentales para la conservación de cualquier hábitat parcheado o fragmentado, así como de las poblaciones cuyas dinámicas dependen de las poblaciones vecinas o las distintas unidades de gestión del taxón (Akçakaya et al., 2007).

El modelo inicial de metapoblación de Levins (1969) parte de la base de la heterogeneidad espacial, asumiendo que todos los fragmentos de hábitat en los que habitan las poblaciones son iguales, sin tener en cuenta la calidad del hábitat en cada parche o las distancias entre cada uno de ellos. La complejidad espacial dentro de los distintos fragmentos no tardó en incorporarse a estos modelos, comenzando a tener en cuenta el tamaño de los fragmentos y la distancia a la que se encuentran entre sí para estimar la probabilidad de extinción y colonización de nuevos fragmentos (Hanski y Ovaskainen, 2003). Estos modelos, que sólo tienen en cuenta la presencia o ausencia de las poblaciones en los parches de hábitat, son utilizados principalmente para estudiar la persistencia de las poblaciones o la importancia de distintos fragmentos para la dinámica poblacional global (Moilanen y Cabeza, 2002; Cabeza y Moilanen, 2003; Ovaskainen y Hanski, 2003) y la viabilidad poblacional (Akçakaya et al., 1995; Lindenmayer y Lacy, 1995). Otros modelos más complejos y que requieren de un mejor conocimiento de las poblaciones que forman la metapoblación son los modelos estructurados, los cuales describen una población de acuerdo a la estructura en edades e incorporan dinámicas espaciales, por ejemplo entre parámetros demográficos entre poblaciones (Kendall et al., 2000; Liebhold et al., 2004; Kerlin et al., 2007). Finalmente, los modelos poblacionales a escala paisajística tienen en cuenta la complejidad espacial de la matriz en la que se localizan estos fragmentos, la calidad del hábitat dentro y fuera de los fragmentos, y la supervivencia o mortalidad asociada a la dispersión atendiendo a la calidad del hábitat y las barreras presentes (Moilanen y Hanski, 1998; Fahrig, 2003; Wiegand et al., 2005; Xu et al., 2006; Hodgson et al., 2009; Robert, 2009).

En las metapoblaciones existen amenazas derivadas de las diferencias de tamaño de las poblaciones y los fragmentos o parches de hábitat. Así, la tasa de extinción es mayor en poblaciones pequeñas y tienen una menor probabilidad de rescate por inmigración en parcelas más aisladas (Hanski, 1994), siendo por tanto su viabilidad menor (Boughton y Malvadkar, 2002; Reed, 2004; Donner et al., 2010). De hecho, las metapoblaciones con varias poblaciones pequeñas pueden tener un mayor riesgo de extinción que una única población grande (Akçakaya et al., 1995).

La estructura genética y las unidades de gestión

La pérdida y fragmentación de hábitats generalmente ejercen un doble efecto en la estructura genética de las poblaciones que sufren estas alteraciones: reducen la diversidad genética dentro de las poblaciones y reducen el flujo génico entre las poblaciones, por tanto reduciendo el fitness adaptativo de las poblaciones (Amos et al., 2012; Harrison et al., 2012). Por tanto, de cara a plantear y priorizar medidas de gestión y conservación de cualquier taxón, en poblaciones pequeñas estructuradas como metapoblaciones (especialmente si se encuentran amenazadas), es necesario conocer el tamaño y el grado de aislamiento de sus poblaciones realizando estimas de la distancia genética y de la evidencia de flujo genético entre ellas (Frankham, 2010), y así tener más argumentos para resolver la cuestión práctica de cómo preservar la máxima diversidad genética de esta especie y, cómo y de qué manera se estructuran las unidades de gestión poblacional.

Para ello, existen diversos conceptos y enfoques acerca de cómo definir las unidades de gestión poblacional de la especie y de las unidades evolutivas significativas (en inglés, ESU) o unidades de gestión (UM), a utilizar para diseñar medidas que permitan conservar la diversidad genética de un taxón y aplicarlos en genética de la conservación y genética paisajística (p.e. Fraser y Bernatchez, 2001; Manel et al., 2003; Hey et al., 2003; DeSalle y Amato, 2004; Hampton et al., 2004; Palsbøll et al., 2006; Frankham, 2010). En este marco, la diferenciación genética entre poblaciones permite conocer el grado de aislamiento entre éstas al evaluar la correlación entre las frecuencias alélicas de genes homólogos de una subpoblación frente a la correlación de estas frecuencias en los genes en toda la población (Pritchard et al., 2000).

Esta información, junto con la referente al flujo genético entre subpoblaciones, no sólo permite identificar las unidades de gestión, sino que además permite identificar, evaluando en el marco de la estructura poblacional, en qué medida factores como la conectividad entre poblaciones o la calidad del hábitat influyen en la dinámica poblacional. Por lo tanto, esta información supone una herramienta imprescindible para definir y priorizar acciones de conservación a escala de la unidad de gestión en los planes de gestión del taxón evaluado (por ejemplo, priorizando acciones de mejora de hábitat para el aumento del tamaño poblacional de las unidades de gestión más amenazadas, o la mejora de la conectividad entre poblaciones entre las que existe un bajo flujo genético).

Los objetivos

El objetivo general de esta tesis ha sido contribuir a mejorar el conocimiento de tres de los aspectos que mayor importancia tienen para la biología de conservación del escribano palustre iberoriental: la estructura genética de sus poblaciones, su estado de conservación y sus preferencias de hábitat a distintas escalas espaciales. De una forma más específica, los objetivos han sido:

1. Determinar la estructura genética y estimar la diversidad genética de las poblaciones ibéricas del escribano palustre iberoriental.
2. Estimar sus tendencias pasadas y futuras en su área de distribución en España.
3. Desarrollar un estudio preliminar para monitorizar su población reproductora en el Parque Nacional de las Tablas de Daimiel.
4. Determinar los requerimientos de hábitat a escala de humedal a lo largo de su área de distribución en España.
5. Identificar los componentes del hábitat y estructura de vegetación seleccionados para el establecimiento de sus territorios, a lo largo de su área de distribución en España.
6. Estudiar la estructura y composición vegetal de sus nidos.
7. Analizar, a partir de sus preferencias de hábitat, los cambios en la vegetación asociados al su declive.

La estructura de la tesis

La tesis se presenta en forma de capítulos que se corresponden con artículos previamente publicados o aceptados, exceptuando un capítulo que se encuentra en fase de revisión en una revista (in rev.). Estos capítulos se complementan con los apartados de discusión general y perspectivas, y conclusiones, los cuales integran los resultados parciales de cada capítulo.

Capítulo I.	Kvist, L., Ponninkas, S., Belda, E.J., Encabo, S.I., Martínez, E., Onrubia, A., Hernández, J.M., Vera, P., Neto, J., Monrós, J.S. 2011. Endangered subspecies of the reed bunting (*Emberiza schoeniclus witherbyi* and *E. s. lusitanica*) in Iberian Peninsula have different genetic structures. *Journal of Ornithology* 152: 681-693.
Capítulo II.	Vera, P., Marín, M., Monrós, J.S. Belda, E.J., Estimating past and future population trends in Spain of endangered Eastern Iberian reed bunting *Emberiza schoeniclus witherbyi* (en revisión).
Capítulo III.	Vera, P. Belda, E.J., Kvist, L., Encabo, S.I., Monrós, J.S. 2011. Habitat preference of endangered eastern Iberian Reed Bunting (*Emberiza schoeniclus witherbyi*). *Bird Study* 58: 238-247.
Capítulo IV.	Vera, P., Belda, E.J., Kvist, L., Encabo, S.I., Marín, M., Monrós, J.S. 2014. Habitat preferences for territory and nest settlement of the endangered Eastern Iberian Reed Bunting *Emberiza schoeniclus witherbyi*. *Ardeola* 61: 97-110.
Capítulo V.	Vera, P., Marín, M., Belda, E.J., Monrós, J.S. Estructura y composición del nido de Escribano Palustre Iberoriental *Emberiza schoeniclus witherbyi*. *Revista Catalana d'Ornitologia* 25: 43-48.
Capítulo VI.	Carrasco, L., Vera, P., Belda, E.J., Monrós, J.S. 2017. Using remote sensing to study the vegetation dynamics of a coastal Mediterranean wetland and its effect on the habitat availability of a threatened passerine. *Journal of Coastal Research* (aceptado)

Justificación de la tesis

En dinámicas poblacionales como la que muestran en las últimas dos décadas tanto el escribano palustre iberoriental como el iberoccidental, es bien conocido que factores como la endogamia, la deriva genética, un flujo restringido de genes y un bajo tamaño poblacional conducen a una reducción de la diversidad genética (Markert et al., 2010, Purvis et al., 2010). A su vez, existen relaciones estrechas entre una baja diversidad genética y un alto riesgo de extinción (Spielman et al., 2004, Furlan et al., 2012), incluyendo hechos como que (1) una reducida diversidad genética puede reducir el tiempo en el que se pueden extinguir los taxones en ambientes cambiantes (Blomqvist et al., 2010), (2) que un cambio en la heterocigosidad entre generaciones es una medida del coeficiente de endogamia y se encuentra relacionado con el estado de las poblaciones (p.e. Melosik et al., 2016), y (3) que la depresión endogámica puede aumentar el riesgo de extinción (p.e. Saccheri et al., 1998, Blomqvist et al., 2010). Las poblaciones de aves fragmentadas y amenazadas, como las del escribano palustre iberoriental y el iberoccidental, se encuentran expuestas a estas condiciones, viendo aumentado su riesgo de extinción y dificultado su rescate (Spielman et al., 2004, Evans y Sheldon, 2008).

Por tanto, resulta fundamental conocer la diversidad genética de ambas subespecies, así como estimar las diferencias genéticas entre las distintas poblaciones fragmentadas. En este sentido, es necesario estimar la cantidad de variación genética existente entre las poblaciones de cara a definir las unidades de gestión o conservación de las poblaciones de ambas subespecies basadas en las diferencias entre poblaciones utilizando medidas genéticas (Capítulo I). Para el estudio genético, se tomaron muestras de escribanos palustres iberorientales en Marruecos, diversas localidades de la zona central, septentrional y oriental de la Península Ibérica e islas Baleares, así como de varias localidades de Portugal y Galicia, para el estudio de la estructura genética del escribano palustre iberoccidental. Un estudio genético de este tipo es un claro ejemplo de la utilidad del desarrollo de una genética de la conservación en poblaciones aisladas y en declive, dado que también permite definir las unidades de gestión de los taxones, imprescindible como base de la redacción de cualquier plan de gestión o recuperación de un taxón que deba redactarse.

Una vez conocidas las unidades de gestión del escribano palustre iberoriental, emerge la necesidad de conocer si existe realmente un declive de la especie, de cómo cuantificarlo y de conocer los factores que actúan sobre esta dinámica. Tradicionalmente, la abundancia ha sido el parámetro utilizado en programas de conservación de especies amenazadas. Sin embargo, es un parámetro muy complejo de estimar adecuadamente, en especial cuando se realiza a una escala geográfica amplia y con especies afectadas por la fragmentación, requiriendo en muchos casos de una fuerte inversión económica. De forma alternativa, la estima de la ocupación (proporción de un área ocupada por una especie o fracciones de unidades paisajísticas donde la especie se encuentra presente) se ha utilizado ampliamente en estudios de ocurrencia (p.e. Engler et al., 2004), selección de hábitat y su modelizado (Reunanen, 2002), estudios a nivel de metapoblación (Hanski, 1998), y programas de seguimiento (Trenham et al., 2003). El principal problema a solventar en este tipo de estudios es conocer la detectabilidad de la especie (la probabilidad de ser detectada estando presente), un factor que necesariamente ha de tenerse en cuenta de cara a evitar sesgos en las estimas realizadas. En este marco, se ha realizado un seguimiento del escribano palustre iberoriental en el Parque Nacional de las Tablas de Daimiel, el humedal que alberga la mayor población reproductora (Capítulo II), con el objetivo de establecer la detectabilidad de la especie y conocer con detalle la tendencia de ésta.

El declive poblacional experimentado por el escribano palustre presenta una preocupación adicional, al ser un ave ligada estrechamente a los humedales. Los humedales son ambientes muy dinámicos en los que la acción del viento, inundación o fuego pueden afectar considerablemente a la estructura y selección de nido y/o alimento, momentos críticos en la vida de un ave. A estos procesos naturales con un fuerte componente de estocasticidad, se suma el hecho de que los humedales son uno de los ecosistemas más amenazados del planeta (Dudgeon et al., 2006). La pérdida o degradación del hábitat, sobreexplotación, contaminación de las aguas, modificación de los ciclos hidrológicos y las especies invasoras amenazan las comunidades biológicas que albergan (Revenga et al., 2005).

A pesar que existe una gran cantidad de bibliografía sobre selección de hábitat de aves palustres, existe escasa información acerca de la selección de hábitat por parte del escribano palustre iberoriental. Los únicos estudios existentes con esta subespecie se restringen a humedales concretos (Martínez-Vilalta et al., 2002) o a inferencias realizadas grosso modo (Bigas y Copete, 2004; Atienza, 2006), incluso mostrando cierta dificultad a la hora de encontrar resultados claros (Poulin et al., 2002). Por ello, resulta de gran importancia aumentar el volumen de conocimiento detallado de las preferencias de hábitat de este paseriforme tanto a escala de humedal (Capítulo III) como a escala de territorios (Capítulo 4), de cara a generar información que pueda ser incorporada por las administraciones en el proceso de elaboración de planes de gestión de estos humedales, designados como zonas ZEPA.

Para ello, se trató de explicar mediante regresiones logísticas binarias la ocurrencia del escribano palustre iberoriental en estos humedales en base a variables relacionadas con la cobertura y dominancia de distintos tipos de vegetación palustre en un total de 25 humedales dentro de su área de distribución en España (Capítulo III). Como segundo paso, se siguió un procedimiento similar para establecer las preferencias de hábitat a nivel de territorios. Con este objetivo, se midieron variables de cobertura y estructura de vegetación dentro de 11 humedales con presencia de escribano palustre iberoriental. Posteriormente, se utilizaron Modelos Mixtos Lineales Generalizados (GLMM) con una distribución de error binomial para explicar la ocurrencia de territorios de escribano palustre iberoriental en base a las variables de cobertura y estructura de la vegetación (Capitulo IV). Con estos resultados, además de obtener las variables seleccionadas positiva o negativamente con la ocurrencia, se desarrollan modelos predictivos con los que potencialmente evaluar la idoneidad de un humedal o un territorio para la ocurrencia de escribanos palustres iberorientales.

Una vez establecido el territorio, existen otras presiones de selección que ocurren a escala de nido. Estas presiones de selección tienen como fin último maximizar la eficacia reproductiva, ya sea reduciendo la probabilidad de ser predados o facilitando el aislamiento de huevos y pollos ante factores climáticos adversos (Alabrudzińska et al., 2003; Pasinelli y Schiegg, 2006; Schiegg et al., 2007). En este sentido, la estructura de nidos naturales y su variación intraespecífica ha sido bien estudiada en muchas especies (Hansell, 2000), aunque los estudios sobre su composición vegetal son escasos o se refieren únicamente a alguno de sus componentes (Mazgajski, 2007). La composición de los nidos constituye también un indicador del uso de hábitat y los requerimientos ecológicos de las aves en el momento crítico de la reproducción. Dado que la estructura y composición de los nidos naturales de aves son resultado de distintas presiones de selección, cada tipo de material usado por cualquier especie en la elaboración del nido tiene una función definida (termorreguladora, aislante, soporte, etc.) de acuerdo a las propiedades físicas del material vegetal (Hansell, 2000). Para el estudio de nidos (Capítulo V), se realizó una búsqueda directa de éstos en el Parque Nacional de las Tablas de Daimiel, recolectándolos tras finalizar la reproducción de la especie. Una vez en el laboratorio, se procedió a la medida de sus dimensiones y a la separación, determinación y pesado de los distintos tipos de vegetación utilizados.

A partir de toda la información disponible, surge la necesidad de comprobar empíricamente la validez de los métodos desarrollados y los resultados obtenidos en uno de los humedales con presencia de escribano palustre iberoriental y sobre la que se ha realizado un seguimiento, y en el que ha tenido lugar un progresivo cambio en la vegetación del humedal por el cambio en la gestión del mismo (Capítulo VI).

El humedal seleccionado fue el Parque Natural del Marjal de Pego-Oliva (Valencia-Alicante, este de España). Como humedal costero mediterráneo, es un ecosistema muy dinámico, lo que dificulta el estudio de los hábitats de las especies que viven en ellos (Mialon, 2005). En estos ambientes dinámicos, dada la necesidad de realizar cartografías con breves intervalos de tiempo, las imágenes de satélite ofrecen un gran ahorro de esfuerzo y coste económico respecto del esfuerzo que representa el mapeo de la vegetación *in situ*, además de ser de gran utilidad para analizar la evolución de poblaciones de aves cuando los datos poblacionales son muy escasos o inexistentes. El estudio tuvo dos objetivos principales: i) obtener una clasificación de la vegetación para diferentes años del Marjal de Pego-Oliva combinando el trabajo de campo y la comparación relativa de firmas espectrales con la técnica de clasificación supervisada mediante el algoritmo de máxima verosimilitud utilizando muti-season SPOT-5 data, y ii) analizar estos cambios en la vegetación en el contexto del declive a escala local del escribano palustre iberoriental utilizando la información de sus preferencias de hábitat a nivel de humedal y para establecer sus territorios.

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Endangered subspecies of the Reed Bunting (*Emberiza schoeniclus witherbyi* and *E. s. lusitanica*) in Iberian Peninsula have different genetic structures

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ENDANGERED SUBSPECIES OF THE REED BUNTING (*EMBERIZA SCHOENICLUS WITHERBYI* AND *E. S. LUSITANICA*) IN IBERIAN PENINSULA HAVE DIFFERENT GENETIC STRUCTURES

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Abstract

In the Iberian Peninsula, populations of two subspecies of the Reed Bunting *Emberiza schoeniclus* have become increasingly fragmented during the last decades when suitable habitats have been lost and/or the populations have gone extinct. Presently, both subspecies are endangered. We estimated the amount of genetic variation and population structure in order to define conservation units and management practices for these populations. We found that the subspecies *lusitanica* has clearly reduced genetic variation in nuclear and mitochondrial markers, has a drastically small effective population size and no genetic differentiation between populations. In contrast, the subspecies *witherbyi* is significantly structured, but the populations still hold large amounts of variation even though the effective population sizes are smaller than in the nonendangered subspecies *schoeniclus*. We suggest several management units for the Iberian populations. One unit includes subspecies *lusitanica* as a whole; the other three units are based on genetically differentiated populations of *witherbyi*. The most important genetic conservation measure in the case of *lusitanica* is to preserve the remaining habitats in order to at least maintain the present levels of gene flow. In the case of the three management units within *witherbyi*, the most urgent conservation measure is to improve the habitat quality to increase the population sizes.

Keywords: genetic diversity, effective population size, microsatellite mtDNA, population structure.

Introduction

Over the last 20 years, there has been a debate on the importance of demographic and genetic processes in the chain of events leading to extinction. Lande (1988) emphasized the importance of demographic over genetic factors, but still sought for integration of both. Caughley (1994), while introducing the small-population paradigm and the declining-population paradigm, argued that the small-population paradigm has contributed significantly to the theory of genetics and dynamics of small populations, but has so far been restricted largely to captive breeding, whereas the declining-population paradigm is still in need for more theory, and is really the one relevant to conservation. He stated that genetics often obscures the real issues, but also that this is not an argument for less conservation genetics, but for more of it. In a large metaanalysis conducted by Spielman et al., (2004), in which 170 threatened taxa and their non-threatened taxonomic relatives were included, heterozygosity was found to be on the average 35% lower in the threatened taxa than the nonthreatened relative taxa, and in 77% of pairwise comparisons, the threatened taxa had lower heterozygosity. The authors argued that reduced genetic diversity indicates that the reproductive fitness is already compromised and extinction risk elevated. Even though Spielman et al., (2004) stated that they were unable to determine whether genetic factors have contributed to the current threatened status of the taxa they studied, there are clear links between reduced genetic diversity and extinction risk. These links include the facts that (1) reduced genetic diversity reduces extinction times in changing environments, (2) change in heterozygosity between generations is a measure of inbreeding coefficient and related to population fitness, and (3) inbreeding depression adversely affect the extinction risk.

Accepting the importance of genetic processes in conservation biology leads to a practical question of how to preserve the maximum genetic diversity in threatened species and how to define the units for management if resources available for the purpose are limited. Since Ryder (1986) presented the need to identify discrete populations within the range of a species, suggesting the use of measures as genetic distances, multitude of concepts of such evolutionary significant units (ESUs) have been proposed. Later, Waples (1991) proposed that an ESU should fill two criteria: it must be substantially reproductively isolated from other conspecific populations and it must represent an important component in the evolutionary legacy of the species. Moritz (1994) firmed up the definition by stating that an ESU should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci. He also introduced the concept of management units (MUs) and defined them as populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of alleles. Crandall et al., (2000) suggested that the rejection of ecological and genetic exchangeability forms the foundation of population distinctiveness and that reciprocal monophyly should be omitted as a criterion because it is too restrictive. The discussion of defining conservation units has been going on with the goal of unifying the concepts (e.g., Fraser and Bernatchez, 2001) and with critics of different definitions (e.g., Patkeau, 1999; Hey et al., 2003). The ultimate aim among conservation biologists is nevertheless the same: to find a common way to define the limits of distinct populations embracing as much evolutionary history and adaptive potential as possible.

In this study, we aimed to estimate genetic distinctiveness and genetic diversity in endangered and still declining fragmented populations of the Reed Bunting *Emberiza schoeniclus* in the Iberian Peninsula. The Reed Bunting is a widely distributed Palaearctic passerine, common in most parts of its distribution range. At the western limits of the range, two subspecies of the Reed Bunting have been described for the Iberian Peninsula, *E. s. lusitanica* in the north-west and *E. s. witherbyi* in the south-east, as well as the nominate subspecies *E. s. schoeniclus*, which breeds throughout north and central Europe and migrates to the south (including the Iberian Peninsula) for wintering. The subspecies *E. s. lusitanica* is endemic to the Iberian Peninsula, while *E. s. witherbyi* is also found in southern France and in one wetland (Loukos) in Morocco. These subspecies are associated with wetlands (whereas *schoeniclus* inhabits a larger variety of habitats especially in northern parts of the distribution range) and consequently their distribution is fragmented. Both *witherbyi* and *lusitanica* have drastically declined in numbers and range since the 1970s, and the decline is still ongoing. For example, in 1995, the species was present in 74 Spanish wetlands, but 10 years later was found in only 35 wetlands. During 1995–2005, declines larger than 70% were estimated for some of the regions from where census data are available. Both subspecies are considered as "Endangered" accordingly to UICN criteria (Atienza and Copete, 2004). This rapid decline in numbers and increased fragmentation has possibly reduced the genetic variation of the populations compared to populations still thriving. Therefore, we specifically aimed to estimate the amount of genetic variation in order to find if it is reduced and to define conservation units for the Iberian populations based on population distinctiveness using genetic measures. These results are discussed in relation to the prospect of extinction of the populations, and suggestions for conservation management are given.

Material and methods

Laboratory protocols

Samples from Reed Buntings were collected during 1995–2008 from northern Finland, Spain, Morocco and Portugal. Most of the samples were collected during the breeding season, but those of the nominate subspecies *schoeniclus* from Spain were collected during winter and most of the samples from the delta of River Ebro during autumn, after the breeding season. In the autumn, both *schoeniclus* and *witherbyi* might co-occur in the delta of Ebro. Therefore, the subspecies was identified according to morphometric measures (for example, the bill of *witherbyi* is larger than the bill of *schoeniclus*; Byers et al., 1994). Samples were feather, blood (Spanish, Moroccan and Portuguese samples) or muscle tissue (Finnish samples). Iberian and Moroccan birds were released after measuring, ringing and sampling, for which the appropriate permits were obtained from the respective authorities. Finnish samples were obtained from tissue collections of Zoological Museum of University of Oulu. Sample sizes and locations are shown in Table 1 and Figure 1.

DNA was extracted from blood and muscle using the traditional phenol–chloroform extraction (Sambrook and Russell, 2001) and from feathers using the lysis method described in Kvist et al., (2003). Six microsatellites *Esc3, Esc4, Esc6* (Hanotte et al., 1994), *Hru6* (Primmer et al., 1995), *Pdo5* (Griffith et al., 1999) and *Pocc6* (Bensch et al., 1997) were amplified in 10 μL reaction volume containing 50–100 ng of template DNA, 0.4 μM of each primer, 0.1 mM of each dNTP, 1 μL of 109 PCR buffer and 0.06 units of DNA-polymerase (Biotools). The following PCR profile was used: 94 ºC

Table 1. Sampling sites and sizes of the Reed Buntings *Emberiza schoeniclus*

Subspecies	Year	Wetland	Locality	Region	*N* from wetland	*N* from region
schoeniclus	2005-2005	-	Oulu	Northern Finland	-	15
schoeniclus	2005-2006	Marjal Pego-Oliva	Oliva	Valencia, Spain	23	23
lusitanica	2006-2008	Carrizales del Ulla	Dodro	Galicia, Spain	13	23
lusitanica	2006-2008	Estuario del Miño	A Guarda	Galicia, Spain	4	
lusitanica	2006	Lestimoño	Ponteceso	Galicia, Spain	6	
lusitanica	2003-2008	Salreu	Salreu	Estarreja, Portugal	29	29
witherbyi	1995, 2006	Delta del Ebro	Delta del Ebro	Cataluña, Spain	11	11
witherbyi	2006-2007	Lagunas de Villafranca de los Caballeros	Villafranca de los Caballeros	Castilla La Mancha, Spain	12	34
witherbyi	2006-2007	Tablas de Daimiel	Daimiel	Castilla La Mancha, Spain	19	
witherbyi	2007	El Masegar	Quero	Castilla La Mancha, Spain	3	
witherbyi	2006-2007	Marjal Pego-Oliva	Oliva	Valencia, Spain	4	4
witherbyi	2006-2008	S'Albufera	Mallorca	Baleares, Spain	12	12
witherbyi	2008	Marismas de Loukos	Larache	Morocco	2	2

for 5 min followed by 35 cycles of 94 ºC for 30 s, annealing in 47–55 ºC for 30 s and 72 ºC for 30 s and a final extension in 72 ºC for 5 min. Annealing temperature for *Pocc6* was 53–55 ºC, for *Esc6, Hru6* and *Pdo5* 45–50 ºC, and for *Esc3* and *Esc4* a touch-down profile from 50 to 45 ºC was used. $MgCl_{2-}$ concentrations varied from 2.0 mM for *Hru6* to 2.5 mM for *Esc 6, Pdo5* and *Pocc6* and 3.0 mM for *Esc3* and *Esc4*. The PCR products were run on ABI 3730 and alleles were scored with Genemapper v.3.7.

Figure 1. Sampling sites of the Iberian Reed Bunting *Emberiza schoeniclus* subspecies

A fragment of the mitochondrial control region about 770 bp long was amplified with primers EmberizaL60 (50-CCCCAGCAACTTTTCTCCTG-30) and PasseriformesH830 (50-GAATGGGGTCAAAGTGCATCAG-30) using a PCR profile of 94 ºC for 5 min followed by 35 cycles of 94 ºC for 30 s, 54 ºC for 30 s and 72 ºC for 30 s and a final extension in 72 ºC for 5 min. The amplification was performed in a 25-ll reaction volume containing about 150 ng of template DNA, 2 lMof each primer, 0.2 mMof each dNTP, 2.5 ll of 109 PCR buffer (2 mM $MgCl_2$) and 0.15 units of DNA-polymerase (Biotools) or 0.25 units of Dynazyme (Finnzymes). Sequencing of the PCR-products was performed with the same primers used for initial amplification with BigDyeTM v.3.1 Dye Terminator Cycle Sequencing Kit (Applied Biosystems) according to the manufacturer's instructions and run with an ABI 3730 automatic sequencer.

Data analyses

Microsatellite data was checked for null-alleles and scoring errors using program Microchecker v.2.2.3 (von Oosterhout et al., 2004). Existence of genetically structured populations was first tested with program Structure v. 2.2 [with no a priori information of the sampling locations, using 10,000 as the length of burn-in periods and 100,000

MCMC replications, setting the number of populations (K) from 1 to 12 for two iterations and from 1 to 3 for additional two iterations, admixture model and correlated allele frequencies; Pritchard et al., 2000] and then by using Analysis of molecular variance (AMOVA) implemented in Arlequin v.3.11 (Excoffier et al., 1992). AMOVA was also used to find if there is genetic subdivision among the three subspecies studied by testing four different hierarchical structures; sampling sites were grouped into three groups according to defined subspecies and also each subspecies was combined with another into one group resulting in three possible combinations. Pairwise F_{ST} values between the sampling sites were calculated with Arlequin v.3.11, and the geographically close sites showing low and nonsignificant pairwise values were combined (one population for *lusitanica* and four for *witherbyi* corresponding to regions in Table 1). Assignment of each individual to the population of origin was also performed with Arlequin. Tests for linkage disequilibrium, Hardy–Weinberg equilibrium and calculation of F_{IS} were performed with Genepop v.4.0 (Raymond and Rousset, 1995) and observed and expected heterozygosities were calculated with Arlequin. Effective population sizes were estimated using the linkage disequilibrium method implemented in program Ne-estimator v.1.3 (Ovenden et al., 2007) for populations which had more than ten sampled individuals. Possible population bottlenecks were searched using the program Bottleneck v.1.2.02 (Cornuet and Luikart, 1996) and by calculating the Garza–Williamson index (M; Garza and Williamson, 2001) implemented in Arlequin. Of the three options for mutation model for the microsatellites in program Bottleneck, we used the infinite allele model and the two-phase model with 70% of stepwise mutations. This program tests whether the heterozygosity is larger than expected given the number of alleles detected in each loci and checks for a mode shift of allele frequency classes, which are both signs of a bottleneck. The Garza–Williamson index compares the number of alleles of a locus to the allelic range. As a consequence of a bottleneck, the number of alleles decrease faster than the allelic range, leading to M values lower than one.

Population structure of mitochondrial sequences was analyzed by calculating pairwise Φ_{ST} between the populations and performing the molecular variance analysis (AMOVA) as described for microsatellites. Φ_{ST} differs from F_{ST} by also taking into account genetic distances between haplotypes instead of only frequencies. Tamura–Nei's distance was used for these analyses, because it was the second best substitution model found by program MultiPhyl (Keane et al., 2007) after the HKY-model and included in program Arlequin (whereas HKY is not). Using the Tamura–Nei's distance instead of HKY is unlikely to influence the results, because the differences between the distance estimates are marginal. Nucleotide diversity, haplotype diversity and theta were estimated with DNAsp v.4.10 (Rozas and Rozas, 1999) for each population. Past changes in population size were studied by calculating Tajima's D, Fu's F and mismatch distributions as well as raggedness index and Ramos-Onsins and Rozas R2 statistics with program DNAsp. In addition, maximum likelihood estimates of the growth rates (g) for the populations were calculated with program Lamarc v.2.1.2 (Kuhner, 2006). This program estimates g based on exponential growth from $\theta_{(t)} = \theta_0 e^{-gt},$ where $\theta_{(t)}$ is θ

at time *t* in the past and θ_0 is θ at present so that a positive value of g represents a growing population, and a negative value a shrinking population. The program was run using the 'likelihood mode' with 10 short chains and 2 final chains, discarding 1,000 samples as burn-in and recording 10,000 genealogies. A parsimony network of the haplotypes was calculated with TCS (Clement et al., 2000).

Results

Microsatellites

Existence of possible null alleles was found in one locus (*Esc4*) in both the Finnish and the Spanish *schoeniclus* populations, in one locus (*Esc3*) in the Portuguese *lusitanica* population and in two loci (*Pocc*6 and *Esc3*) in the *witherbyi* population from Delta del Ebro. Otherwise, no evidence of scoring errors, stuttering or null-alleles was found. As these loci were not constantly suspect of having null-alleles across different populations, it is likely that they rather show excess of homozygotes from other reasons than null-alleles and therefore all loci were used for analyses. No linkage was detected when tested across all the populations. When linkage was tested for each population separately, it was found in three populations; in the Spanish *schoeniclus* population (*Pocc6* and *Hru6*), in the Spanish *lusitanica* population (*Esc4* and *Hru6*) and in the *witherbyi* population from Ebro (*Esc4* and *Hru6*).

Program Structure could not distinguish the populations or subspecies [$K = 1$, LnP = -3,232.4 to -3,233.5, $var(LnP)$ = 43.0–43.9, second best was for $K = 2$, LnP = -3,252.3 to -3,260.4, $var(LnP)$ = 293.5–322.6]. Pairwise F_{ST} values between sampling sites were low and nonsignificant between sampling sites of *schoeniclus* (F_{ST} = -0.0078) and *lusitanica* (F_{ST} = 0.00826) and between geographically close *witherbyi* populations from Villafranca (El Masegar included) and Daimiel (F_{ST} = 0.00878). These sampling sites were therefore combined in further analyses as *schoeniclus* (including sampling sites in Finland and Spain), *lusitanica* (sampling sites in Spain and Portugal), and Castilla La Mancha (including sampling sites of *witherbyi*, Villafranca, El Masegar and Daimiel in Spain). For these combined populations, pairwise F_{ST} values (Table 2) were significant in all other comparisons except between *lusitanica* and *schoeniclus* and between the Mallorcan *witherbyi* population and other populations. The sample size from Marjal Pego-Oliva was small (n = 4; the population is now probably extinct), so the results concerning this population should be treated cautiously. Morocco was excluded from calculations of F_{ST} due to the small sample size. F_{ST} values estimated between the subspecies pairs were all significant, though relatively small (*schoeniclus–witherbyi*: 0.03381, *schoeniclus–lusitanica*: 0.02285 and *lusitanica–witherbyi*: 0.04288, all P-values < 0.05). Now, the pairwise F_{ST} value between *schoeniclus* and *lusitanica* also became significant when *witherbyi* populations were grouped into subspecies. Results of molecular variance analyses using four different kinds of hierarchies are shown in Table 3. The analyses revealed that 2.68% of the total variance occurred between groups ($P < 0.05$) when the groups were formed according to subspecies. Also, when *schoeniclus* and *lusitanica* were combined into one group, the variance between groups was almost as high (2.55 %, $P < 0.05$). This is also supported by the pairwise F_{ST} values (Table 2).

Table 2. Pairwise F_{ST} values from microsatellite data

	E. s. schoeniclus	*E. s .lusitanica*	*E. s. witherbyi* Ebro	*E. s. witherbyi* Castila La Mancha	*E. s. wtherbyi* Marjal Pego-Oliva
E. s. lusitanica	0.02285				
E. s. witherbyi Ebro	**0.03335**	**0.04644**			
E. s. witherbyi Castila La Mancha	**0.04458**	**0.05859**	**0.03806**		
E. s. wtherbyi Marjal Pego-Oliva	**0.09214**	**0.10788**	**0.09113**	**0.09564**	
E. s. witherbyi Mallorca	0.00211	0.00882	-0.01530	0.00464	0.03027

Values in bold are significant at $P < 0.05$

Table 3. AMOVA results

Marker	Hierarchy	Variance components	Percentage of variation	P	F_{ST}
Microsatellites	3 groups: *schoeniclus, lusitanica* and *witherbyi,* and 9 samplig sites	Among groups	2.68	0.0059	0.0433
		Among sites within groups	1.65	< 0.001	
		Within sites	95.67	< 0.001	
	2 groups: *schoeniclus* and *lusitanica* combined, and 9 samplig sites	Among groups	2.55	0.0117	0.0484
		Among sites within groups	2.28	< 0.001	
		Within sites	95.17	< 0.001	
	2 groups: *schoeniclus* and *witherbyi* combined, and 9 samplig sites	Among groups	1.52	0.175	0.0443
		Among sites within groups	2.91	< 0.001	
		Within sites	95.57	< 0.001	
	2 groups: *lusitanica* and *witerhbyi* combined, and 9 samplig sites	Among groups	0.66	0.3851	0.041
		Among sites within groups	3.44	< 0.001	
		Within sites	95.9	< 0.001	
mtDNA	3 groups: *schoeniclus, lusitanica* and *witherbyi,* and 9 samplig sites	Among groups	3.11	0.1701	0.1399
		Among sites within groups	10.89	0.0449	
		Within sites	86.01	< 0.001	
	2 groups: *schoeniclus* and *lusitanica* combined, and 9 samplig sites	Among groups	6.92	0.0176	0.1628
		Among sites within groups	9.36	0.001	
		Within sites	83.73	< 0.001	
	2 groups: *schoeniclus* and *witherbyi* combined, and 9 samplig sites	Among groups	1.03	0.2659	0.1378
		Among sites within groups	12.77	< 0.001	
		Within sites	86.2	< 0.001	
	2 groups: *lusitanica* and *witerhbyi* combined, and 9 samplig sites	Among groups	-2.96	0.5621	0.1209
		Among sites within groups	15.5	< 0.001	
		Within sites	87.91	< 0.001	

Sampling sites: *E. s. schoeniclus* Finland, *E. s. schoeniclus* Spain, *E. s. lusitanica* Portugal, *E. s. lusitanica* Spain, *E. s. witherbyi* Delta del Ebro, *E. s. witherbyi* Castilla La Mancha, *E. s. witherbyi* Marjal Pego-Oliva, *E. s. witherbyi* Mallorca, *E. s. witherbyi* Morocco.

The lowest heterozygosity values were found in *lusitanica* populations (*He* = 0.6543 and 0.6781) and in *witherbyi* populations from Marjal Pego-Oliva and Mallorca (*He* = 0.5631 and 0.6865, respectively), while highest values (He = 0.7553 and 0.7602) were found a little surprisingly in *witherbyi* populations from Delta del Ebro and Castilla La Mancha (Table 4). Allele richness was the highest in *schoeniclus* (11.786) and the lowest in *lusitanica* (10.290). The value from *witherbyi* was close to that of *schoeniclus* (11.758). Differences between these values were non-significant (t tests: *schoeniclus–lusitanica*, *P* = 0.102, *schoeniclus–witherbyi P* = 0.493, *witherbyi–lusitanica P* = 0.073). Estimates of the effective population sizes using the linkage-disequilibrium-based method show the largest population sizes (87 and 133) for Spanish and Finnish *schoeniclus*, respectively, smaller estimates (21 and 53) for *witherbyi* (Delta del Ebro and Castilla La Mancha) and the smallest estimates (11 and 13) for Portuguese and Spanish *lusitanica* (Table 4). Program Bottleneck found no signs of a bottleneck in any of the populations (Wilcoxon test $P >$ 0.05, no mode shifts), but the *M* ratio varied from 0.53 to 0.88. A ratio < 0.68 can, according to Garza and Williamson (2001), be assumed to indicate a reduction in size in any population analyzed for more than seven loci. With the six loci we analyzed, M ratios were less than 0.68 in two *witherbyi* populations, Marjal Pego-Oliva and Mallorca (0.58 and 0.53, respectively). However, the sample sizes from these populations are small, which might affect the ratios. The ratios from Spanish *lusitanica* and *witherbyi* from Ebro were just slightly higher (0.682 and 0.685). Here again, these values need to be considered with some caution, because in addition to small sample sizes, the number of loci is smaller than used by Garza and Williamson (2001). Assignment test classified almost all the individuals correctly to the population of origin. There were only seven exceptions, two individuals from the Spanish *schoeniclus* population were assigned to the Finnish *schoeniclus*, one bird from Spanish *lusitanica* was assigned to the Portuguese *lusitanica* population, one to the Spanish *schoeniclus*, one bird from the Portuguese *lusitanica* was assigned to the Spanish *schoeniclus* population, and one individual from Castilla La Mancha was assigned to the Spanish *lusitanica* and one to the Portuguese *lusitanica*. All samples from Delta del Ebro, which were collected during autumn when overwintering individuals from northern populations of *schoeniclus* might have occurred at this site, were assigned to Ebro, so we concluded that this population sample is not likely to include misidentified individuals from *schoeniclus*.

Mitochondrial control region sequences

The 745-bp-long alignment of the total of 125 sequences (GenBank accession numbers FJ794476–FJ794600) included 41 segregating nucleotide sites resulting in 38 haplotypes (haplotype diversity was 0.778). There were no double-peaks and no systematic differences that could be related to the tissue from which DNA was isolated, thus supporting the mitochondrial origin of the sequences. In addition, all obtained sequences overlapped in the central region and many were sequenced completely from both strands. Of the 36 sequences from *schoeniclus*, 23 haplotypes were found: in *lusitanica* there were only 5 haplotypes out of 48 sequences and in *witherbyi* 13 out of 41 sequences. One common haplotype (Es1; Fig. 2) was found from 56 individuals and it was represented in all three subspecies. The

Table 4. Polymorphism measures from the study populations.

	n	*Ho*	*He*	F_{IS}	N_e *(95 % CI)*	*n/#hapl*	π	θ	$\hat{h}$	Fu's F	Tajima's D
E. s. schoeniclus	38	0.6655	0.6923	0.0412	-	36/21	0.00306	0.871	0.871	-26.7609 $P < 0.001$	-2.1842 $P < 0.001$
Finland	15	0.6667	0.6778	0.0170	132.8 (43-inf)	14/10	0.00423	0.890	0.890	-14.0699 $P < 0.001$	-1.9079 $P < 0.001$
Spain	23	0.6625	0.7037	0.0607	87 (43-1097)	22/14	0.00234	0.874	0.874	-27.3521 $P < 0.001$	-2.1224 $P < 0.001$
E. s. lusitanica	52	0.6632	0.6850	0.0222	-	48/5	0.00060	0.330	0.330	- inf $P < 0.001$	-1.7474 $P < 0.001$
Spain	23	0.6006	0.6543	0.0445	13.4 (1-19)	21/2	0.00013	0.095	0.095	- inf $P < 0.001$	-1.1636 $P = NS$
Portugal	29	0.6951	0.6781	-0.0242	10.9 (9-13)	27/5	0.00095	0.484	0.484	-inf $P < 0.001$	-1.6435 $P < 0.001$
E. s. witherbyi	57	0.7028	0.7584	0.0751	-	41/13	0.00312	0.866	0.866	-26.8519 $P < 0.001$	-1.2745 $P = NS$
Ebro	11	0.6368	0.7553	0.1688	20.6 (11-99)	6/4	0.00314	0.867	0.867	-4.0049 $P < 0.001$	0.1965 $P = NS$
Castilla La Mancha	31	0.7398	0.7602	0.0288	53.4 (34-110)	21/9	0.00236	0.829	0.829	-27.462 $P < 0.001$	-1.3347 $P = NS$
Marjal Pego-Oliva	4	0.5972	0.5631	-0.0685	-	4/3	0.00439	0.833	0.833	-1.1571 $P = NS$	-0.1345 $P = NS$
Mallorca	9	0.6865	0.6604	-0.0491	-	8/3	0.00331	0.679	0.679	-6.5008 $P < 0.001$	1.0923 $P = NS$

From left to right: sample sizes used in microsatellite analyses (*n*), observed and expected heterozygosities (*Ho, He*), inbreeding coefficient (F_{IS}), Ne estimates using linkage disequilibrium method (95% confidence interval), sample sizes and haplotype numbers from mitochondrial data (n/#hapl), nucleotide diversity (π), number of segregating sites (θ) haplotype diversity ($\hat{h}$), Fu's F and Tajima's D and their significance.

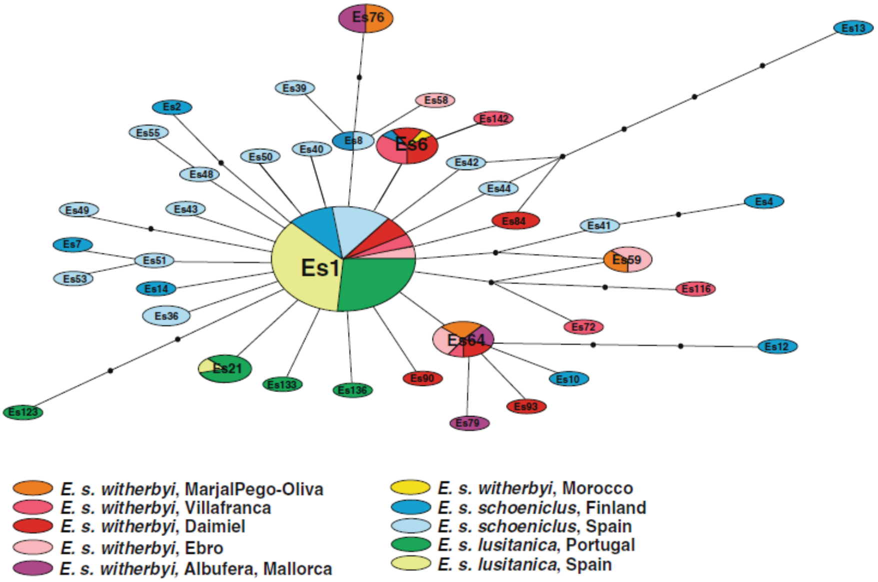

Figure 2. Parsimony network from the mitochondrial control region sequences. Sizes of the *circles* are proportional to the number of haplotypes found and *shadings* infer the origins of the individuals possessing the haplotypes. Each *connecting bar* represents one substitution.

other eight haplotypes (Es6, Es8, Es21, Es36, Es59, Es64, Es76 and Es84; Fig. 2) were shared between two or more individuals and the remaining haplotypes were found only in one individual each (Fig. 2; Appendix A). The parameters describing polymorphism within the subspecies (Table 4) showed low diversity in *lusitanica* and relatively high in *schoeniclus* and *witherbyi*. Theta was the highest in *schoeniclus* (0.00835), medium in *witherbyi* (0.00525) and the lowest in *lusitanica* (0.00188). *Witherbyi* and *schoeniclus* had high nucleotide diversities (0.00312 and 0.00306, respectively), while it was low in *lusitanica* (0.00060). The nucleotide diversity in *lusitanica* was statistically highly different from that of *schoeniclus* and *witherbyi* (both t tests resulted in $P < 0.0001$).

Pairwise Φ_{ST} values estimated between the subspecies pairs were again all significant (*schoeniclus*–*witherbyi* = 0.05331, *schoeniclus*–*lusitanica* = 0.04318 and *lusitanica*–*witherbyi* = 0.13968, all *P* values < 0.05). Estimates between *schoeniclus* and the two other subspecies were quite small, but the estimate between *witherbyi* and *lusitanica* was relatively large. There was no differentiation between sampling sites of *schoeniclus* (Φ_{ST} = -0.00527, *NS*) and *lusitanica* (Φ_{ST} = -0.01437, *NS*). Also, no differentiation was detected between *witherbyi* samples from Villafranca and Daimiel (Φ_{ST} = 0.00173, *NS*). Therefore, these sampling sites were combined as was done with microsatellite data into *schoeniclus*, *lusitanica* and *witherbyi* of Castilla La Mancha (we did not succeed in sequencing any samples from El Masegar, the third sampling site from this area). The Castilla La Mancha population differed significantly from the other *witherbyi* populations. In addition, significant differentiation was found between populations from Mallorca and Delta del Ebro and between populations from Marjal Pego-Oliva and Mallorca and Delta del Ebro (Table 5). The population of Marjal Pego-Oliva is represented by just four samples and therefore the pairwise Φ_{ST} -values do not necessarily reliably represent the true values. Morocco is again excluded from estimating the pairwise Φ_{ST} s. Hierarchical AMOVA showed that the among group variance was the largest and significant when the grouping was formed based on the three subspecies or by grouping *schoeniclus* and *lusitanica* (Table 3), i.e. *witherbyi* is differentiated from the two other subspecies (though variance among sampling sites is higher than among groups). Also, differentiation between *lusitanica* and *schoeniclus* is supported especially by the pairwise Φ_{ST}-values.

Mismatch distributions from all the sequences combined followed closely the expected distribution for 'recent' population growth/decline. θ initial (θ before the population size change) and τ (time of the size change in mutational time $2ut$, where u is the mutation rate and t is time in generations) describing the shape and mean of the distribution were 0.671 and 0.956, respectively (0.969 and 1.239 for *schoeniclus*, 0.360 and 0.072 for *lusitanica* and 0.000 and 2.251 for *witherbyi*). θ final was 1,000 for all. Raggedness statistics was 0.0384 ($P = 0.058$) and Ramos-Onsins and Rozas R2 statistics 0.0201 ($P < 0.001$) for the combined set of sequences. The mismatch distributions and diversity values of the subspecies compared to each other and to the combined values show that the peak of the mismatch distribution and all the diversity values are clearly the lowest in *lusitanica*, especially in the Spanish population, indicating a loss of haplotypes and diversity. Growth rates (g) estimated with program Lamarc were very large for *schoeniclus* (2,315, with 95 % CI of 1,727–2,879), large also for *witherbyi* (819; 95 % CI 521–1,086) and negative for *lusitanica* (-1,413; 95 % CI -2,408 to -684).

Table 5. Pairwise Φ_{ST} -values from mitochondrial sequence data.

	E. s. schoeniclus	*E. s .lusitanica*	*E. s. witherbyi* Ebro	*E. s. witherbyi* Castilla La Mancha	*E. s. wtherbyi* Marjal Pego-Oliva
E. s. lusitanica	**0.04318**				
E. s. witherbyi Ebro	0.04669	**0.3637**			
E. s. witherbyi Castila La Mancha	**0.08165**	**0.2168**	**0.1299**		
E. s. wtherbyi Marjal Pego-Oliva	0.05345	**0.4545**	-0.1510	**0.1465**	
E. s. witherbyi Mallorca	**0.19073**	**0.5365**	**0.1250**	**0.2778**	-0.1236

Values in bold are significant at $P < 0.05$

Discussion

Diversity within populations

Mitochondrial DNA sequences showed that genetic diversity was significantly reduced in the Iberian subspecies of the Reed Bunting, *E. schoeniclus lusitanica*. Some indications of reduction in diversity could also be seen in microsatellites (allelic richness was the lowest), but this was not significant. Furthermore, the Spanish *lusitanica* population had reduced heterozygosity values and both the Portuguese and Spanish populations had extremely low effective population sizes (N_e 10.9 and 13.4, respectively). The differences in the magnitude of the reduction in genetic diversity in the two marker systems are likely due to the different effective population sizes of the markers. The decrease of the census population sizes has affected the mitochondrial sequence diversity faster, because the effective size and therefore also the coalescent time of mitochondrial markers is only one-quarter of the nuclear markers, and thus the genetic drift may act four times more strongly, rapidly removing rare haplotypes from the small populations. Usually, the extremely fast mutation rate of the microsatellite markers is thought to result in easier detection of very recent demographic events than would be possible with mitochondrial markers (see Zink and Barrowclough, 2008). But in our study, especially in the case of the *lusitanica* populations, drift has reduced much more variation in mitochondrial markers than in microsatellites.

The Iberian subspecies *witherbyi*, on the other hand, did not show as strong a reduction of genetic diversity as expected based on the rapid decrease of the census sizes. The three populations with adequate sample sizes (Delta del Ebro, Castilla La Mancha and Mallorca) had mitocondrial nucleotide diversity and nuclear heterozygosity values that were at the same level as in the nominate *schoeniclus* populations, even though for Delta del Ebro and Mallorca the decline of the population has been above 70 % in the last decade (no census data available for Castilla La Mancha but the population is probably more or less stable). Only the number of alleles and the allelic richness in four of the six studied microsatellite loci (*Esc3, Esc4, Esc6* and *Pdo5*; Appendix B), haplotype diversities and theta values were slightly lowered. It is possible that the decline is still so recent that drift has only just begun to reduce the number of rare haplotypes and alleles, but this is not yet detectable by different bottleneck tests or diversity values. In the case of the Castilla La Mancha population, it is also possible that even though *F* statistics did not find differences between the sampling sites within this area, we had sampled individuals from distinct populations, which might have increased the genetic variation via Wahlund's effect. Some additional evidence of decreased census size affecting genetic patterns in *witherbyi* was obtained from low Garza–Williamson indexes (Delta del Ebro and Mallorca populations) and relatively small effective population sizes (20.6 for Delta del Ebro and 53.4 for Castilla La Mancha).

Overall, the heterozygosity values were somewhat lower than previously reported in a study by Matessi (1999), where four loci were used (three of those were same as here). One of our study populations, the Delta del Ebro population, was also included in Matessi (1999), and then the observed and expected heterozygosities for that population were 0.781 and 0.823, respectively (n = 16). It is possible that heterozygosity has decreased during the years between the sampling for Matessi's and for our study. Our first sampling period from this population was in 1995, and including only those individuals resulted in slightly higher value of expected heterozygosity (0.7874), which anyhow was still lower than the value obtained by Matessi (1999). It is therefore more likely that our values were in general lower due to the marker set used or small sample size. In a Swiss population, belonging to the nominate subspecies, heterozygosity in 11 autosomal microsatellite loci varied from 0.756 to 0.933 (n = 45; Mayer et al., 2008).

Differentiation of subspecies and populations

The number of subspecies in the Reed Bunting varies from 30 to 15 depending on authors, and these subspecies are grouped into two to four groups (Byers et al., 1994; Cramp and Perrins, 1994). The subspecies are designated largely based on bill size and plumage color. Genetic differentiation between the subspecies groups, subspecies or populations of the Reed Bunting has not been studied in detail and only a couple of subspecies have been included in published studies. Graputto et al., (1998) have shown that subspecies *intermedia* of southern, thick-billed *pyrrhuloides*- group and *schoeniclus* of the northern thin-billed *schoeniclus*-group are slightly genetically differentiated in nuclear loci (F_{ST} from four microsatellite loci was 0.0444), but not in mitochondrial DNA. Our microsatellite data resulted in very similar F_{ST} values (0.0229–0.0429) between the subspecies, but also showed significant differentiation with mitochondrial data (pairwise Φ_{ST} values 0.0432–0.1397). This difference may be explained by the highly variable mitochondrial control region sequences used here, which are more suitable for detection of genetic structures within species than the more conservative mitochondrial cytochrome b and ND5 sequences used by Graputto et al., (1998). Also, hierarchical molecular variance analyses from both marker sets supported some genetic differentiation between the three subspecies.

Genetic differentiation among populations within subspecies was not evident in *schoeniclus* or *lusitanica*, whereas among populations of *witherbyi*, the differentiation was surprisingly large in many cases. Within *witherbyi*, pairwise F_{ST} values were high and significant (range 0.0381–0.1402) between all populations except comparisons to Mallorca. In addition, Φ_{ST} values were significant (range 0.1299–0.2861) in all except some comparisons involving Marjal Pego-Oliva, which could be just due to the small sample size. Notably, many of the values within *witherbyi* were much higher than values estimated between subspecies. Even though the sample sizes were not large for some of the populations, it seems that the *witherbyi* populations are more differentiated from each other than *lusitanica* populations or the migrant *schoeniclus* populations. Unfortunately, estimates of pairwise population differentiation presented by Graputto et al., (1998) and Matessi (1999) were calculated using co-ancestry coefficients or Nei's genetic distances, and cannot be directly compared with our results. However, estimates of F_{ST} were given among populations of *schoeniclus* (0.0361) and among populations of intermedia (0.0277), which are clearly higher than our estimates for *schoeniclus* and *lusitanica*, but much lower than our estimates for *witherbyi*.

The difference in the magnitude of genetic structure reflects the different amounts of gene flow among populations within the subspecies. Both *lusitanica* and *witherbyi* have inhabited a larger number of wetlands in the past, but now have gone extinct especially from small wetlands. It is possible that in *lusitanica* the gene flow, i.e. dispersal between the fragmented habitats, is more effective, aiding recolonizations after local extinctions (following more or less the metapopulation model). On the other hand, the geographical distances between populations of *lusitanica* are shorter than distances between populations of *witherbyi* because the current distribution area of *lusitanica* is much smaller than that of *witherbyi*. This might be the reason why gene flow seems to be more effective in *lusitanica*. In any case, differentiation between populations of *witherbyi* is stronger than in *lusitanica*, suggesting low amounts of gene flow. Unfortunately, this might indicate that the now extinct populations are lost for good.

Implications for conservation

Habitat loss was probably the main cause of decline in the 1970s and 1980s. However, already in the last decade, most of the populations were located within protected areas and therefore the loss of wetlands cannot account for the continuing decline. Belda et al., (2008) suggested that changes associated to reed and water management in wetlands are also an important cause for the decline of the species. Traditional activities, such as grazing, cutting, etc., have been abandoned or banned in these protected areas, and the decline or extinction of the Reed Bunting in these areas has been recorded as following those changes in management (unpublished data). Most of the management practices have been devoted to favor other species, such as endangered ducks or egrets, without knowing how the consequences affect other bird species, such as several endangered passerines like the species studied here. Therefore, there is an urgent need to undertake studies on habitat requirements of *lusitanica* and *witherbyi* and to understand how reed management affects demographic parameters. As for now, it could be a promising idea to allow or even encourage the traditional use of the wetlands, at least in some parts, in order to get a more diverse habitat, which would fulfill the requirements for a variety of species.

In the light of the estimated genetic differentiation, there are no evolutionary significant units in Iberian Reed Buntings, but we suggest several management units for their populations. One unit includes subspecies *lusitanica* as a whole. *Lusitanica* is differentiated from other subspecies, has reduced genetic variation especially in mitochondrial markers, a drastically small effective population size, and a negative growth rate. The Salreu population in Portugal is presently estimated to be around 350–400 breeding pairs, while for Galicia, Spain, the estimate is around 50–60 breeding pairs, distributed in 14–15 wetlands. Given that there is no differentiation between populations and some of the populations hold only a few breeding pairs, it is quite likely that those small populations receive immigrants from the 'large' Salreu population and possibly also from other smaller populations. If this is the case, the most important genetic conservation measure would be to increase or at least maintain the present levels of gene flow. To achieve this aim, the remaining habitat network needs to be preserved.

Other suggested management units are *witherbyi* populations from Delta del Ebro, Castilla La Mancha and Mallorca. These populations show some genetic differentiation in one or both markers and therefore are likely to hold variation not present in other *witherbyi* populations. The population from Marjal Pego-Oliva also fulfils these criteria, but in this case the sample size is too low to make any suggestions (and the population might actually be already extinct). Even with a moderate amount of gene flow in general, recolonizations of small and geographically isolated habitats located far from each other are highly unlikely. At present, the remaining census sizes for Castilla La Mancha (in Daimiel about 100 pairs) and Delta del Ebro (50–100 pairs) are already alarmingly low. The most urgent conservation measures should therefore be guided to maintain these two mainland populations in addition to the even more threatened population in Mallorca. The only way to do this is to offer enough proper habitats to help to increase the population sizes. In other words, there is an uttermost need to understand the habitat requirements and demography of the endangered Iberian subspecies before it is too late.

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Appendix A. Haplotype distribution

Haplotype	Population									
	schF	schS	lusS	lusP	witEb	witVFr	witDa	witMPO	witMa	witMo
Es1	5	7	20	19	1	1	3			
Es2	1									
Es4	1									
Es7	1									
Es8	1	1								
Es10	1									
Es12	1									
Es13	1									
Es14	1									
Es36		2								
Es39		1								
Es40		1								
Es41		1								
Es42		1								
Es43		1								
Es44		1								
Es48		1								
Es49		1								
Es50		1								
Es51		1								
Es53		1								
Es55		1								
Es21			1	5						
Es123				1						
Es133				1						
Es136				1						
Es58					1					
Es59					2			4		
Es64					2	1	1	2	4	
Es6						3	5			2
Es72						1				
Es116						1				
Es142						1				

Haplotype	Population									
	schF	schS	lusS	lusP	witEb	witVFr	witDa	witMPO	witMa	witMo
Es76								1	3	
Es79									1	
Es84							2			
Es90							1			
Es93							1			
Total	14	22	21	27	6	8	13	4	8	2

Abbreviations for population names: schF = *E. s. schoeniclus,* Finland, schS = *E. s. schoeniclus* Spain, lusS = *E. s. lusitanica*, Spain, lusP = *E. s. lusitanica*, Portugal, witEb = *E. s. witherbyi*, Delta del Ebro, witVFr = *E. s. witherbyi*, Villafranca, Castilla La Mancha, witDa = *E. s. witherbyi* Daimiel, Castilla la Manca, witMPO = *E. s. witherbyi*, Marjal Pego-Oliva, witMa = *E. s. witherbyi,* Mallorca, witMo = *E. s. witherbyi,* Morocco.

Appendix B. Number of alleles (#A) and allelic richness (R) for each locus and study population.

Locus	Poplation																			
	schF		schS		lusS		lusP		witEb		witVFr		witDa		witMPO		witMa		witMo	
	#A	R	#A	R	#A	R	#A	R	#A	R	#A	R	#A	R	#A	R	#A	R	#A	R
Escmu3	13	1.913	14	1.930	7	1.782	9	1.780	9	1.895	7	1.804	12	1.850	3	1.600	7	1.894	2	1.667
Escmu4	14	1.924	13	1.910	15	1.888	11	1.890	9	1.908	8	1.900	12	1.900	3	1.679	7	1.909	3	1.833
Escmu6	9	1.841	11	1.869	6	1.754	10	1872	6	1.817	6	1.850	7	1.803	3	1.600	5	1.703	2	1.667
.Pdo5	17	1.952	19	1.947	14	1.845	16	1.917	10	1.918	8	1.908	13	1.85	4	1.786	8	1.894	2	1.667
Pocc6	2	1.370	2	1.359	4	1.418	4	1.572	4	1.592	5	1.549	5	1.346	3	1.464	2	1.167	2	2.000
HrU6	2	1.067	5	1.207	4	1.241	2	1.037	4	1.403	5	1.621	7	1.677	2	1.250	4	1.396	2	1.667
Total	57	1.678	64	1.704	50	1.655	52	1.678	42	1.756	39	1.772	56	1.744	18	1.563	33	1.661	13	1.750

Abbreviations for population names: schF = *E. s. schoeniclus,* Finland, schS = *E. s. schoeniclus* Spain, lusS = *E. s. lusitanica*, Spain, lusP = *E. s. lusitanica*, Portugal, witEb = *E. s. witherbyi*, Delta del Ebro, witVFr = *E. s. witherbyi*, Villafranca, Castilla La Mancha, witDa = *E. s. witherbyi* Daimiel, Castilla la Manca, witMPO = *E. s. witherbyi*, Marjal Pego-Oliva, witMa = *E. s. witherbyi,* Mallorca, witMo = *E. s. witherbyi,* Morocco.

Capítulo II

Estimating past and future population trends in Spain of endangered Eastern Iberian reed bunting *Emberiza schoeniclus witherbyi*

Pablo Vera · Marcial Marín · Juan S. Monrós · Eduardo J. Belda

En revisión

ESTIMATING PAST AND FUTURE POPULATION TRENDS IN SPAIN OF ENDANGERED EASTERN IBERIAN REED BUNTING *EMBERIZA SCHOENICLUS WITHERBYI*

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Abstract

Estimates of occupancy (proportion of an area occupied by a species or fraction of landscape units where the species is present) based on presence –absence data may be used to monitor population trends. This approach is especially useful when dealing with rare species with fragmented distribution such as the Eastern Iberian Reed Bunting, with a recently estimated population of 122-136 breeding pairs in Spain. We used estimates of occupancy to: i) monitor population trends in the past (2002-2015) using published presence-absence data in the 10 x 10 km UTM squares and conduct a population viability analysis of the endangered population of the Eastern Iberian Reed Bunting, and *ii*) monitor the main breeding population of the Eastern Iberian Reed Bunting in Spain between 2006 and 2009. The probability that an area that was occupied in a previous period was also occupied in the next period was 0.891 ± 0.056 for the period 2002-2005 and 0.942 ± 0.031 for the period 2005-2015 with a probability of detection ranging from 0.709 ± 0.089 to 0.823 ± 0.051. The annual growth rate was 0.929 ± 0.054 (95 % CI 0.726-0.984) for 2002-2005 and 0.942 ± 0.031 (95 % CI 0.842-0.980) for 2005-2015. Probability of a decline greater than 80 % in a 25-year projection was 0.886, and probability of a decline greater than 90 % in a 50-year projection was 1. In Tablas de Daimiel, the main breeding population, proportion of territories occupied declined from 2006 to 2009 from 71 % to 17 %. Between 2006 and 2008 (the only period that was possible to analyse), growth rate was of 0.568 ± 0.294. The study shows the utility of the use of presence absence data to monitor rare species. Approval of Eastern Iberian Reed Bunting Conservation Plan at national level and management actions need to be taken urgently to assure the conservation of this Reed Bunting endemic subspecies in the short term.

Keywords: occupancy, detection probability, growth rate

Introduction

Monitoring population trends is a required tool in management programs of endangered species. Nonetheless, and especially when dealing with rare species, this is a challenging task. Abundance has been widely used in conservation programs of endangered species. Nonetheless, abundance is a parameter that it is both difficult and costly to estimate. In addition, abundance estimation has serious problems when wide ranges are covered for relative scarce and fragmented species. In these cases, a different approach is required to monitor these type of species. Alternatively, the use of occupancy (proportion of an area occupied by a species or fraction of landscape units where the species is present) based on presence–absence data may be used to monitor population trends (Joseph et al., 2006, MacKenzie et al., 2006). This type of metrics (estimates of occupancy) has been widely applied in ecology to studies of species occurrence, range and distribution (Engler et al., 2004), habitat selection and modelling (Gu and Swihart, 2004, Kéry et al., 2010, Gormley et al., 2011), metapopulation studies (Hanski, 1999, Moilanen, 2002), and monitoring programs (Trenham et al., 2003, Rhodes et al., 2006).

The problem when using occupancy studies is that the species may stay undetected even if the species is present (false absence). The imperfect detection of a species may lead to underestimate the true level of occupancy (Moilanen, 2002, Gu and Swihart, 2004, Wintle et al., 2005). This implies that the probability of detection and its possible variation needs to be considered, in order to obtain unbiased estimation of occupancy and make reliable, informed management decisions (MacKenzie, 2005). Thus, field studies should be designed to minimize false absences (e.g. Moilanen, 2002). MacKenzie et al., (2002) proposed a likelihood-based method for estimating site occupancy rates when detection probabilities are < 1, allowing obtaining unbiased estimates of occupancy (ψ). By introducing two additional parameters representing the processes of colonization (γ) and local extinction (ε) it is possible to model changes in multiple seasons (MacKenzie et al., 2003). This modeling framework developed is more flexible than others (see for example Barbraud et al., 2003) and allow estimating not only occupancy, but also rates of change, and estimates of colonization and extinction (see MacKenzie et al., 2006).

Similarly, to monitor the trend of a species in a wetland as described above, we can use the data of presence of a species in several wetlands and years to monitor the trends of the population over time. In this approach, we may treat the data to estimate survival of the population as in classical capture-recapture models for open populations using the Cormack-Jolly-Seber approach (Lebreton et al., 1992). This may allow us to estimate survival of populations. Pradel (1992) proposed an approach to estimate realised population growth rate using capture recapture data for open populations through estimating apparent survival. In a classical survival estimation, the parameter includes both survival and fidelity to the area (we cannot estimate emigration on the individuals to other areas). When the parameter estimated is apparent survival of the population, the estimated parameter includes both survival and recolonization of the area.

In this study, we used the available data for the Eastern Iberian Reed Bunting to estimate occupancy, apparent survival and realised population growth rate in order to monitor population trends in the past and conduct a population viability analysis of the Spanish population. The Reed Bunting is a widely distributed Palaearctic passerine, common in most of its distribution range. In the Iberian Peninsula, two subspecies of Reed Bunting have been described, the Western Iberian Reed Bunting *E. s. lusitanica* in north-west and the Eastern Iberian Reed Bunting *E. s. witherbyi* in the south-east. *E. s. witherbyi* breeds only in Spain, Southern France and in Morocco with an estimated population in 2005 of 254-360 pairs (Atienza, 2006) but only 122-136 in 2015 (Monrós et al., 2017). Both *witherbyi* and *lusitanica* subspecies are considered as “Endangered” according to IUCN criteria (Madroño et al., 2004) and are included with this category in the Spanish List of Endangered Species (Catálogo Español de Especies Amenazadas, Real Decreto 139/2011). Thus, studies of occupancy may relay very valuable information about its population trends. Complementarily, we conducted a preliminary study to monitor its breeding population in the Tablas de Daimiel National Park, one of the main breeding population in Spain.

Material and methods

Monitoring population trends

We collect the presence data published in the breeding atlas in 2002 (Martí and del Moral, 2003), first national survey in 2005 (Atienza, 2006) and second national survey in 2015 (Monrós et al., 2017). Considering data from these atlases together, we had three issues to solve always a following conservative position (the null hypothesis is that there are no population changes between years):

a) In 2002 atlas are considered different categories for certainty of reproduction. We only considered 10 x 10 km UTM squares with probable/reliable reproduction.

b) The 2002 atlas covered several years (1998-2002, respectively). As a conservative approach, we considered the Eastern Iberian Reed Bunting as breeder in 2002 if it was present as a breeder in a square between 1998 and 2002.

c) The 2002 atlas occasionally considered data collected between 1985 and 1997 from observations registered in regional atlas and regional ornithological yearbooks, meaning a partial overlap between the data of both atlases. For the grids with probable/reliable reproduction obtained with regional atlas and yearbooks, we checked the references and removed all the data taken previously to the atlas fieldwork.

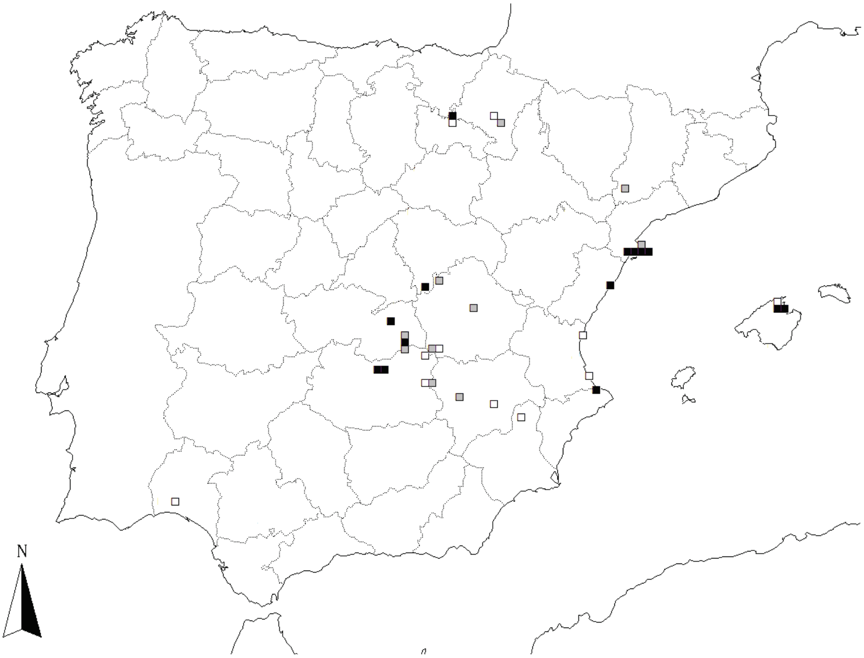

Figure 1. Wetlands (10 x 10 UTM squares) with historic presence of the Iberian Reed Bunting. Open squares represent areas where the species was present as a breeder in 2002 but not afterwards. Grey squares represent areas with Reed Bunting as a breeder by 2005 but not in 2015, and black squares represent areas where Reed Bunting was breeding in 2015.

Thus, a total of 34 squares were considered (Figure 1). For each of these 10 x 10 squares, we generated capture-recapture histories based on the presence/absence data that were of the type *hi* = 1 1 0 (i.e. the species was detected in 2002 and in 2005, but detected in 2015). This data was used to estimate realised population growth rate (λ) following Pradel (1996).

Occupancy, growth rate and extinction estimation

A monitoring program of the Eastern Iberian Reed Bunting in "Tablas de Daimiel National Park" was carried out from 2007 to 2009. We sampled 30 randomly selected points (Figure 2). In 2006 11 points were sampled and from 2007-2009 the same 30 points were sampled (MacKenzie and Royle 2005). A point survey of five minutes was carried out to detect the presence of the species. Once we finished, we used playback of local Eastern Iberian Reed Bunting male songs for one minute to increase the probability of detection (Matessi et al., 2000, Atienza 2006). We consider male Eastern Iberian Reed Buntings singing observed within a radio of 100 m. Thus, we were studying presence of males in territories. Two visits were conducted to each of the plots within two weeks during the breeding season (May-July).

Figure 2. Localization of Tablas de Daimiel National Park in the Iberian Peninsula. Position of survey points in Tablas de Daimiel National Park.

Statistical methods

Presence/absence data for the period 2002-2015 was treated as if it was capture-recapture data traditionally used in survival studies of open populations (e.g. Lebreton et al., 1992). The individual site detection history h_i (e.g. h_i = 1 0 1) was analysed using capture-recapture models for open populations based in the Cormack-Jolly-Seber model (CJS). We estimated realised population growth rate (λ) using Pradel Survival and Lambda models (Pradel, 1996) using program MARK 5.1 (White and Burnham 1999). In our approach, for example for the above *hi*, the CJS considers that in the second year the species was present but go undetected. This approach differs from the robust design used by Barbraud et al., (2003), where the species it is not necessarily present in the second sampling period. Instead, it is possible that it became extinct, but was colonised again in the third year (MacKenzie et al., 2003). With the available data, we can only assume that the species was present but go undetected. Fieldwork and raw data for the atlas do not exist, so specific extinction and recolonization rates could not be estimated. The estimated apparent survival refers to survival and recolonization probability. The Akaike Information Criterion (AIC; Akaike, 1973) was used for ranking the fit of models to the data (Burnham and Anderson 2002, Johnson and Omland, 2004). The modelling procedure was set to verify that survival was always equal or less than the population growth rate ($\Phi_i \leq \lambda_i$). Thus, we used a Clogit link function for survival and growth rate and a logit link function for recapture. We considered that models within 2 AIC units fitted similarly the data and used model averaging to obtain estimates (Anderson et al., 2000).

As there is no information available about demographic parameters and metapopulation structure of the Spanish population, it was not possible to run a population viability analysis. Therefore, we used the annual growth rate and standard deviation in an estimation of future trends following White et al. (2002). We considered future growth rate (λ_f) to be random with mean equal to the annual growth rate and standard deviation as the annual growth rate standard deviation assuming a normal distribution of λ_f. We generated 10.000 population projections for 25 and 50 years, we took the product of 25 and 50 randomly generated values of λ_f to obtain the amount of change in the population expected to occur in 25 and 50 years. The strength of this approach is that it gives rigorous of the mean and process variance of λ_f that are used to project the population forward in time, based on temporal variation in the encountered histories observed in the field (White et al., 2002). However, this approach assumes that demographic stochasticity is not included (White et al., 2002). To incorporate it into the projections, we would need data on survival and reproduction, not available for the species.

Occupancy (ψ) was estimated using software PRESENCE 2.3 (Hines 2006) and following MacKenzie et al., (2002). Probability of occupancy given that the species was not detected at a site was estimated according to MacKenzie et al. (2006). Probability of colonization and extinction of the territories sampled in Tablas de Daimiel from 2007-2009 was analysed accordingly to the framework exposed in MacKenzie et al. (2003) and analysed using program PRESENCE 2.3. Models with or without heterogeneity in detection probability were considered. The Akaike Information Criterion (AIC) was used for ranking the fit of models to the data.

Results

Population trend

The Eastern Iberian Reed Bunting was recorded as a breeder in 24 10 x 10 UTM squares in Spain in 2002. By 2005, the species was found being still present in 12 of them, but was recorded in another 10 (i.e. the species was present in 22 sampling units). In 2015, the species was recorded only in 14 squares. Therefore, there has been a decline of 42 % in the 10 x 10 UTM squares distribution of the Eastern Iberian Reed Bunting from 2002 to 2015.

We used the above presence-absence data to estimate realised population growth rate. There were 3 models within 2 AIC units fitting similarly the data (Table 1). According to model averaging, the probability that an area occupied in a period was also occupied in the following period (i.e. apparent survival probability) 0.891 ± 0.056 for the period 2002-2005 and 0.942 ± 0.031 for the period 2005-2015. The detection probability was estimated of 0.709 ± 0.089

in 2002, 0.780 ± 0.093 in 2005 and 0.823 ± 0.051 in 2015. The annual growth rate was 0.929 ± 0.054 (95 % Confidence Interval: 0.726-0.984) during the interval 2002-2005 and 0.942 ± 0.031 (95 % CI: 0.842-0.980) for 2005-2015. The survival probability and annual growth rate estimated for the second period are equal, indicating that there has not being recruitment of new populations during this period.

A histogram of the amount of change expected over the 25 and 50-year period is shown in Figure 3. The projections show a future very strong decline in the population. According to the projections frequencies, probability of a decline greater than 80 % ($\lambda_f < 0.2$) in a 25-year projection is 0.886, and probability of a decline greater than 90 % ($\lambda_f < 0.1$) in a 50-year projection is 1.

Table 1. Model selection for to explain the dynamics in occupancy of Eastern Iberian Reed Bunting in Spain based on atlas data. Model procedure was set to verify that $\Phi_i \leq \lambda_i$. For each model, Akaike's Information Criterion (AICc), differences between that model and the model with the lowest AICc (ΔAICc), AICc weights (w), number of estimable parameters (K) and the values for deviance are shown. Model notation is as follows: Φ, survival probability; p, detectability; λ, population growth rate; c, constant; t, time dependent.

Id.	Model	AICc	ΔAICc	w	K	Deviance
1	Φ (t) p (c) λ (t)	128.974	0.000	0.326	4	6.888
2	Φ (c) p (t) λ (c)	129.069	0.095	0.311	3	9.277
3	Φ (c) p (c) λ (c)	129.390	0.415	0.265	2	11.811
4	Φ (t) p (t) λ (t)	131.351	2.377	0.099	5	6.888

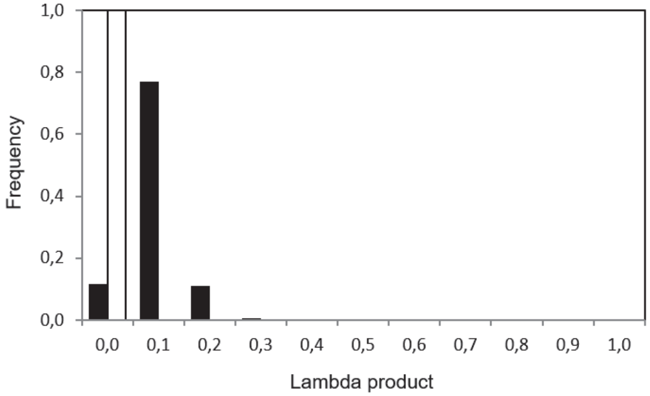

Figure 3. Frequency of the amount of change expected after 25 (in black) and 50 years (in white) for a population with λ = 0.929 and standard deviation σ = 0.054.

Occupancy in Tablas de Daimiel National Park

According to parameter estimates (Table 2), detection probability in our surveys ranged from 0.450 to 0.500 between 2006 and 2008. In 2009, detection probability was too low (0.080 ± 0.040), and therefore occupancy estimation was not reliable ($\psi = 1.0 \pm 0.0$). The naive estimation of the proportion of area occupied was 16% (Figure 4).

Table 2. Model selection statistics, parameter estimates and associated standard errors for the multi-season models. K represents the number of parameters in the model. Akaike Information Criteria (AIC), differences between that model and the model with the lowest AIC (ΔAIC) and Akaike weight (w) were calculated for each model. Ψ represents occupancy, and p represents detection probability, noted with (s) when spatial heterogeneity was considered and with (·) when considered as fixed.

Year	Model	K	AIC	ΔAIC	w	p
2006	$\Psi, p(\cdot)$	2	41.090	0.000	0.534	0.450 ± 0.150
	$\Psi, p(s)$	3	41.410	0.320	0.460	
2007	$\Psi, p(\cdot)$	2	64.120	0.000	0.719	0.459 ± 0.010
	$\Psi, p(s)$	3	65.970	1.850	0.284	
2008	$\Psi, p(\cdot)$	2	47.210	0.000	0.731	0.500 ± 0.220
	$\Psi, p(s)$	3	49.210	2.000	0.269	

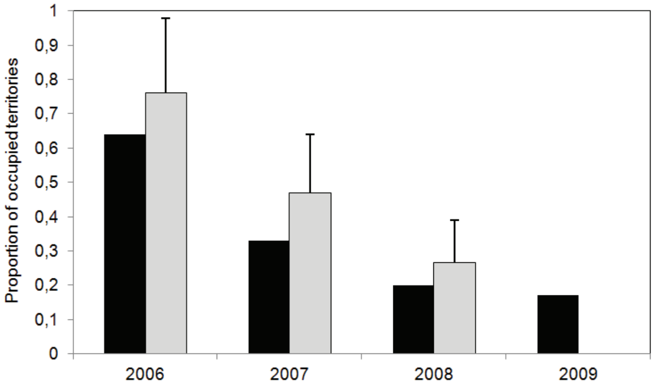

Figure 4. Variation of territories occupied by the Reed Bunting in Daimiel National Park in the period 2006-2009 in the proportion. Solid bars represent the naïve estimation. Open bars indicate the model estimates for each year in occupancy. Error bar are ± 1 s.e. Occupancy for 2009 was not reliable due to low probability of detection.

Naive estimation of the proportion of territories occupied declined from 64 % to 16 % and estimates of occupancy using model selection declined between 71 % and 27 % (Figure 4). Between 2007 and 2008 (the only period that was possible to analyse), growth rate was = 0.568 ± 0.294 (95 % Confidence Interval 0.074 - 1.126). The probability of extinction for a territory was below unity (0.733 ± 0.169; 95 % CI: 0.337 - 0.937) and the probability of colonization of a new territory was low (0.267 ± 0.156; 95 % CI: 0.071 - 0.635). Thus, there was a clear decline in territory occupancy with time.

Discussion

The Eastern Iberian Reed Bunting is considered as Endangered in the Red Book of birds in Spain (Madroño et al., 2004). It is claimed that the species has declined in its range of distribution in the last decades (Madroño et al., 2004, Atienza, 2006, Monrós et al., 2017). The results of this study confirm such trend both at national scale and at the wetland that held the highest population in 2005 (Atienza, 2006). The realised population growth rate for the period analysed showed that the reed bunting declined in both periods as the estimate and the 95 % confidence interval is below 1. According to the future projections of the population, our results suggest that there is a high risk of extinction in the close future and therefore urgent measures are needed to preserve it. In addition, genetic studies revealed that there is already differentiation in the genetic structure between the main wetlands where the species is found (Castilla La Mancha, Delta del Ebro and Baleares) and suggest low gene flow between subpopulations, what increase the risk of extinction (Kvist et al., 2011). This low gene flow would be reducing, as the range distribution has been reduced and our results show that there has not being recruitment of new populations between 2005 and 2015. Thus, our approach is conservative and probably underestimates the extinction risk.

Athough we are aware than a period of four years is too short to establish a population trend, our results suggest a declining trend for the population of Daimiel. Recent estimates support the decline in this wetland. Although Jiménez et al., (2015) state that a marked local decline of the Eastern Iberian Reed Bunting cannot be confirmed with any certainty, their population estimate (10-20 territorial males in 2014) and the estimate of 11-15 territorial males in 2015 (Monrós et al., 2017), complementarily with our data, confirm such trend. This decline is probably associated to declining conditions (prolonged drought) at the National Park between 2005 and 2009. However, in 2010 this wetland recovered significantly from that dry period but the monitoring of the Eastern Iberian Reed Bunting population has showed how this changing flooding conditions have affected negatively the habitats preferred by the Reed Bunting for the species occurrence at the wetland scale and to settle territories (own data, for details see Vera et al., 2011, 2014). In 2007 a severe hailstorm affected the National Park during the breeding season and several nests of Reed Bunting were destroyed (2 out of seven nest being monitored, one female killed). This storm may have affected the population and the significant decline observed between 2007 and 2008 may be caused by the consequences if this catastrophe.

One of the aims of this study was to evaluate the possibility of using presence-absence studies to monitor this species at the National Park. We may conclude that the method applied (survey points and analysis of occupancy controlling for detection probability) is a valid alternative to census studies. Depending on the precession required some changes should be made to the methodology. For example, according to the effect of date on detectability, a sampling period from 20th April to 7th June was suggested by Jiménez et al. (2015). It is interesting to note that at the same time, this methodology may be used to monitor other passerine species.

On the other hand, the results of this study clearly showed that the probability of detection of the Iberian Reed Bunting is below unity, as is the case in most species (e.g. MacKenzie et al., 2005). In both analyses carried out in this study showed similar estimate for the detection probability (ranging from 0.724 to 0.823 in the population trend analysis and ranging from 0.450 to 0.500 in Tablas de Daimiel between 2006 and 2008). Given this detection probability of this subspecies during the breeding season, it is quite likely than previous studies have infra-estimated the range of distribution of it. In any case, we suggest that future studies of this endangered subspecies need to consider modelling the probability of detection to obtain unbiased estimates of occupancy (see MacKenzie et al., 2005, 2006).

More relevant, this study shows that management actions need to be taken urgently to assure the conservation of this Reed Bunting endemic subspecies in the short term. Although the endangered status of the Eastern Iberian Reed Bunting has been recognized by the Spanish List of Endangered Species (Real Decreto 139/2011) as Endangered, only the Valencia region has developed a draft of recovery plan for it, as is recquired by law. Also, only few regional or local administrations have started or continued the monitoring of some populations (i.e. Tablas de Daimiel, Delta del Ebro, Marjal de Pego-Oliva and s'Albufera de Mallorca). According to our results, not only monitoring programs, but also recovery plans for the species and management plans for the wetlands where it is present (as all of them are included as SPAs in the Natura 2000 network), must be urgently developed and put into practice to preserve the small populations and its genetic diversity (Kvist et al., 2011).

We agree with Madroño et al., (2004) and Atienza (2006) that the low population size and fragmented, scarce distribution probably are enough to qualify for an endangered status in Spain. However, our results and the recent population estimation (Monrós et al., 2017) urge to review its status, so the subspecies would qualify as "Critically Endangered" in Spain according to IUCN parameters. We are not able to assess the overall status of this subspecies, as there is not accurate population census and trends in the other areas of its range of distribution out of Spain (southern France and Morocco).

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Habitat preference of endangered eastern Iberian Reed Bunting (*Emberiza schoeniclus witherbyi*)

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HABITAT PREFERENCE OF ENDANGERED EASTERN IBERIAN REED BUNTINGS *EMBERIZA SCHOENICLUS WITHERBYI*

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Capsule Careful management is required to maintain or create habitats with the correct proportions of rush with reeds that are preferred by this subspecies.

Aims To determine the habitat requirements of Eastern Iberian (Western Iberian Reed Buntings were not included in the study) Reed Buntings Emberiza schoeniclus witherbyi, a subspecies endemic to a few marshes in France, Spain and Morocco, with a population of 254–360 breeding pairs.

Methods Twenty-five wetlands in Spain were surveyed and presence/absence of Iberian Reed Buntings was deteremined together with data on 41 environmental variables. The relationships between the birds and habitat data were investigated using GLM.

Results Proportion of rush with reeds, proportion of reed–bulrush patches and perimeter length of rush–reed patches, were the variables that primarily explained the present distribution of Eastern Iberian Reed Buntings. Other vegetation classes traditionally associated with the presence of the Eastern Iberian Reed Buntings, such as sedges, were not found to be important in the selected models.

Conclusion Conservation planning and management guidelines for this subspecies should focus on encouraging these specific-vegetation parameters. Flood control and grazing are proposed as the best practices that will favour these vegetation variables and avoid simplification of the plant community. Keywords: occupancy, detection probability, growth rate.

Introduction

Wetlands are environments of high conservation interest for the diversity and status of flora and fauna. These habitats are especially important for many globally endangered birds (Butchart et al., 2004). However, Mediterranean wetlands have been seriously affected by human activities through dessication and exploitation (Fernández-Alés 1992), soil and water quality loss (Zalidis et al., 2002), and loss of connectivity through landscape homogenization (Gallego-Fernández et al., 1999). It is likely that almost all wetlands in Mediterranean Europe are presently managed for human activities, such as agriculture, hunting, reed cutting and also conservation purposes. These activities may have negative impacts, especially on birds (Tscharntke, 1992, Graveland, 1998, 1999, Martínez-Vilalta et al., 2002, Kozulin et al., 2004) and, within the EU, about 110 bird species protected by EU Bird Directive (92/43/EEC) depend on wetlands for survival. Despite the fact that many bird species depend on these types of habitats, quantitative information on the habitat requirements of many of these species is lacking and so it is often not possible to propose adequate conservation measures (Tanneberger et al., 2009).

Although some birds species associated with wetlands are at serious risk of extinction, such as Aquatic Warblers *Acrocephalus paludicola*, only a few studies have analysed the habitat requirements of endangered passerines linked to wetlands (but see Poulin et al., 2002, Tanneberger et al., 2009, 2010). For example, the population trend of Reed Buntings *Emberiza schoeniclus* in Europe since 1980 has been one of decline (Voríšek et al., 2010). Several studies have indicated the loss of suitable habitats (Siriwardena et al., 2000, Brickle and Peach, 2004, Surmacki, 2004, Orłowski 2005) and the importance of over-winter survival (Peach et al., 1999) to explain the decline of Reed Buntings. These studies were done for the subspecies *Emberiza schoeniculus schoeniculus*, which inhabits agricultural and wetland-associated landscapes. Although this decline is severe in some parts of Europe, including Norway, Sweden and the UK (Bufield and Van Bommel, 2004), in the Iberian Peninsula the decline has been dramatic, with a loss of 80% of the population in some regions in recent decades (Atienza and Copete, 2004). However, the habitat requirements for Reed Buntings at the southern range of their breeding distribution, are not well-known (Poulin et al., 2002).

In Spain there are fewer than 500 pairs of breeding Reed Buntings left (Atienza, 2006). They belong to two different subspecies: Eastern Iberian Reed Buntings *Emberiza schoeniclus witherbyi* and Western Iberian Reed Buntings *E. s. lusitanica* (Belda et al., 2009), with a highly fragmented distribution (Atienza, 2006). Eastern Iberian Reed Buntings are a subspecies that is endemic to very few western Mediterranean marshes in France, Spain and Morocco (Fig. 1). At present, there are only 254–360 breeding pairs in Spain (Atienza, 2006), which are distributed in 21 different wetlands; therefore, distribution of this subspecies is highly fragmented. Indeed, fragmentation of populations has been confirmed by genetic analysis involving genetic estimates of migration rates and gene flow of this nonmigrating subspecies (Kvist et al., in press). The subspecies is considered 'endangered' (Spanish Catalogue of Threatened Species, RD 139/2011). Loss of suitable habitats is suggested to be the main cause of its decline (Atienza 2006). Thus, the adequate management of the wetlands which it presently inhabits is needed to avoid its extinction. Little is known about the habitat requirements of Eastern Iberian Reed Buntings at either the landscape level or on finer scales. Reed *Phragmites australis* and sedge *Cladium mariscus* have been proposed as the most important variables in habitat selection for Eastern Iberian Reed Buntings (Martínez-Vilalta et al., 2002, Bigas and Copete, 2004, Atienza, 2006).

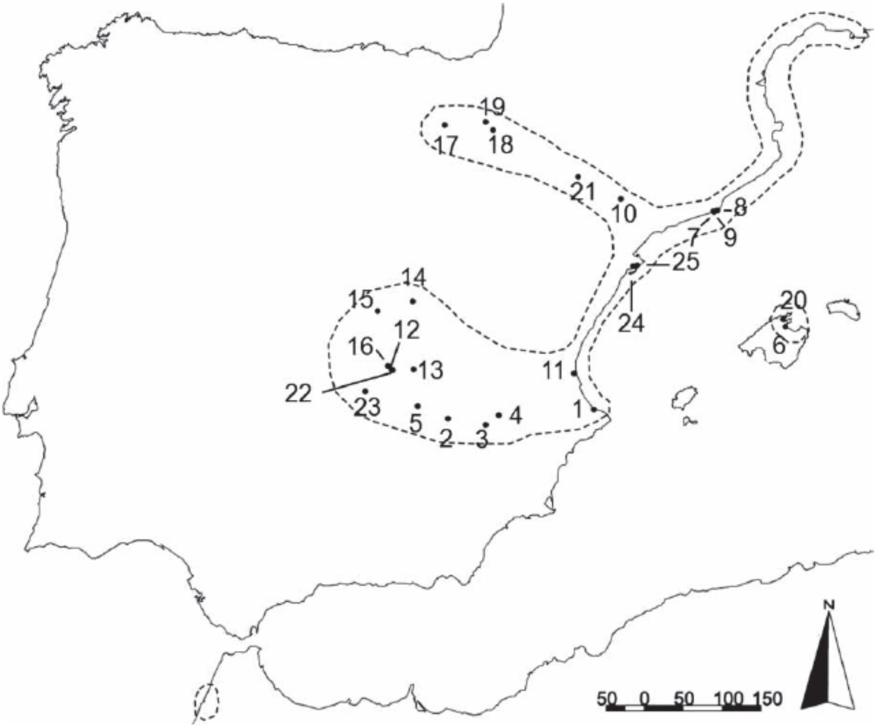

Figure 1. World distribution of Eastern Iberian Reed Buntings and location of the wetlands surveyed in the Iberian Peninsula: (1) Marjal de Pego-Oliva (404 ha, P); (2) Ojos de Villaverde (49 ha, P); (3) Laguna de Ontalafia (45 ha, A); (4) Pétrola (47 ha, A); (5) Laguna del rey (45 ha, A); (6) s'Albufera (1448 ha, P); (7) Delta del Llobregat 1 (30 ha, A); (8) Delta del Llobregat 2 (82 ha, A); (9) Delta del Llobregat 3 (80 ha, A); (10) Pantà d'Utxesa (204 ha, P); (11) l'Albufera (2686 ha, A); (12) la Veguilla (74 ha, P); (13) Laguna Pueblo (42 ha, A); (14) Embalse de Almoguera (108 ha, P); (15) Laguna de San Juan (24 ha, A); (16) Villafranca de los Caballeros (198 ha, P); (17) Embalse de las Cañas (95 ha, P); (18) Laguna de Pitillas (187 ha, A); (19) Laguna del Juncal (8 ha, P); (20) s'Albufereta (76 ha, A); (21) Laguna de Sariñena (229 ha, A); (22) Laguna de yeguas (269 ha, A); (23) Tablas de Daimiel (1593 ha, P); (24) Encanyissada (Delta del Ebro) (803 ha, P); (25) Tancada (Delta del Ebro) (246 ha, A). P, Eastern Iberian Reed present; A, absent.

Predictive models are one of the most interesting and important research fields in biodiversity and habitat selection studies (Guisan and Zimmermann, 2000). Practical applications of predictive distribution models demonstrate their usefulness, particularly for managing endangered species (Engler et al., 2004, Norris, 2004, Balbotín, 2005). Their use in modelling distribution patterns and habitat selection has not increased as much as the use for other purposes in the scientific literature (but see Beard et al., 1999, Segurado and Araújo, 2004), and they are scarce on local scales (Suárez-Seoane et al., 2002). This is because of the need of great detail in field data measurements to obtain reliable results, especially when measuring vegetation or habitat features. Such problems have been solved through exhaustive field mapping of vegetation. In these vegetation maps functional classes of vegetation, and not vegetation classes, should be taken into account (Vanreusel and Van Dyck, 2007).

This study aimed to analyse the environmental parameters that influence the presence of endangered Eastern Iberian Reed Buntings at the wetland level. The results are used to suggest management guidelines for their conservation.

Material and methods

Study area

The study area includes 25 wetlands located in Spain, southwest Europe (Figure 1). First, we surveyed wetlands where the presence of Eastern Iberian Reed Buntings was detected in the National Census carried out in 2005, ranging from 90 to 120 breeding pairs at Tablas de Daimiel, to only one pair at Embalse Las Cañas (Atienza 2006). Then, we selected the nearest wetlands to the previously selected wetlands where the Eastern Iberian Reed Bunting presence was not registered in the National Census, which were used as possible negative controls. Regardless of previous available information on presence/absence in these wetlands in 2005, the presence of Eastern Iberian Reed Buntings was verified in the 25 wetlands in 2006 to provide real presence/absence data. Each wetland was surveyed twice by conducting transects within the first 4 hours after dawn during the breeding period (April–May). In order to increase the detection probability, a digital recording was played during transects. The records played were of natural songs recorded in a wetland as near as possible to the surveyed wetland (a reduction in detectability has been found when playing recordings made in geographically remote localities Matessi et al., [1997, 2000]). Both visual and counter-singing data were used to determine numbers of birds in a locality. Eastern Iberian Reed Buntings were considered absent when the censuses carried out in 2006 gave a negative result.

Environmental variables

A total of 42 variables were measured or calculated in all studied wetlands (Table 1). The area of the wetland and 41 biotic variables (relating to vegetation) were considered as possible explanatory factors of the distribution of Eastern Iberian Reed Buntings in the Iberian Peninsula and on the Balearic islands. In each wetland, vegetation was

Table 1. Measured variables for each vegetation patch type in all surveyed wetlands and the nomenclature used.

Vegetation class	Formations	Measured parameters	Reasons for inclusion
Reed	Reed dominant (5)	Total area, perimeter, fragmentation, proportion, greater patch	Martínez-Vilalta et al., (2002) found that Eastern Iberian Reed Buntings' abundances were greatest in areas of drier soils and a dense basal stratum (also called emergent vegetation)
Bulsrush	Bulrush-dominant (4) Reed–bulrush (4) Reed with bulrush (4)	Total area, perimeter, fragmentation, proportion	Used to place the nests (Vera et al., 2009)
Sedge	Sedge-dominant (4) Reed–sedge (4) Reed with sedge (4)	Total area, perimeter, fragmentation, proportion	Used to place the nests (Vera et al., 2009), and foraging sites in search of prey (Cramp and Perrins 1994)
Rushes	Rush-dominant (4) Reed–rush (4) Reed with rushes (4)	Total area, perimeter, fragmentation, proportion	Selection of reed-beds characterized by presence of plants adapted to saline soils, such as *Juncus* and others (Martínez-Vilalta et al., 2002), and foraging sites in search of prey (Cramp and Perrins, 1994)

Numbers in parentheses following the patch type refer to the number of measured parameters for those patch types; see Methodology for the definition of the patch types and measured parameters.

systematically mapped using intensive transects covering the whole area of the studied wetlands. These maps were digitalized using the ARCGIS tools and digital maps.

The vegetation classes studied were patches dominated by Common Reeds *Phragmites australis*, Bulrushes *Typha* spp., Saw Sedge *Cladium mariscus*, rushes *Juncus acutus* and *Scirpus holoschoenus* structural and ecological type (hereafter called rushes), and dominance combinations among them (Table 1). Estimations of abundance ratios were made de visu (Sutherland 1996) according to coverage of each species, as it was very important to avoid overestimation of smaller, emergent species coverage. Mapping of these habitat patches was performed by walking systematically within the vegetation. Patches were considered to be of one type when one species represented between 95% and 100% of the polygon area. A nomenclature of the mixed patches was established with three categories: (1) dominance, when a species represented between 75% and 95% of the polygon area; (2) co-dominance, when two species had similar areas close to 50% (i.e. reed–rush); (3) semi-dominance when one species represented 60–75% and a second species represented 25–40% of the polygon area (i.e. reed with rushes). For each vegetation patch, the following variables were calculated:

(a) Total area (hectares): surface resulting from the sum of the partial area of polygons belonging to the same vegetation class.

(b) Perimeter (hectometers): sum of the perimeters length of polygons belonging to the same vegetation class.

(c) Fragmentation: ratio between the perimeter and the total area (according to Pasinelli and Schiegg, [2006]).

(d) Proportion: ratio between the total area for each vegetation class and the wetland's total area. This variable was transformed with the arcsine rule (Zar 1996) in order to normalize the distribution of the variable.

Model development and selection

We applied GLM techniques with binomial error distribution to explain the presence or absence of Eastern Iberian Reed Buntings in the surveyed wetlands. Only those variables with $P \leq 0.15$ according to the Wald's test (Hosmer and Lemeshow, 2000) were included in the subsequent models. This procedure allowed us to reduce the number of possible explanatory variables. We also included as potential predictors the quadratic terms for these variables (Guisan and Thuiller, 2005). The AIC (Akaike, 1973) was used to select the models that best fitted the data (Burnham and Anderso,n 2002, Johnson and Omland, 2004). Correction of Akaike's index (AICc) was performed for small sample sizes, given that fewer than 40 wetlands were surveyed (Burnham and Anderson, 2002, Johnson and Omland, 2004). We considered models within two AICc units of the best model as competing models (Burnham and Anderson, 2002). Co-linearity between the selected variables was evaluated by Spearman's test. Akaike's weights (ω_i) were calculated for the whole set of models. For this set of models, ω_i sum to 1. For a variable k, we can calculate the sum of the values of ω_i of all the models including k, being this sum the probability that variable k, of the variables considered in the analysis, is in the best approximating model (Burnham and Anderson, 2002). All the statistical procedures were performed with SPSS 16.0 (SPSS Inc., Chicago, Illinois).

Results

The results of the wetland surveys revealed 11 instances of presence and 14 instances of absence of Eastern Iberian Reed Buntings (Figure 1). Results of previous surveys in the National Census in 2005 were very similar. Nevertheless, in two wetlands not surveyed in the National Census the presence of Eastern Iberian Reed Buntings was detected: La Veguilla (Ciudad Real, central Spain) and Encanyissada (Tarragona, northeast Spain).

Only 11 of the 42 vegetation variables went beyond the threshold of $P \leq 0.15$ in the Wald's test (Table 2). The variables that better described the occurrence of Eastern Iberian Reed Buntings in single models were the proportion of rushes with reed (correctly classified 85.7 % of presences and 72.7 % of absences) and the proportion of reeds as the dominant vegetation (78.6 % of presences and 45.5 % of absences). The total area of reeds as the dominant vegetation (92.9 % of presences and 27.3 % of absences) and the perimeter of patches composed of reeds and rushes (85.7 % of presences and 45.5 % of absences) fitted the data worst, thus showing the importance of reed-dominant, rush-dominant and rush–reed habitat patches in the distribution of Eastern Iberian Reed Buntings. Only one variable relating to sedge patches, traditionally correlated with the presence of Eastern Iberian Reed Buntings, was selected for the development of the model – total area of sedge as the dominant vegetation – and it was not among the variables that better explained the data set. Dominant reed formations were the only formations necessarily present for the occurrence of Eastern Iberian Reed Buntings. Most variables showed mean values with a high standard deviation for wetlands where the Eastern Iberian Reed Buntings were present or absent (Table 2), reflecting the heterogeneity in the size and typology of the surveyed wetlands. According to Student's t-test results, only the means of proportion of rushes and proportion of reeds as dominant vegetations were significantly different between wetlands with presence and absence of Eastern Iberian Reed Buntings (proportion of rushes: $t = -3.373$; df = 23; $P = 0.003$; proportion of reeds: $t = -2.393$; df = 23; $P = 0.025$). Differences in the mean size of occupied and non-occupied wetlands were not found ($t = 0.620$; df = 23; $P = 0.541$).

We obtained four models with the lowest AICc which fitted our data perfectly (100 % presences and 100 % absences) (Table 3). These models included four different variables. Three variables were constant in the four models (proportion of reed–bulrush patches, proportion of rushes with reed, and perimeter of reed–rush patches) and another three were present in only one model (total area, greater patch, and perimeter of dominant reed). The three variables present in the best-fitting models were the variables with highest Akaike's weights (proportion of reed–bulrush $\omega_1 = 0.993$; perimeter of reed–rush $\omega_2 = 0.990$; proportion of rushes with reed $\omega_3 = 0.641$), calculated as the sum of the Akaike's weights of the models including these variables. That is, of all the variables considered in the analysis, they were the variables with the highest probability of being included in the best-approximating model. Correlation between these variables was not significant (proportion of reed–burush versus perimeter of reed–rush, Spearman's $r = 0.000$, $P = 1.000$; proportion of reed– bulrush versus proportion of rushes with reed, $\rho = 0.050$, $P = 0.811$; perimeter of reed–rush versus proportion of rushes with reed, $\rho = 0.341$, $P = 0.096$).

Table 2. Maximum, minimum, and mean + sd values for the variables used in the development of predicted models after exceeding the acceptation threshold in the Wald's test (Hosmer and Lemeshow 2000) according to the presence/absence of Eastern Iberian Reed Buntings in surveyed wetlands.

		Presence of Eastern Iberian Reed Buntings (n = 11)			Absence of Eastern Iberian Reed Buntings (n = 14)		
Variable	Wald's test	Max.	Min.	Mean ± sd	Max.	Min.	Mean ± sd
Total area of dominant reed	0.065	1124.99	4.43	251.50 ± 422.76	234.15	0	34.65 ± 63.47
Perimeter of dominant reed	0.127	2629.76	20.40	416.49 ± 759.50	513.78	0	99.96 ± 134.08
Fragmentation of dominant reed	0.150	0.06	0.01	0.03 ± 0.01	0.22	0	0.05 ± 0.05
Proportion of dominant reed	0.026	61382	17.52	39.27 ± 15.37	53.19	0	23.98 ± 16.23
Greater patch of dominant reed	0.102	972.10	1.58	153.79 ± 307.26	92.61	0	17.73 ± 27.69
Total area of dominant sedge	0.126	16.78	0	3.55 ± 6.25	5.84	0	0.85 ± 1.85
Proportion of reed-bulrush	0.085	14.91	0	2.68 ± 5.35	51.80	0	4.39 ± 13.89
Perimeter of rushes with reed	0.094	365.40	0	64.09 ± 106.17	139.12	0	12.35 ± 36.81
Proportion of rushes with reed	0.004	36.50	0	15.31 ± 10.96	18.84	0	3.71 ± 6.04
Perimeter of reed-rush	0.068	154.17	0	24.71 ± 46.84	9.69	0	1.27 ± 3.23
Proportion of reed-rush	0.086	39.52	0	7.95 ± 12.84	14.06	0	1.57 ± 4.17

Areas are measured in ha; perimeters are measured in hm; proportions are arcsine-transformed. Wald's test: *P*-value.

We obtained four models with the lowest AICc which fitted our data perfectly (100 % presences and 100 % absences) (Table 3). These models included four different variables. Three variables were constant in the four models (proportion of reed–bulrush patches, proportion of rushes with reed, and perimeter of reed–rush patches) and another three were present in only one model (total area, greater patch, and perimeter of dominant reed). The three variables present in the best-fitting models were the variables with highest Akaike's weights (proportion of reed–bulrush $\omega_1 = 0.993$; perimeter of reed–rush $\omega_2 = 0.990$; proportion of rushes with reed $\omega_3 = 0.641$), calculated as the sum of the Akaike's weights of the models including these variables. That is, of all the variables considered in the analysis, they were the variables with the highest probability of being included in the best-approximating model. Correlation between these variables was not significant (proportion of reed–burush versus perimeter of reed–rush,

Table 3. Model selection according to the corrected AICc. Only models within five AICc units of the best models are shown.

Variables included in the model	*K*	AICc	Δ_i	Weight	-2log likelihood
Proportion of rushes with reed; Perimeter of reed–rush; Total area of dominant reed; Proportion of reed–bulrush	5	13.158	0	0.121	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Greater patch of dominant reed	5	13.158	0	0.121	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Perimeter of dominant reed	5	13.158	0	0.121	< 0.001
Perimeter of reed–rush; Proportion of dominant reed; Proportion of reed–bulrush; Perimeter of rushes with reed	5	13.158	0	0.121	< 0.001
Proportion of rushes with reed; Proportion of rushes with reed^2; Perimeter of reed–rush; Total area of dominant reed; Proportion of reed–bulrush	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Perimeter of reed–rush^2; Total area of dominant reed; Proportion of reed–bulrush	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Total area of dominant reed; Total area of dominant reed^2; Proportion of reed–bulrush	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Total area of dominant reed; Proportion of reed–bulrush; Proportion of reed–bulrush^2	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Proportion of rushes with reed^2; Perimeter of reed–rush; Proportion of reed–bulrush; Greater patch of dominant reed	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Perimeter of reed–rush^2; Proportion of reed–bulrush; Greater patch of dominant reed	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Proportion of reed–bulrush^2; Greater patch of dominant reed	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Greater patch of dominant reed; Greater patch of dominant reed^2	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Proportion of rushes with reed^2; Perimeter of reed–rush; Proportion of reed–bulrush; Perimeter of dominant reed	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Perimeter of reed–rush^2; Proportion of reed–bulrush; Perimeter of dominant reed	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Proportion of reed–bulrush^2; Perimeter of dominant reed	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Perimeter of dominant reed; Perimeter of dominant reed^2	6	16.667	3.509	0.021	< 0.001
Perimeter of reed–rush; Perimeter of reed–rush^2; Proportion of dominant reed; Proportion of reed–bulrush; Perimeter of rushes with reed	6	16.667	3.509	0.021	< 0.001
Perimeter of reed–rush; Proportion of dominant reed; Proportion of dominant reed^2; Proportion of reed–bulrush; Perimeter of rushes with reed	6	16.667	3.509	0.021	< 0.001

Variables included in the model	*K*	AICc	Δ_i	Weight	-2log likelihood
Perimeter of reed–rush; Proportion of dominant reed; Proportion of reed–bulrush; Proportion of reed–bulrush^2; Perimeter of rushes with reed	6	16.667	3.509	0.021	< 0.001
Perimeter of reed–rush; Proportion of dominant reed; Proportion of reed–bulrush; Perimeter of rushes with reed; Perimeter of rushes with reed^2	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of rushes with reed^2; Perimeter of reed–rush Proportion of reed–bulrush; Total area of dominant sedge	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Proportion of reed–bulrush^2; Total area of dominant sedge	6	16.667	3.509	0.021	< 0.001
Proportion of rushes with reed; Perimeter of reed–rush; Proportion of reed–bulrush; Total area of dominant sedge; Total area of dominant sedge^2	6	16.667	3.509	0.021	< 0.001
Rest of the models		> 20.588	> 7.430	< 0.003	

[2] Quadratic terms; *K*, number of descriptive variables included in the development of the model; Δ_i, difference between the AICc of the model and the lower AICc value of the models; weight, Akaike's weight calculated for all the models.

Spearman's ρ = 0.000, *P* = 1.000; proportion of reed– bulrush versus proportion of rushes with reed, ρ = 0.050, *P* = 0.811; perimeter of reed–rush versus proportion of rushes with reed, ρ = 0.341, *P* = 0.096).

Discussion

We found that the presence of Eastern Iberian Reed Buntings at the wetland level relates to the mixed patches of reed–bulrush, reed–rush and the proportion of rushes with reed as secondary vegetation. This suggests that these vegetation variables may be important for the establishment of Eastern Iberian Reed Bunting populations and to provide wetland vegetation management guidelines.

This is, to our knowledge, the first study to find a strong relationship between Eastern Iberian Reed Bunting occurrence and mixed patches of reed and bulrushes. Previous detailed analysis in Spain (Martínez- Vilalta et al., 2002) did not take into account these kinds of patches in the habitat types studied to assess habitat selection by Eastern Iberian Reed Buntings and other marshland species. In the Camargue, Poulin et al., (2002) did not find any significant association between habitat features and the presence of Eastern Iberian Reed Buntings. A possible explanation of this result may lie in the lack of detail in the classification of habitats, as they included bulrushes with *Scirpus*, *Juncus* and *Atriplex* in a unique category (emergent species). In contrast, Vera et al., (2009) found that nests can be placed in bulrushes in central Spain, and Surmacki (2004) found that bulrushes significantly influenced territory occupation, but not in all years. Surmacki (2004) also proposed that bulrushes and rushes could play a secondary role as singing posts in territory establishment.

Reeds and reed–rush patches (referred to by some authors as emergent vegetation) have been considered within the determinant vegetation classes for the presence/absence of this passerine in the Iberian Peninsula on a local scale (Martínez-Vilalta et al., 2002, Atienza, 2006) and also for the nominal subspecies *schoeniclus* in western Poland (Surmacki, 2004). In these studies, no information was available concerning the vegetation feature that played an important role in habitat selection. Our results show that proportion of rushes as dominant vegetation (with reeds) and the perimeter of reed–rush mixed patches play an important role in explaining the variance in habitat. As in the case of the proportion of reed–bulrushes, these variables are, as far as we know, the first known features for wetland selection by Eastern Iberian Reed Buntings on a distribution scale. Previous knowledge is based on observations made at specific wetlands (the Ebro Delta) and was considered to be representative of the whole distribution range (Martínez-Vilalta et al., 2002, Bigas and Copete, 2004). Those studies showed that Eastern Iberian Reed Buntings preferred sedge-dominant patches with medium height and avoided reed patches with high vegetation height and water depth (Martínez-Vilalta et al., 2002).

Reed patches are used as breeding areas (at least marginally) (Surmacki, 2004), feeding areas, or both (Brickle and Peach, 2004). Surmacki (2004) showed the importance of reed patches with old reeds for the establishment of male territories. We found no evidence for the selection of pure (old) reed patches. The pure reed patches in our study area had permanent flooding conditions, a limiting factor for the development of other emergent vegetation, except for bulrushes. Nests need to be placed close to these other emergent vegetation classes (Vera et al., 2009), so pure reed patches should not be an optimum habitat for Eastern Iberian Reed Buntings to nest in. Furthermore, areas where reeds dominate are also used as feeding areas by adults. As in northern Reed Buntings, whose diet is composed of invertebrates in the breeding season (Cramp and Perrins, 1994), Eastern Iberian Reed Buntings feed on insect larvae extracted from reed stems (Isenmann, 1990, Goater, 1993). This resource is more available in areas with seasonal fluctuation in water level, where plant stems are less thick (Goater, 1993), but not in dry, thick stems found in pure reed-beds. Reed–rush and rush-dominant patches, which could be also considered emergent vegetation, are cryptic habitats for nesting, especially in the borders of large reed beds (Brickle and Peach, 2004). Similar studies have postulated that the presence of emergent vegetation is an important factor in establishing breeding territories (Martínez-Vilalta et al., 2002). The fact that the perimeter of reed–rush patches is important to wetland selection has strong implications for management. The perimeter of reed–rush patches can be very different, even though they may cover the same area. As the proportion of reed–rushes patches has not been selected as a relevant variable, those more irregular, heterogeneous formations are selected by Eastern Iberian Reed Buntings. These patches hold major arthropod diversity and abundance, being related more to flooding duration than to vegetation structure (Poulin et al., 2002), especially for small arthropods that are assumed to be an important part of the nestlings' diet (Brickle and Peach, 2004).

Other vegetation classes traditionally associated with the presence of Eastern Iberian Reed Buntings, such as sedge *Cladium mariscus* being dominant or mixed with reed in different dominance rates (Martínez-Vilalta et al., 2002, Atienza, 2006), were not of interest for the selected models. This absence of explanatory power could be related to the scale of this study and the distribution of sedge in the Iberian peninsula, and also to the fact that its ecological function (rush-like structure of 1.0–1.5 m high and coriaceous leaves) could be substituted for other species grouped in the vegetation class of rushes (i.e. *Juncus acutus* or *Scirpus holoschoenus*) in wetlands where sedge is not present. The fact that rushes are a limiting factor for the distribution of Eastern Iberian Reed Buntings supports this hypothesis.

Management implications

The most important application of our results is that the variables relevant to wetland selection in Eastern Iberian Reed Buntings could be managed in order to increase the probability of their occurrence. As Poulin et al., (2002) demonstrated in the French Mediterranean for other marshland birds, and on the basis of our results, flooding fluctuations seem to determine the presence of Eastern Iberian Reed Buntings through the presence of bulrushes, reed–rush mixed patches and food availability. In fact, the effects of flooding duration, and the depth and salinity of water are especially relevant for competition between reeds and other emergent vegetation (Hellings and Gallagher, 1992, Coops et al., 1994).

As pure, high patches of reed are not preferred habitats, reed cutting (Poulin and Lefebvre, 2002, Tannenberger et al., 2009) would not be a useful management action, as this favours reed dominance. Burning has not proved useful in restoring habitats for birds, given the consequent lack of food resources (Valkama et al., 2008). However, cattle grazing could be used to recommence vegetation succession processes and favour emergent species other than reed, such as *Juncus* and *Scirpus* (Mesléard et al., 1999). Grazing pressure needs to be modelled to avoid over exploitation of these plant species. For example, year-round grazing (1.3 heads/ha) occurs in a small area in the Encanyissada lagoon (Martínez-Vilalta et al., 2002), where a breeding population of Eastern Iberian Reed Buntings is present.

On the basis of our results, wetland size is not an important factor in determining the occurrence of Eastern Iberian Reed Buntings. This is supported by Pasinelli et al., (2008), who found that small and large reed-beds were equally suitable for breeding Reed Buntings. Thus, restoring a small proportion of reed-beds in areas with reed–bulrush and reed–rush mixed patches, mainly through water level management, but also with complementary grazing, would favour the presence of Eastern Iberian Reed Buntings in Iberian wetlands.

Implementing vegetation management practices in accordance with our results could generate a conflict with the habitat selection of other endangered marshland species. These species should at least be taken into account to achieve optimal, integrated wetland management.

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Habitat preferences for territory and nest settlement of the endangered Eastern Iberian Reed Bunting *Emberiza schoeniclus witherbyi*

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HABITAT PREFERENCES FOR TERRITORY SELECTION BY THE ENDANGERED EASTERN IBERIAN REED BUNTING *EMBERIZA SCHOENICLUS WITHERBYI*

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Summary

Given the 80% decline of the eastern Iberian reed bunting *Emberiza schoeniclus witherbyi* breeding population in recent decades, our aim was to identify the habitat components selected during territory establishment and to characterise the vegetation features that are positively or negatively selected at the territory scale. GLMM were used to explain the occurrence of territories in 11 wetlands. Fourteen variables with four vegetation dominance categories were analysed with respect to habitat composition, while occupancy of seven vegetation classes and 12 reed structural parameters were analysed with respect to habitat structure. The proportion of reed-cattails (Typha) measured by the habitat approach was the variable with the greatest likelihood of being the model that best fitted our data, but showed poor discriminative ability. The proportion of reed with tussocks was higher in occupied territories than in non-occupied territories. The main results are consistent with a previous study of habitat preference at a wetland scale and seem to be associated both with reduced predation risk and provision of nesting and feeding opportunities. Management guidelines to enhance the presence of the vegetation classes preferred by the species are discussed.

Key words: habitat selection, predation risk, reed structure, wetland management.

Introduction

Wetlands are among the most threatened habitats in the world (Dudgeon et al., 2006) and they support specific and valuable species diversity (Gibbs, 2000). Among them, Mediterranean wetlands have been seriously affected by human activities in recent decades, especially those on plains and in littoral areas as they become not only embedded within human-modified landscapes but also smaller in size (Benassi et al., 2007). It is likely that almost all European Mediterranean wetlands are currently managed for human activities, such as agriculture, hunting and reed-cutting, as well as for conservation purposes. In addition, wetlands are highly dynamic ecosystems where fire, wind and flooding conditions can cause major interannual changes in the structure and composition of the predominant vegetation (White et al., 2007). For wetland-associated birds, all these factors affect nest site selection and food availability, which are critical for specialist species. In fact, a large number of threatened or endangered birds breed in European wetlands (Bufield and van Bommel, 2004). Landscape-scale habitat availability and preferences, and vegetation structure and composition at different scales, have not been extensively studied in relation to endangered European passerines, except for the globally endangered aquatic warbler *Acrocephalus paludicola* (Tanneberger et al., 2009, 2010).

The reed bunting *Emberiza schoeniclus* shows a declining population trend in Europe (Voříšek et al., 2010). This decline is most severe in Norway, Sweden and the United Kingdom (Bufield and Van Bommel, 2004), and is dramatic in the Iberian Peninsula, where an 80% loss of breeding population and local extinctions have been reported in recent decades (Atienza and Copete, 2004). The eastern Iberian reed bunting *Emberiza schoeniclus witherbyi* is endemic to a very few western Mediterranean marshes in France, Spain and morocco (Atienza, 2006). In 2005, there were only 254-360 breeding pairs left, distributed between 21 different wetlands (Atienza, 2006). Therefore, this subspecies' distribution is highly fragmented and it is included in the Spanish Red List as an endangered Species (Atienza and Copete, 2004). Since then, the eastern Iberian reed bunting has either become extinct in several wetlands or its population has severely declined.

Recent studies indicate that a heterogeneous habitat structure is important for the occurrence of the eastern Iberian reed bunting at a landscape scale. This includes the presence of large, irregular patches of reed-rush formations within reedbeds, and reed-cattail formations (Vera et al., 2011), also referred to as emergent vegetation (Martínez-Vilalta et al., 2002). It has been suggested that availability of nest sites and foraging habitats is the reason for preference of heterogeneous reedbeds (Vera et al., 2011). Several studies have indicated that loss of suitable habitats is the main reason for the decline of reed buntings in Europe (Siriwardena et al., 2000; Brickle and Peach, 2004; Surmacki, 2004; Orłowski, 2005), where this species is linked to farmlands and wetlands (Cramp and Perrins, 1994). Agricultural intensification and wetland destruction have been proposed to be the main causes for this decline in eastern Iberian reed bunting (Atienza and Copete, 2004), but habitat requirements at a territory scale, and landscape variables and micro-habitat structure relating to establishment of territories, are poorly known, even for the nominate subspecies (Pasinelli and Schiegg, 2006). For example, Poulin et al. (2002) found no significant relationship between the structural parameters studied and the occurrence of this endangered bird.

The aims of the present study were twofold: to identify the habitat components preferred by eastern Iberian reed buntings during the breeding season, which enable them to establish their territories and nests, and to characterise the vegetation structure that is positively or negatively selected on a territory scale. The results obtained from these analyses will prove most useful to implement wetland management guidelines that focus on the conservation of this highly endangered passerine.

Material and methods

Study area

Eastern Iberian reed bunting territories were studied in 11 wetlands in the centre and east of the Iberian Peninsula, as well as at a site in Majorca (Table 1). The surveyed wetlands represent half of the 22 known localities of this species in Spain and they hold 65% of the breeding population estimated in 2005 (Atienza, 2006). One locality, La Veguilla (Ciudad Real), was not included in the 2005 census, despite the eastern Iberian reed bunting being present there in 2006 (Vera et al., 2011). According to the results of the national census carried out by Atienza (2006), the number of territories sampled during the study period agrees with the number of breeding pairs estimated for each wetland in 2005.

Table 1. Wetlands surveyed and number of territories sampled.

Id	Wetland	Coordinates	Area (ha)	Territories sampled (occupied + non-occupied)
1	Embalse de Almoguera	40º 16' N; 2º 56' W	108	(3 + 3)
2	Las Tablas de Daimiel	39º 08' N 3º 42' W	1593	(8 + 4)
3	Delta del Ebro	40º 39' N 0º 44' W	803	(3 + 3)
4	Embalse de Las Cañas	42º 29' N 2º 24' W	95	(1 + 1)
5	Marjal de Pego-Oliva	42º 30' N 0º 03' W	404	(5 + 5)
6	S'Albufera de Mallorca	39 º 47' N 3º 06' E	1448	(5 + 1)
7	Laguna del Juncal	42º 30' N 1º 42' W	8	(1 + 1)
8	Pantà d'Utxesa	41º 30' N 0º 30' E	204	(4 + 2)
9	La Veguilla	39º 23' N 3º 14' W	74	(1 + 1)
10	Villafranca de los Caballeros	39º 27' N 3º 20' W	198	(2 + 2)
11	Ojos de Villaverde	38º 42' N 2º 22' W	49	(1 + 1)

Reed bunting surveys and habitat mapping

The 11 wetlands were surveyed in April and May 2006, a period determined by the timing of the breeding season and the peak period of territorial behaviour (Atienza, 2006). At each wetland, four intensive surveys were conducted, in the mornings (07:00-11:00 h) avoiding adverse weather conditions. Playback of reed bunting song was employed to increase the probability of detection. Song was played for one minute periods alternating with one minute of silence. The recordings used were made as near to the surveyed wetland as possible (Atienza, 2006). Local songs were employed because responses to playback are weaker if songs of different subspecies, or of the same subspecies but recorded at distant localities, are employed (Matessi et al., 1997, 2000). Based on this methodology, the probability of recording a false-negative was estimated as very low (Matessi et al., 2000). Thus, if the reed bunting was not detected after four surveys, it was considered absent at that location. Special attention was paid to territorial behaviour (singing or territory defence), which was georeferenced using a GPS device.

Habitat mapping by intensive field sampling, which covered the whole wetland area, was conducted to study which vegetation factors affected territory establishment. Habitat mapping was conducted between May and June 2006. Mapped vegetation classes included reed *Phragmites australis*, cattail *Typha spp*, saw-sedge *Cladium mariscus*, rushes (*Juncus acutus, Scirpus holoschoenus*, and other rushes of similar structure), tussocks (clumps of saw-sedges or rushes, considering both classes to be a functional vegetation type), club-rushes (thin, sparse sedges, such as *Scirpus maritimus*, *S. tabernaemontani* and *S. lacustris*) and grasslands (formations of grasses). Croplands, forests and infrastructures were not mapped and so were not included in the analyses.

Fifteen vegetation variables were measured (Table 2). Four different dominance categories were established for vegetation: a) *pure formation*, when one species represented between 95 % and 100 % of the cover of the vegetation patch mapped; b) *dominant*, when a species represented 75-95 % of the mapped patch (for example, sedge dominant); c) *co-dominant*, when two species each covered similar areas of 40-60 % (for example, reed-rush); d) *semidominant*, when one species represented 60-75 % and a second species represented 25-40 % of the patches mapped (for example, reed with rushes). A territory was considered to be a 100-m radius circle centred at a georeferenced point and where the eastern Iberian reed bunting was present, following Brickle and Peach (2004). When a male was observed in more than one position, the centre of the territory was considered the mid-point, or centroid, of the polygon formed by these positions. Afterwards, in each wetland where territorial males were not detected, the same number of points were randomly established. These points were considered non-occupied territories. We used a random number generator to select the random coordinates in the study area. At these random points, song playback was replayed to confirm the absence of the eastern Iberian reed bunting. During the field

Table 2. Variables measured at each surveyed wetland and nomenclature used. See methods for the definition of the formations and measured parameters.

	Formations	Reasons for inclusion in the analysis
Water	Open water	Related to nest placement and predation risk (Pasinelli & Schiegg, 2006).
Reed	Pure reedbed	Foraging sites (Isenmann, 1990; Goater, 1993).
Cattail	Pure cattails Reed-cattails Reed with cattails	Selected vegetation parameter on the wetland scale (Vera et al., 2011); used to place nests when dry (Vera et al., 2009) and as singing posts (Surmacki, 2004)
Sedge	Sedge dominant Reed with sedge	Used as nest sites (Vera et al. 2009), and for foraging (Cramp & Perrins, 1994)
Rushes	Rushes dominant Reed–rushes Reed with rushes	Selection of reedbeds with *Juncus* and other halophytes (Martínez-Vilalta et al. 2002), and foraging sites (Cramp & Perrins 1994). Selected vegetation parameter on the wetland scale (Vera et al., 2011).
Tussocks	Tussocks dominant Reed-tussocks Reed with tussocks	Rushes and sedges equally play a functional role in habitat selection (Vera et al. 2001)
Grassland	Formations dominate by herbaceous species and/or grasses	Present in territories (Bricke and Peach, 2004) and used for nest sites (Surmacki, 2004) by subspecies *schoeniclus*

surveys, we recorded 5 false-negative errors out of 28 points (territories initially considered non-occupied but actually occupied) after four field surveys had been conducted at each point (producing disparity from the 1:1 ratio of occupied and random, non-occupied territories in Table 1). Thus, a ratio of 5:28 can be considered high, but we reduced the probability of a false negative error remaining in other territories by resurveying each point 4 times.

We first examined the proportions of each habitat type within each territory. To calculate the proportion of each variable, we measured the percentage of all the vegetation variables in each territory using Arcmap 9.0 software (ESRI, Redlands, California, USA). In non-occupied territories, we calculated the proportion of each variable following the same method as that employed in occupied territories. Vegetation proportion percentages were arcsine-transformed prior to the analysis (Zar, 1996).

We next examined habitat proportions and reed structure in plots within the territories. Within each occupied territory and non-occupied territory, a direction (0-359º) was randomly selected by a random number generator, and these variables were calculated in the 0.5 × 0.5 m plots located in the centre of the circle and every 10 m following the randomly selected direction. We used a 0.5 × 0.5 quadrat frame to standardise all the plot vegetation measures. In each plot, we measured the proportion of open water and the six vegetation classes (reed, sedge, rushes, tussocks, bulrushes and cattail). The density, height and width of the green and dry stems or inflorescences were also measured for all the vegetation classes (following Passinelli and Schiegg, 2006). However, only reed variables were used in further analyses (Table 3) because the sample size of the other vegetation classes was small. To avoid any bias between wetlands due to timing (i.e. affecting the phenology of vegetation), all these measurements were taken after reed flowering. Plant measurements and counts were carried out in these plots. Thus, the vegetation data were taken in a maximum of 11 plots in each territory or non-territory. In those plots, where the sampling direction cut across a free water mass or large expanses of farmland, it was not possible to measure the variables in the 11 plots, and the minimum number of sampled plots was four (mean 5.59 ± 1.78 plots). The mean measurements were calculated for each plot and were used in the subsequent analyses.

Table 3. Variables measured in relation to reed structure in each plot and the nomenclature used.

Variable	Reed type	Measures
Green density	Green reed stems	Number of stems/m^2
Dry density	Dry reed stems	Number of stems/m^2
Mean density	All stems	Number of stems/m^2
Green thickness	Green reed stems	mm
Dry thickness	Dry reed stems	mm
Mean thickness	All stems	mm
Reed youth	All stems	Green density/dry density
Green height	Green reed stems	cm
Dry height	Dry reed stems	cm
Mean height	All stems	cm
Inflorescences	Flowering stems	Number of stems/m^2
Lying reed	All stems	Percentage of lying stems

Statistical analyses

Generalised Linear mixed models (GLMM), with a binomial error distribution, were used to explain the occurrence of eastern Iberian reed bunting territories in the surveyed areas by combining all the variables taken by both approaches (habitat and structure). Site was included as a random effect in GLMMs. Only those variables with $P \leq 0.15$ (according to the Wald's test) in a binomial regression model (Hosmer and Lemeshow, 2000) were included in the subsequent models. This procedure allowed us to reduce the number of possible explanatory variables. As potential predictors, we included the quadratic terms of the variables (Guisan and Thuiller, 2005). The colinearity between the selected variables was evaluated using Spearman's correlation test: when two variables correlated significantly ($P < 0.05$), only the variable with the lower P in the Wald's test was included in the analysis. A Principal Components Analysis approach was not considered a good option to reduce the number of variables because the main aim of the study was to determine the habitat preferences of the eastern Iberian reed bunting that are measurable and can be directly managed.

All the possible models were fitted and the Akaike information criterion (AIC) (Akaike, 1973) was used to select the models that best fitted the data (e.g., Burnham and Anderson, 2002; Johnson and Omland, 2004). Correction of Akaike's index (AICc) was performed for small sample sizes (Burnham and Anderson, 2002; Johnson and Omland, 2004), and was calculated for the whole set of models that contained all the variables and their combinations. We considered models within 2 AICc units of the best model to be competing models (Burnham and Anderson, 2002).

In addition, Akaike's weights (w_i) were calculated for the whole set of models. For the set of models, the w_i values were summed to 1. w_i were used to calculate the probability that a variable k, from among all the variables considered in the analysis, was the best model to account for our data (Burnham and Anderson, 2002; Johnson and Omland, 2004). This probability was calculated as the sum of the w_i values of all the models that included k.

A ROC (Receiver Operating Characteristic) curve was used to test the model's predictive ability. ROC curves relate true positive cases (sensitivity) and the corresponding false-positive cases (1-specificity) in a range of thresholds (Hanley and mcNeil, 1982). For these curves, we calculated the area under the curve (AUC), which varied from 0.5 (a model whose discriminative ability was no better than by random) to 1 (a model with perfect discriminative ability) (Fielding and Bell, 1997; Pearce and Ferrier, 2000). All the statistical procedures were performed with SPSS 19.0.

A partial mantel test was performed to assess the role of geographic distances in the relation between the variation of number of territories and the vegetation parameters identified in the previous analyses. For each wetland, similarity matrices of number of territories, vegetation parameters (calculated as the mean of the parameters data for each territory in each wetland) and geographic distances were calculated according to Euclidean distances. The analysis was performed using PAST v. 3.01 software (Hammer et al., 2001).

Results

Of the initial 33 variables (14 habitat and 19 structural variables), only 10 variables were below the threshold for inclusion in variables were excluded as they correlated strongly, and 22 were removed from further analyses as they showed a high degree of correlation. After reducing the variables, logistic regressions were performed with four habitat variables (proportions of reed with dominant cattails, reed-cattail, reed with tussocks and rushes), three structural variables (proportions of cattails, water and sedge) and their quadratic terms.

Relative support for the candidate models of effects of vegetation on territory establishment showed the importance of reed with cattails and rush patches (Table 4). However, the effects of the four variables in the best supported models were not significant (Table 5). So the model with the best AICc score showed poor discriminative ability and correctly classified only 62.1 % of cases (AUC = 0.542 ± 0.078; *P* = 0.591). The proportion of reed-cattails scored the highest Akaike's weight ($w_1 = 0.392$). The use of quadratic terms did not improve the fit of the models, so a quadratic relationship as considered not to occur.

Significant differences were found between occupied and non-occupied territories in the proportion of reed with tussocks ($t = 2.521$, df = 43.721, $P = 0.015$), with higher values in occupied territories. None of the variables measured by the vegetation structure approach, and retained after the correlation analysis, showed significant differences between occupied and non-occupied territories.

These vegetation parameters did not correlate with territory abundance in each wetland (reed-cattails: mantel's r = −0.073, P = 0.439; proportion of reed with tussocks: Mantel's $r = -0.062$, $P = 0.509$). The results did not vary when controlling for geographic distances between wetlands (reed-cattails: partial Mantel's $r = -0.077$, $P = 0.452$;

Table 4. Model selection according to the corrected Akaike's Information Criterion (AICc) using the habitat and structural variables. Only competing models are shown. K: Number of parameters estimated. Δ_i: Difference between the AICc of the model and the lower AICc value of the whole set of models. w_i: Akaike's weight calculated for the whole set of models developed with all the variables. H_ is used to denote habitat variables.

Id	Model	K	AICc	Δ_i	w_i
1	H_Reed-cattails	2	256.611	0	0.311
2	H_Rushes dominant	2	258.044	1.433	0.152
3	H_Reed with cattails	2	258.313	1.702	0.133
4	H_Reed with tussocks	2	258.377	1.766	0.129

Table 5. Results from the models shown in table 4 for the effects of habitat variables on eastern Iberian reed bunting territory selection.

Model ID	Variable	ß	se	t	*P*
1	Intercept	0.429	0.273	1.571	0.122
	H_Reed-cattails	-0.070	0.079	-0.880	0.383
2	Intercept	0.155	0.285	0.543	0.509
	H_Rushes dominant	0.036	0.023	1.79	0.120
3	Intercept	0.431	0.275	1.568	0.122
	H_Reed with cattails	-0.035	0.031	-1.115	0.269
4	Intercept	0.089	0.289	0.295	0.769
	H_Reed with cattails	0.043	0.023	1.838	0.071

proportion of reed with tussocks: partial Mantel's r = −0.064, P = 0.511). This indicates that geographic distances had no effect on the relation of these vegetation parameters to the abundance of reed bunting territories.

Discussion

Habitat preferences at the territory scale

Our study shows that in the 11 wetlands comprising our study, the proportion of cattails is a variable that better explains the occurrence of territories of the eastern Iberian reed bunting. According to the Akaike weights, the proportion of reed with cattail is also important among the variables studied for occurrence in territories. However, both models offer poor predictive accuracy. These results support previous studies conducted at single wetlands, such as those carried out in the Ebro Delta (Martínez-Vilalta et al., 2002; Bigas and Copete, 2004) and Camargue (Poulin et al., 2002), which did not find a relationship between cattails and the abundance of territorial eastern Iberian reed buntings.

A previous study found that eastern Iberian reed buntings preferred wetlands with cattails (Vera et al., 2011). The different results obtained by all these studies may reflect a different interaction with cattails on wetland and territory scales since cattail presence is related to the occurrence of stable water levels between seasons and years (Asaeda et al., 2005; White et al., 2007; Chun and Choi, 2009). Moreover, presence and cover of cattails may act as an indicator of wetlands with stable hydrological conditions. The territory scale, as in the present study, may indicate stable flooding conditions, which have been related to increased predation probabilities at the nest stage in the northern reed bunting *Emberiza schoeniclus schoeniclus* (Passinelli and Schiegg, 2006), since reed buntings are small ground-nesting passerines (Cramp and Perrins, 1994). In fact, evidence for the direct employment of cattails by reed buntings implies their use as singing posts (Sumarcki, 2004), sources of nest material and nest sites, but only when cattails are found on dry substrates (Vera et al., 2009), which suggests that their importance with respect to territory siting is secondary and non-definitive.

Reed cover with tussocks was higher in occupied territories than in non-occupied territories, being a good predictor of territory occurrence. Mixed formations of reed and tussocks were a determinant of species occurrence at the wetland scale (Vera et al., 2011). In addition to the good food availability for adults in reeds (Insemann, 1990; Goater, 1993) and for fledglings in tussocks or rushes (Cramp and Perrins, 1994), a preference for less fragmented areas (largely covered by one vegetation class) has been related to reduced nest predation probability (Lahti, 2001; Bátary et al., 2004; Schiegg et al., 2007), since nests located in small reed patches were more likely to be depredated (Pasinelli and Schiegg, 2006; Schiegg et al., 2007). According to our results, tussocks are preferred for territory establishment, but not in pure formations. A proportion of tussocks in a given territory can greatly enhance nestling feeding opportunities (Cramp and Perrins, 1994) and tussocks also provide singing posts (Surmacki, 2004) and nest sites (Vera et al., 2009).

Therefore, the fact that the habitat preferences at the territory scale studied here and those preferred at the wetland scale (reed patches with rushes/tussocks, see Vera et al., 2011) coincide may reflect the probability of occurrence of eastern Iberian reed buntings in a given wetland according to habitat composition, as determined by the probability of territory establishment in terms of habitat availability.

Finally, we cannot ignore the fact that other factors such as food availability, density of predators and/or the density of conspecific breeding pairs, may also determine territory selection by the eastern Iberian reed bunting. In addition, other variables extrinsic to habitat, such as local knowledge, the experience of older males and a lack of suitable alternative habitats, can dissociate territory siting from habitat quality (Musilova et al., 2011). Nonetheless, this has been described in populations that strongly compete for territories, and this is not the case in Iberian reed buntings. Territory choice may also depend, at least in part, on the presence of predators rather than on habitat characteristics, when there is only one main predator (Trnka et al., 2011). In our study area however, the diversity of potential predators was high and included mammals, reptiles and birds (pers. obs.), suggesting that selection pressure due to predation avoidance does not favour the selection of a given habitat.

Implications for conservation and wetland management

The presence of a high proportion of sedge, tussocks or mixed formations of these with reeds appears to be important in territory selection by the eastern Iberian reed bunting and this finding is similar to that reported at a wetland scale (Vera et al., 2011). Hence, wetland management should maximise the presence of reed patches with tall stems and tussocks to increase not only the likelihood of occurrence of eastern Iberian reed buntings but also their population size or number of territories (assuming the latter is a limiting factor).

Furthermore, predation is a highly relevant factor that should be considered as it is the main source of nest failure in reed buntings (Crick et al., 1994). Thus, intensive wetland management may lead to higher nest failure levels due to increased predation (Schiegg et al., 2007), and also to the mid- and long term abandonment of a reproduction area, as reported for other reedbed passerines (Báldi, 1999). In those areas that are managed to promote the species' occurrence, the limitation or exclusion of potential predators, such as rodents, rails, marsh harriers *Circus aeruginosus*, red foxes *Vulpes vulpes* and wild boars *Sus scrofa*, should also become a principal but complex consideration.

Reed cutting and burning are discretionary management practices. Large-scale reed cutting is usually harmful for reedbed passerines making nesting harder for species, such as eastern Iberian reed buntings, that breed early in the season (Poulin and Lefrebvre, 2002). In addition, reed burning can significantly stunt stem height (Valkama et al., 2008). Regarding food availability, both reed cutting and reed burning on a large scale can diminish the abundance of Lepidoptera (Schmidt et al., 2005; Valkama et al., 2008), among which moths (specifically *Archanara geminipunctata*) are one of the main components in the eastern Iberian reed bunting's diet during the breeding season (Goater, 1993). This moth does not appear in burned and mown reedbeds because its eggs remain in stems throughout winter and its larvae do not disperse until after hatching, around May (van der Toorn and mook, 1982). Hence, such practices can drastically reduce the abundance of this main element in the species' diet, especially where there has been intensive management over at least 3-5 years during which the moth overwintering stages are repeatedly being removed (Valkama et al., 2008). Recent studies have revealed that small-scale, mosaic reed cutting does not negatively affect food abundance and nest survival in *Acrocephalus* warblers and bearded tits *Panurus biarmicus* (Trnka et al., 2013). However, no comparable data are currently available for reed buntings.

Flood control appears to be a useful method to manage the presence, density and proportion of reeds, tussocks and cattails as it regulates competition between reeds and other emergent species (Hellings and Gallagher, 1992; Coops et al., 1994; Asaeda et al., 2005; Chun and Choi, 2009).

Finally grazing, although complementary to other management practices, may facilitate the presence and density of tussocks through the control of reedbed spread, although grazing pressure must be low to avoid grassland development (Vulink et al., 2000). For example, low-density grazing (1.3 animals/ha) occurs in the Encanyissada lagoon (Ebro Delta) where eastern Iberian reed buntings breed (Martínez-Vilalta et al., 2002). This management practice must be carried out only in those areas where predator pressure from wild boars and red fox is low because grazing increases not only habitat heterogeneity (van Oene et al., 1999), but also the presence of edge habitats, which favour predator presence (Seymour et al., 2003).

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Estructura y composición del nido de Escribano Palustre Iberoriental *Emberiza schoeniclus witherbyi*

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ESTRUCTURA Y COMPOSICIÓN DEL NIDO DEL ESCRIBANO PALUSTRE IBERORIENTAL *EMBERIZA SCHOENICLUS WITHERBYI*

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Abstract

We studied the plant composition and structure of Eastern Iberian Reed Bunting *Emberiza schoeniclus witherbyi* nests in Las Tablas de Daimiel National Park (Ciudad Real, Spain). Nests were cup-shaped, with materials finely interwoven in spirals or in simple wave forms. Plant matter such as reed sheaths and leaves formed the basic structure, and other materials such as small fragments of plant stems and grass helped in compacting and reinforcing the structure. The inner layer of the nest bowl was lined with wild boar hairs, with a probably thermoregulatory and insulation function. The weight distribution of the different materials varied greatly between nests.

Key words: nest structure, nest composition, plant matter, Reed Bunting, *Emberiza schoeniclus witherbyi*, Tablas de Daimiel.

Introducción

La estructura y composición de los nidos naturales de aves son resultado de distintas presiones de selección, como la protección frente a predadores o el aislamiento de huevos y pollos ante factores climáticos adversos (Slagsvold 1989, Lens et al. 1994, Hansell 2000, Alabrudziñska et al. 2003), y tienen como fin último el maximizar la eficacia reproductiva. En este sentido, la estructura de nidos naturales y su variación intraespecífica ha sido bien estudiada (Kern 1984, Slagsvold 1989, Hoi et al. 1996, Palomino et al. 1998, Soler et al. 1998, Suárez et al. 2005, Tomás et al. 2006), aunque los estudios sobre su composición vegetal son escasos (Calvelo et al. 2006) o se refieren únicamente a alguno de sus componentes (Clark & Mason 1988, Lambrechts & Dos Santos 2000, Mazgajski 2007). La composición de los nidos constituye un buen indicador del uso de hábitat y los requerimientos ecológicos de las aves en el momento crítico de la reproducción, ya que cada tipo de material usado por cualquier especie en la elaboración del nido tiene una función definida (termorreguladora, aislante, soporte, etc.) de acuerdo a las propiedades físicas del material vegetal (Martínez Vilalta et al. 2002, Calvelo et al. 2006).

El Escribano Palustre Iberoriental *Emberiza schoeniclus witherbyi* se encuentra clasificado como "En Peligro de Extinción" en el último Libro Rojo (Atienza & Copete 2004), ya que sus tamaños poblacionales son de los más exiguos de entre los paseriformes nidificantes en España (Atienza 2006). Sus requerimientos para la nidificación no han sido estudiados en detalle, a diferencia de la subespecie nominal, la cual muestra una clara preferencia por nidificar sobre vegetación bien desarrollada, recurriendo a los herbazales anexos en busca de alimento (Brickle & Peach 2004, Orlowsky 2005). En el caso del Escribano Palustre Iberoriental únicamente se ha descrito someramente su preferencia por establecer poblaciones reproductoras en humedales caracterizados por la presencia de masegares y carrizales poco o nada inundados, con una altura de la vegetación menor de 3 m (Martínez Vilalta et al. 2002). La estructura y composición de sus nidos no ha sido estudiada hasta la fecha. El propósito del presente estudio es explorar la estructura y composición vegetal de los nidos de Escribano Palustre Iberoriental del Parque Nacional de las Tablas de Daimiel. En una fase vital tan crítica como es la reproducción, el uso concreto o exclusivo de unos determinados materiales vegetales puede suponer un recurso limitante que afecte directamente a la conservación de este paseriforme palustre amenazado.

Material y métodos

El estudio fue realizado en el Parque Nacional de las Tablas de Daimiel (1928 ha; Ciudad Real, C de España), entre abril y julio de 2007. La vegetación de las Tablas de Daimiel está formada mayoritariamente por carrizales densos (*Phragmites australis*). En los lugares que acumulan una mayor humedad edáfica, o permanecen con una pequeña lámina de agua durante mayor tiempo, resulta frecuente encontrar vigorosas formaciones de eneas (*Typha dominguensis*) y juncales (*Juncus* spp., *Scirpus* spp.). En épocas secas, comenzando en mayo y hasta las lluvias otoñales, los herbazales terofíticos y de hemicriptófitos toman mayor relevancia, extendiéndose en aquellos lugares ocupados anteriormente por la lámina de agua y los juncales.

La población de Escribano Palustre Iberoriental del Parque Nacional de las Tablas de Daimiel, estimada en el último censo nacional en 90-120 parejas (Atienza 2006), resulta el principal núcleo poblacional de la subespecie (de una estima total de 254-360 parejas). El hecho de que la población haya aumentado de forma significativa desde los censos realizados en la última década y las condiciones climáticas del año en que se realizó el censo nacional inducen a pensar que el Parque Nacional puede ejercer de refugio de poblaciones de otros humedales manchegos.

Para localizar nidos de Escribano Palustre Iberoriental, se prospectó el área de estudio en busca de machos territoriales. Posteriormente se realizó un seguimiento de los territorios encontrados con el fin de detectar la construcción de nidos o la ceba de pollos. Se llevó a cabo durante estas fases de la reproducción ya que resulta más sencillo que durante la puesta o el período de incubación. Una vez detectadas dichas actividades, se procedía a la búsqueda del nido. Tras su localización, y en función de la fase de construcción en que se encontraba, se realizó al menos una visita de comprobación y otra para proceder al anillamiento de los pollos. En las ocasiones en que se encontró una puesta completa se hicieron una o dos visitas más. La recogida del nido se efectuó entre cinco y diez días después de observar el vuelo de los pollos o constatar el fracaso de la reproducción (por predación o causas ambientales), guardándose en una bolsa de cierre hermético.

A cada nido se le tomó medida del diámetro mayor, menor y altura del nido, diámetro interno mayor, menor y profundidad del cuenco (Ponz et al. 1997, Palomino et al. 1998, Hansell 2000, Herranz et al. 2004) (Figura 1). Los materiales fueron separados atendiendo a si participaban de la estructura de la base o del propio nido. Dentro de estos grupos estructurales, se separaron los materiales en 5 clases: tallos finos (Ø=1 mm), tallos y ramas (Ø>1 mm), hojas de gramíneas herbáceas, hojas de carrizo y material no vegetal. Los materiales que no formaran parte de la estructura del nido fueron determinados y tratados por separado. Los diferentes componentes del nido fueron analizados con lupa binocular para determinar la especie a la que pertenecía. Con el fin de determinar la importancia relativa de los distintos componentes, éstos fueron pesados por separado en una balanza electrónica (precisión ± 0,01 g).

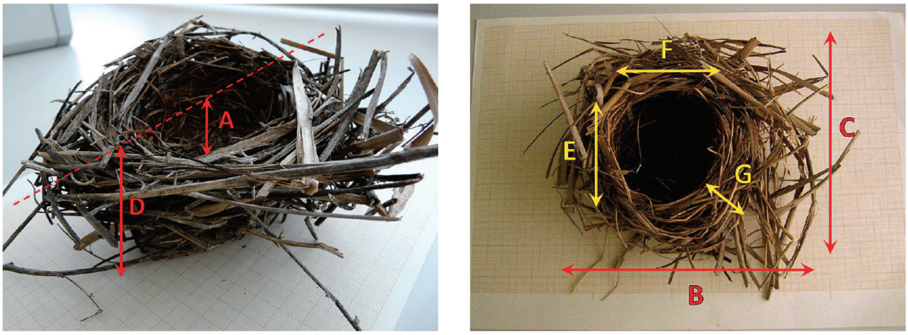

Figura 1. Vista superior y lateral de nido de Escribano Palustre Iberoriental mostrando las medidas tomadas. A = Profundidad del cuenco; B = Diámetro mayor de la estructura; C = Diámetro menor de la estructura; D = Altura de la estructura; E = Diámetro mayor de la estructura; F = Diámetro menor de la estructura; G = grosor del cuenco.

Resultados y discusión

Fueron recogidos un total de siete nidos de Escribano Palustre Iberoriental. Los valores promedios para las medidas realizadas se muestran en la Tabla 1. El diámetro mayor y menor del cuenco así como su profundidad fueron los parámetros que tuvieron menor variación, pudiendo ser el origen de tal variación las diferencias en el tamaño de las hembras. El resto de parámetros, mostraron una mayor variación entre nidos, ya que dependen de las características del lugar donde ha sido construido el nido o las preferencias de las hembras. El peso del nido fue el parámetro más variable, siendo dependiente de los porcentajes de cada tipo de material empleado en su construcción. Siguiendo las directrices de Hansell (2000), los nidos de Escribano Palustre Iberoriental pueden ser clasificados como "de copa" y, según el lugar en el que han sido construidos, tres de ellos se encuentra en la categoría de "herbazal y carrizo" y cuatro en la categoría de "árboles y arbustos". Los nidos presentaban una base que proporcionaba estabilidad, encontrándose asentados sobre el sustrato vegetal o el suelo.

Los materiales fueron tejidos de forma mixta, enrollándose en espiral y mediante ondas simples (Hansell 2000), llegando alguno de los componentes vegetales de los nidos a medir más de 70 cm de longitud. Se pudo determinar el origen del material vegetal hasta nivel de especie en cuatro casos, mientras que en otros ocho casos únicamente se llegó a nivel genérico, no quedando materiales vegetales sin determinar. El grupo funcional de hojas de carrizo estuvo formado únicamente por material foliar seco de *Phragmites australis*, pudiendo estar recortado longitudinal o transversalmente. Se emplea en todas las capas del nido, siendo menor la representación en la capa inmediatamente inferior al cuenco del nido.

Tabla 1. Medidas de los nidos (en centímetros) y peso (en gramos) de Escribano Palustre Iberoriental en el Parque Nacional de las Tablas de Daimiel (n =7). D.T. = Desviación típica.

	Media	D.T.
Profundidad del cuenco	3.27	1.26
Diámetro interno mayor del cuenco	7.04	0.38
Diámetro interno menor del cuenco	5.93	0.45
Altura de la estructura	8.24	2.02
Diámetro mayor de la estructura	17.59	3.45
Diámetro menor de la estructura	15.14	2.90
Grosor del cuenco	4.67	1.21
Peso	17.51	7.97

Tabla 2. Distribución en pesos de los materiales pertenecientes a las distintas clases (medidas tomadas en gramos); — = ausente.

	Nido 1	Nido 2	Nido 3	Nido 4	Nido 5	Nido 6	Nido 7
Peso	9.90	8.95	25.3	29.03	13.92	23.15	12.34
Base del nido							
Tallos finos	-	0.09	0.00	0.16	0.57	0.12	0.29
Tallos gruesos/ramas	-	1.34	1.01	5.95	0.27	4.01	2.18
Material no vegetal	-	0.04	0.05	0.10	0.04	0.07	0.07
Hojas gramíeas	-	1.63	4.85	0.00	0.00	0.44	0.21
Hojas carrizo	-	0.11	1.36	10.28	3.41	2.30	1.95
Peso total base	-	3.21	10.27	16.49	4.29	6.94	4.70
Nido							
Tallos finos	1.13	0.28	0.43	1.84	1.47	0.39	3.16
Tallos gruesos/ramas	2.82	0.38	1.76	1.72	1.76	7.37	1.89
Material no vegetal	1.77	1.37	1.96	2.60	1.89	4.77	1.16
Hojas gramíeas	3.13	2.64	7.82	0.00	1.78	1.35	0.33
Hojas carrizo	0.13	0.69	1.74	2.74	2.48	1.93	0.82
Otros restos	0.92	0.27	1.32	3.61	0.16	0.40	0.28
Material exógeno	0.00	0.11	0.00	0.03	0.09	0.00	0.00
Sustrato	Suelo	Masiega	Enea	Suelo	Masiega	Masiega	Masiega

La presencia de hojas de carrizo en el cuenco del nido fue más reducida que su participación en la formación de las bases de los nidos. La razón más probable para este hecho es la mayor dificultad existente en el manejo de estas hojas para la estructuración del nido, empleándose para tal fin tallos de juncos, ramas y tallos finos, que tienen un mayor contenido en lignina, siendo por tanto más resistentes a movimientos mecánicos que pueden ocurrir de manera natural sobre el sustrato del nido o sobre éste mismo.

Dentro de los tallos finos, destacó la presencia de gramíneas anuales (*Poa* spp. y *Polypogon monspeliensis*) de las que se emplearon tanto los tallos como las hojas e inflorescencias. En el nido 5 se observó la presencia de zarcillos de vid (*Vitis vinífera*). Frecuentemente encontramos los tallos finos entretejidos formando el armazón del cuenco, aunque son materiales muy poco utilizados en la base debido a su escasa consistencia para formar la estructura del nido. Sin embargo, resultan muy útiles para afianzar la estructura del nido al ser entretejidos transversalmente al resto de materiales que forman el cuenco del nido. En el caso del grupo funcional de tallos gruesos y ramas, encontramos gramíneas, todo tipo de material procedente de la crucífera *Cochlearia glastifolia*, inflorescencias de *Daucus* spp., hojas de castañuela (*Scirpus maritimus*) y frutos de *Erodium* spp. La flexibilidad de las hojas acintadas de gramíneas o juncos permite entrecruzarlas en el exterior del cuenco, para dar mayor consistencia. En algunos de los restos de este material se encuentran vestigios de barro, por lo que se deduce que fueron recogidos del suelo. En el caso del material correspondiente a plantas herbáceas como *Cochlearia glastifolia*, *Erodium* spp y *Daucus* spp, el material utilizado se encuentra siempre seco, independientemente de si se trata de frutos, inflorescencias o ramas, a pesar de la presencia en el entorno de elementos frescos.

El material no vegetal correspondió a pelo de jabalí *Sus scrofa*. A causa de su baja consistencia como material estructural, creemos que su presencia en el revestimiento del cuenco sugiere una función termorreguladora durante la incubación (Hansell 2000).

El material exógeno es aquél que no forma parte directa de la estructura del nido. En este grupo se detectaron plumas de los padres, restos de cáscaras de los huevos eclosionados, escamas de los plumones de los pollos y restos de los pequeños artrópodos consumidos por los pollos, como fue el caso de *Armadillium vulgare*, Oniscidea: Isopoda (Brickle & Peach 2004). Estos materiales se encontraron en el interior del cuenco.

La distribución en pesos de los materiales empleados en la base del nido (Tabla 2) sugiere un papel determinante de las hojas de carrizo (10,28 g en el nido 4, lo que representa aproximadamente un 62% del peso total). Tienen también un papel destacado en la fijación del resto de material, los tallos de juncos y ramas de herbáceas, aunque no en todos los nidos. Coincidiendo con aquellos nidos construidos sobre carrizo o eneas, el peso parcial de las hojas de gramíneas resulta un parámetro relevante en el peso de la base de los nidos de los que se disponen de estas medidas. Al igual que ocurre con otros paseriformes (Calvelo et al. 2006), el uso predominante de un material en las capas externas y base de los nidos parece indicar una función mimética contra el ataque de depredadores (Hansell 2000). En este sentido, la predación de nidos es un fenómeno muy frecuente en paseriformes palustres (Neto 2006), habiéndose demostrado que la presión predadora sobre nidos del Escribano palustre norteño *Emberiza schoeniclus schoeniclus* es mayor cuanto mayor grado de fragmentación presentan los ambientes palustres (Schiegg et al. 2007).

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Capítulo VI

Using remote sensing to study the vegetation dynamics of a coastal Mediterranean wetland and its effect on the habitat availability of a threatened passerine

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COMBINING REMOTE SENSING AND FIELD MAPPING METHODS TO STUDY THE VEGETATION DYNAMICS WITHIN A COASTAL WETLAND AND DETERMINE THE HABITAT EFFECTS OF A THREATENED BIRD SPECIES (*EMBERIZA SCHOENICLUS WITHERBYI*)

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Abstract

Coastal wetlands are highly dynamic changing ecosystems because of the effects of meteorology, wildlife interactions and human activities. They are one of the world’s most threatened ecosystems, and threats to them drive the most specialist species to unfavorable conservation status and population trends. It is, therefore, very important to frequently monitor the coverage changes of the different vegetation types in order to understand these species’ population dynamics. However, frequent and detailed cartography entails costly efforts. Here, satellite images with field mapping were combined to create vegetation classification maps for past years from SPOT-5 images in the Pego-Oliva coastal wetland (Spain), and obtained classification accuracies above 85%. Together with habitat selection models, this information was used to understand the changes in the habitat of a threatened bird species, the Eastern Iberian reed bunting (*Emberiza schoeniclus witherbyi*), whose population has sharply declined in recent decades in Spain. A statistically significant reduction in reed-rush patches (positively selected habitat) and an increase in homogeneous reed patches (negatively selected habitat) were observed in those areas where the species disappeared as breeders. This study shows the potential of remote sensing and GIS techniques for the *a posteriori* monitoring of variation in the habitats available for threatened species in order to set up management and conservation measures.

Keywords: Habitat selection, Mediterranean wetland, reed bunting, SPOT-5, vegetation classification map.

Introduction

Wetlands are among the world's most threatened ecosystems (Dudgeon et al., 2006; Strayer and Dudgeon, 2010). Loss or degradation of habitat, over-exploitation, water pollution, modification of hydrological cycles and invasive species all threaten the biological communities of wetlands (Allan and Flecker, 1993; Darwall et al., 2009; Revenga et al., 2005). High productivity levels and strong selection pressure make these ecosystems excellent sites for biodiversity, which include species of notable conservation interest, *e.g.*, marshland birds (Dudgeon *et al.*, 2006; Haig and Mehlman, 1998), some of which are very sensitive to habitat changes (Martínez-Vilalta *et al.*, 2002; Poulin and Lefebvre, 2002; Poulin, Lefebvre, and Mauchamp, 2002; Tanneberger et al., 2009). As coastal wetlands are highly dynamic ecosystems, studying the habitats of the species that live there is very difficult (Mialon, Roger, and Fily, 2005), which is why new methodologies based on mapping techniques are being rapidly developed in order to monitor and plan conservation strategies for these ecosystems (Davranche, Lefebvre, and Poulin, 2009; Klemas, 2011; Poulin *et al.*, 2010).

In these dynamics systems, given the need to create cartographies in short time intervals, satellite images greatly reduce the effort required and economic costs of systematically mapping vegetation *in situ*. Nevertheless, the selection of appropriate satellite images and vegetation classification methodologies is not a trivial issue (Klemas, 2014). Suitable spectral and spatial resolutions, together with sufficient satellite revisiting frequency, are crucial in order to identify the complex wetland vegetation types correctly (De Roeck *et al.*, 2008; Melack and Hess, 2004). Accurate vegetation mapping is especially important for those ecologists studying how habitat changes are affecting animal populations (Rocchini *et al.*, 2011).

Combining maps of habitat changes with predictive habitat models using GIS methodologies provides us with an excellent tool for analyzing the dynamics of bird populations when population data are scarce or non-existent. Until quite recently, most analyses of bird habitats have used low-spatial resolution images, such as Landsat images (Gottschalk, Huettman, and Ehlers, 2005; Shirley *et al.*, 2013). However, higher-spatial-resolution maps allow researchers to deal with new studies of the combined dynamics of habitats and species' populations based on predictive habitat models created on a small spatial scale (Keith et al., 2009; Leyequien et al., 2007; Turner et al., 2003).

The species selected for this study was the Eastern Iberian reed bunting (*Emberiza schoeniclus witherbyi*, hereafter referred to as reed buntings), an endemic subspecies of the Western Mediterranean Basin (Byers, Olson, and Curson, 1995). The population of this subspecies has sharply declined in the last decades and its Spanish population includes only 250-350 breeding pairs, according to a census in 2005, which were found mainly in wetlands in the Castilla-La

Mancha region (Atienza, 2006). For this reason, this subspecies is listed as “Endangered” in the Red Book of Spanish Birds (Madroño, González, and Atienza, 2004) following IUCN criteria and is also listed in the Spanish List of Threatened Species (Catálogo Nacional de Especies Amenazadas, *Real Decreto 139/2011*). In the Marjal de Pego-Oliva Natural Park, a small coastal wetland of Eastern Spain, this subspecies was recorded as a breeder between the 1990s and 2007 (Atienza, 2006; Vera *et al.*, 2009).

The present study had two objectives: i) to obtain a classification of the vegetation in Marjal de Pego-Oliva, a highly dynamic coastal wetland, for previous years by combining fieldwork and SPOT-5 images; and ii) to analyze vegetation changes in association with the local-scale decline of the reed bunting, a species with strong habitat selection.

Methods

The methodology is based on two main phases: the creation of vegetation maps and the analysis of the changes in the key habitats for the study species. A field-based map of the study area was combined with satellite images of previous years to obtain vegetation classification maps. These maps were then used to analyze temporal changes, at different scales, in the positively and negatively selected habitats of the study species.

Study area

This study was carried out in the Marjal de Pego-Oliva Natural Park, a 1290-hectare wetland located in the east of the Iberian Peninsula (38º52’ N, 0º3’ W; Figure 1), which is included in the Natura 2000 Network. Vegetation is dominated mainly by common reed (*Phragmites australis*), cattails (*Typha angustifolia*), rushes (*Juncus acutus, J. maritimus*) and bulrushes (*Scirpus maritimus, S. lacustris, S. holoschoenus*) and presents interannual variations that correspond to the superficial or phreatic water levels, and to the management of the habitat for hunting purposes. The surroundings of the wetland habitats are characterized by the presence of a mosaic of crops, rice fields, dispersed reed patches, humid grasslands and temporary ponds.

Field map

In order to perform a multiseason analysis of vegetation, a vegetation map of Marjal de Pego-Oliva charted *in situ* between May and June of 2008 was used as a reference. The following vegetation types were charted: common reed, cattails and rushes (*J. acutus, S. holoschoenus* and other rushes with similar ecological roles). Water channels, farmland tracks, paddy fields and buildings were also charted, with each variable mutually exclusive from the other variables. Given the need for high-spatial-resolution vegetation mapping, aerial photographs close in time to 2008

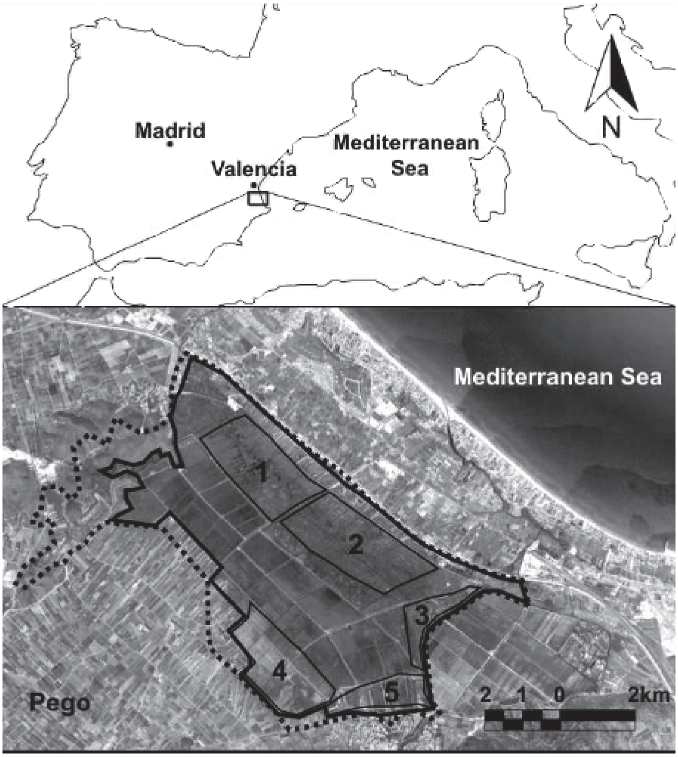

Figure 1. Location map of the study area. Dotted line represents the Marjal de Pego-Oliva Natural Park limits and the thick solid line comprises the palustrian vegetation and rice fields. Thin solid lines represent the high-interest regions. These regions were by delimited by considering the areas with a high probability of occurrence of a territorial male (>80 %) based on the habitat selection models in Vera et al. (2014).

were used to help to georeference the vegetation unity limits with GPS. Subsequently, field data were transformed into digital polygons using the ArcMap software (Environmental Systems Research Institute, 2009).

Processing and classifying SPOT-5 images

SPOT-5 images were obtained through the Programa Nacional de Teledetección (PNT; Spanish National Geographical Institute). Images taken between June and August in 2005, 2006, 2008 and 2009 were used. No images of sufficient quality taken in 2007 were available because of high cloud coverage on the satellite over-pass dates required for this study. SPOT-5 multispectral images have four bands (b1: 0.50-0.59 µm; b2: 0.61-0.68 µm; b3: 0.79-0.89 µm; b4: 1.58-1.75 µm), presenting a spatial resolution of 10 m for bands b1, b2 and b3, and of 20 m for b4. This spatial resolution is adequate for performing vegetation classification studies in wetlands (Poulin *et al.*, 2010). Satellite images were preprocessed at level 1A (www.spotimage.com) and geometric correction with the nearest neighbor interpolation algorithm was applied (Davranche et al., 2009).

Following this, a relative atmospheric correction, using the dark subtract algorithm (Chuvieco, 2002), was performed. The dark subtract correction allows us to perform a multitemporal analysis without obtaining the absolute reflectance values of the vegetation for each image, which thus provides a much simpler and more reliable work flow (Keith et al., 2009; Martin, Howarth, and Holder, 1998). Masks were applied to the clouds and the clouds' shadows, and these areas were left out from the classification process.

The vegetation classification process was carried out by applying a supervised classification (Richards, 2006). Regions of interest (ROI) were created for each image by identifying 12 land-cover types that form the wetland and those detectable by satellite images (Table 1). Field map vegetation types were used to identify these land-cover classes and to create the ROI for the year 2008. For all the other years, the visual interpretation was combined with the comparison of the spectral signatures to create ROI (Martin, Howarth, and Holder, 1998). The vegetation patches for the years 2005, 2006 and 2009 were visually identified, with limits that coincided with the same patches in the 2008 image for all the bands. This allowed the identification of temporary stable patches. To test the validity of this

Table 1. Description of land-cover classes used for the supervised classification. Four different dominance categories were established for vegetation formations: a) pure, when one species represented 95-100% of the cover of the vegetation patch mapped; b) dominance, when a species represented 75-95%; c) co-dominance, when two species covered similar areas of 40-60% (i.e., reed-rush); d) semi-dominance, when one species represented 60-75% and a second species represented 25-40% of the patch (i.e., reed with rushes).

Land-cover class	Description	Correspondence to field-map formations
Reed	Common reed (*Phragmites australis*)	Pure reedbed
Reed-rushes	Common reed with *Juncus* and other structurally similar species.	Co-dominance and semi-dominance of reedbeds with rushes
Reed-cattail	Common reed with cattails (*Typha angustifolia*)	Co-dominance and semi-dominance of reedbeds with cattails
Grassland	Herbaceous species and/or grasses	Pure grassland
Rushes	Juncus and other structurally similar species	Pure or semi-dominance of rushes
Reed-bulrushes	Common reed with bulrushes (*Scirpus maritimus, S. lacustris, S. holoschoenus*)	Co-dominance or semi-dominance of reedbeds and bulrushes
Water	Ponds and channels	Open water
Paddy field	Rice cultivations	Paddy field
Flooded paddy	Rice cultivations with the presence of a thin water layer	Paddy field
Crops	Vegetable cultivations	Crops
Citrus	Citrus fruits cultivations	Citrus
Building	Buildings, roads, and other constructions	Building

methodology, the spectral signatures of these patches were compared with those of the image taken from 2008 (Richards, 2006). If these geometrically constant patches had been completely replaced by another vegetation type, the spectral signature would have changed. After selecting some of these patches as our ROI, a spectral separability analysis (Richards, 2006) was performed to avoid identifying land regions that were too complex, which could affect the quality of the vegetation classification. With the selected ROI, a supervised classification was made using a maximum likelihood algorithm. ENVI 4.3 (ITT Visual Information Solutions, Boulder, CO, USA) was used to perform the spectral separability analysis and the supervised classification.

To measure the validity of the classification for the 2008 map, 100 random points were created and the classified land use was compared with that of the vegetation field map. ArcMap and the Hawth's Tools for ArcMap (Beyer, 2002) were employed to create random points and to compare land uses between the two maps. Some land-use classes on the field map were joined to meet the supervised classification classes. In order to test the accuracy of the classification for the other years, a confusion matrix (Richards, 2006) was created by comparing the results with the ROI data, and then calculating the overall accuracy index and the kappa coefficient (Congalton, 1991).

Reed bunting population

Each survey consisted of three linear transects. These covered all the habitats within the study area, and gave a total length of 15.02 km (Tr.1: 5.47 km; Tr.2: 5.08 km; Tr.3 4.49 km) and a lateral coverage of 100 m. Surveys were conducted weekly from May to July between 2005 and 2009, to avoid coming into contact with late-migrating individuals belonging to the *schoeniclus* subspecies, which are located in the area until mid-April. Surveys lasted 4 hours and started at dawn or before sunset. Adverse weather conditions were always avoided. After visual or audio contact, the location of a territorial individual (singing, adding nest material, *etc.*) of feeding nestlings was georeferenced using a GPS, laser telemeter and compass.

Temporal analysis of Reed buntings' preferred habitats

In order to study reed buntings' habitat preferences on both the wetland and territory scales, the same methodology as used in previous studies with this species was followed (Vera et al., 2011, 2014). At both scales, the reed bunting selects heterogeneous habitats such as reed-rush and reed-cattail, habitats that are associated with provision of nesting and feeding resources and reduced predation risk. With the habitat variables measured on the wetland scale, the classified vegetation maps were used and the proportion of pixels of each vegetation type was calculated in relation to the number of the wetland's total pixels. We also identified the biggest patch for each class in order to detect changes on key pieces of habitat. Five high-interest regions within the wetland were defined (Figure 1). For these five regions, changes in the preferred vegetation types of reed buntings were analyzed to study their territories based on the previous habitat preferences studies of this species (Vera et al., 2014).

To study the habitat variables measured on the territory scale, 50 random points were plotted in the study area. Random points were different for each study year. Then 100-metre radius circular areas were created around those points (following the methodology implemented in Vera et al. (2014)), which represented 50 possible breeding territories for reed buntings. Finally, the percentages of each vegetation type for each circular area were calculated using ENVI 4.3. ArcMap and Hawth's Analysis Tools (Beyer, 2002) were used to create the random points and circular areas.

Results

A vegetation classification was obtained for the years 2005, 2006, 2008 and 2009 (Figure 2). When comparing the classification of 2008 with the field-based map, an accuracy of 74% was obtained. Some misclassified points were found in small-sized crops or on bordering paths between different land types.

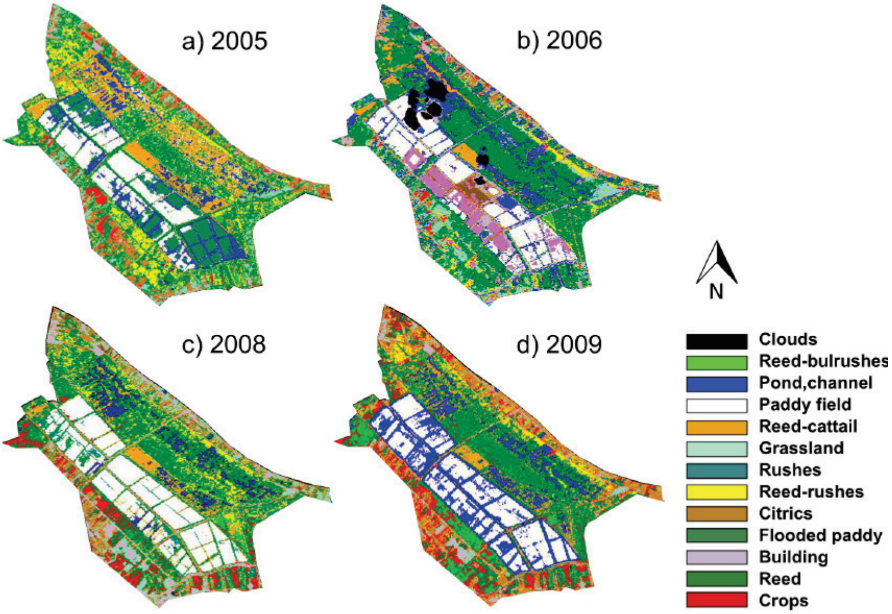

Figure 2. Vegetation classification maps for the four study years. The general darkening of the classifications from the year 2006 (excluding the central stripe, formed by paddy fields at different flooding stages) corresponds to an overall substitution of mixed vegetation formations to pure reed.

The classification algorithm obtained values above 85% accuracy compared with the ROI for all the study years, with the most accurate at 96%. The kappa coefficient values were always above 0.8 (Table 2). The classification accuracy for each class also varied from year to year, with reed and reed-bulrushes generally being the most accurate of the main wetland classes, while grassland and reed-rushes presented lower accuracies (see confusion matrices and user/producer accuracies in Online Appendix A).

Table 2. Accuracy test results for the classification maps.

Map year	2005	2006	2008	2009
Overall accuracy (%)	96.38	95.86	89.31	85.4
Kappa coefficient	0.95	0.95	0.86	0.81

Monitoring reed bunting data revealed the existence of five territorial males when the study began. In 2006, five territorial males were also detected, but only three males were found in 2007. No territorial males were detected in 2008 and 2009. All the breeding territories were located in Region 1 (2005: one male; 2006: one male; 2007: zero males) and Region 2 (2005: four males; 2006: four males; 2007: three males).

Using the whole wetland as a reference, the areas and proportions of the main wetland vegetation classes, as well as the total pure reed surface and the biggest pure reed patch size, were estimated (Table 3; Figures 3, 4). The proportions of reed-cattail and reed-rush, habitats positively selected by reed buntings on the wetland scale (Vera et. al, 2014), had reduced by more than 50% between 2005 and 2006 (Figure 3), while the pure reed surface had increased over the same period by more than 20% (Figure 4). This tendency was reversed in the following years as the reed surface had reduced (Figure 4) and the proportion of mixed formations, preferred by reed buntings, had increased (Figure 3).

Similarly, a general increase in the surface of reed habitats and fewer reed-rush formations were observed when the analysis was performed for high-interest regions (Figure 5). The variation in the reed-rush formations' surface area was analyzed during the period prior to the extinction of reed buntings (between 2005 and 2006) with a chi-square test of equality of proportions. This decrease was significant in Regions 1 ($\chi^2 = 7.12$, $p < 0.01$) and 3 ($\chi^2 = 7.12$, $p < 0.01$). For the other regions, the differences between 2005 and 2006 were not significant (Region 2: $\chi^2 = 0.23$, $p = 0.63$; Region 4: $\chi^2 = 3.14$, $p = 0.07$; Region 5: $\chi^2 = 3.33$, $p = 0.06$). At the same time, the surface occupied by pure reed increased in all the regions, and this increase was significant for Regions 1 and 4 (Region 1: $\chi^2 = 20.21$, $p < 0.01$; Region 2: $\chi^2 = 1.77$, $p = 0.18$; Region 3: $\chi^2 = 0.17$, $p = 0.67$, Region 4: $\chi^2 = 8.38$, $p < 0.01$; Region 5: $\chi^2 = 0.08$, $p = 0.78$).

Table 3. Changes in area coverage for the main wetland vegetation classes.

	Area (ha)				Relative change in area (%)			
Land cover class	2005	2006	2008	2009	05-06	06-08	08-09	05-09
Reed	294.50	358.07	334.83	270.95	21.59	-6.49	-19.08	-7.99
Reed-rush	106.12	37.93	60.66	27.83	-64.25	59.92	-54.12	-73.77
Reed-cattail	117.94	41.22	46.32	114.75	-54.05	12.37	147.73	-2.70
Grassland	50.50	60.12	48.33	13.20	19.04	-19.61	-72.68	-73.86
Rushes	20.64	50.78	12.38	34.88	146.02	-75.62	181.74	68.99
Reed-bulrushes	7.25	2.32	14.97	42.20	-68.00	545.26	181.89	482.06

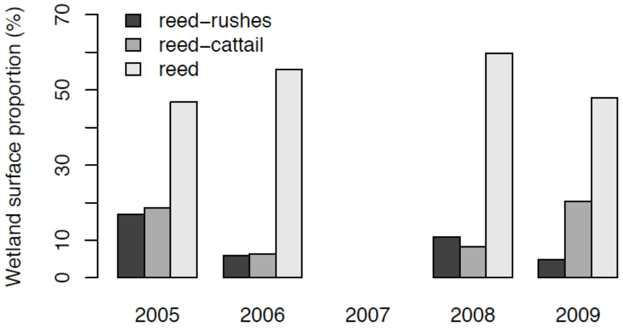

Figure 3. Proportions of the key vegetation formations on a wetland scale, showing an abrupt general decrease of mixed reed formations (habitats positively selected by the study species) together with an increase of pure reed (negatively selected) between 2005 and 2006.

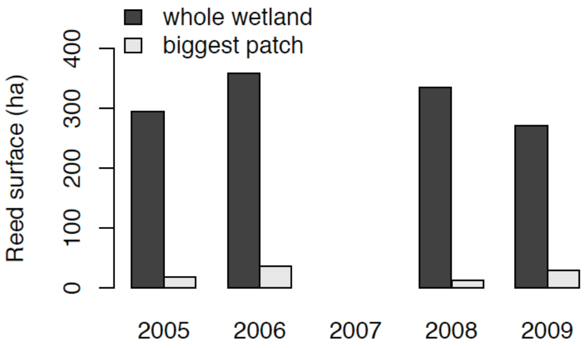

Figure 4. Total pure reed surface on a wetland scale (ha) and the surface of the biggest reed patch (ha) for each study year. A general increase of pure reed surface together with the increase of the patch sizes of these formations could indicate a general decrease of the habitat suitability for the study species. The figure shows an increase of pure reed surface between 2005 and 2006, although the rest of the values fluctuate for the rest of the years.

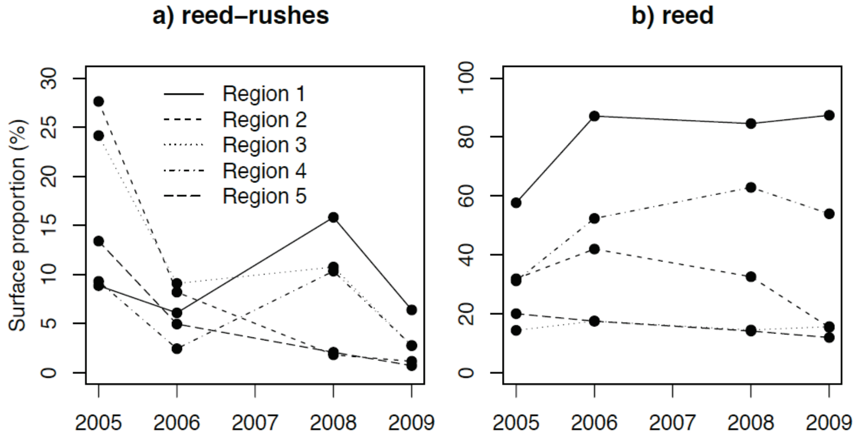

Figure 5. Surface proportions of reed-rushes (a) and pure reeds (b) for all the analyzed regions of interest for each study year. A general decrease of the reed-rushes proportions was observed between 2005 and 2006 within the regions of interest, areas with high probability of occurrence for the study species. Similar patterns can be observed between 2008 and 2009. An increase of the proportion of reed was observed between years 2005 and 2006 for the regions where the study species was recorded during the study period (Region 1 and 2).

When analyzing vegetation variation inside the random circular areas, the proportion of reed-rush was higher at the beginning of the study (Figure 6), with significant differences found between study years (ANOVA: $F_{3,200} = 3.133$, $p = 0.026$). A *post hoc* Tukey's test analysis almost showed significant differences between 2005 and 2009 ($p = 0.02$) and between 2005 and 2006 ($p = 0.09$).

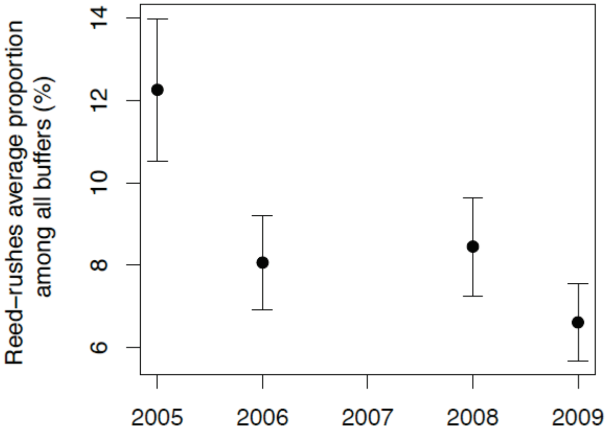

Figure 6. Average of the proportion of reed-rush formations inside the analyzed random circular areas, showing a significant decrease of suitable habitats for the species at a territorial scale. Error bars indicate the standard error of the mean.

Discussion

This study demonstrates how basic processing and classification techniques combined with medium-high resolution satellite images can be applied to obtain a satisfactory classification of several key vegetation types of small-sized coastal wetlands and, complementarily, to assess the habitat suitability of endangered species. Here it is discussed how the selection of suitable spatial resolution for images, appropriate image corrections and validation methods, provides us with an opportunity to obtain useful and reliable contemporary and past ecological information to study habitats of animal species (Fuller et al., 2005; Gillespie et al., 2008; Keith et al., 2009).

The spatial resolution of the SPOT-5 images (10 meter) was high enough to conduct the habitat analysis for the studied species. The small breeding territories of reed buntings (following Brickle and Peach (2004) and Vera *et al.* (2014)) led to us to rule out other medium-resolution satellite images (such as Landsat images) as the number of pixels inside each territory would have been too small to perform a proper analysis of the habitat within all these territories. The results of the global classification accuracy of each map confirmed that the band number and the spectral resolution of the SPOT-5 images were appropriate for making a supervised classification in the study area.

The accuracy analysis of the 2008 classification based on the field map gave 74 % accuracy, a lower value than that obtained with the global accuracy analysis (89 %, accuracy based on the selected ROI). This smaller value could be due to the inconsistency of the spatial and temporary scales in the accuracy measurement methodology performed with the field map. Firstly, field-based validations should be planned beforehand (Strahler et al., 2006). However, this was not possible, as satellite images from previous years were used and the only field information available was from the year 2008. Predicting the dates on which images will be captured can be of considerable help in appropriate validation analyses. Secondly, classification validations should be performed on either the same or a comparable spatial scale as the satellite images (Strahler et al., 2006). In this study, the field map was created on a smaller scale in certain zones (narrow paths, small crops) and on bigger scales in other zones (some central vegetation patches of the wetland). ROI were created in areas where mapping was more intense (smaller scale) in order to ensure that each Region of Interest was a uniform vegetation unit. Field map-based validation was performed for the whole map to obtain classification errors associated with scale differences between the field map and satellite image resolution.

It is quite common to find such scale inconsistency when validating classification maps with field data. Hence, it is also important to calculate global accuracy and the kappa coefficient using the ROI at the same time (Richards, 2006). In this case, relatively high accuracy values were obtained for all the classification maps compared with previous works conducted in wetlands (Baker et al., 2006; Davranche et al., 2010; Ozesmi and Bauer, 2002). Pure reed formations showed high accuracy values, but lower accuracy values and poorer separability indices were obtained for grasslands and mixed vegetation formations (see Online Appendices A and B), as previous studies conducted in wetlands using SPOT-5 images have reported. For example, in their wetland vegetation classification, Davranche et al. (2009) obtained 98 % accuracy values for pure reeds, while for other vegetation types they obtained smaller values (around 86 %). Conchedda et al. (2007) also obtained accuracy values that ranged from 73 % to 98 % depending on the vegetation type. Future developments for wetland classifications, such as the use of multi-seasonal or hyperspectral data, should focus on improving the accuracy of mixed-formations and partially-flooded vegetation, as these formations are often key for the study of the distribution of many animal species living in these ecosystems.

The observed vegetation dynamics were used to understand the population dynamics of reed buntings in relation to the availability of suitable habitats. Regions 1 and 2, where all observations of territorial males were recorded, suffered a homogenization process with a decrease in the reed-rush surface, the most important vegetation formation for the species, and suffered an important decrease in pure reed, a habitat that reed buntings avoid (Vera et al., 2011). Despite observing a general increase in the reed-rush coverage in 2008, the percentage of this key formation decreased again in the following year in most of the regions as well as on a wetland scale. In accordance with the lack of recovery of suitable habitats in Regions 1 and 2, as well as in the rest of the regions of interest, no colonizing territorial males were detected in the study area from 2008. In addition, on the territory scale, the randomly selected areas showed a significant decrease in preferred habitats and a significant increase in habitats avoided by the reed buntings, suggesting a generalized reduction of suitable habitat for the species.

Differences in the vegetation changes between regions could indicate differential land management for different parts of the wetland. Abandonment of crops and livestock activities could have affected the vegetation dynamics of some regions (Urios and Menargues, 2005), while having very limited influence on other regions. Further analysis should investigate which particular areas could have been altered by these management changes in order to observe correlations with the vegetation dynamics. Because the most drastic changes in terms of management took place prior to the present study, the analysis of satellite images prior to 2005 could help to clarify the effect of these transformations. Our results suggest that longstanding monitoring in these type of wetlands, naturally driven by severe meteorological events such as flooding and droughts, as well as by human-related uses (*i.e.* reed cutting and grazing), should be oriented to detect interannual vegetation changes. Long-term variability studies are often unable to detect severe, rapid changes in the habitat availability of small animal populations. Monitoring programs with rapid and systematized methods would help to reveal habitat changes, easing the decision-making process to avoid wetland degradation.

The observed interannual vegetation changes suggest a relationship between the decline in reed buntings and the reduction in suitable habitats for their territory establishment, and also with landscape homogenization. Despite the fact that the sudden habitat change occurred between 2005 and 2006, in the form of a rush-reed dominancy change, and that the suitable vegetation types for territory establishment continued to reduce, reed bunting extinction occurred in the wetland under study between 2007 and 2008. Similarly to other animal species, a reduction in the number of bird territories occurred with a certain time lag, which varied between species and alteration types (Brooks et al., 1999; Findlay and Bourdages, 2001). Campbell (1988) observed a two-year delay between habitat alteration and the reduction in the number of territories of reed buntings in a riparian habitat.

Beyond the scope of vegetation dynamics, particular factors exist that can lead to the decline and extinction of reed bunting populations. Among them we find interspecific competition (Báldi, 2004, 2006), availability of trophic resources (Martin, 1992, 1995; Pärt, 2001) and nest predation risk (Musilová et al., 2014; Schiegg, et al., 2007; Trnka et al., 2011). These factors cannot be directly analyzed by remote sensing techniques, but are closely linked to the structure and coverage of vegetation (*e.g.*, Pasinelli and Schiegg, 2006). Recently, Musilová et al. (2014) found that the eutrophication and deterioration of tussock sedges led to an increased probability of predation in nests built on top of this vegetation type. It is also fundamental to consider, alongside previously discussed processes, stochastic environmental changes and population fluctuations, because they can lead to the extinction of small and isolated populations, or species with a metapopulation structure, such as reed buntings.

Conclusions

This study showed how *a posteriori* monitoring can help us to understand the vegetation dynamics of coastal wetlands and the rapid changes that can take place in the habitats of threatened species that live in them. On the basis of this study, we encourage other ecologists and land managers to select appropriate images and classification workflows carefully, and to plan field validation campaigns in detail by focusing on scale factors and relatively identifiable land types from satellite imagery (Wang *et al.*, 2009). Satellite images, when combined with field-based maps to produce high-accuracy vegetation mapping, are key to monitoring biodiversity habitat availability, especially among endangered species. The medium-high resolution images increasingly available from high revisiting-frequency satellites, such as those from the recently launched Sentinel satellites (Berger *et al.*, 2012), have the potential to be a game-changer for researchers monitoring rapid habitat changes of threatened ecosystems.

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Appendix: Separability Indices of 2008 Map Regions of Interest (ROI)

ROI Name: (Jeffries-Matusita Index, Transformed Divergence Index

Reed-bulrushes 60 pixels:
Reed-catttails 1154 pixels: (1.81870831 1.94569098)
Pond-channel 150 pixels: (1.99999999 2.00000000)
Rushes 93 pixels: (1.93412277 2.00000000)
Paddy field 1545 pixels: (1.99995543 2.00000000)
Reed-rushes 70 pixels: (1.03942975 1.13823516)
Grassland 145 pixels: (1.42898534 1.99451566)
Building 71 pixels: (1.98833616 2.00000000)
Reed 324 pixels: (1.44229400 1.70981012)

Reed-catttails 1154 pixels:
Reed-bulrushes 60 pixels: (1.81870831 1.94569098)
Pond-channel 150 pixels: (1.98240506 1.99943998)
Rushes 93 pixels: (1.98062186 2.00000000)
Paddy field 1545 pixels: (1.99250648 1.99500897)
Reed-rushes 70 pixels: (1.64991048 1.90757226)
Grassland 145 pixels: (1.59700279 1.97264456)
Building 71 pixels: (1.99823120 2.00000000)
Reed 324 pixels: (1.31909097 1.41348959)

Pond-channel 150 pixels:
Reed-bulrushes 60 pixels: (1.99999999 2.00000000)
Reed-catttails 1154 pixels: (1.98240506 1.99943998)
Rushes 93 pixels: (2.00000000 2.00000000)
Paddy field 1545 pixels: (1.99999999 2.00000000)
Reed-rushes 70 pixels: (1.99999999 2.00000000)
Grassland 145 pixels: (1.99999996 2.00000000)
Building 71 pixels: (2.00000000 2.00000000)
Reed 324 pixels: (1.97201744 1.99756196)

Rushes 93 pixels:
Reed-bulrushes 60 pixels: (1.93412277 2.00000000)
Reed-catttails 1154 pixels: (1.98062186 2.00000000)
Pond-channel 150 pixels: (2.00000000 2.00000000)
Paddy field 1545 pixels: (1.99842216 2.00000000)
Reed-rushes 70 pixels: (1.99224506 2.00000000)
Grassland 145 pixels: (1.67896747 1.73095288)
Building 71 pixels: (1.90331223 2.00000000)
Reed 324 pixels: (1.96544675 2.00000000)

Paddy field 1545 pixels:

```
        Reed-bulrushes 60 pixels: (1.99995543 2.00000000)
        Reed-catttails 1154 pixels: (1.99250648 1.99500897)
        Pond-channel 150 pixels: (1.99999999 2.00000000)
        Rushes 93 pixels: (1.99842216 2.00000000)
        Reed-rushes 70 pixels: (1.99997993 1.99999999)
        Grassland 145 pixels: (1.99556856 1.99999999)
        Building 71 pixels: (1.99987373 2.00000000)
        Reed 324 pixels: (1.99998232 1.99999934)

Reed-rushes 70 pixels:
        Reed-bulrushes 60 pixels: (1.03942975 1.13823516)
        Reed-catttails 1154 pixels: (1.64991048 1.90757226)
        Pond-channel 150 pixels: (1.99999999 2.00000000)
        Rushes 93 pixels: (1.99224506 2.00000000)
        Paddy field 1545 pixels: (1.99997993 1.99999999)
        Grassland 145 pixels: (1.22649421 1.93094568)
        Building 71 pixels: (1.99772701 2.00000000)
        Reed 324 pixels: (1.09326012 1.69664462)

Grassland 145 pixels:
        Reed-bulrushes 60 pixels: (1.42898534 1.99451566)
        Reed-catttails 1154 pixels: (1.59700279 1.97264456)
        Pond-channel 150 pixels: (1.99999996 2.00000000)
        Rushes 93 pixels: (1.67896747 1.73095288)
        Paddy field 1545 pixels: (1.99556856 1.99999999)
        Reed-rushes 70 pixels: (1.22649421 1.93094568)
        Building 71 pixels: (1.95211751 2.00000000)
        Reed 324 pixels: (1.62699264 1.97438788)

Building 71 pixels:
        Reed-bulrushes 60 pixels: (1.98833616 2.00000000)
        Reed-catttails 1154 pixels: (1.99823120 2.00000000)
        Pond-channel 150 pixels: (2.00000000 2.00000000)
        Rushes 93 pixels: (1.90331223 2.00000000)
        Paddy field 1545 pixels: (1.99987373 2.00000000)
        Reed-rushes 70 pixels: (1.99772701 2.00000000)
        Grassland 145 pixels: (1.95211751 2.00000000)
        Reed 324 pixels: (1.99663380 2.00000000)

Reed 324 pixels:
        Reed-bulrushes 60 pixels: (1.44229400 1.70981012)
        Reed-catttails 1154 pixels: (1.31909097 1.41348959)
        Pond-channel 150 pixels: (1.97201744 1.99756196)
        Rushes 93 pixels: (1.96544675 2.00000000)
```

Paddy field 1545 pixels: (1.99998232 1.99999934)
Reed-rushes 70 pixels: (1.09326012 1.69664462)
Grassland 145 pixels: (1.62699264 1.97438788)
Building 71 pixels: (1.99663380 2.00000000)

Pair Separation (least to most):
Reed-bulrushes 60 pixels and Reed-rushes 70 pixels - 1.03942975
Reed-rushes 70 pixels and Reed 324 pixels - 1.09326012
Reed-rushes 70 pixels and Grassland 145 pixels - 1.22649421
Reed-catttails 1154 pixels and Reed 324 pixels - 1.31909097
Reed-bulrushes 60 pixels and Grassland 145 pixels - 1.42898534
Reed-bulrushes 60 pixels and Reed 324 pixels - 1.44229400
Reed-catttails 1154 pixels and Grassland 145 pixels - 1.59700279
Grassland 145 pixels and Reed 324 pixels - 1.62699264
Reed-catttails 1154 pixels and Reed-rushes 70 pixels - 1.64991048
Rushes 93 pixels and Grassland 145 pixels - 1.67896747
Reed-bulrushes 60 pixels and Reed-catttails 1154 pixels - 1.81870831
Rushes 93 pixels and Building 71 pixels - 1.90331223
Reed-bulrushes 60 pixels and Rushes 93 pixels - 1.93412277
Grassland 145 pixels and Building 71 pixels - 1.95211751
Rushes 93 pixels and Reed 324 pixels - 1.96544675
Pond-channel 150 pixels and Reed 324 pixels - 1.97201744
Reed-catttails 1154 pixels and Rushes 93 pixels - 1.98062186
Reed-catttails 1154 pixels and Pond-channel 150 pixels - 1.98240506
Reed-bulrushes 60 pixels and Building 71 pixels - 1.98833616
Rushes 93 pixels and Reed-rushes 70 pixels - 1.99224506
Reed-catttails 1154 pixels and Paddy field 1545 pixels - 1.99250648
Paddy field 1545 pixels and Grassland 145 pixels - 1.99556856
Building 71 pixels and Reed 324 pixels - 1.99663380
Reed-rushes 70 pixels and Building 71 pixels - 1.99772701
Reed-catttails 1154 pixels and Building 71 pixels - 1.99823120
Rushes 93 pixels and Paddy field 1545 pixels - 1.99842216
Paddy field 1545 pixels and Building 71 pixels - 1.99987373
Reed-bulrushes 60 pixels and Paddy field 1545 pixels - 1.99995543
Paddy field 1545 pixels and Reed-rushes 70 pixels - 1.99997993
Paddy field 1545 pixels and Reed 324 pixels - 1.99998232
Pond-channel 150 pixels and Grassland 145 pixels - 1.99999996
Pond-channel 150 pixels and Reed-rushes 70 pixels - 1.99999999
Pond-channel 150 pixels and Paddy field 1545 pixels - 1.99999999
Reed-bulrushes 60 pixels and Pond-channel 150 pixels - 1.99999999
Pond-channel 150 pixels and Building 71 pixels - 2.00000000
Pond-channel 150 pixels and Rushes 93 pixels – 2. 000000

Resumen ampliado

Los humedales mediterráneos se han visto fuertemente alterados a lo largo de los dos últimos siglos, sufriendo la desecación, pérdida de hábitat, de calidad del agua y del suelo, conduciendo a una progresiva homogeneización del paisaje. Gran parte de los humedales mediterráneos o su entorno directo se encuentran gestionados para actividades humanas, como la agricultura, la caza o la siega de carrizo. Todas estas actividades pueden tener impactos negativos en los humedales, y especialmente, a través de los impactos en el hábitat, en las poblaciones de aves (Tscharntke, 1992; Graveland, 1998; Kozulin et al., 2004; Tanneberger et al., 2009, 2010). Las aves ligadas a los humedales son, junto con las aves agrícolas, el grupo de aves que sufre una mayor amenaza por la pérdida y degradación de su hábitat (Butchart et al., 2004; Dudgeon et al., 2006). En consecuencia, estos hábitats son especialmente importantes para las aves (alrededor de 110 especies dependientes de los humedales se encuentran protegidas por la Directiva Aves 2009/147/CE), entre ellas varias especies globalmente amenazadas (Butchart et al., 2004).

La pérdida de hábitats, fragmentación del paisaje alrededor de los humedales y en consecuencia la pérdida de conectividad ha sido un proceso especialmente intenso y negativo en los humedales de las regiones mediterráneas (Gallego-Fernández et al., 1999; Silva et al., 2007; Valiela y Fox, 2008) y ha llevado a las especies más íntimamente ligadas a ellos, para las que la matriz paisajística es menos permeable o con menor capacidad dispersiva, a aumentar su aislamiento y ver empeorado su estado de conservación (Cuttelod et al., 2008).

El escribano palustre (*Emberiza schoeniclus*), es una de estas especies, y especialmente en el caso de las poblaciones o subespecies con un marcado carácter sedentario. Se trata de un ave paseriforme que extiende sus áreas de reproducción desde la península Ibérica hasta China (Copete y Christie, 2017) y que se reproduce en todo tipo de ambientes naturales asociados al agua. A pesar de que la especie no se encuentra amenazada a nivel mundial, sí lo están las poblaciones de algunos países (Bufield y Van Bommel, 2004; Voříšek et al., 2010), entre ellos España (Atienza y Copete, 204; Atienza, 2006; Monrós et al., 2017), asociándose este declive con la pérdida y alteración del hábitat tanto durante la época de reproducción como la invernada (Siriwardena et al., 2000; Brickle y Peach 2004; Voříšek et al., 2010). De las 20 subespecies de escribano palustre que se reconocen actualmente (Copete y Christie, 2017), dos de ellas se distribuyen en la península Ibérica: el escribano palustre iberoriental (*E. s. witherbyi*), que se reproduce de forma irregular en humedales del interior de la península Ibérica y costa mediterránea española y francesa, así como la vertiente atlántica de Marruecos; y el escribano palustre iberoccidental (*E. s. lusitanica*), reproductor en humedales de la cornisa cantábrica y atlántica de la península Ibérica. En el caso del escribano palustre iberoriental, las últimas estimas del tamaño de población en España corresponden a los años 2005 y 2015. El I Censo Nacional, realizado en 2005, reflejó un tamaño poblacional de entre 250 y 360 parejas distribuidas en 21 humedales, concentradas en su mayoría en los humedales de Castilla-La-Mancha y el Delta del Ebro (Atienza, 2006). En 2015, en el marco del II Censo Nacional, reflejó un tamaño poblacional de 122-136 parejas distribuidas en 9 humedales, afectando la mayor reducción precisamente a la población reproductora en Castilla-La Mancha (Monrós et al., 2017). Conocer y entender la estructura de las poblaciones de taxones amenazados es una cuestión crítica para definir las estrategias y actuaciones de gestión de la biodiversidad. Una información especialmente importante en aquellos taxones que se distribuyen y ocupan el espacio de una manera parcheada en una matriz paisajística heterogénea o en ambientes fragmentados (Akçakaya et al., 2007; van Teeffelen et al., 2012), como es el caso del escribano palustre iberoriental.

En el capítulo I se presentan los resultados del estudio de la estructura y diversidad genética de las dos subespecies ibéricas de escribano palustre. Para ello, se recogieron muestras de ADN de aves procedentes de España, Marruecos y Portugal (correspondientes a las dos subespecies) y Finlandia (correspondientes a la subespecie nominal, *E. s. schoeniclus*) durante el período reproductor o post-reproductor. El ADN se extrajo mediante los métodos recomendados para sangre y tejido (Sambrook y Russell, 2001) y plumas (Kvist et al., 2003). Los distintos análisis realizados mostraron que el escribano palustre iberoccidental presentaba una reducida variación genética tanto en los marcadores nucleares como mitocondriales, teniendo un muy pequeño tamaño poblacional efectivo y sin encontrarse diferenciación genética entre las poblaciones muestreadas de Galicia y Portugal. En cambio, la subespecie iberoriental se mostró significativamente estructurada, pero las poblaciones mantenían una gran cantidad de variación genética a pesar de los bajos tamaños poblacionales efectivos con respecto a la subespecie norteña. Los datos sugieren un mayor intercambio genético entre las poblaciones gallegas y portuguesas de escribano palustre iberoccidental, probablemente como respuesta a una menor distancia entre humedales y la existencia de un mayor flujo génico entre poblaciones. Las poblaciones de la subespecie iberoriental se encontrarían más aisladas, reflejándose en la mayor variación genética encontrada, aunque no se encontraron evidencias de que ninguna población hubiera sufrido los efectos de haber pasado por un cuello de botella. De acuerdo a los resultados, propusimos distinguir cuatro unidades de gestión del conjunto de poblaciones de escribano palustre estudiadas: una primera que englobaría al escribano palustre iberoccidental, y otras tres unidades basadas en las poblaciones genéticamente diferenciadas de escribano palustre iberoriental (Delta del Ebro, Castilla La Mancha y Mallorca). Por tanto, las medidas de conservación inferidas de estos resultados deben focalizarse en la conservación de los humedales y hábitats remanentes del escribano palustre iberoccidental para al menos mantener los niveles de flujo génico, mientras que en el caso del escribano palustre iberoccidental, los esfuerzos deben centrarse en mejorar la calidad del hábitat, aumentar los tamaños poblacionales de estas unidades y mejorar o recuperar la conectividad entre humedales que mantienen su presencia, así como con aquellos en los que ya se ha producido la extinción.

Teniendo en cuenta el declive que sugieren los datos de las poblaciones del escribano palustre iberoriental, el planteamiento de estrategias de conservación de la especie requiere de estimas concretas sobre su tendencia. Así, en el Capítulo II utilizamos los datos disponibles de censos para estimar su ocupación, supervivencia aparente y tasa de crecimiento poblacional real, y conocer sus tendencias poblacionales pasadas y futuras. Para ello, se recopilaron los datos referentes a cuadrículas de 10 x 10 km publicados en el Atlas de Aves Reproductoras de España de 2002 (Martí and del Moral 2003) y los dos censos nacionales de escribano palustre iberoriental (Monrós et al., 2017; Atienza 2006). Para cada una de las 34 cuadrículas en las que el escribano palustre se encontró presente entre 2002 y 2015 se generaron historiales de captura-recaptura basados en datos de presencia/ausencia, que fueron analizados utilizando modelos de Lambda y Supervivencia de Pradel, diseñados para poblaciones abiertas y basadas en el modelo Cormack-Jolly-Seber (Pradel, 1996). Los análisis fueron realizados con el programa MARK 5.1 (White y Burnham, 1999). Durante el intervalo 2002-2005, la tasa de crecimiento anual fue de 0.929 ± 0.054 (Intervalo de confianza al 95 %: 0.726-0.984), mientras que durante el intervalo 2005-2015 fue de 0.942 ± 0.031 (IC 95 %: 0.842-0.980), poniendo de manifiesto su declive al no incluir los intervalos de confianza a 1. La probabilidad de supervivencia y la tasa anual de crecimiento estimadas para el segundo período fueron iguales, indicando que no hubo reclutamiento de nuevas poblaciones durante este periodo. La tasa de crecimiento anual y su desviación estándar fueron utilizadas para proyectar las tendencias futuras considerando una distribución normal de la tasa de crecimiento y la ausencia de estocasticidad demográfica, mostrando éstas un declive muy importante en el futuro: una probabilidad de 0.886 de sufrir un declive mayor del 80 % en los próximos 25 años, y una probabilidad de 1 de sufrir un declive mayor del 90 % en los próximos 50 años. De acuerdo a estos resultados, resulta urgente elaborar y poner en marcha los planes de recuperación de la especie y los planes de gestión de los humedales en los que habita (todos ellos pertenecientes a la Red Natura 2000) para preservar todas las poblaciones y su diversidad genética.

De manera complementaria, entre 2007 y 2009 desarrollamos en el Parque Nacional de las Tablas de Daimiel un estudio preliminar para hacer un seguimiento de su población reproductora, una de las principales en España. Se muestrearon en dos ocasiones entre mayo y junio los mismos 30 puntos cada año, realizando puntos de escucha de 5 minutos, y posteriormente incrementando la probabilidad de detección mediante el uso de un reclamo durante un minuto (Matessi et al., 2000; Atienza, 2006). La ocupación (ψ) y la probabilidad de colonización y extinción de los puntos muestreados fueron estimadas usando el programa PRESENCE 2.3 (Hines, 2006), considerando que la detectabilidad podía tener heterogeneidad. La estimación Naive de la proporción de territorios ocupados se redujo de 64 % a 16 %, mientras que las estimas de ocupación utilizando los modelos se redujeron entre 71 % y 27 %. El intervalo de confianza al 95 % de la probabilidad de extinción de los territorios se encontró por debajo de 1 y la probabilidad de colonizar un nuevo territorio fue baja (0.267 ± 0.156; 95 % CI: 0.071 - 0.635), evidenciando un claro declive en la ocupación de los territorios a lo largo del tiempo de estudio. Tanto en análisis de la tendencia poblacional como en el estudio de la ocupación en las Tablas de Daimiel, las estimas de la detectabilidad del escribano palustre iberoriental se mostraron por debajo de 1 (entre 0.724 y 0.823, y entre 0.450 y 0.500 respectivamente). Por tanto, es probable que estudios anteriores hayan subestimado el rango de distribución o su grado de ocupación y, en cualquier caso, sugerimos que futuros estudios consideren la necesidad de modelar la detectabilidad para obtener unas estimas del grado de ocupación sin sesgos.

El conocimiento de las características del hábitat que influyen en la ocurrencia de las especies y, por tanto, también en su declive o crecimiento poblacional, es una cuestión esencial en los estudios dirigidos a establecer las actuaciones destinadas a mejorar el estado de conservación de una especie. En el caso del escribano palustre iberoriental, existen pocos estudios que analicen los requerimientos de hábitat tanto a escala paisajística como a escala más pequeña, y únicamente se han propuesto a grandes rasgos la cobertura de carrizo (*Phragmites australis*) y la de masiega (*Cladium mariscus*) como las variables más importantes en la selección de hábitat (Martínez-Vilalta et al., 2002; Atienza, 2006). En el Capítulo III estudiamos a lo largo de gran parte de su área de distribución en España las variables de hábitat que intervienen en la selección de hábitat del escribano palustre iberoriental a escala de humedal, con el objetivo de sugerir líneas de actuación y gestión que permitan aumentar la disponibilidad de hábitat adecuado y por tanto, sus tamaños poblacionales. En un total de 25 humedales en los que se registró la presencia de escribano palustre iberoriental (11 humedales) o ausencia (14 humedales) se midieron o calcularon un total de 42 variables ambientales. Para ello, utilizando transectos intensivos que cubrieron todo el área de los humedales estudiados, se mapearon sistemáticamente los parches de vegetación dominados por carrizo, eneas (*Typha* spp.), masiega, juncos (tipos ecológicos de *Juncus acutus* y *Scirpus holoschoenus*), con diferentes clases de dominancia entre ellas de acuerdo a las coberturas relativas de los parches.

Tras aplicar modelos GLM encontramos que la ocurrencia de escribano palustre iberoriental en un humedal fue independiente de su tamaño, pero sí se encontraba relacionada con la cobertura de parches mixtos de carrizo y enea (menor en humedales ocupados), cobertura de parches de juncos con carrizo, y perímetro de parches mixtos de carrizo y juncos (mayor en humedales ocupados). Las formaciones de enea y carrizo pueden ser utilizadas como indicadores de condiciones de inundación, aunque fluctuantes y favorables para el desarrollo de las formaciones de juncos y carrizo en distintos grados de dominancia y para aumentar las oportunidades de alimentación tanto de los adultos como de los volantones (Isenmann, 1990; Goater, 1993), principalmente en aquellos parches de vegetación más irregulares (Poulin et al., 2002; Brickle y Peach, 2004), y por tanto con un mayor perímetro. Por tanto, la gestión del hábitat para favorecer la idoneidad de los humedales para albergar poblaciones de escribano palustre iberoriental no se encuentra influido por el tamaño del humedal, y deben estar dirigidas a alcanzar una mayor cobertura de especies emergentes y una menor dominancia general del carrizo mediante el control de las condiciones de inundación y el desarrollo de otras prácticas de gestión de la vegetación. Estudios de modelado de idoneidad del hábitat a escala paisajística como el realizado tienen la posibilidad de determinar espacialmente las áreas más idóneas para realizar prácticas de gestión y conservación, y establecer áreas y prácticas prioritarias (Store y Jokimäki, 2003).

Además de conocer qué factores intervienen en la idoneidad del hábitat a escala paisajística, el análisis de las preferencias de vegetación a escala de territorio resulta fundamental para entender de qué manera trabajan las fuerzas de selección para que las aves escojan territorios, factores que pueden actuar de manera diferente dependiendo de la escala (Söderströn y Pärt, 2000; Brambilla et al., 2009). En este contexto, el Capítulo IV tiene por objetivo identificar los componentes del hábitat seleccionados para el establecimiento de los territorios. Para ello, en 11 de los 22 humedales en los que el escribano palustre iberoriental se encontraba presente se localizaron 35 territorios ocupados y 23 áreas del mismo tamaño, en las que se comprobó su ausencia (territorios no ocupados). En todos ellos se midieron 14 variables de coberturas de vegetación, con los mismos grados de dominancia que a escala de humedal, junto con 12 parámetros estructurales del carrizo (densidad, altura y grosor de tallos verdes y secos, así como juventud, densidad de inflorescencia y cobertura de carrizo tumbado). El análisis de esta información mediante GLMM permitió identificar que la cobertura de parches de carrizo y enea resultaba relevante en la selección de hábitat, y la cobertura de carrizo con formaciones similares a los juncos era superior en los territorios ocupados que en los no ocupados, de manera consistente a lo ocurrido a escala paisajística. Esta coherencia a distintas escalas espaciales reflejaría que la probabilidad de ocurrencia de escribano palustre iberoriental en un humedal dado se encuentre determinado por la probabilidad de establecer un territorio de acuerdo a la disponibilidad de hábitat.

Estos resultados son igualmente coherentes con los resultados expuestos en el Capítulo V. La estructura y composición de los nidos naturales de aves son resultado de distintas presiones de selección, como la protección frente a predadores o el aislamiento de huevos y pollos ante factores climáticos adversos (Hansell 2000), y tienen como fin último el maximizar la eficacia reproductiva. Dado que el uso concreto o exclusivo de unos determinados materiales vegetales puede suponer un recurso limitante que afecte directamente a la conservación de este paseriforme palustre amenazado, con el objetivo de conocer la estructura y composición vegetal de los nidos de escribano palustre iberoriental se prospectó un área del Parque Nacional de las Tablas de Daimiel en busca de machos territoriales. Posteriormente se realizó un seguimiento de los territorios encontrados con el fin de detectar la construcción de nidos o la ceba de pollos. Una vez se observó el vuelo de los pollos o se constató el fracaso de reproducción se recogieron los nidos. En total, 7 nidos fueron recogidos y estudiados. Los nidos se localizaron en el suelo, sobre eneas o masiega. Tuvieron forma de copa y tanto su base como estructura estuvo formada por hojas y vainas secas de carrizo finamente tejidos en espiral u onda, reforzada con pequeños fragmentos de tallos de gramíneas y otras hierbas. La capa interna estuvo recubierta en todos los casos de pelo de jabalí (*Sus scrofa*), con una proabable función termorreguladora. Esta estructura fue común a todos los nidos, aunque la distribución de pesos de los distintos materiales varió entre nidos. El uso predominante de un material en las capas externas y base de los nidos parece indicar una función mimética contra el ataque de depredadores (Hansell 2000), un fenómeno frecuente tanto en el propio escribano palustre (Schiegg et al., 2007, Musilová et al., 2014) como en otros paseriformes palustres ibéricos (Neto, 2006).

Con el objetivo de analizar el efecto de cambios ocurridos en la disponibilidad de hábitat sobre la población de escribano palustre iberoriental, entre 2005 y 2009 realizamos en el Marjal de Pego-Oliva un estudio en el que se combinó el trabajo de campo de mapeo de hábitat y seguimiento de machos territoriales. Dado que los humedales son ecosistemas muy dinámicos, las herramientas para el seguimiento de los procesos biológicos y apoyo al desarrollo de planificación de gestión mediante técnicas de mapeo a través de imágenes satélite son de gran utilidad (Klemas, 2013; Rocchini et al., 2011; Poulin et al., 2010; Davranche et al., 2009), gracias a la disponibilidad de imágenes de alta resolución con una frecuencia corta de tiempo (Keith et al., 2009; De Roeck et al., 2008; Leyequien et al., 2007). En nuestro caso, se utilizaron imágenes SPOT-5 de alta resolución (10 m para las bandas b1, b2 y b3, y de 20 m para b4), adecuadas para el estudio de la vegetación de humedales (Poulin et al., 2010). Las imágenes fueron tomadas siempre en el mes de agosto entre 2005 y 2009 (excepto 2007, cuyas imágenes no son analizables por la cobertura de nubes). Tras aplicar las correcciones necesarias a las imágenes se realizó un proceso de clasificación tutelado utilizando la cartografía de detalle realizada a pie en 2008. Los resultados, que se recogen en el capítulo VI, muestran en primer lugar cómo un importante esfuerzo de cartografía detallada de las formaciones vegetales permite obtener una elevada exactitud en la clasificación tutelada posterior, por encima del 85 %. En segundo lugar, en aquellas zonas donde todos los machos habían establecido sus territorios se observó una reducción significativa de la superficie ocupada por parches de carrizo y junco y un incremento de los parches puros de carrizo, cambios que se dieron de la misma forma al analizar potenciales territorios seleccionados aleatoriamente en el humedal. Por tanto, de acuerdo a los resultados de los capítulos III a V, a lo largo del período de estudio los resultados obtenidos sugieren una reducción generalizada del hábitat adecuado para el escribano palustre iberoriental en el Marjal de Pego-Oliva. En consecuencia, no se observaron recolonizaciones posteriores ni establecimiento de territorios en áreas con hábitat no adecuado, conduciendo estos cambios aparentemente a la extinción local de la especie entre 2006 y 2008.

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Discusión general y perspectivas

El escribano palustre iberoriental (*Emberiza schoeniclus witherbyi*) es un paseriforme palustre endémico de algunos humedales de Marruecos, España y Francia. Desde que se dispone de información cuantitativa de esta subespecie se reconoce que su distribución en España se encuentra en retroceso (p.e., Purroy, 1995). Sin embargo, sus hábitos retraídos y su estructura metapoblacional (con poblaciones localizadas en grandes humedales y su entorno, y pequeñas poblaciones en pequeños humedales, muy dispersas y que seguían dinámicas de colonización, extinción y recolonización), posiblemente han hecho menos evidente su desaparición. En consecuencia, hasta la primera evaluación de su estado de conservación (Atienza y Copete, 2004) no se pudo determinar su estado de conservación y la necesidad de disponer información representativa de su ecología en todo su rango de distribución en España para poder definir y poner en marcha acciones de gestión y conservación. En la actualidad, se encuentra catalogado en el Catálogo Nacional de Especies Amenazadas como “En Peligro de Extinción” (Real Decreto 139/2011) y “En Peligro” en el Libro Rojo de las Aves de España (Atienza y Copete, 2004).

Esta tesis estudia de una manera integrada la selección del hábitat en el escribano palustre iberoriental, su estructura genética y su tendencia poblacional. Por tanto, ofrece información relevante para ser utilizada en la redacción de sus correspondientes planes de gestión. Al mismo tiempo, los resultados obtenidos plantean nuevas preguntas que requieren de líneas de investigación específicas que deben ser tomadas en cuenta para mejorar el grado de conocimiento de su ecología y, por tanto, aumentar la eficacia de las actuaciones a desarrollar para revertir su dinámica poblacional y mejorar su estado de conservación.

Los resultados del capítulo I muestran la evaluación de la estructura genética del escribano palustre iberoriental. En el momento del estudio las poblaciones no presentaban evidencias de haber sufrido la reducción de la diversidad genética (medida como diversidad de nucleótidos mitocondriales y valores de heterocigosidad nucleares) esperable de acuerdo a la reducción ya experimentada tanto de los tamaños poblacionales en los humedales muestreados, como a la reducción de su área de distribución (Purroy, 1995; Martí y del Moral, 2002; Atienza, 2006; Atienza y Copete, 2006). Resulta destacable que las poblaciones de escribano palustre iberoriental se encuentran más diferenciadas entre ellas que lo están las poblaciones de escribano palustre iberoccidental (*Emberiza schoeniclus lusitanica*, presente en humedales de la costa cantábrica y atlántica de la península Ibérica) o que las poblaciones migratorias e invernantes de escribano palustre norteño (*Emberiza schoeniclus schoeniclus*). A pesar de que ambas subespecies ibéricas han desaparecido de numerosos humedales pequeños en su rango de distribución, este resultado pone de manifiesto un mayor aislamiento de las poblaciones de escribano palustre iberoriental que en el caso del escribano palustre iberoccidental. Probablemente, el hecho de que las distancias entre humedales con presencia de escribano palustre sean considerablemente menores en el escribano palustre iberoccidental, facilita que el flujo génico sea más efectivo. Es fundamental considerar que en especies con estructura metapoblacional y en poblaciones pequeñas y aisladas, como en el caso de este estudio, entran en juego procesos de estocasticidad demográfica y ambiental que pueden conducir, por sí solos, a la extinción de la población (p.e. Melbourne y Hastings, 2008; Eriksson et al., 2014). Por ello, y teniendo en cuenta el grado de diferenciación entre poblaciones, los resultados sugieren la necesidad de tomar como unidades de gestión de la subespecie las poblaciones de Castilla-La Mancha, Delta del Ebro y Baleares, estableciendo como medida prioritaria la mejora de la calidad del hábitat para aumentar los tamaños poblacionales y preservar la máxima diversidad genética de esta subespecie.

Los resultados plantean la urgente necesidad de recuperar la conectividad entre humedales grandes y pequeños dentro de las unidades de gestión para facilitar los procesos de colonización y recolonización, la mejora del flujo génico y un menor aislamiento genético, tal y como ocurre en el escribano palustre iberoccidental. En este sentido, en un futuro sería necesario profundizar en el conocimiento de la estructura metapoblacional de la especie y, especialmente, en conocer qué factores intervienen y cómo, en la conectividad de la especie a escala poblacional (estructura en edades de la población, productividad), a escala de comunidad (interacciones con las poblaciones invernantes y migratorias de escribano palustre norteño u otras especies) y a escala paisajística (teniendo en cuenta la complejidad espacial de la matriz en la que se localizan estos fragmentos, la calidad del hábitat dentro y fuera de los fragmentos, y la supervivencia o mortalidad asociada a la dispersión atendiendo a la calidad del hábitat y las barreras presentes) (Moilanen y Hanski, 1998; Fahrig, 2003; Wiegand et al., 2005; Xu et al., 2006; Hodgson et al., 2009).

De igual manera, ante la posibilidad de favorecer el efecto rescate de algunas poblaciones mediterráneas (o incluso proyectos de reintroducción) resultaría importante profundizar en el conocimiento de la estructura genética de las poblaciones francesas y marroquíes de escribano palustre iberoriental y, específicamente en el caso de las poblaciones francesas, conocer el flujo génico y el grado de aislamiento existente con las poblaciones del Delta del Ebro y Baleares.

A pesar que los resultados no evidencian efectos de cuello de botella en las poblaciones analizadas, el aumento del aislamiento de las poblaciones de escribano palustre iberoriental y la reducción del flujo y diversidad génica podrían tener efectos sobre la aptitud adaptativa de estas poblaciones a corto plazo (Amos et al., 2012; Harrison et al., 2012). Los resultados del Capítulo II muestran cómo el declive experimentado a nivel del rango de distribución determina un alto riesgo de extinción en el futuro cercano (con una probabilidad de 0.886 de sufrir un declive mayor al 80 % en los próximos 25 años). De manera complementaria, se muestra el declive de la población reproductora en las Tablas de Daimiel, el humedal más importante para el escribano palustre iberoriental en el interior de la península Ibérica, donde la ocupación de territorios pasó del 71 % en 2006 al 17 % en 2009, con una tasa de crecimiento de la población de 0.568 ± 0.294 entre 2006 y 2008. Estos resultados se encuentran en sintonía con las últimas estimas poblacionales para este humedal (Jiménez et al. 2015, Monrós et al. 2017). Los resultados muestran que el seguimiento de la población mediante puntos de escucha y análisis de la ocupación (MacKenzie et al. 2003, 2006; Brotons et al. 2004) es adecuado para el seguimiento del escribano palustre en las Tablas de Daimiel. De acuerdo a los resultados, la metodología propuesta para futuros estudios y programas de seguimiento requiere tener en cuenta que la probabilidad de detección es menor a la unidad para obtener estimas de la ocupación no sesgadas (MacKenzie et al. 2005, 2006). En este sentido, estudios anteriores que no modelizaron la detectabilidad del escribano palustre pueden haber infraestimado su rango de distribución.

El capítulo II pone en relieve la urgencia requerida para la redacción de planes de gestión del escribano palustre iberoriental tanto a nivel regional como de los espacios protegidos que ocupa (todos ellos espacios de la Red Natura 2000), y la puesta en marcha de acciones para asegurar la conservación a corto plazo. En la actualidad, únicamente la Comunidad Valenciana ha redactado un borrador de plan de gestión para la especie, y algunas comunidades autónomas como La Rioja o Madrid aparentemente han visto extinguirse la especie sin haber planificado ni puesto en marcha medidas para su conservación. La situación mostrada de acuerdo a los resultados y al último censo nacional (Monrós et al., 2017) debería poner en marcha los procedimientos de evaluación del estado de conservación de la especie a nivel nacional y, en consecuencia, la redacción de una estrategia nacional para su conservación.

La pérdida de hábitat y sus efectos a escala paisajística es considerada como una de las causas más relevantes de extinción de especies (Butchart et al., 2010). Un proceso que ha llevado a las especies más íntimamente ligadas a los humedales de la región mediterránea a aumentar su aislamiento y ver empeorado su estado de conservación (Cuttelod et al., 2008). Por tanto, la redacción de esta planificación debe incluir y dirigir los esfuerzos en recuperar hábitat de calidad de acuerdo a sus requerimientos. Los Capítulos III y IV muestran por primera vez qué variables ambientales determinan su presencia o ausencia durante la época de cría y el establecimiento de territorios dentro de este humedal en todo su rango de distribución en España. Los resultados a escala de humedal ponen de manifiesto la importancia de la cobertura de parches de vegetación mixta de carrizo (*Phragmites australis*) y enea (*Typha* spp.), y de carrizo y juncos (*Scirpus* spp.) en diferentes grados de dominancia. Una de las principales conclusiones del estudio es que la cobertura de masiega (*Cladium mariscus*) no es un factor importante para determinar la presencia de escribano palustre en su rango de distribución en España, aunque esta relación sí se encontró o propuso en estudios realizados en una única localidad (Martínez-Vilalta et al., 2002, Jiménez et al., 2015) o valoraciones a escala regional (Bigas y Copete, 2004). La distribución del escribano palustre iberoriental en España no se solapa con la de la masiega, por lo que su papel ecológico parece ser sustituido por la de otras especies de estructura similar que en nuestro estudio clasificamos como juncos (p.e. *Scirpus holoschoenus* o *Juncus acutus*) y que sí muestran una relación significativa con la presencia de la especie. Aunque estudios previos con la subespecie nominal encontraron esta relación con la enea para el establecimiento de territorios por su función como lugar para defender territorios (Sumarcki 2004), otros estudios realizados en el Delta del Ebro y Camarga no encontraron relación (Martínez-Vilalta et al. 2002, Poulin et al. 2002), posiblemente debido a no tratarla de manera independiente. La enea probablemente tiene un papel indicador de condiciones de inundación permanentes, aunque fluctuantes (White et al., 2007; Chun y Choi, 2009), factor que permite una mayor diversidad de vegetación emergente. De igual manera, estas condiciones se relacionan con una mayor accesibilidad al alimento durante la época de cría. La dieta, principalmente compuesta de larvas de insectos que extrae de los tallos de carrizo (Isenmann, 1990; Goater, 1993), es más diversa (Poulin et al. 2002) y accesible ya que los tallos de carrizo son más estrechos en condiciones de inundación permanente que en condiciones de sequía donde se desarrollan carrizales densos (Goater 1993).

Por lo que respecta al análisis de los requerimientos de hábitat para establecer los territorios, realizado en 11 humedales, la cobertura de eneas y la cobertura de carrizo y eneas fueron las variables que mejor explicaron la ocurrencia de los territorios, aunque con baja capacidad predictiva, por lo que aparentemente tienen un papel secundario para el establecimiento de territorios y simplemente indiquen condiciones estables de inundación, tal y como ocurre a escala de humedal. La cobertura de carrizo con formaciones de juncos y/o la masiega fue mayor en los territorios ocupados que en los no ocupados, siendo un resultado consecuente con el análisis realizado a escala de humedal. Estas formaciones proporcionan lugares para alimentación de adultos y volantones (Cramp y Perrins, 1994), así como lugares para percharse y defender territorios (Sumarcki 2004) y establecer sus nidos, tal y como se muestra en el Capítulo V. Dado que el escribano palustre iberoriental es un ave que construye sus nidos muy cerca del suelo, las altas coberturas de vegetación y la escasa fragmentación que tienen sus territorios se relacionarían con la reducción de la probabilidad de predación (Lahti, 2001; Bátary et al., 2004; Schiegg et al., 2007), ya que la predación es la principal causa de pérdida de nidos del escribano palustre (Crick et al., 1994) y los nidos de escribano palustre localizados en pequeños parches tienen una mayor probabilidad de ser predados (Pasinelli y Schiegg, 2006; Schiegg et al., 2007).

En base a los resultados obtenidos, el tamaño de los humedales no es un factor determinante en la ocurrencia del escribano palustre iberoriental, tal y como también demostraron Passinelli et al. (2008). Por tanto, en base a los resultados de modelización y uso de hábitat obtenidos, para aumentar la superficie de hábitat adecuado para establecer territorios e incrementar las poblaciones de escribano palustre iberoriental, la restauración de pequeños humedales o de zonas concretas dentro de grandes humedales debe contemplar básicamente cuatro aspectos:

i) Control de los niveles de inundación, como herramienta para gestionar la presencia, densidad y proporción de carrizo, eneas y matas de juncos y masiega a través de la competencia entre el carrizo y el resto de especies emergentes (Hellings and Gallagher, 1992; Coops et al., 1994; Poulin et al., 2002; Chun y Choi, 2009).

ii) Fomento de formaciones poco fragmentadas de carrizo mixtas con otros tipos de vegetación emergente, principalmente eneas, y juncos/masiega, mediante el pastoreo y de manera complementaria al control de los niveles de inundación (Vulink et al., 2000, Martínez-Vilalta et al. 2002, Mesléard et al. 2002).

iii) Desarrollo de prácticas de gestión compatibles con el mantenimiento de la abundancia y disponibilidad de alimento en los tallos de carrizo, evitando por tanto hacer extensivas siegas que afectan la disponibilidad de hábitat durante el inicio de la primavera (Poulin y Lefebvre, 2002) y quemas que impidan el desarrollo en altura del carrizo (Valkamma et al., 2008) y disminuyan la abundancia de insectos que componen la dieta del escribano palustre iberoriental (van der Toorn y Mook, 1982; Schmidt et al. 2005).

Asimismo, el estudio de nidos mostró un importante impacto de predadores, de forma coherente con otros estudios con el escribano palustre en Europa (Schiegg et al., 2007; Musilová et al., 2014). Po tanto, parece recomendable establecer un control de predadores, como son los roedores, rálidos, zorros (*Vulpes vulpes*) y jabalíes (*Sus scrofa*), especialmente en aquellas zonas en las que la gestión de los niveles de inundación y de la vegetación aumentan temporalmente la fragmentación y el borde o margen de los hábitats (van Oene et al., 1999; Seymour et al., 2004).

Los resultados plantean nuevos aspectos a profundizar, como es el papel en el establecimiento de territorios de la disponibilidad de alimento, la densidad de predadores, la experiencia de machos adultos y la falta de hábitats alternativos adecuados, aspectos que pueden disociar el establecimiento del territorio de la calidad del hábitat (Söderström, 2001; Musilová et al. 2011). En este sentido, es importante profundizar en las variables que determinan los hábitats óptimos para la especie, relacionando los requerimientos de hábitat con variables como el éxito reproductor o la productividad (Arlt y Pärt, 2007; Berg, 2008), aspectos que permitirían determinar áreas prioritarias para su restauración o reintroducción (Guisan y Zimmermann, 2000; Austin, 2007).

En el Capítulo VI se muestra mediante el estudio de un humedal concreto (Marjal de Pego-Oliva) la posibilidad de analizar la variación en la cobertura de los hábitats seleccionados positivamente por el escribano palustre iberoriental mediante el uso de técnicas de clasificación de vegetación correspondientes a varios años, a partir de imágenes de satélite de alta resolución (SPOT-5, resolución de 10 m) apoyadas en la cartografía de campo. En nuestro caso, se han obtenido altos valores de exactitud para todos los mapas de clasificación considerados (> 85 %), en comparación a otros trabajos realizados en humedales (Ozesmi 2002, Baker 2006, Davranche 2010) gracias al grado de detalle del trabajo de campo. Los sectores con hábitat adecuado (clasificación apoyada por la localización de machos territoriales) muestran una rápida homogeneización de la vegetación entre 2005 y 2006, coincidiendo con el abandono del pastoreo. Este proceso es especialmente importante en las formaciones de carrizal-juncal, hábitat seleccionado positivamente por el escribano palustre iberoriental para establecer territorios, y que a lo largo del período del estudio fue sustituido en uno de los sectores por formaciones puras de carrizo, hábitat evitado por la especie. En el resto de sectores la vegetación, dominada por carrizales homogéneos, no se observó un aumento o disminución significativa de los tipos de vegetación adecuados para el escribano palustre, sectores en los que no fue detectado ningún macho territorial durante el período de estudio. El escribano palustre iberoriental desaparece de las zonas donde se ha perdido su hábitat y aparentemente se extingue del Marjal de Pego-Oliva entre 2007 y 2008, suponiendo una diferencia de dos años respecto a los cambios rápidos de vegetación, de igual manera que ocurre con otras especies (Brooks et al., 1999; Findlay & Bourdages, 2001), incluyendo el escribano palustre norteño (Campbell, 1988).

De acuerdo a los resultados, son necesarios nuevos estudios para mejorar el grado de exactitud alcanzado por las clasificaciones de formaciones mixtas, así como métodos que permitan evaluar factores clave para esta y otras especies, como es la disponibilidad de recursos tróficos (Martin, 1992, 1995; Pärt, 2001) o riesgo de predación de nidos (Schiegg et al., 2007, Musilová et al., 2014, Trnka et al., 2011), aunque se encuentran estrechamente ligados a la estructura y cobertura de la vegetación (p.e. Pasinelli & Schiegg, 2006). Esperamos que los resultados de este capítulo sirvan de estímulo para que las administraciones pongan en marcha programas de seguimiento del hábitat adecuado del escribano palustre iberoriental, y pueda profundizarse *a posteriori* en los factores de pérdida de hábitat subyacentes a las extinciones locales y los declives poblacionales en todo su rango de distribución. El uso de este método, además, permite planificar las campañas de validación con trabajo de campo y las categorías de vegetación con las que realizar evaluaciones de la idoneidad de hábitats de una manera rápida, así como de su dinámica temporal (Fuller, 2005; Gillespie, 2008; Keith, 2009) para un amplio rango de fauna, incluso de manera integrada.

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Conclusiones

1. El escribano palustre iberoriental no presenta en el momento del estudio evidencias de haber sufrido reducción de la diversidad genética (medida como diversidad de nucleótidos mitocondriales y valores de heterocigosidad nucleares) esperable de acuerdo a su declive.

2. Las poblaciones de escribano palustre iberoriental tienen una mayor diversidad genética y se encuentran más diferenciadas genéticamente entre ellas de lo que lo están las poblaciones de escribano palustre iberoccidental (*Emberiza schoeniclus lusitanica*). Este resultado pone de manifiesto un mayor aislamiento del escribano palustre iberoriental, debido a que las distancias entre humedales en los que se encuentra presente son considerablemente mayores que en el caso del escribano palustre iberoccidental, dificultando que el flujo génico sea más efectivo.

3. Los resultados sugieren la idoneidad de tomar como unidades de gestión de escribano palustre iberoriental las poblaciones de Castilla-La Mancha, Delta del Ebro y Baleares, estableciendo como medida prioritaria la mejora de la calidad del hábitat para aumentar los tamaños poblacionales y preservar la máxima diversidad genética de esta subespecie y recuperar la conectividad entre pequeños humedales.

4. El declive experimentado a nivel del rango de distribución, sin prácticamente reclutamiento de nuevas poblaciones entre 2005 y 2015, determina un alto riesgo de extinción en el futuro cercano (con una probabilidad de 0.886 de sufrir un declive mayor al 80 % en los próximos 25 años). En las Tablas de Daimiel, el humedal más importante para el escribano palustre iberoriental en el interior de la península Ibérica, la ocupación de territorios pasó del 71 % en 2006 al 17 % en 2009, con una tasa de crecimiento de la población de 0.568 ± 0.294 entre 2006 y 2008.

5. Los resultados muestran que el seguimiento de la población mediante puntos de escucha y análisis de la ocupación de territorios es adecuado para el seguimiento del escribano palustre en las Tablas de Daimiel, requiriendo modelizar la detectabilidad para obtener estimas de la ocupación no sesgadas.

6. La cobertura de juncos con carrizo, de carrizal-eneal y el perímetro de los juncales-carrizales son las variables que mejor explicaron la distribución del escribano palustre iberoriental en su rango de distribución en España. Por tanto, los planes de gestión y estrategias de conservación deben poner el foco en mejorar el hábitat recuperando estas formaciones y evitando la homogeneización de la vegetación. Los carrizales-juncales proveen lugares de alimentación para adultos y jóvenes, así como lugares de nidificación. La enea probablemente tiene un papel indicador de condiciones de inundación permanentes, aunque fluctuantes, factor que permite una mayor diversidad de vegetación emergente.

7. La cobertura de carrizo con formaciones de juncos y/o masiega fue mayor en los territorios ocupados que en los no ocupados, en un resultado consecuente con el análisis realizado a escala de su distribución. El escribano palustre iberoriental es un ave que construye sus nidos muy cerca del suelo, por lo que las altas coberturas de vegetación y la escasa fragmentación que tienen sus territorios, así como la composición del nido, se relacionarían con la reducción de la probabilidad de predación, la principal causa de pérdida de nidos del escribano palustre.

8. Dado que el tamaño de los humedales no es un factor determinante en la ocurrencia del escribano palustre iberoriental, y de acuerdo a los requerimientos de hábitat a escala de humedal y territorio, la restauración de pequeños humedales o de zonas concretas dentro de grandes humedales debe contemplar el fomento de formaciones poco fragmentadas de carrizo con otros tipos de vegetación emergente, principalmente juncos/masiega y eneas. Para ello se proponen prácticas de control de los niveles de inundación y/o el pastoreo, teniendo en cuenta prácticas de gestión compatibles con el mantenimiento de la abundancia y disponibilidad de alimento en los tallos de carrizo (p.e. evitando por tanto hacer extensivas siegas y quemas), y el control de predadores.

9. En el Marjal de Pego-Oliva el uso de técnicas de clasificación de vegetación correspondientes a varios años a partir de imágenes de satélite de alta resolución (SPOT-5, resolución de 10 m) validadas con cartografía de campo, muestra la homogeneización rápida del carrizal y reducción de la cobertura de las formaciones vegetales seleccionadas positivamente por el escribano palustre iberoriental (proceso ocurrido tras el abandono del pastoreo y ausencia de gestión activa en zonas ocupadas por machos territoriales). Este proceso coincide con su aparente extinción, con un retraso de dos años similar al mostrado por la especie en otros estudios.

10. La obtención de altos valores de exactitud en la clasificación de los tipos de vegetación para todos los mapas de clasificación considerados permite considerar esta herramienta como idónea para poner en marcha programas de seguimiento del hábitat del escribano palustre iberoriental (pudiendo complementarse con el de otras especies). Asimismo, puede ser utilizada para profundizar en los factores de pérdida de hábitat subyacentes a las extinciones locales y los declives poblacionales en todo su rango de distribución y proponer, en base a esta información, prioridades de gestión y restauración de hábitats.

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