



TESIS DOCTORAL

**PAPEL DE LAS POBLACIONES DE AVES ACUÁTICAS
EN HUMEDALES ANTRÓPICOS DEL SUR DE EUROPA:
ECOLOGÍA DE LAS ANÁTIDAS MIGRATORIAS DE
LARGAS DISTANCIAS INVERNANTES EN
EXTREMADURA**

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A mis padres

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Resumen

A lo largo del siglo XX y principio del XXI la continua transformación y degradación de las zonas húmedas naturales, a consecuencia del Cambio Global, ha ocasionado un declive generalizado de las poblaciones de aves acuáticas migratorias de largas distancias. Esta situación ha originado que humedales antrópicos como los campos de arroz, ampliamente distribuidos a escala global, puedan proporcionar hábitats favorables para las aves acuáticas y tener un papel importante en la conservación de estas especies. Dentro de la Ruta Migratoria del Atlántico Este, Extremadura, una de las principales regiones productoras de arroz del suroeste de Europa, ha emergido como un área de importancia internacional para diferentes grupos de aves acuáticas durante el otoño e invierno. Numerosas especies de ánades de superficie (*Anatidae*, género *Anas*) utilizan los arrozales como áreas de invernada y escala durante sus migraciones de largas distancias, por lo que representan un excelente modelo a la hora de valorar el papel que los arrozales tienen, o pueden llegar a tener, como sustitutos potenciales de los humedales naturales.

El objetivo general de esta tesis doctoral es profundizar en el conocimiento sobre el uso de los arrozales como áreas de forrajeo por aves acuáticas migratorias, con especial énfasis en los ánades de superficie.

Entender cómo la conectividad geográfica influye en las diferentes etapas del ciclo anual de las especies migratorias es un componente central en el diseño de las estrategias de conservación de tales especies. A pesar de ello, el origen geográfico de los ánades de superficie invernantes en los arrozales del sur de Europa es bastante desconocido. En los ánades de superficie, al igual que en otras muchas especies de aves migratorias, los sexos suelen diferir en la distancia recorrida entre las áreas de reproducción e invernada. Conocer el origen geográfico de ambos sexos en las principales áreas de invernada, algunas de ellas inexistentes hasta hace pocas décadas, permitiría establecer la actual conectividad migratoria en especies de gran interés en conservación. Este conocimiento también ayudará a entender los patrones de flujo genético en estas especies, ya que en los ánades de superficie la pareja se forma durante el invierno y luego se desplazan juntos a la zona de reproducción. Dentro de este contexto hemos analizado, por un lado, las concentraciones de isótopos estables de deuterio ($\delta^2\text{H}_p$) en plumas crecidas en las áreas de reproducción, lo cual permitió determinar el origen geográfico de machos y hembras juveniles de ánades rabudos *Anas acuta* y cercetas comunes *Anas crecca* invernantes en Extremadura, un área de invernada clave para las poblaciones de ambas especies que utilizan la Ruta Migratoria del Atlántico Este. Por otra parte, equipamos con transmisores GPS-GSM machos

y hembras de ánades rabudos para establecer las áreas de cría y complementar así la información proporcionada por el análisis de isótopos. Los resultados indicaron que la mayoría (> 70 %) de los ánades rabudos de primer año proceden de regiones situadas en latitudes superiores a los 55°N, llegando a desplazarse entre 2600 km y 5600 km desde las áreas de reproducción hasta Extremadura. Los valores medios de ($\delta^2\text{H}_p$) variaron significativamente entre machos y hembras de ánade rabudo, indicando diferencias en cuanto a sus orígenes geográficos. Los datos obtenidos de los individuos equipados con transmisores apoyaron los resultados isotópicos, recorriendo alguno de los individuos más de 5000 km hasta alcanzar las zonas de cría en la costa del mar de Pechora (Rusia). La mayor parte (> 70 %) de las cercetas comunes fueron asignadas a un área geográfica amplia, situada entre los 48°N y los 60°N, por lo que deben desplazarse entre 1500 km y 4500 km hasta llegar a Extremadura. Las diferencias entre los valores de ($\delta^2\text{H}_p$) de machos y hembras de cercetas comunes fueron próximas a la significación. Los ánades de superficie migratorios pueden reproducirse el primer año tras su nacimiento, lo que sugiere que al menos en el caso de los ánades rabudos la formación de la pareja durante la invernada en estos arrozales podría favorecer la variabilidad genética de sus poblaciones.

La pérdida de humedales naturales es un fenómeno global que tiene graves consecuencias para las poblaciones de aves acuáticas y sus servicios ecosistémicos asociados. Un gran número de estudios sugieren que los arrozales pueden reducir el impacto que la pérdida de hábitats naturales tiene en las aves acuáticas migratorias. Sin embargo, a pesar de la gran cantidad de información disponible, los factores que determinan el uso de los arrozales por los ánades de superficie son muy desconocidos en aquellas especies que forrajean durante la noche. Con el fin de contribuir a suplir esta falta de conocimiento, se realizó un estudio cuyo objetivo fue identificar los efectos de las actividades de manejo de los arrozales, las características del paisaje y las condiciones ambientales en el uso nocturno de los arrozales por el ánade rabudo, una especie ampliamente distribuida en todo el mundo. Para ello se examinó su área de campeo en los arrozales extremeños de las Vegas Altas del Guadiana, así como la selección de recursos a pequeña escala a lo largo de la invernada. Los individuos fueron monitorizados utilizando transmisores GPS-GSM, y los patrones espaciales de uso de hábitat fueron analizados mediante la utilización de modelos lineales generalizados mixtos, integrando las observaciones de campo con los datos de telemetría GPS. Todas las aves se alimentaron durante la noche. Para ello se desplazaron diariamente desde el embalse utilizado como dormitorio diurno hasta los arrozales próximos, donde forrajean desde la puesta de sol hasta el amanecer. El área de campeo (9.653 ± 1.589 ha) y la distancia máxima de forrajeo nocturno ($11,4 \pm 0,6$ km) aumentaron con la disminución de la superficie de balsas inundadas, y ambas variables estuvieron positivamente correlacionadas con la iluminación nocturna procedente de la luna. Las aves seleccionaron tablas de arroz inundadas (rango de profundidad: 9 - 21 cm), provistas de rastrojo, y con un sustrato con grava de menos de 0,5 cm de diámetro. La densidad de alimento (semillas de arroz), la superficie total de la tabla de arroz y otras características ambientales y paisajísticas no fueron predictores significativos del uso nocturno de las tablas de arroz por los ánades. Nuestros hallazgos indican que el forrajeo nocturno de los ánades rabudos dentro de los campos de arroz está

condicionado principalmente por la manipulación del rastrojo, el nivel del agua y el tamaño de la grava del sustrato. De este modo, desde el punto de vista de los ánades de superficie, se deben priorizar tablas de arroz inundadas, con rastrojo y partículas finas en el sustrato. Estas prácticas de manejo no incrementarían los costes ni afectarían a la producción de arroz, y podrían ser aplicadas para la conservación de los ánades de superficie en todo el mundo.

Antes de la migración de primavera, los ánades de superficie que migran largas distancias deben acumular una gran cantidad de grasa y, en menor medida, de proteínas como fuentes de energía para realizar con éxito su viaje migratorio. Sin embargo, a pesar de que la masa corporal alcanzada en los lugares de invernada antes de emprender la migración es un parámetro esencial en el estudio de la migración de las aves, la información disponible sobre los cambios fisiológicos de los ánades de superficie en las áreas de invernada y escala, en relación a la distancia que han de volar ininterrumpidamente, es muy escasa. En este estudio realizado en los campos de arroz de Extremadura, se han investigado los cambios en la masa corporal de los ánades rabudos a lo largo del invierno, incluyendo el período pre-migratorio. Además, también se han medido los cambios en los niveles plasmáticos de triglicéridos y proteínas totales como índices del metabolismo de lípidos y proteínas, respectivamente. Los ánades rabudos incrementaron significativamente su masa corporal al final del invierno (período pre-migratorio), y ambos sexos presentaron un patrón similar. Los niveles plasmáticos de triglicéridos y proteínas mostraron un patrón comparable al del incremento de la masa corporal, si bien estadísticamente sus incrementos no fueron significativos. El incremento de masa corporal en Extremadura no siguió las predicciones de la ‘estrategia de invernada’ propuesta para ánades de superficie migratorios invernantes en el oeste de Europa, el cual señala que los valores más altos de masa corporal se alcanzan a mediados del invierno. Ello podría ser debido a las condiciones ambientales (clima y disponibilidad de alimento) más benignas en el suroeste de Iberia en relación al oeste de Europa.

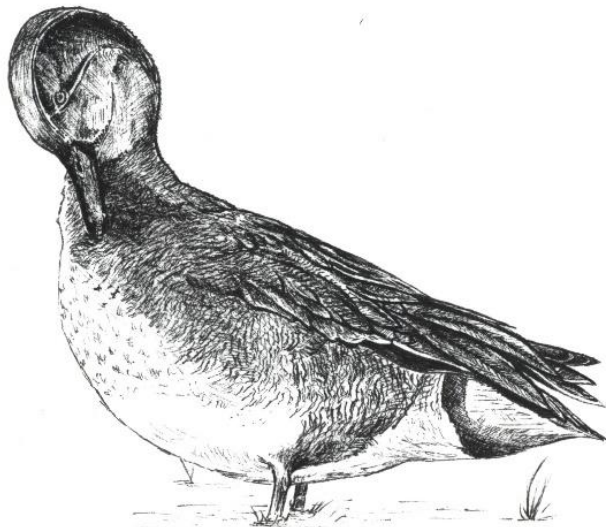
Las aves acuáticas son un componente clave en los flujos de masa y energía dentro de las redes tróficas de los humedales, proporcionando importantes servicios ecosistémicos. Este grupo de aves puede consumir una importante proporción de la producción vegetal y animal (macroinvertebrados) anual, mientras que sus excrementos representan una fuente natural de nutrientes como el nitrógeno (N) y el fósforo (P). En los campos de arroz de las regiones templadas, los cuales son utilizados por grandes números de aves acuáticas durante el invierno boreal, se espera que este flujo de nutrientes sea muy elevado. Sin embargo, los efectos de las aves acuáticas en los ciclos biogeoquímicos han sido raramente cuantificados. En este estudio se han examinado tales efectos en los campos de arroz de Extremadura, una de las áreas más importantes para la producción de arroz en el suroeste de Europa. Con este fin hemos estimado, por un lado, el número de aves en estos arrozales, la dieta (análisis de isótopos estables) de las principales especies, así como la disponibilidad y consumo de alimento por las aves acuáticas. Por otro, se modeló el reciclaje de nutrientes (N y P) en los campos de arroz y su transporte hacia los embalses. Los campos de arroz proporcionaron un significativo ‘subsidio trófico’ a las aves acuáticas invernantes, principalmente (90%) a través del consumo de las semillas de arroz que quedan

abandonadas en el suelo tras la cosecha. La energía consumida por las aves acuáticas (96.605 ± 18.311 individuos) en los arrozales durante el invierno se estimó en $89,9 \pm 39,0 \text{ kJ}\cdot\text{m}^{-2}$. Las aves retiraron el 26 % de las semillas que quedan en el suelo tras la cosecha (estimadas en $932,5 \pm 504,7 \text{ semillas}\cdot\text{m}^{-2}$ al inicio del invierno), siendo los consumidores más importantes la grulla común *Grus grus* y los ánades de superficie. Las aves acuáticas fueron responsables del reciclaje de más de 24,1 y 5,0 toneladas de N ($1,0 \text{ kg}\cdot\text{ha}^{-1}$) y P ($0,2 \text{ kg}\cdot\text{ha}^{-1}$) dentro de los campos de arroz. Por otro lado, los movimientos que realizan algunas especies entre los campos de arroz y los embalses adyacentes generaron una relocalización de 2,3 toneladas de N y 550 kg de P hacia los embalses que actúan como áreas de descanso. El reciclaje de nutrientes aporta importantes beneficios directos a los agricultores con respecto a la fertilización artificial. Por tanto, estos resultados pueden llegar a ser especialmente relevantes para la toma de decisiones de gestión y manejo de los hábitats asociados a la producción de arroz, los cuales también son importantes áreas para la conservación de las aves acuáticas migratorias.

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1

Introducción general

Humedales antrópicos e importancia internacional de Extremadura

Las modificaciones del paisaje ligadas a la historia de la humanidad, junto con los efectos globales del Cambio Climático, han provocado que los humedales naturales sean hoy en día uno de los hábitats más amenazados del planeta (Sebastián-González y Green 2016). En 1971 se firmó la Convención Ramsar (Convención Relativa a los Humedales de Importancia Internacional especialmente como Hábitat de Aves Acuáticas), con el fin de garantizar la protección y conservación de estos hábitats (Kleijn *et al.* 2014). No obstante, pese a esta y otras acciones de conservación, las zonas húmedas naturales han seguido desapareciendo durante el siglo XX y principios del XXI, de modo que más del 64 % de los humedales originales del planeta han desaparecido (Perennou *et al.* 2012, Davidson 2014). Sin embargo, la creación de humedales antrópicos (p.e. salinas, campos de arroz o acuicultura extensiva) ha mitigado hasta cierto punto los efectos de esta pérdida y degradación (Hagy *et al.* 2016), dado que estos humedales pueden proporcionar hábitat alternativos o complementarios a una gran variedad de especies de fauna acuática silvestre (Masero 2003, Machado y Maltchik 2010, Sirami *et al.* 2013, Elphick 2015). Especialmente importante es el papel actual, o potencial, de los humedales artificiales en la conservación de las aves acuáticas, reconocido por investigadores y gestores de la vida silvestre en todo el mundo (Ma *et al.* 2010). No obstante, la riqueza de estos hábitats de origen humano en términos de biodiversidad y proporción de especies amenazadas es inferior a la de los humedales naturales o restaurados (Sebastián-González y Green 2016). En este contexto, es de vital importancia identificar y valorar el papel de aquellos humedales antrópicos que amortigüen de algún modo los efectos negativos de la pérdida de zonas húmedas naturales en las aves acuáticas migratorias.

La posición estratégica de Extremadura (SO de España) dentro de la Ruta migratoria del Atlántico Este, junto a numerosos embalses próximos a grandes extensiones de campos de arroz, ha propiciado que esta región emerja como un área de importancia internacional para diferentes especies de aves acuáticas migratorias (Sánchez-Guzmán *et al.* 2007, Navedo *et al.* 2012). La creación de este agroecosistema a partir de la década de 1960 (**Figura 1**), ha modificado, entre otros, los lugares de invernada y alimentación de numerosas especies de aves acuáticas que siguen esta ruta migratoria, entre las que se incluyen la grulla común *Grus grus* (Sánchez-Guzmán *et al.* 2007), la aguja colinegra *Limosa limosa* (Masero *et al.* 2011, Santiago-Quesada *et al.* 2014) y diferentes especies de ánades de superficie (Navedo *et al.* 2012). Al igual que sucede en otras muchas regiones, en Extremadura este cultivo recibe subvenciones económicas de la Unión Europea, pero a diferencia de la mayoría de ellas, no existen planes o guías de manejo que indiquen y/o regulen dónde, cuándo y cómo deberían ser aplicados diferentes tratamientos pre- y post-cosecha para favorecer a las aves acuáticas, siendo claramente compatibles con la producción agrícola. A lo largo del invierno, la mayoría de los arrozales extremeños pueden inundarse de forma ‘natural’ por el agua de lluvia. La duración de la lámina de agua dependerá de los diferentes tratamientos de manejo post-cosecha, los cuales incluyen dejar o no el rastrojo (Sánchez-Guzmán *et al.* 2007). Este hecho genera, al igual que en otras zonas de cultivos de arroz del

planeta, un ‘mosaico de hábitats’ donde los arrozales inundados a diferentes profundidades, que mantienen o no el rastrojo, favorecen su uso por los distintos grupos de aves acuáticas como áreas de forrajeo o descanso durante el día y/o la noche (Elphick 2015).

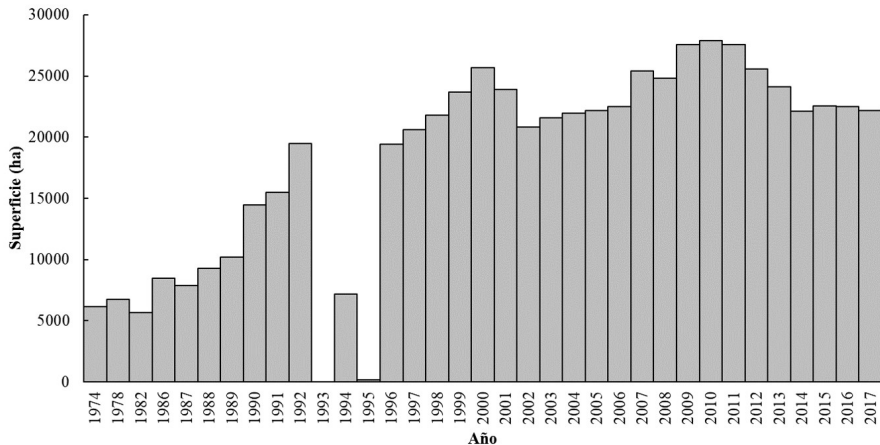


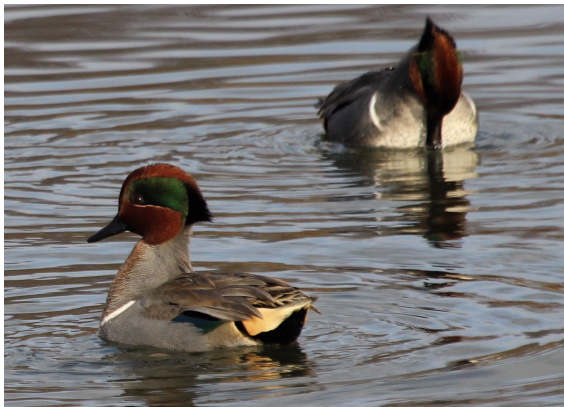
Figura 1: Evolución histórica (1974-2017) de la superficie del cultivo de arroz en Extremadura. Datos procedentes del anuario de estadísticas del Ministerio de Agricultura y Medio Ambiente (www.mapama.gob.es).

Ánades de superficie migratorios

Los ánades de superficie (Tribu *Anatini*) forman parte del orden *Anseriformes*, perteneciente a la familia *Anatidae*, un grupo que incluye a las especies de Anátidas más abundantes y cosmopolitas del planeta (Carboneras 1992). Dentro del género *Anas* existen ‘especies hermanas’ en términos biogeográficos como el silbón europeo *Anas penelope* y el silbón americano *Anas americana* (Johnson y Sorenson 1999), y otras especies como el ánade real *Anas platyrhynchos*, el ánade rabudo *Anas acuta* o la cerceta común *Anas crecca*, las cuales se distribuyen ampliamente a lo largo de diferentes regiones geográficas del planeta (Carboneras 1992, Kear 2005). Algunas especies migratorias realizan viajes de varios miles de kilómetros desde las áreas de reproducción, situadas en latitudes próximas a los círculos polares, hasta las áreas de invernada localizadas en las zonas templadas de ambos hemisferios, donde se reúnen miles de individuos con diferentes orígenes geográficos (Scott y Rose 1996, Guillemain *et al.* 2017a). La estrategia migratoria de los ánades de superficie se basa en combinar largos vuelos ininterrumpidos de hasta 1.300 km, con escalas de varios días en zonas donde reponen las reservas de energía necesarias para finalizar la migración (Arzel *et al.* 2006, O’Neal *et al.* 2012). Los estudios realizados durante los últimos cincuenta años sobre la distribución geográfica de diferentes especies de ánades de superficie migratorios del Paleártico occidental, han demostrado de forma repetida la disminución

de la distancia recorrida por estas especies durante la migración otoñal, así como la utilización de nuevas áreas de invernada (ver Guillemain y Hearn 2017).

Comportamientos relacionados con la reproducción como el cortejo y la formación de la pareja en los ánades de superficie, descritos detalladamente en los clásicos estudios de Konrad Lorenz (1941, 1951–1953, 1971), tienen lugar durante la estancia de estas especies en las zonas de invernada (Tamisier *et al.* 1995, Guillemain *et al.* 2005, Rodway 2007). Por tanto, los ánades de superficie tienen que ajustar la obtención de reservas de energía necesarias para la migración y la reproducción con las actividades de cortejo, de modo que al finalizar la invernada los individuos se encuentren emparejados y en la mejor condición corporal posible para comenzar la migración (Tamisier *et al.* 1995, Guillemain *et al.* 2005, 2008).



Machos de cerceta común *Anas crecca* realizando la exhibición de cortejo para formar pareja. Fotografía: P. Courteau - winter-wren, 2013 (www.flickr.com).

A lo largo del ciclo anual los ánades de superficie están ligados a distintos ambientes acuáticos, y se han adaptado a utilizar humedales antrópicos como embalses, zonas de cultivos piscícolas, salinas o cultivos de arroz (Kurechi 2007, Eadie *et al.* 2008, Navedo *et al.* 2012, Li *et al.* 2013). La capacidad para adaptarse a esta diversidad de hábitats se debe en gran medida a que los ánades de superficie migratorios presentan dietas mixtas basadas principalmente en semillas, granos y materia vegetal, así como en anfibios, peces pequeños e invertebrados acuáticos, dependiendo de las necesidades nutricionales y las fuentes de alimento disponibles (Olsen *et al.* 2011, Dessborn *et al.* 2014, Petrovan y Leu 2017).

Los campos de arroz se extienden por todos los continentes a excepción de la Antártida, y constituyen valiosos humedales artificiales de los que dependen, en alguna etapa de su ciclo anual, casi la mitad de las 147 especies de anátidas existentes en el mundo (Carboneras 1992, Elphick 2015). En el este y centro de Asia y en el sur de Norteamérica, donde se localizan las principales regiones productoras de arroz del mundo, millones de ánades de superficie se concentran durante el invierno boreal (Fujioka *et al.* 2010, Sundar y Subramanya 2010, Petrie *et al.* 2014). En Iberia,

los hábitats asociados a la producción de arroz como los situados en las marismas del Guadalquivir o Vegas Altas del Guadiana (SO de la Península Ibérica), también constituyen áreas de invernada para miles de ánades de superficie (Rendón *et al.* 2008, Navedo *et al.* 2012). La percepción de este grupo de aves varía geográficamente dependiendo en gran medida del contexto social y ambiental. Así, mientras que en Asia los ánades de superficie silvestres son considerados beneficiosos para el cultivo de arroz, en las regiones subsaharianas de África son considerados una plaga (Pernollet *et al.* 2015). En Estados Unidos los campos de arroz son gestionados a través de planes de manejo (North American Waterfowl Management Plan) desarrollados para proporcionar hábitats favorables a este grupo de aves durante la época de invernada, con el objetivo de conservar a estas especies (Petrie *et al.* 2014). Mientras que en Europa existen programas como los proyectos ‘Life Project Ebro Delta’ (Proyecto Life 96 NAT/E/3133) o ‘Life Project ECORICE’ (Vercelli Progetto Life 09 NAT/IT/000093), que promueven la inundación de algunas zonas de cultivo de arroz y así proporcionar hábitats para las aves acuáticas. En este escenario cabe preguntarse si las nuevas áreas de importancia internacional para la conservación de los ánades de superficie se encuentran suficientemente protegidas y se gestionan de forma adecuada para garantizar la existencia de hábitats favorables a estas especies.

A pesar del creciente número de estudios que versan sobre campos de arroz y ánades de superficie, hoy en día aún se desconocen aspectos muy importantes sobre cómo utilizan estos humedales artificiales desde el punto de vista de la obtención de recursos tróficos. Por ejemplo, en los hábitats antrópicos los ánades de superficie forrajean principalmente durante la noche (Guillemain *et al.* 2002), lo cual conlleva que desconozcamos en gran medida los determinantes del uso nocturno que hacen de los arrozales. Tampoco existe información, que nos permitan conocer los ajustes fisiológicos existentes detrás de los cambios en la condición corporal adquirida por estas especies invernantes en los arrozales de la zona templada, en relación a sus migraciones de largas distancias.

Conectividad migratoria y análisis del isótopo estable de H ($\delta^2\text{H}$)

En la actualidad, a consecuencia de la pérdida y degradación de los hábitats acuáticos mencionada anteriormente, más del 40 % de las especies de aves acuáticas migratorias de largas distancias paleárticas muestran un fuerte declive poblacional (Merken *et al.* 2015). Esta situación hace que sea necesario conocer los efectos del Cambio Global sobre la distribución geográfica de las aves acuáticas migratorias, y cómo sus poblaciones reproductoras y no reproductoras se encuentran interconectadas, lo cual es un requisito previo para diseñar planes adecuados de conservación y establecer una red de áreas clave para las diferentes especies (Madsen *et al.* 2014, Guillemain y Hearn 2017).

La ‘conectividad migratoria’ entre las poblaciones reproductoras e invernantes de las aves puede considerarse fuerte o débil, dependiendo de la medida en que los indivi-

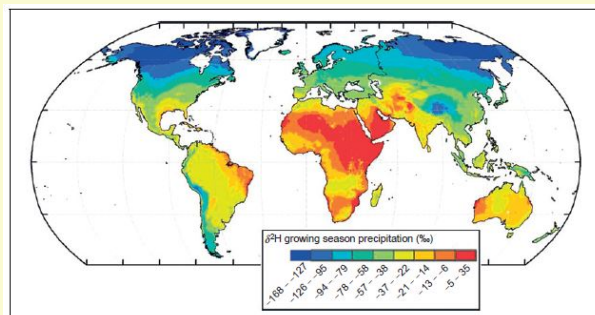
duos de determinadas áreas de reproducción viajen a las mismas o a diferentes áreas de invernada y viceversa (Newton 2008). Ello conlleva implicaciones para la ecología y estructura genética de las poblaciones, así como para su conservación (Finch *et al.* 2017). Desde otro punto de vista, los estudios de conectividad migratoria permiten evaluar los posibles riesgos de transmisión de enfermedades, dado que en sus viajes de largas distancias, las aves migratorias pueden actuar como vectores de parásitos y patógenos (Olsen *et al.* 2006, Krauss *et al.* 2016, Kwon *et al.* 2016). Especies con patrones de migración paralelos, como por ejemplo las poblaciones de barnacla cariblanca *Branta leucopsis* de Groenlandia, Noruega y Rusia, migran cada otoño a zonas separadas de Europa occidental, con muy poco intercambio de individuos de las tres poblaciones (Newton 2008). La fuerte conectividad migratoria de esta especie la hace más proclive a la disminución poblacional que otras cuya conexión migratoria es más débil (Carboneras 1992, Kear 2005). En los ánades de superficie la conectividad migratoria es débil, por lo general en una misma área de invernada los machos y hembras difieren tanto en la ruta migratoria como en la distancia recorrida durante la migración otoñal (Anderson *et al.* 1992, Scott y Rose 1996, Caizergues *et al.* 2011, Guillemain *et al.* 2017a). El hecho de que formen la pareja en los cuarteles de invierno puede tener posibles implicaciones directas sobre la variabilidad genética de la especie (Liu *et al.* 2012). Por lo tanto, designar el origen geográfico de las principales poblaciones invernantes de ánades de superficie migratorios proporciona un avance en el conocimiento de la conectividad migratoria de la especie (Newton 2008).

La aplicación del análisis de isótopos estables de H ($\delta^2\text{H}$) a los estudios de designación del origen geográfico de las especies ha generado un aumento en el conocimiento de la conectividad migratoria de las aves acuáticas (Hobson y Wassenaar 2008, Hobson 2011). La utilidad del análisis de isótopos estables se basa en el grado de conocimiento del proceso de enriquecimiento isotópico asociado al metabolismo, que se da entre la fuente de agua y alimento que ingiere el animal y sus tejidos (Bearhop *et al.* 2002, Caut *et al.* 2009). La utilización de tejidos metabólicamente inertes como las plumas o las uñas, permite una asignación probabilística del lugar donde se formaron estos tejidos (Hobson y Wassenaar 2008). La ventaja de utilizar las plumas en los estudios de conectividad migratoria de aves, es que la cronología de muda es relativamente conocida para numerosas especies migratorias (p.e. Baker 2016). Mediante algoritmos que relacionan los valores de $\delta^2\text{H}$ en plumas ($\delta^2\text{H}_{\text{pl}}$) con los valores de $\delta^2\text{H}$ ponderados del área de crecimiento, según las precipitaciones de dicha área ($\delta^2\text{H}_{\text{p}}$), se generan ‘isoscapes’ de los valores de $\delta^2\text{H}_{\text{pl}}$, que pueden usarse para determinar áreas geográficas potenciales donde los individuos reemplazan el plumaje (**Cuadro A**). Por otra parte, combinar la utilización del análisis de isótopos estables y el de otros marcadores extrínsecos como la recuperación de anillas o dispositivos GPS, o intrínsecos como los marcadores genéticos, mejoraría la certeza de la asignación del origen geográfico a una población invernante (Bridge *et al.* 2014, Rushing *et al.* 2014). La combinación de los datos proporcionados por estas herramientas sobre la conectividad migratoria y el desarrollo de nuevos modelos matemáticos, prometen aportar luz a los estudios sobre la dinámica poblacional y las causas del declive generalizado de las poblaciones de aves migratorias de largas distancias (Bridge *et al.* 2014, Rushing *et al.* 2016, Guillemain *et al.* 2017a).

Cuadro A. Modelos de distribución isotópica ‘Isoscapes’

La variación isotópica a nivel del paisaje refleja (1) la fuente isotópica disponible, (2) las condiciones ambientales locales, y (3) la organización espacial de diferentes procesos físicos (escorrentía, flujo de agua subterránea o circulación atmosférica) que determinan tanto la fuente isotópica como los procesos de fraccionamiento ambientales a gran escala (Hobson y Wassenaar 2008). La variación espacial de los valores isotópicos del $\delta^2\text{H}$ y el $\delta^{18}\text{O}$, se atribuyen principalmente a las precipitaciones. Por otro lado la actividad fotosintética y el intercambio gaseoso de las plantas generan la variación de los valores de $\delta^{13}\text{C}$, y la absorción del nitrógeno del suelo y su metabolismo por parte de las plantas producen la variación del $\delta^{15}\text{N}$ (Hobson 2011). El término Isoscapes, acuñado por el Dr. Jason B. West y el Dr. Gabriel J. Bowen, hace referencia a cualquier predicción de relaciones isotópicas específicas a nivel del paisaje, en un dominio espacio-temporal de interés. Para crear los mapas de Isoscapes, los patrones de fraccionamiento han de ser modelados, mapeados y por último combinados con Sistemas de Información Geográfica (West *et al.* 2008, Bowen 2010).

Los isoscapes de $\delta^2\text{H}$, principalmente los basados en los valores isotópicos de precipitación, han sido ampliamente utilizados en estudios de migración, dado que la principal fuente de ^2H en los tejidos es el agua ambiental, consumida o derivada de la dieta (Bearhop *et al.* 2005, van Wilgenburg y Hobson 2011). Los isoscapes de ^{18}O , utilizados con la misma finalidad, han sido menos aplicados a la investigación migratoria (Hobson *et al.* 2004). Por otro lado, los valores de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ han sido aplicados principalmente a estudios de dieta animal (Podlesak y McWilliams 2006, Caut *et al.* 2009), pero pueden ofrecer información espacial significativa a partir de sus isoscapes, ya que permiten realizar predicciones a escalas espaciales más pequeñas (Hebert y Wassenaar 2005, Catry *et al.* 2016). Incluso los valores de diferentes elementos isotópicos se pueden combinar para predecir el origen geográfico de las aves migratorias de forma más precisa (Hobson *et al.* 2012).



Ejemplo de isocape global del isótopo estable de H, basado en los valores medios de $\delta^2\text{H}$ de las precipitaciones, extraído de (Hobson y Wassenaar 2008).

Función de selección de Recursos

Determinar cuáles son los principales recursos seleccionados por las aves acuáticas migratorias proporciona información crucial sobre los requisitos necesarios para asegurar la supervivencia de estas especies. Cualquier función cuyo valor sea proporcional a la probabilidad de que un recurso sea seleccionado por un organismo, se considera una función de selección de recursos (en adelante FSR; Manly *et al.* 2002). Para llegar a conclusiones válidas sobre dicha selección, hay que comparar los recursos utilizados frente a los recursos potencialmente disponibles pero no usados (Johnson *et al.* 2006, Beyer *et al.* 2010). En los estudios de uso y selección de recursos los investigadores han de tener en cuenta la escala estudiada, dado que la selección puede darse a diferentes niveles espaciales y temporales; desde la distribución geográfica de una especie a la selección de un atributo del hábitat con unas características particulares en un momento concreto del ciclo anual (Boyce 2006). Numerosos factores contribuyen a que un recurso sea seleccionado o evitado, como por ejemplo la competencia inter e intra-específica, la depredación, las perturbaciones humanas, el tamaño del parche de hábitat o la distancia entre parches (Chudziriska *et al.* 2015).

La vinculación de la FSR a los Sistemas de Información Geográfica (SIG) ha supuesto un importante avance en el diseño de planes de conservación, ya que tiene numerosas aplicaciones en el manejo de recursos naturales (Boyce *et al.* 2002). Sin embargo, es la combinación de SIG con los datos de ubicaciones de los animales lo que permite desarrollar modelos de FSR espacialmente explícitos (Clevenger *et al.* 2002, Johnson *et al.* 2004, Millspaugh *et al.* 2006). Los datos de Sistema de Posicionamiento Global (GPS; **Cuadro B**) a pequeña escala temporal y espacial, permiten describir la relación entre las características del paisaje y un comportamiento (p. e. alimentación, descanso o nidificación), lo cual ofrece una visión más real de cómo percibe las características del entorno el animal (Dzialak *et al.* 2015, Austin *et al.* 2016). Tener un conocimiento detallado de la sincronía entre los movimientos y las características de hábitat a las que se encuentran asociados es decisivo, por ejemplo, a la hora de identificar los atributos del paisaje críticos para la especie (Beatty *et al.* 2014a, Benson *et al.* 2015, Salazar *et al.* 2016).

La mayoría de los trabajos sobre el uso y la selección de recursos se han desarrollado en hábitats naturales, donde las características del hábitats son fácilmente cuantificadas a distintas escalas (Dzialak *et al.* 2013, 2015). Sin embargo, en los hábitats antrópicos la diversidad topográfica es muchas veces baja o nula, y la abundancia de recursos fluctúa o es efímera (Meager *et al.* 2012, de la Cruz *et al.* 2014). Además, durante su estancia en estos hábitats las especies silvestres se encuentran expuestas a la influencia de las perturbaciones humanas producidas, por ejemplo, por las actividades agrícolas, la caza, los contaminantes u otras alteraciones físicas del hábitat (Meager *et al.* 2012). A pesar de que existen numerosos planes de conservación que gestionan ciertos humedales antrópicos con el objetivo de favorecer a diferentes especies de aves acuáticas migratorias, estos no se basan en datos empíricos sobre el uso y selección de alimento por estas especies dentro de una escala espacial y temporal adecuada (Callicutt *et al.* 2011). Dado el incremento en la dependencia de las aves acuáticas migratorias por los humedales antrópicos, la falta de conocimiento sobre

la selección de recursos restringe el desarrollo de medidas de gestión adecuadas que puedan beneficiar a sus poblaciones (Pernollet *et al.* 2016, Guillemain *et al.* 2017b). A fecha de hoy, los modelos de selección de recursos diseñados a partir de ubicaciones de las aves nos dan una visión fundamental de los mecanismos que subyacen a su distribución y abundancia en diferentes escalas (Beatty *et al.* 2014a; b, de la Cruz *et al.* 2014).



Grupo de ánades de superficie (género *Anas*) abandona al caer la tarde el embalse utilizado como zona de descanso durante las horas de luz del día y se dirige hacia las áreas de forrajeo nocturno. Fotografía: Eileen y Harry Bickerstaff, 2013 (www.flickr.com).

Cuadro B. Tecnología de seguimiento de aves

En los últimos años, como consecuencia de los avances en la tecnología de seguimiento, los estudios de ‘ecología del movimiento’ han experimentado un impulso de gran valor (Nathan *et al.* 2008, Kays *et al.* 2015, Edelhoff *et al.* 2016). El movimiento de las aves ha despertado el interés de la humanidad desde la antigüedad; de hecho, hace más de 2000 años Aristóteles se preguntaba dónde iban las aves en invierno. Sin embargo, hasta la llegada de esta tecnología a finales de la década de 1950, nuestra ignorancia sobre los movimientos de las aves continuaba siendo muy elevada, a pesar de que en Europa los primeros anillamientos científicos ocurrieron en 1899 (Newton 2008, López-López 2016).

A lo largo de las últimas cinco décadas los diferentes tipos de dispositivos se han ido miniaturizando hasta alcanzar en la actualidad 0,3 gramos, en el caso de los geolocalizadores. Los dispositivos adecuados para una especie determinada se limitan a aquellos que no superen entre el 3 y el 5 % de la masa corporal de los individuos (Kays *et al.* 2015). El aumento de la capacidad de la memoria interna y la alta frecuencia de adquisición de posiciones permite que existan dispositivos capaces de proporcionar miles de localizaciones al día. Por otro lado, la posibilidad de la descarga remota de los datos y la configuración de los distintos parámetros de registro en función de las necesidades de los investigadores, permiten seguimientos casi a tiempo real. Finalmente, en los últimos años se han ido incorporando diferentes tipos de sensores (altímetros, acelerómetros, pulsómetros, termómetros, conductímetros e incluso sensores de vídeo), permitiendo una resolución de las trayectorias y un conocimiento de los complejos comportamientos de vuelo con una sutileza sin precedentes (López-López 2016).



Ánade rabudo *Anas acuta* equipado con transmisor GPS-GSM alimentado por una placa solar (aproximadamente 35 g; Fotografía: J. M. Abad, 2013).

Cuadro B. Continuación

La tecnología de seguimiento puede ser clasificada en función de cómo se recuperan los datos registrados por los dispositivos (**Tabla B1**).

Tabla B1

Características clave de la tecnología de seguimiento de aves, adaptado de Bridge *et al.* (2011) y López-López (2016)

Sistema de recuperación de datos	Tecnología de seguimiento	Peso mínimo del dispositivo (gramos)	Coste mínimo por unidad (euros)	Máximo número de localizaciones al día	Máxima precisión (metros)	Rango de operación
Sistema de transmisión por satélites (datos registrados y recuperados por satélites)	Efecto Doppler	5	3200	1	100	global
	GPS	15	3200	20	5	global
Receptores terrestres (antenas fijas o móviles)	Torre de identificación	-	desconocido	10	30000	80 % superficie terrestre
	GPS/GSM	15	2000	>2000	5	global
	Telemetría de radio	0,3	200	200	100	local (o móvil)
	GPS con transmisor	5	1000	100	5	global
	Geolocalizador solar con transmisor	-	desconocido	2	200000	global
Dispositivos que requieren su recuperación	GPS	5	600	100	5	global
	Geolocalizador solar	0,3-0,5	80	2	200000	global
Radar	Radar marino, X-band radar		variable	1000	5	local
	Radares meteorológicos de vigilancia		gratuito	144	500	Norte de América y Europa

¹Dependiendo del tamaño de la batería.

²Capaz de obtener datos de localización global, pero la transmisión de los datos sólo ocurre cuando existe cobertura de telefonía móvil.

³Descarga local.

⁴La precisión es limitada en la región ecuatorial durante alguna parte del año y en la región polar.

⁵El coste del seguimiento X-band puede variar desde aproximadamente 20000 euros para el alquiler de equipos y el procesamiento hasta 200000 euros por la compra de un dispositivo ensamblado y el análisis de los datos. El equipo de radares de seguimiento especializado u otros sistemas portátiles de alta gama pueden alcanzar los 820000 euros.

GPS Global Positioning System; GSM Global System for Mobile Communications.

Servicios ecosistémicos y aves acuáticas migratorias

El término ‘servicios ecosistémicos’ describe los recursos que proporciona un ecosistema para beneficio de la humanidad (Green y Elmberg 2014). Los humedales son uno de los ecosistemas que más beneficios aportan al bienestar humano, entre los que se incluyen purificación del agua, conservación de la biodiversidad, protección frente a los efectos de la erosión del suelo e inundaciones, regulación de gases atmosféricos o secuestro de carbono (Costanza *et al.* 1997). Las aves acuáticas son responsables, dentro de los humedales, de una serie de servicios ecosistémicos únicos como la dispersión de semillas o el control de plagas, además de proporcionar alimento y poseer un gran valor cultural (**Tabla 1**; Soons *et al.* 2016). Las aves acuáticas también juegan un importante papel en el ciclo de los nutrientes y son responsables de la concentración y relocalización de estos en los cuerpos de agua (Hahn *et al.* 2008). A la hora de determinar estos servicios ecosistémicos, es esencial profundizar en el conocimiento de los niveles de interacción entre las aves acuáticas y el resto del ecosistema, y la variación espacio-temporal de dichas interacciones, dado que una misma especie se puede comportar de manera diferente a lo largo del ciclo anual (Dessborn *et al.* 2014). Además, los servicios ecosistémicos aportados por las aves suelen depender de gremios formados por diferentes especies con un comportamiento ecológico similar (Whelan *et al.* 2008). El declive generalizado del tamaño de las poblaciones de aves acuáticas migratorias y su cada vez mayor dependencia de los humedales antrópicos (Green y Elmberg 2014), donde las aves acuáticas pueden competir por recursos limitados de interés humano, hace aún más urgente la valoración de los servicios proporcionados por estas especies (ver Fox *et al.* 2017). Finalmente avanzar en el conocimiento a pequeña escala de los servicios ecosistémicos aportados por las aves acuáticas migratorias mejoraría la comprensión y la opinión de la sociedad sobre la necesidad de conservar estas especies, siendo además argumentos sólidos a favor de un desarrollo económico sostenible.



Representación de un ánade de superficie en un mosaico romano de la sinagoga de Hammam-Lif, Túnez, Siglo III d.C. Fotografía: Dilek Murgul, 2014 (www.flickr.com).

Tabla 1

Ejemplos de servicios ecosistémicos proporcionados por algunos grupos de aves acuáticas, adaptado de (Green y Elmberg, 2014)

Servicio ecosistémico	Grupo taxonómico	Referencia
Materia prima		
Alimento	Anátidas	(Zwarts <i>et al.</i> 2009, Krcmar <i>et al.</i> 2010, Fox <i>et al.</i> 2017)
Plumón, plumas y grasa impermeabilizante	Anátidas	(MacMillan y Leader-Williams 2008, Buij <i>et al.</i> 2017)
Sostenibilidad		
Dispersión de propágulos	Anátidas, ráldos	(Soons <i>et al.</i> 2016, Lovas-Kiss <i>et al.</i> 2018)
Ciclo de nutrientes y fertilización del suelo	Anátidas, grullas, limícolas	(Gauthier <i>et al.</i> 2006, Kameda <i>et al.</i> 2006, Hahn <i>et al.</i> 2008, Klimaszuk <i>et al.</i> 2014)
Estimulación de producción primaria	Anátidas	(Mayhew y Houston 1999, Nolet 2004, Brogi <i>et al.</i> 2015)
Estimulación de descomposición	Anátidas	(Bird <i>et al.</i> 2000, Brogi <i>et al.</i> 2015)
Reducción de producción de metano	Cisnes	(Bodelier <i>et al.</i> 2006)
Diversidad de plantas	Anátidas, ráldos	(Green <i>et al.</i> 2002, García-Álvarez <i>et al.</i> 2015, Lovas-Kiss <i>et al.</i> 2018)
Diversidad de animales	Anátidas, limícolas y otros	(Arzel <i>et al.</i> 2015)
Bioindicador de plantas y animales	Anátidas, ráldos, limícolas y otros	(Ogden <i>et al.</i> 2014a; b, Samraoui <i>et al.</i> 2015)
Bioindicador de nutrientes/contaminantes	Garzas, podicipédidos, anátidas	(Ferreira <i>et al.</i> 2009; 2014, Burger <i>et al.</i> 2015, Holman <i>et al.</i> 2015)
Control		
Control de plagas	Anátidas	(Takao Furuno 2012)
Disminución de malas hierbas	Anátidas	(van Groenigen <i>et al.</i> 2003, Fogliatto <i>et al.</i> 2010; 2011)
Indicador de enfermedades	Ánades de superficie	(Ziegler <i>et al.</i> 2010, Rollo <i>et al.</i> 2012)
Configuración del paisaje	Anátidas, cormoranes	(Dirksen <i>et al.</i> 1995, Cowx 2007, Klimaszuk <i>et al.</i> 2014, Kleyheeg <i>et al.</i> 2017, Lovas-Kiss <i>et al.</i> 2018)
Cultural y deportivo		
Observación de aves	Anátidas, limícolas, grullas	(MacMillan y Leader-Williams 2008, Mattsson <i>et al.</i> 2018)
Emblema de conservación	Anátidas, limícolas, grullas	(Sánchez-Guzmán <i>et al.</i> 2007; Masero <i>et al.</i> 2011, Navedo <i>et al.</i> 2012)
Arte	Flamencos, grullas, anátidas	(Arnott 2007)
Caza	Anátidas, limícolas	(Eadie <i>et al.</i> 2008, Petrie <i>et al.</i> 2014, Mattsson <i>et al.</i> 2018)

Objetivos

El objetivo general de la presente tesis doctoral es comprender el papel de los arrozales como áreas de forrajeo para las aves acuáticas migratorias, con especial atención al uso de los arrozales por los ánades de superficie migratorios.

- *Objetivo I.* Establecer el origen geográfico de los ánades rabudos *Anas acuta* y cercetas comunes *Anas crecca* invernantes en Extremadura (**Capítulo 2**).
- *Objetivo II.* Evaluar el uso y la selección a pequeña escala de los campos arroz como áreas de forrajeo nocturnas por los ánades de superficie migratorios (**Capítulo 3**).
- *Objetivo III.* Conocer los ajustes fisiológicos de los ánades de superficie durante la invernada y período pre-migratorio en relación a su estrategia migratoria (**Capítulo 4**).
- *Objetivo IV.* Determinar el papel en los flujos de energía y en los ciclos biogeoquímicos de las poblaciones de aves acuáticas en campos de arroz (**Capítulo 5**).

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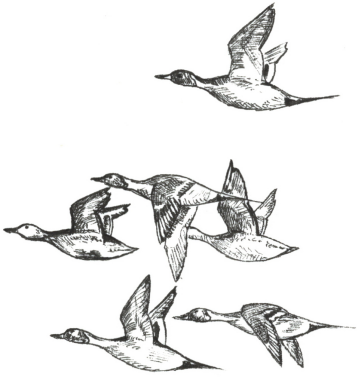
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2

Geographical origin of dabbling ducks wintering in Iberia: sex differences and implications for pair formation

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Abstract

Natural and anthropogenic Iberian wetlands in southern Europe are well known for supporting large numbers of migratory Palaearctic waterbirds each winter. However, information on the geographical origin of dabbling ducks overwintering in these wetlands is scarce and mostly limited to data from ringing recoveries. Here, we used intrinsic isotopic markers to determine the geographical origin of male and female northern pintails *Anas acuta* and Eurasian teal *Anas crecca* in Extremadura, inland Iberia, a key site for overwintering dabbling ducks. Additionally, we fitted six northern pintails with GPS-GSM tags to complement the data derived from stable isotope analysis. Most (> 70 %) first calendar-year northern pintails were assigned to regions above 55°N, flying 2,600–5,600 km from their main natal regions to Extremadura. Mean values of $\delta^2\text{H}_f$ varied significantly between male and female northern pintails, suggesting that the sexes had different geographical origins. Data from tagged adult northern pintails supported the isotopic data, one male flying more than 5,000 km to the coast of the Pechora Sea (Russia). Most (> 70 %) first calendar-year Eurasian teal were assigned to the region between 48° and 60°N, travelling 1,500–4,500 km to arrive in Extremadura. Male and female Eurasian teal showed marginal differences in mean values of $\delta^2\text{H}_f$. In migratory dabbling ducks, pairing typically occurs on the wintering grounds, and ducks in their first winter can breed the following spring. For northern pintails, pair formation in Extremadura could occur between individuals with different geographical origins, which could contribute to the genetic variability of their offspring.

Introduction

The long-term stability of migratory bird populations is to a large extent determined by geographically separated events that occur during different periods of the annual cycle (reproduction, pre- and post-breeding migration and winter) (Newton 2008). Protecting migratory birds poses a great challenge, as they constitute more than 80% of avian species in temperate regions (Rappole 1995) and strongly influence ecosystem functioning (Wilcove and Wikelski 2008, Bauer and Hoye 2014). In this context, understanding how geographical connectivity influences the different stages of the annual cycle of migratory species is a central component of designing conservation strategies for such populations. For example, establishing geographical connectivity will help to predict how changes in the quality of breeding areas, stopover sites and/or wintering areas influence the migratory behaviour of birds (Martin *et al.* 2007, Reichlin *et al.* 2013).

Many populations of migratory waterbirds are declining (Mundkur and Nagy 2012), mainly due to continuous loss and/or deterioration of natural wetlands (Rendón *et al.* 2008, Quesnelle *et al.* 2013). Iberian wetlands are among the main wintering areas for migratory Palaearctic waterfowl populations in Europe. Among these wetlands, the Doñana marshes, Ebro delta and Tagus estuary support large numbers of dabbling ducks (*Anas* spp.) (Scott and Rose 1996, Rendón *et al.* 2008, SEO/BirdLife 2012). Recently, other anthropogenic habitats such as rice fields and the reservoirs of Extremadura, inland Iberia, have emerged as key international sites for the populations of several dabbling ducks, such as northern pintail *Anas acuta* and Eurasian teal *Anas crecca* (Navedo *et al.* 2012). Available information on the geographical origin of dabbling ducks in Iberia comes from ringing recovery data (SEO/BirdLife 2012). Previously available information on the geographical origin of northern pintails and Eurasian teal wintering in Spain, based on historical records (1977–2011) of ringed bird recovery (SEO/BirdLife 2012), suggests that northern pintails mainly originate from Russia, Finland and Sweden, whereas Eurasian teal come from Finland, the Netherlands, France and the UK. However, such information is sparse and can be biased by banding effort and/or hunting pressure in different geographical regions (Hobson 2011). The recovery rate of individuals of both species ringed in Spain during the winter (November to February) and recovered in other countries during the breeding season (May to August), and of birds ringed in other countries during the breeding season and recovered in Spain during the wintering season is very low: only two northern pintails and four Eurasian teal were recovered during the last 30 years (1982–2012, data from Bird Migration Centre (CMA) of the Spanish Ornithological Society; www.anillamientoseo.org).

In many species of migratory birds, males and females differ in some ecological aspects, such as the distance covered between the breeding and wintering grounds (Cristol *et al.* 1999, Newton 2008). Such sex-related differential migration also occurs among dabbling ducks, in which males typically migrate shorter distances than females (Perdeck and Clason 1983, Rodway 2007a; b, Newton 2008, Guillemain *et al.* 2009a). Understanding the geographical origin of males and females in the main wintering areas would therefore provide a range-wide perspective of migratory con-

nectivity in dabbling ducks. As many waterfowl species pair up in winter (Rohwer and Anderson 1988), patterns of gene flow and population structure might be defined during this period of the annual cycle (Robertson and Cooke 1999), so determining the geographical origin of the sex classes would also be useful to explain these patterns.

The measure of stable isotopes in feathers and other avian tissues has been shown to be a useful tool for determining migratory connectivity in numerous bird species (Hobson 2011). This tool is based on the existence of a relationship between the values of deuterium in the precipitation water at a geographical location ($\delta^2\text{H}_p$) and its incorporation into growing feathers or other tissues ($\delta^2\text{H}_f$) (Hobson 2011). The analysis of $\delta^2\text{H}$ of juvenile feathers grown in the breeding grounds and collected during winter can therefore be used to estimate the geographical origin of overwintering birds (Newton 2008). In Europe, several studies have used stable isotope analysis to determine the geographical origin of migratory birds sampled during winter (e.g. Bowen *et al.* 2005, Guillemain *et al.* 2013, Hobson *et al.* 2013a; b, Van Dijk *et al.* 2013). Furthermore, fine-scale methods such as global positioning systems (GPS) allow researchers to locate the spatial position of tagged individuals at discrete time intervals and enable the reconstruction of their migratory routes with more precision and accuracy than is possible with stable isotope analysis (Akesson and Weimerskirch 2014, Willemoes *et al.* 2014).

The aim of this study was to assess the geographical origin of male and female northern pintails and Eurasian teal overwintering in Extremadura. We analysed concentrations of $\delta^2\text{H}_f$ in juveniles of both species captured during the winter and tagged adult northern pintails with GPS-GSM transmitters to obtain additional information regarding their breeding grounds.

Methods

Study site, species and capture

The anthropogenic wetlands of Extremadura (SW Spain) are a key site for many migratory waterbirds (Sánchez-Guzmán *et al.* 2007, Masero *et al.* 2009), including dabbling ducks (Navedo *et al.* 2012). Our study site was located at Vegas Altas del Guadiana (Figure 1), where several large reservoirs provide roosting areas for waterbirds (Navedo *et al.* 2012). These reservoirs, together with adjacent rice fields (25,000–30,000 ha), create an environmental mosaic that has promoted the populations of anatids and other wintering waterbirds in the area (Sánchez-Guzmán *et al.* 2007, Masero *et al.* 2011, Navedo *et al.* 2012).

The mean number of northern pintail and Eurasian teal overwintering in Vegas Altas del Guadiana was 7,235 and 9,389 individuals, respectively (2007–2010, Navedo *et al.* 2012). During early winter (15 November to 31 December) 2008–2010, we captured juvenile individuals of both species using cannon nets. In total, we caught 24 northern pintail and 15 Eurasian teal juveniles. Most individuals could be sexed

and aged according to plumage characteristics. Nevertheless, we took a small blood sample from the brachial vein for molecular sexing (Santiago-Quesada *et al.* 2014).

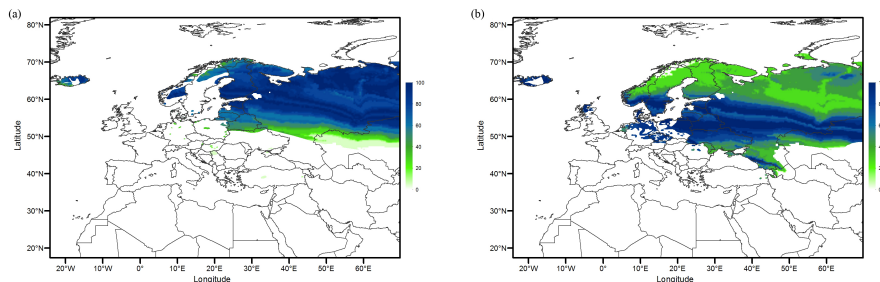


Figure 1: Geographical origin of first calendar-year (a) northern pintail and (b) Eurasian teal (males and females combined) overwintering in Extremadura (\blacktriangle). These maps represent the relative proportions of the individuals whose isotopic signatures ($\delta^2\text{H}_f$) matched the values of each cell of the isoscape within the European breeding range for each species, with a probability index of 2 : 1 (see Methods). The whole coloured area represents the potential breeding area according to the base maps provided by Birdlife International and NatureServe (2012). The correspondence between colour and origin probability for the population is shown in the legend inside the figures.

Stable isotope analysis and assignment of geographical origin

In both species the outermost primary feathers were retained juvenile feathers (often contrasting in colour with inner primary and/or replaced secondary feathers) and so reflected the isotope ratios of natal origin. A small portion (< 0.5 cm) of the tip of the outermost primary feather was collected from each individual for the $\delta^2\text{H}_f$ analysis. Feathers were placed in labelled plastic bags and stored at -30 °C until further assay at the Iso-Analytical Laboratory (Cheshire, UK). Analyses were performed using elemental analysis – isotope ratio mass spectrometry. Each feather was washed using sodium hydroxide solution and purified water, and oven-dried at 50 °C for one night. Samples (1 mg each) were weighed into silver capsules, and filled capsules were left open (all samples at the same time) for a period of at least 4 days to allow the exchangeable hydrogen in the feather keratin to equilibrate fully with the moisture in the laboratory air (Wassenaar and Hobson 2003). Deuterium (D) values based on non-exchangeable hydrogen were expressed as the deviation (δ ; in parts-per-thousand) in the ratio of $^2\text{H}/^1\text{H}$, normalized according to the VSMOW-SLAP (Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation) scale using keratin isotope reference materials (mean \pm sd; BWB-II, whale baleen, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -108.00\text{‰}$, observed value = $-108.00 \pm 1.31\text{‰}$; IA-R002, mineral oil, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -111.20\text{‰}$, observed value = $-111.11 \pm 0.93\text{‰}$; IEA-CH-7, polyethylene foil, expected non-exchangeable $\delta\text{D}_{\text{V-SMOW}} = -100.30\text{‰}$, observed value = $-101.42 \pm 1.13\text{‰}$; RSPB, eggshell membrane standard, expected nonexchangeable $\delta\text{D}_{\text{V-SMOW}} = -99.0\text{‰}$, observed value = $-100.37 \pm 1.55\text{‰}$), which received identical times of exposure to laboratory air as feather samples. Each feather was measured in duplicate and the results are presented as mean values (repeatability was > 90 %).

To assign the geographical origin of birds, we followed the protocol of van Wilgenburg and Hobson (2011). This approach provides a probability surface of areas consistent with potential origins. Information on the breeding distribution in the Western Palaearctic and the GIS-based model for $\delta^2\text{H}_p$ were extracted from the maps of the *Birds of the World* (Birdlife International and NatureServe 2012) and from Bowen *et al.* (2005), respectively. The latter was converted into $\delta^2\text{H}_f$ isoscape, following the equation $\delta^2\text{H}_f = -30.44 + 0.93 \delta^2\text{H}_p$, which accounts for 88 % of the variance in $\delta^2\text{H}_f$ among anatids and passerines of known origin (Clark *et al.* 2006, 2009, Ashley *et al.* 2010). Mean values of $\delta^2\text{H}_f$ were extracted for the breeding ranges of each species using ARCGIS SPATIAL ANALYST. We assessed the probability that any given cell within the $\delta^2\text{H}_f$ isoscape represented the origin of an individual, using a normal probability density function:

$$f(y^* | \mu_c \sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c} \right) \exp \left[-\frac{1}{\sqrt{2\pi}\sigma_c^2} (y^* - \mu_c)^2 \right]$$

where $f(y^* | \mu_c \sigma_c)$ represents the probability that the cell (c) was the natal origin of an individual with an isotopic signature $\delta^2\text{H}_f(y^*)$, given the expected mean of $\delta^2\text{H}_f$ (i.e. isoscape prediction) for that cell (μ_c) and the expected standard deviation (σ_c) of $\delta^2\text{H}_f$ among individuals whose feathers grew in the same locations. Probability densities resulting from this equation were normalized, dividing the probability of a cell to be the origin of an individual between the sum of all the probabilities of the cells from where the individual might originate, to produce an origin probability map for each individual:

$$\pi_b = \frac{f(y^* | \mu_c \sigma_c)}{\sum_{b=1}^B f(y^* | \mu_c \sigma_c)}$$

To represent the origin of each sample, we converted the individual origin probability map, using a probability index 2 : 1 (odds ratio), considering the more probable origins against the more unlikely. Therefore, the region we assigned to each individual was twice as likely to be correct as the rest. We then selected the group of cells in the map that encompassed 67 % of the origin probabilities; those cells were estimated and codified as 1, whereas the remaining cells were codified as 0, to obtain a binary map for each individual. To obtain the origin probability for the population, the results of the assignation for each individual were grouped and represented in a $\delta^2\text{H}_f$ isoscape. All GIS analyses were performed using ARCGIS (ESRI, Redlands, CA, USA).

Transmitters

Six overwintering northern pintails (three adult males and three adult females) were cannon-netted and fitted with GPS-GSM tags (ECOTONE, model Duck 3). Transmitters were attached using a Teflon ribbon breast harness with a cotton weak link in the sternum. The weight of the transmitter was 35 g, thus being < 3.3 % and 3.9 %

of the body mass of males and females, respectively. Transmitters recorded one GPS fix every 2 h and sent the data when five fixes were collected or when GSM coverage was reached, in areas with low or no GSM coverage.

Statistical analyses

We used a general linear model, with backward stepwise procedure, to test the effect of sex (fixed factor; two levels) on $\delta^2\text{H}_f$. Capture date (1 November = day 1) was included in the model as a covariate. Prior to analyses, data were examined for normality and homogeneity of variance. Analyses were performed using STATISTICA (version 10, Statsoft Inc., Tulsa, OK, USA). Throughout, two-tailed $P < 0.05$ was used as the level of significance.

Results

$\delta^2\text{H}_f$ variation between sexes

Mean $\delta^2\text{H}_f$ values for male (-111.83 ± 10.72 , $n = 11$) and female (-100.72 ± 8.04 , $n = 13$) northern pintails were significantly different (sex: $F_{1,22} = 8.39$, $P < 0.01$). Mean $\delta^2\text{H}_f$ values for male (-97.7 ± 8.66 , $n = 9$) and female (-89.93 ± 7.03 , $n = 6$) Eurasian teal did not differ significantly (sex: $F_{1,13} = 3.37$, $P = 0.09$). Date was dropped from the models ($P \geq 0.50$).

Geographical origin

According to the isotopic values, 90–100% of northern pintail juveniles overwintering in Extremadura originated from the central and northeastern parts of their distribution in the Western Palaearctic (Figure 1a). The geographical distribution of females ranged from 55° to 65°N (Figure 2a), whereas males typically originated at higher latitudes, between 58° and 70°N , the northern part of the potential breeding range described for the species (Figure 2c). Two of the three adult males equipped with transmitters completed migration: ‘Pint 02’ flew to the west coast of Denmark, near the locality of Højer (55°N), after covering 2,342 km; and ‘Pint 04’ covered 5,545 km to reach the coast of the Pechora Sea (Russia, above 68°N) (Figure 3). In both cases, the individuals remained in those areas from 12 June to 1 October 2013. ‘Pint 03’ stopped transmitting when crossing the Swiss Alps (Figure 3). Of the three tagged adult females, only one (‘Pint 06’) reached a potential breeding area close to the border between the Netherlands and Germany (near the town of Emden, 54°N ; Figure 3) after covering 2,236 km. This individual remained there between 14 June and 27 July 2013. The other two tagged individuals, ‘Pint 01’ and ‘Pint 05’, were found dead along the coast of northern France and thus did not complete migration (Figure 3).

For the Eurasian teal, between 90 and 100 % of the juvenile individuals came from the central parts of their breeding area in the Western Palaearctic, within the central part of the Volga river basin (Figure 1b). The natal origin of females (probability 90–100 %) ranged from 50° to 55°N (Figure 2b), whereas that of males (probability 90–100 %) ranged from 48° to 60°N (Figure 2d).

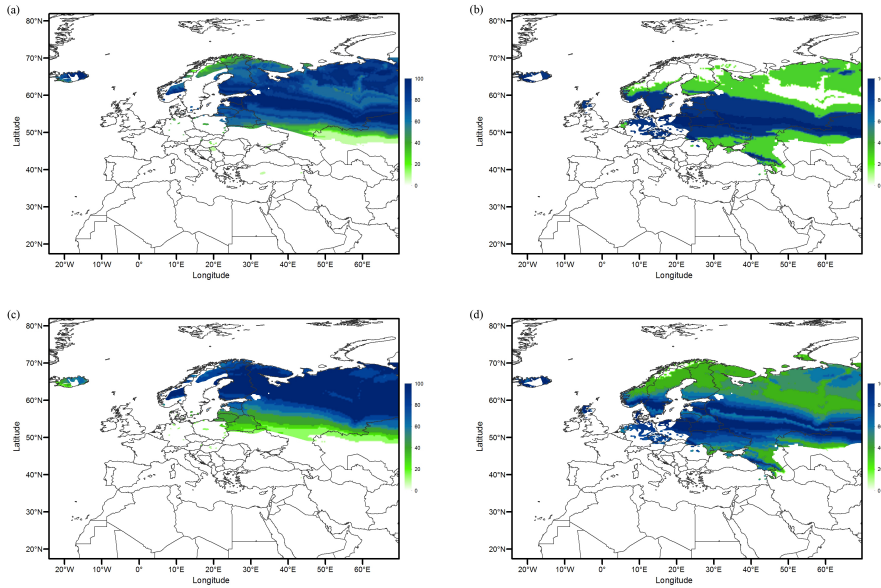


Figure 2: Geographical distributions for assigned origins for: (a) female northern pintails, (b) female Eurasian teal, (c) male northern pintails and (d) male Eurasian teal, captured between 2008 and 2010 in Extremadura (see the legend to Figure 1).

Discussion

Isotope analyses suggested that more than 70 % of northern pintails that spent their first winter in Extremadura came from latitudes above 55°N. Most came from Fennoscandinavia as well as northern and central Russia, entailing a 2600–5600 km migration distance from the main breeding areas to the wintering grounds in Extremadura. First-winter males in Extremadura came from breeding areas located further north than those of females. Therefore, areas such as the northern Scandinavian Peninsula or northern Russia represent the most probable origin of these males (80 %), whereas the probability of females being born in those areas was 60 %. The most probable origins of females (80 %) were central Russia, Finnish Lapland and northern Iceland. Unfortunately, only three individuals with tags completed their migration (two males and one female). Despite the low sample size, our data show that male northern pintails can migrate more than 5000 km to reach their breeding areas. The two males

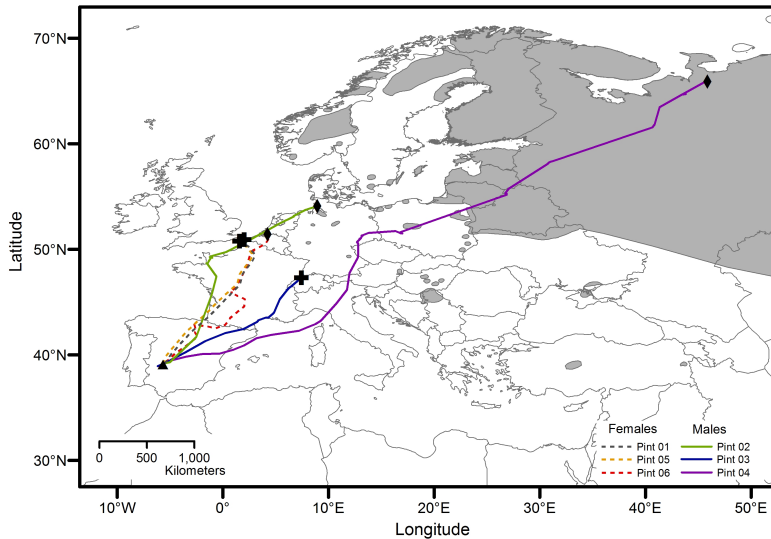


Figure 3: Migratory routes of three males (dashed lines) and three females (solid lines) equipped with GPS-GMS transmitters during the winter in Extremadura. The birds left Extremadura between 14 March and 2 May 2013; three of them died during northward migration (+) and the rest remained within the potential breeding areas between 12 June and 1 October 2013 (◆).

migrated further north than the female, consistent with the pattern derived from the isotope analysis.

In North America and Japan, a large number of northern pintails have been marked with platform transmitter terminal (PTT) tags to study their migratory movements (Miller *et al.* 2005; 2010, Haukos *et al.* 2006). These studies have shown that they migrate long distances (over 4,000 km during spring migration) but unfortunately there is no information on differential migration of males and females. In birds, there is increasing evidence that spatial segregation of sexes during the nonbreeding season is a widespread phenomenon, and in many sexually dimorphic species, males (usually the larger sex) winter further north than females (Newton 2008). Among migratory dabbling ducks, most species show differential migration, with males migrating shorter distances to winter further north than females (Rodway 2007a;b, Guillemain *et al.* 2009a and references therein). In the case of northern pintail, unfortunately, there are no published data on sex ratios in the main wintering sites through the East Atlantic flyway and other major flyways. Males and females overwintering in Extremadura come from different geographical breeding areas. Therefore, females of the same population as the overwintering males at Extremadura could spend the winter further south, in Doñana or West Africa, whereas males of the same geographical areas as females overwintering at Extremadura could winter further north, in France, the Netherlands or the UK.

There are three commonly (non-mutually exclusive) hypotheses to explain this sex-specific differential migration (Cristol *et al.* 1999, Newton 2008). The dominance hypothesis states that the socially dominant sex occupies better non-breeding habitat, forcing subordinates to migrate further or occupy less suitable habitats. The body-size hypothesis suggests that the larger sex usually winters at higher latitudes due to superior fasting endurance and thermal efficiency. The arrival-time hypothesis suggests that the sex that benefits most by arriving on the breeding grounds will minimize migration distance. In migratory dabbling ducks, however, these hypotheses do not apply to most species due to their pairing behaviour during winter (see below) or fail to explain their differential migration (Guillemain *et al.* 2009a).

Over 70 % of the wintering population of Eurasian teal in Extremadura originates from 48° to 60°N, a biogeographical area located between central Europe and the Ural Mountains. The area where females most probably originate was narrower than that for males. Hence, more than 80 % of the females originated from southeast Iceland, Denmark, northern Poland and central Russia, where in addition to these areas, males also come from northern Iceland, southern Norway, northern and southern Finland and north of the Russian Plain.

Recently, Guillemain *et al.* (2013) analysed the geographical origin of Eurasian teal hunted in France using stable isotopes in feathers and recoveries of ringed birds, finding that Eurasian teal wintering in France originated from areas further north in Europe (Finland to the Ural Mountains) than those wintering in Extremadura. Nevertheless, Eurasian teal overwintering at Extremadura, France and the UK (Guillemain *et al.* 2009a;b, 2013) migrate similar distances between wintering and breeding areas (about 3,100 km). Like Guillemain *et al.* (2005; 2013), we did not find sex differences in isotope ratios of Eurasian teal overwintering at Extremadura.

Waterfowl are unusual in showing female-biased philopatry (Greenwood 1987, Anderson *et al.* 1992, Ely and Scribner 1994, Blums *et al.* 2002). Differences in the patterns of gene correlations for maternally inherited and nuclear genes have shown that females show greater natal philopatry than do males (Scribner *et al.* 2001, Liu *et al.* 2012). The acquisition of nutrient storage by pre-breeding females and arguments concerning the adaptive consequences of promoting or avoiding inbreeding have been proposed to explain these dispersal patterns and winter pairing (Rohwer and Anderson 1988, Chesser 1991a;b). It is known that many species of migratory waterfowl can breed 1 year after their birth (Rohwer and Anderson 1988), and thus pair formation can occur in Extremadura among juvenile northern pintails from distant geographical regions. This supports the possibility that winter pairing contributes to the avoidance of inbreeding. The level of genetic variation within northern pintail and other dabbling duck populations might result from gene flow that is determined in the wintering grounds (Robertson and Cooke 1999, Scribner *et al.* 2001, Liu *et al.* 2013).

We show that, at least in the case of northern pintail, overwintering male and female juveniles in the south of Europe have different geographical origins. As pairing typically occurs on the wintering grounds, pair formation can occur among juvenile northern pintails from distant geographical regions, perhaps contributing to the avoidance of inbreeding. Further research is needed to assess the degree to which this

pairing behaviour and migration strategy contribute to a higher degree of genetic variability.

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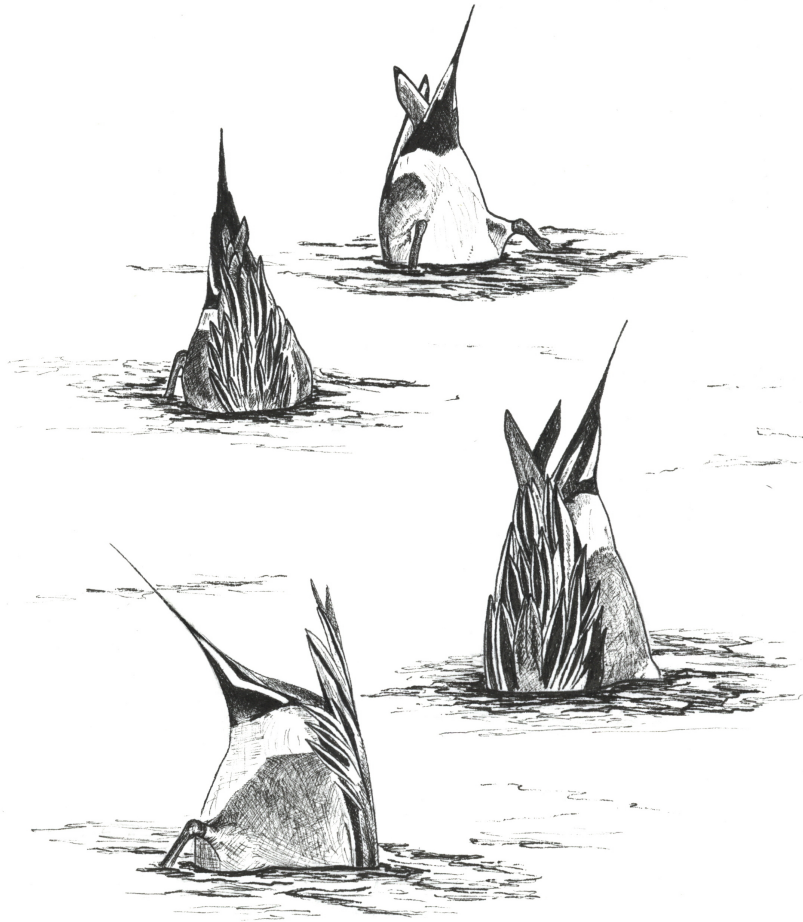
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3

Fine-scale resource selection by nocturnally foraging dabbling ducks in an agroecosystem landscape: crop management matters

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Abstract

Loss of natural wetlands is a global phenomenon that has severe consequences for waterbird populations and their associated ecosystem services. Although agroecosystems can reduce the impact of natural habitat loss, drivers of use of such artificial habitats by waterbirds remain poorly understood. Here, we report the effects of rice field management, landscape and environmental features upon the nocturnal foraging strategy of migratory dabbling ducks overwintering on an agricultural landscape in Southern Europe. Using the cosmopolitan northern pintail *Anas acuta* as a model species, we monitored home-range and fine-scale resource selection across the agricultural landscape. Individuals were tracked using GPS-GSM transmitters, and a suite of environmental and landscape features were measured throughout the season. Spatial patterns of habitat use were analysed using generalized linear mixed effect models by integrating field-observations with GPS telemetry. All birds used rice fields as foraging grounds at night and commuted to an adjacent reservoir to roost during daylight. Home-ranges and maximum foraging distances of nocturnally foraging birds increased with decreasing availability of flooded fields, and were positively correlated with moonlight levels. Birds selected flooded rice paddies (water depth range: 9 - 21 cm) with standing stubble and substrate with pebbles smaller than 0.5 cm in diameter. Food abundance, rice paddy size, and other environmental and landscape features did not emerge as significant predictors. Our findings indicate that nocturnal foraging of northern pintails within rice fields is driven primarily by straw manipulation, water level and substrate pebble size. Thus, the presence of standing stubble in flooded paddies with soft bottoms should be prioritized to improve foraging areas for dabbling ducks. These management procedures in themselves would not increase economic costs or affect rice production and could be applied for dabbling-duck conservation throughout the world.

Introduction

Globally, natural wetlands have lost around 64 - 71 % of their area since the beginning of the 20th century (Davidson 2014). In Europe and North America the rate of wetland loss has decreased or remains constant, but in many other regions, such as Asia, natural wetlands are disappearing at alarming rates (Xia *et al.* 2016). Direct human alterations, often in conjunction with climate change, make natural wetlands one of the most threatened habitats on the planet (Čížková *et al.* 2013). The lost or degradation of these aquatic ecosystems has a great impact on biodiversity conservation (Gibbs 2000). Even though the ecosystem functions of natural wetlands cannot be totally replaced by human-made wetlands, the latter can provide suitable habitats that partly mitigate the impact of wetland loss on aquatic biota (e.g. Ghermandi *et al.* 2010).

Flooded rice fields occupy over 1 % of the Earth's ice-free land surface (Maclean *et al.* 2013). The high number of rice (*Oryza sativa*) varieties has enable its growth in every continent (except Antarctica), spanning 163 million hectares from 50° N to 40° S (FAO-STAT 2014). These flooded agricultural fields are often classified as functional wetlands (Lourenço and Piersma 2009), and they have a huge potential to contribute to the conservation of wetland biota worldwide (Elphick 2000).

Most waterbird species depend on wetlands throughout their life cycle. Waterbird use of rice fields has increased as natural wetlands continue to decline (e.g. Czech and Parsons 2002), and currently many migratory waterbird species on several flyways depend on them (Elphick 2015). Thus, there is a growing interest in how to manage rice fields in order to increase their value for waterbirds (e.g. Sesser *et al.* 2016), which is especially relevant in the case of duck species given the important ecosystem services they provide (Green and Elmberg 2014, Fox *et al.* 2017).

Generally, migratory dabbling ducks forage in rice fields at night and rest in reservoirs or lakes nearby during the day (e.g. Eadie *et al.* 2008, Casazza *et al.* 2012). This nocturnal regime has hampered the study of micro- and macro-habitat use and selection in rice fields by nocturnal foragers, which is imperative to design appropriate management strategies for these species (Guillemain *et al.* 2002a, Kloskowski *et al.* 2009). To our knowledge, no study to date has assessed the factors influencing the selection of nocturnal foraging areas by dabbling ducks and other waterbirds within their home-range, i.e. at a relevant scale (Callicutt *et al.* 2011). The only studies available are based on direct censuses at night using spotlights or light amplifiers (Tajiri and Ohkawara 2013, Pernollet *et al.* 2016).

Here, we evaluated fine-scale use and selection of rice field areas by nocturnally foraging dabbling ducks in one of the most important areas for rice production in Western Europe (Extremadura, SW Spain; Navedo *et al.* 2015). Specifically, we focused on the northern pintail *Anas acuta* as a model — a cosmopolite and widely distributed species, present in North America, Asia, Europe and North of Africa (Fox 2005). To this end, we tagged several individuals with GPS-GSM devices and used resource selection functions (RSF; Manly *et al.* 2002) at fine-scale spatiotemporal resolution. On one hand, RSF provide an excellent framework to understand the distribution of

organisms and they are essential to design and develop successful management and conservation strategies (de la Cruz *et al.* 2014). On the other hand, GPS-GSM devices provide an extremely fine spatial and temporal resolution to describe bird movement patterns (e.g. Duerr *et al.* 2012; 2015), and they allow us to understand how individuals perceive and react to environmental changes (Flack *et al.* 2016). Our main goal was to identify the post-harvest treatments and environmental and landscape variables that determine the home-range and the selection of nocturnal foraging areas by dabbling ducks during the winter. Our results can be applied to improve habitat features for dabbling ducks in the world's most important crop (Elphick 2010).

Methods

Study area

We carried out the study at rice fields located in Extremadura (SW Spain), in the Guadiana river basin (39°N, 6°W; Figure 1). These rice fields and associated reservoirs are one of the main wintering grounds for dabbling ducks in the south of Europe, such as northern pintails, Eurasian teals *Anas crecca* or northern shovelers *Anas clypeata* (Navedo *et al.* 2012). Northern pintails wintering in Extremadura migrate from breeding grounds located above 55° N (Parejo *et al.* 2015). Although their populations increased between 1996 and 2007 (Mundkur and Nagy 2012), numbers have dropped by 25 - 50 % in the last decade (BirdLife International 2017). In Extremadura management of rice fields for waterbirds is not yet implemented, and while northern pintails are not hunted, other dabbling duck species such as Eurasian teals and northern shovelers are permitted to be hunted during the winter.

Post-harvest treatment

Extremadura rice fields are a continuum that occupies around 25,000 ha (Figure 1), divided into paddies surrounded by a raised earthen levee (usually < 0.5 m high). The average size of a paddy is 2.4 ± 0.2 ha, and most of them (> 80 %) range from 1 to 4 ha. Paddies are owned by a number of particulars and cooperatives that carry out different treatments once the harvest is finished in September and October. Similar to other parts of the world, when rice paddies are flooded or partially flooded with the first rainfalls, many are ploughed and the straw is incorporated into the soil (Figure 2a), which accelerates its decomposition (Fogliatto *et al.* 2010). However, many other rice paddies are not ploughed (Figure 2b), and standing stubble (25 - 45 cm high) remains in the paddies until they are prepared for seed plantation in spring. Upon these management practices, rice paddies can remain flooded or dry up rapidly, depending on whether drainage channels remain closed or open, respectively. Stubble burning is forbidden.

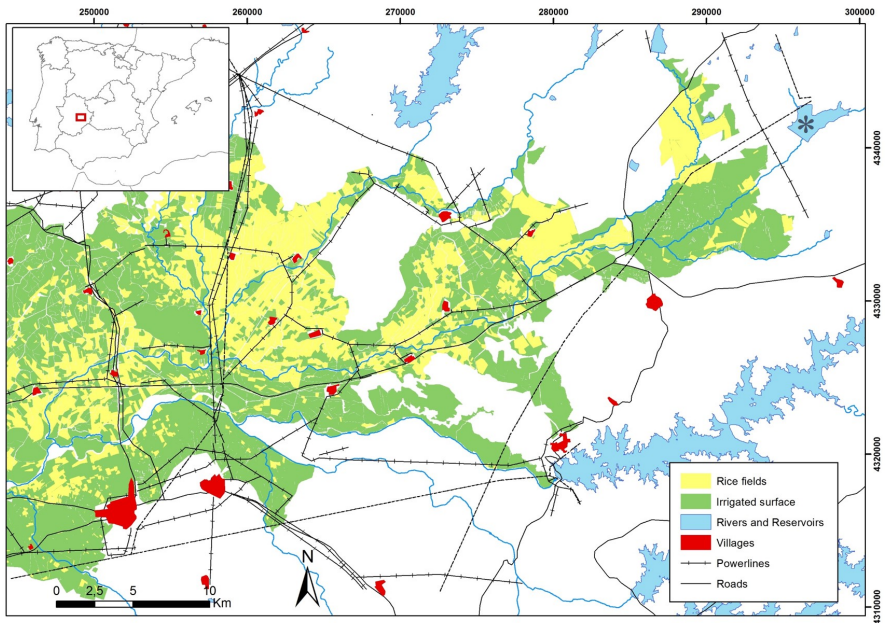


Figure 1: Study area (Extremadura rice fields; SW Spain) showing reservoirs, rice fields, main infrastructures and urban areas. The asterisk indicate the reservoir (Gargáligas) used by northern pintails as roosting site during daylight.

Tag deployment and tracking individuals

In early December 2012 and 2014, we cannon-netted twelve adult northern pintails (9 females and 3 males) at Gargáligas reservoir (Figure 1). This reservoir is used as a roosting site during daylight by over 7,000 individuals ($\sim 1\%$ of the population from the East Atlantic Flyway; Navedo *et al.* 2012). Upon capture, all individuals were ringed, weighted and measured. Age and sex were determined according to plumage and cloacal examination (Mouronval 2014, Baker 1993).

Pintails were tagged with solar powered GPSs using Teflon harnesses (Parejo *et al.* 2015). The six devices deployed in 2012 were GPS-GSM Duck-3 (35 g; Ecotone Telemetry, Gdynia, Poland) and the six deployed in 2014 were GiPSy-4 (25 g; Technosmart, Roma, Italy). The mass of the devices represented 2 - 4% of body mass in early winter. Duck-3 devices collected locations every 2 h, and sent the data when GSM signal was available and at least five positions had been recorded. GiPSy-4 devices recorded three positions during daylight (dawn, midday, dusk) and hourly positions at night; positions were downloaded using Zigbee base stations placed within 1 km range (Monsarrat *et al.* 2013). Both models had a location error < 20 m (average distance between consecutive locations of stationary devices).

(a)



(b)



Figure 2: (a) Image showing a rice farmer ploughing their rice paddies after the first rains. In the foreground we can observe rice paddies with standing stubble, while in the background there are rice paddies ploughed and partially flooded, with the straw incorporated into the soil. (b) Flooded rice paddy with standing stubble; the stubble-free furrows created by the harvester are visible.

Home-range

Space use was estimated daily and then averaged weekly throughout the season (December-February). Home-range was defined as 100 % of the minimum convex polygon (MCP), the best estimator to determine the exploratory activity of an individual (Bengtsson *et al.* 2014). We used R (ver. 2.12.0, R Development Core Team 2010), the Geospatial Modelling Environment (GME; Beyer 2012) and ArcGIS (ver. 10.1, Esri, Redlands, CA, U.S.A.) to calculate the weekly MCPs. Maximum daily foraging distance was defined as the longest distance between the foraging positions (10 pm - 2 am) and the roosting positions (12 - 4 pm), using Euclidean distance in ArcGIS (Legagneux *et al.* 2009).

We examined how fluctuations in food availability, flooded area, climate, and moon light could affect home-range area used by pintails. The proportion of flooded rice paddies was estimated following Santiago-Quesada *et al.* (2014). We established four transects (10 - 15 km) across the rice fields within the 20 km radius ($\sim 12,000$ ha) of the main roosting site, which were visited twice a week from December to March. This 20 km radius was the maximum distance covered by radio tagged northern pintails, Eurasian teals and northern shovelers when commuting between roosting and nocturnal foraging sites (unpublished data from radio tagged birds in Extremadura). The percentage of flooded rice paddies with stubble, percentage of flooded and ploughed rice paddies (straw incorporated into the soil), and percentage of flooded rice paddies (independently of straw manipulation) were estimated from these transects.

Food abundance was estimated as the density of rice seeds in rice paddies within that 20 km radius. Data from stable isotope analysis showed rice seeds left on the ground after harvest are the main food source for dabbling ducks in Extremadura (Navedo *et al.* 2015). Every week, we randomly sampled 25 flooded rice paddies assumed to be available for foraging dabbling ducks (see below). Using a soil core sampler (7.5 cm diameter, 10 cm depth), we sampled the sediment of each rice paddy at five randomly selected points and used the mean values in the analyses (Elphick 2000). Samples were stored and preserved at -24 °C for later analysis. In the laboratory, soil cores were defrosted and sieved (mesh size = 1 mm), and the number of rice seeds was counted (Santiago-Quesada *et al.* 2014, Navedo *et al.* 2015).

Finally, daily records of the moonlight intensity (percentage of full moon) and climate (rain, wind speed, and minimum temperature) were taken from the ‘Observatorio Astronómico Nacional’ (<http://www.oan.es/servidorEfem/>; Centro Nacional de Información Geográfica) and from the weather station in the Gargáligas reservoir (Confederación Hidrográfica del Guadiana), respectively. The values were averaged weekly.

Resource selection

Each rice paddy was assumed to be an experimental unit (Elphick 2000). To test whether northern pintails preferred certain rice paddies over others, we developed RSFs using a use vs. availability design (Dzialak *et al.* 2015). Every week, we selected four

random locations within the MCP of a given individual and established a relationship between the available and the used rice paddies of 3:1 (McDonald *et al.* 2006, Salazar *et al.* 2016). To avoid telemetry errors and confounding effects on the estimation of the probability of occurrence, these random locations were > 20 m away from used rice paddies (Dzialak *et al.* 2011). We only considered locations that were flooded and had GPS locations recorded between 10 pm and 2 am, since dabbling ducks always forage in flooded areas and their maximum foraging activity occurs during this time (Tamisier and Dehorter 1999, Pernollet *et al.* 2016; personal observations). In general ($> 80\%$ of cases), after 8 pm tagged pintails remained in the same rice paddy for several consecutive hours (see Results).

For each paddy (both used and not used), we recorded food density (see above), pebble size, water depth, paddy size, straw manipulation, distance to diurnal roosting site (Gargáligas), and distance to the closest power line, paved road and urban area. The pebbles found in these soil corers were classified into three different categories according to their diameter (< 0.5 cm, $0.5 - 1.0$ cm, and > 1.0 cm; Gurd 2006), because pebble size can affect foraging in dabbling ducks (Guillemain *et al.* 2002b, Arzel *et al.* 2007). We also measured water depth at five different points following the diagonal of the rice paddy and maintaining a constant distance between sampling points (Pernollet *et al.* 2016). To estimate the size of the rice paddies and landscape variables, we used raster images of the study area (Centro Nacional de Información Geográfica 2014). The distance to the closest urban area, paved road and power line was estimated from the centre of each rice paddy (Larsen and Madsen 2000, Milsom *et al.* 2000, Santiago-Quesada *et al.* 2014).

Statistical analysis

We used generalized linear mixed models (GLMM) to test the effect of several variables on weekly MCP (ha) and maximum foraging distance (km). In both cases, we included food density ($\text{seeds}\cdot\text{m}^{-2}$), percentage of flooded rice paddies (%), percentage of flooded rice paddies with standing stubble (%), percentage of ploughed and flooded rice paddies (%), rain ($\text{l}\cdot\text{m}^{-2}$), minimum temperature ($^{\circ}\text{C}$), wind speed ($\text{km}\cdot\text{h}^{-1}$), moonlight intensity (%), and Julian date (days after 1 November) as potential predictive variables. To test for potential collinearity among predictors, we calculated Pearson's correlation coefficients, and removed highly correlated covariates ($r > 0.50$). Prior to analysis, we log-transformed rain, wind speed and minimum temperature, and arcsine-transformed flooded area and moonlight. Given the high correlation among covariates, we only kept in the analysis percentage of flooded rice paddies, minimum temperature, wind speed and moonlight intensity. We also included bird ID as a random effect, since locations from the same individual are not independent.

To perform the RSF analysis we used a GLMM with a binomial distribution and a logit-link function. Our binary response was used (1) versus non-used (0) rice paddies. Straw manipulation (two levels: standing stubble and straw incorporated into the soil) and pebble size (three levels: < 0.5 cm, $0.5 - 1.0$ cm, and > 1.0 cm) were included

as fixed factors. Food density (seeds·m⁻²), water depth (cm), paddy size (ha), Julian date, distance to diurnal roosting site (km), and distances to the closest power line (km), paved road (km), country road (km) and urban area (km), were included as covariates. Distance to the closest urban area, country road, and Julian date were excluded from the model due to collinearity issues (see above procedure). Candidate models were built using all possible combinations of explanatory variables. Models were evaluated using the Akaike information criterion with a correction for small sample sizes (AIC_c; Burnham and Anderson 2002). Models within 2 units of ΔAIC_c were considered equally good. In the RSF analysis, we also performed ‘full-model averaging’ of the subset of models with ≤ 0.95 accumulated weight (Burnham and Anderson 2002), an appropriate approach when there is uncertainty in the selection process (i.e. the best model has a low weight; Symonds and Moussalli 2010). We further calculated the relative importance (RI) of each variable as the sum of the weight of the models where that variable was present. For all the models we used the lme4 package in R3.3.3 (Bates *et al.* 2014). All values are expressed as a mean \pm standard error.

Results

Space use

Northern pintails followed a common routine throughout the winter: they left the diurnal roosting site 16.1 ± 1.9 min after sunset, spent the night in the foraging areas (rice fields), and left them 29.7 ± 1.2 min before dawn to go back to the diurnal roosting site.

MCP and maximum foraging distance were $9,652.6 \pm 1,588.9$ ha and 11.4 ± 0.6 km, respectively. In the MCP analysis, the best-supported model included the proportion of flooded rice fields and intensity of moonlight (Table 1; Figure 3). The MCP model indicated that northern pintails’ home-range was larger when the proportion of flooded rice fields was lower (Figures 4a - 4b) and the moonlight was more intense (Table 1; Figures 4c - 4d). The best model for maximum foraging distance showed that the proportion of flooded rice fields had a positive effect on the travelled distance ($w_i = 0.457$; Table 1).

Table 1

Nocturnal home-range (defined using minimum convex polygon; MCP) and maximum foraging distance results for overwintering northern pintails at Extremadura rice fields. Models (MCP: $n = 16$; Foraging distance: $n = 16$) were sorted using the Akaike information criterion with a correction for small sample sizes (AIC_c), the increase in AIC_c compared to the best model (ΔAIC_c), the weight of each model (w_i), and the values of the $-2\log$ -likelihood (logLik) function. Only models following $\Delta AIC_c < 2$ are displayed.

Model variables	df	logLik	AIC_c	ΔAIC_c	w_i
Home-range (MCP)					
Flooded rice paddies + Moonlight	5	-121.135	253.1	0.00	0.358
Flooded rice paddies + Moonlight + Wind speed	6	-120.481	254.1	1.04	0.213
Flooded rice paddies	4	-123.011	254.6	1.47	0.172
Maximum foraging distance					
Flooded rice paddies	4	-38.814	86.2	0.00	0.457
Flooded rice paddies + Moonlight	5	-38.211	87.3	1.08	0.266

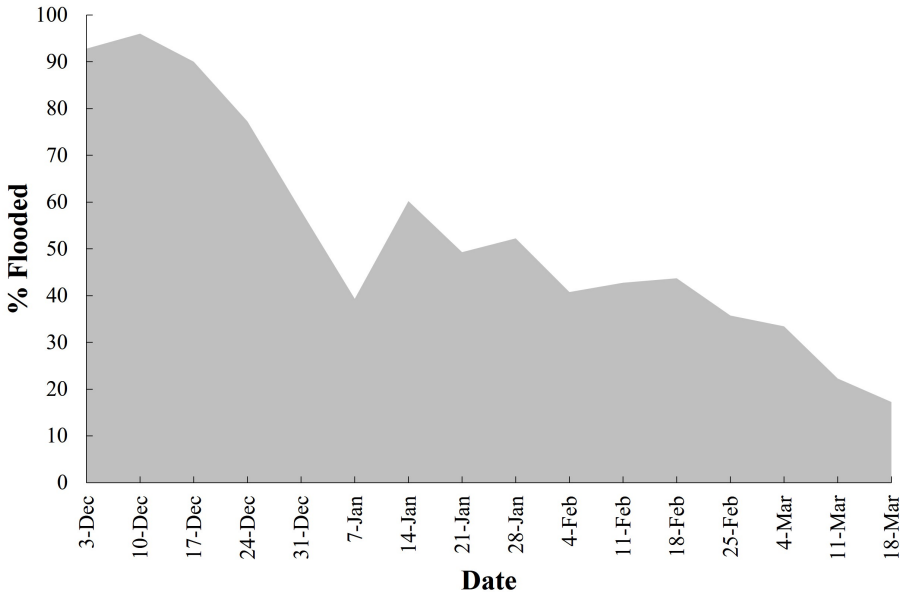


Figure 3: Variation in the proportion of flooded rice paddies (with and without standing stubble) through the winter season in a 20 km radius from the diurnal roosting area.

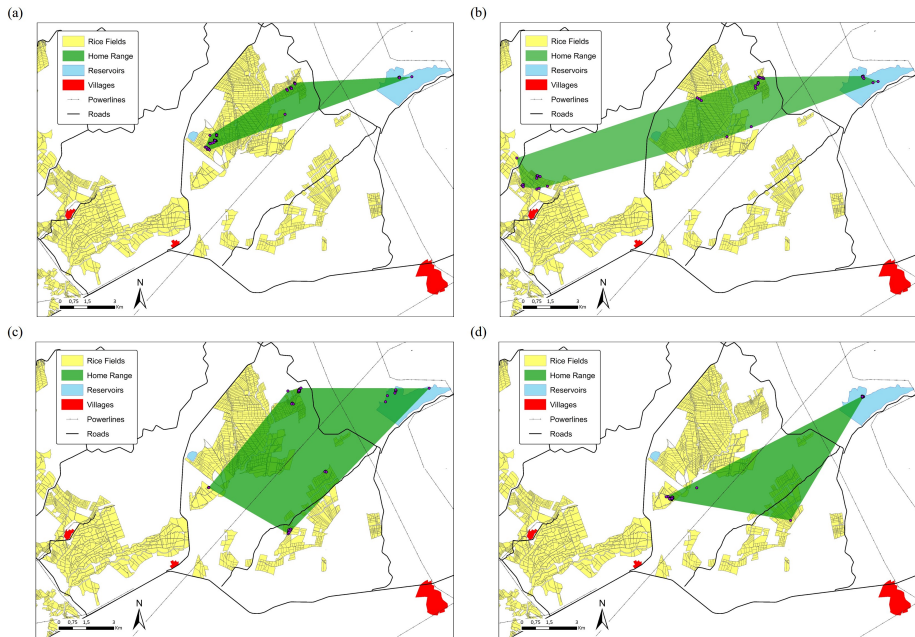


Figure 4: Nocturnal home-ranges of northern pintails overwintering at Extremadura rice fields. (a) Pint 06 during the second week of December 2012 (MCP = 1,312 ha; 96 % of rice paddies flooded and moonlight intensity 6 %). (b) Pint 06 during the second week of January 2013 (MCP = 4,082 ha; 39 % of rice paddies flooded and moonlight intensity 10 %). (c) Pint 05 during the fourth week of January 2013 (MCP = 4,765 ha; 45 % of rice fields flooded and moonlight intensity 88 %). (d) Pint 05 during the second week of January 2013 (MCP = 2,637 ha; 39 % of rice fields flooded and moonlight intensity 10 %).

Resource selection

The four top-ranked candidate models explaining rice paddy selection by foraging northern pintails included water depth, standing stubble and pebble size (Table 2). Of these, three also included food density, and one included distance to paved roads and rice paddy size (Table 2). There was high model selection uncertainty (the best AIC model was not strongly weighted, $w_i = 0.136$); thus, inference was based on all models in the candidate set using full-model averaging. Estimates from the model averaging showed that water level (14.10 ± 0.31 cm depth) and stubble presence had a strong influence on rice paddy selection (Table 3). Moreover, presence of pebbles larger than 0.5 mm in diameter had a negative effect on rice field selection by pintails (Table 3). Food density was present in three of the four best-ranked models (Table 2); nonetheless, its effect was only marginally significant when full-model averaging was performed (Table 3).

Table 2

Results for the resource selection model (RSF) using the GPS locations obtained from northern pintails during the winter. Models ($n = 256$) were sorted using the Akaike information criterion with a correction for small sample sizes (AIC_c), the increase in AIC_c compared to the best model (ΔAIC_c), the weight of each model (w_i), and the values of the $-2\log$ -likelihood ($\log\text{Lik}$) function. Only models following $\Delta AIC_c < 2$ are displayed.

Model variables	df	logLik	AIC_c	ΔAIC_c	w_i
Pebble size + Food density + Water depth + Straw	7	- 102.337	219.1	0.00	0.136
Pebble size + Distance to road + Food density + Water depth + Straw	8	- 101.595	219.8	0.65	0.098
Pebble size + Food density + Paddy size + Water depth + Straw	8	- 101.791	220.2	1.04	0.081
Pebble size + Water depth + Straw	6	- 104.341	221.0	1.89	0.053

Table 3

Estimates for the averaged resource selection model (RSF, using models within an Akaike accumulated weight ≤ 0.95) and relative importance of the parameters (RI) for the nocturnal home-range (minimum convex polygon; MCP) and maximum foraging distance analysis. Variables are sorted by the p-value.

Variable	β	SE	RI	P
Water depth	- 0.96	0.27	1.00	< 0.001
Straw	4.64	1.46	1.00	0.001
Pebble size	- 1.56	0.62	0.97	0.011
Food density	0.49	0.25	0.75	0.053
Distance to road	- 0.38	0.34	0.40	0.254
Paddy size	0.30	0.34	0.33	0.376
Distance to power line	- 0.21	0.44	0.28	0.640
Distance to roosting site	- 0.06	0.32	0.24	0.857

Discussion

Winter management of rice fields can have important consequences for the conservation of migratory waterbirds worldwide (Elphick 2015). Our GPS-GSM data revealed that northern pintails roosted during daylight in a reservoir near the foraging areas visited at night. Home-range area and maximum foraging distance from this reservoir were mainly influenced by the surface of flooded rice fields and moon phase. Northern pintails selected to forage flooded rice paddies where stubble was present and where pebble size was relatively small. By contrast food abundance and other landscape variables were not strong predictors of rice paddy use at night. These results are es-

essential to delineate appropriate management strategies in rice fields that underpin conservation efforts of migratory dabbling ducks (Guillemain *et al.* 2017).

Northern pintails' home-ranges were up to 35,000 ha. These home-ranges are larger than those of pintails using coastal marshes in West Europe (Legagneux *et al.* 2009) as well as of other ecologically similar dabbling ducks (Kleyheeg *et al.* 2017). Home-range size and maximum foraging distance increased with decreasing surface of flooded rice paddies. Soil softening, seed hydration and water availability are key to efficient feeding by dabbling ducks relying on rice seeds (Guillemain *et al.* 1999, Bird *et al.* 2000, Pernollet *et al.* 2015); thus, as the surface of flooded rice paddies decreased, northern pintails were probably forced to increase their home-ranges to find adequate foraging grounds. We also showed a consistent (positive) relationship between moonlight and the spatial use of rice fields by pintails. Previous studies have shown that waterbirds can take advantage of the moonlight to increase feeding opportunities (Dwyer *et al.* 2013), since they can detect predators more easily and increase their exploratory activity to find new foraging areas (Sauter *et al.* 2012, Korner *et al.* 2016).

Water depth and stubble presence were the most important predictors of rice paddy selection by northern pintails. Previous studies performed in rice fields showed that depths of 14 - 22 cm lead to the greatest densities of dabbling ducks during daylight (Elphick and Oring 2003), and overall, suitable water depth for dabbling ducks in rice fields is assumed to be > 16 cm (Strum *et al.* 2013). These water levels fall within the water depth range (9 - 21 cm) of flooded rice paddies used by pintails at Extremadura rice fields. On the other hand, studies based on nocturnal counts in rice fields in Japan (Tajiri and Ohkawara 2013) and France (Pernollet *et al.* 2016) also found that rice paddies with stubble harboured higher abundances of dabbling ducks. This positive association seems to be caused by the higher density of rice seeds available where stubble was present, compared to ploughed paddies (see Pernollet *et al.* 2016 and references therein). Moreover, it has been suggested that foraging in paddies with standing stubble could enhance crypsis (Whittingham and Evans 2004, Whittingham *et al.* 2006), which could compensate the reduction in the ability to detect predators during nocturnal foraging (Guillemain and Fritz 2002).

By contrast we found no evidence that northern pintails habitat selection patterns during nocturnal foraging were affected by the proximity to urban areas, paved roads or power lines. These results are consistent with other studies that did not detect an effect of these landscape variables on the use of foraging areas by migratory waterbirds (Gill *et al.* 2001, Gill 2007, de la Cruz *et al.* 2014). Nevertheless, power lines can influence the choice of nocturnal roosting sites in some waterbird species, such as the black-tailed godwit *Limosa limosa* (Santiago-Quesada *et al.* 2014). It is important to note that, in our study area, population density is relatively low (9 villages, with 200-1800 people each; Figure 1), infrastructures are scarce, and northern pintail hunting is forbidden (hunting of other duck species is unusual too).

Noticeably, ducks avoided paddies where pebbles > 0.5 cm were abundant (Gurd 2006). Dabbling ducks generate a water flow through a lamellar structure in the margins of the bill (Guillemain *et al.* 2002b), a feeding mechanism that could be impaired by large pebbles and thus reducing foraging efficiency (Gurd 2006). The greater pre-

sence of these pebbles in the superficial soil layer is related to soil properties but also to pre- and post-harvest treatments (Haefele *et al.* 2014). During these treatments, the soil is compacted to form an impermeable layer (i.e. hardpan). This layer avoids root penetration and water loss by percolation and increases rice capacity to efficiently use water and nutrients (Busscher 2011). On top of the hardpan, farmers create a fertile layer with a high content of organic matter and nutrients, where the roots of the rice develop (Hamza and Anderson 2005). When this fertile layer is too thin, ploughing can increase the number of big pebbles in the upper part of this layer (Hemmat and Taki 2003, Fusi *et al.* 2014), thus transforming a potential foraging area into an unavailable one, at least for dabbling ducks. Since our results also support that rice seed density is not a limiting resource in our study area (Navedo *et al.* 2015), management of rice paddies arise essential to integrate a worldwide productive crop into conservation efforts of migratory dabbling ducks.

Management implications

To date, conservation plans of non-breeding migratory dabbling ducks in Western Europe have focused on the conservation of diurnal roosting areas, and nocturnal foraging grounds are usually unprotected (Guillemain *et al.* 2002a, Navedo *et al.* 2015) with no management measures yet implemented. In Extremadura, for example, some reservoirs were designated Special Protection Areas owing to the high numbers of dabbling ducks they support during daylight, but most adjacent rice fields used as nocturnal foraging grounds are currently unprotected and unmanaged (Navedo *et al.* 2015). Our study highlights the need to include nocturnal foraging grounds under protection, as well as to account for large home-ranges when designing appropriate conservation measures for these species using agroecosystem landscape features.

Nowadays, the flooding of rice fields is promoted by various conservation policies across the world (Pernollet *et al.* 2015). This action not only provides a suitable habitat for waterbirds, but also benefits farmers by improving the rate of vegetation decomposition and reducing weed biomass (e.g. Bird *et al.* 2000). Moreover as recently demonstrated in California Central Valley (Reynolds *et al.* 2017) habitat ‘rent’ by external entities (government, NGOs) to rice farmers on a seasonal basis will provide habitat for waterbirds during critical periods.

Currently, large areas of rice fields are being lost in Spain. In Extremadura alone, almost 6000 ha of rice fields have been replaced mainly by fruit, almond and olive tree intensive crops (MAPAMA 2017). Recently announced reductions in personal income tax rates by the Spanish government for rice farmers could contribute to the maintenance of this crop. The implementation of management actions for waterbird conservation could be included as part of the greening measures of the Common Agriculture Policy and as a condition for reductions in tax rates, which would increase farmers’ commitment towards the development of sustainable farming.

Our findings suggest the following low-cost and easy management measures that would benefit dabbling duck conservation and rice farming sustainability:

1. In order to benefit migratory dabbling ducks, farmers should maintain their rice paddies flooded and with stubble throughout the wintering season. It is important to highlight that maintaining rice fields flooded does not incur any economic cost for farmers (Bird *et al.* 2000, Lourenço and Piersma 2009, Elphick *et al.* 2010). In Extremadura, rice paddies' drains remain closed when the fields are flooded to grow rice but are left open throughout the winter, so it would suffice to keep them closed so that the rainwater remained as long as possible.
2. To identify depth ranges, rather an optimal depth, is more appropriated when designating guidelines for water depth management in flooded rice fields after harvest (Elphick and Oring 1998). In absence of diving ducks, which need a water depths > 25 cm (Taft *et al.* 2002), we propose the water depth range found in our study (9 - 21 cm), which would benefit medium-large dabbling ducks.
3. In 45% of rice paddies sampled, pebbles > 0.5 cm in diameter were abundant and pintails avoided them. In those areas, creating a fertile layer of 40 - 50 cm and levelling of the soil every 3 - 4 years could avoid an increment of pebbles in the upper part of the fertile layer during ploughing (Hamza and Anderson 2005, Fusi *et al.* 2014). This would not only promote its use by nocturnally foraging dabbling ducks but also increase rice production (Haeefele *et al.* 2014).

Lastly, other migratory waterbird populations using rice fields such as shorebirds or cranes have different water depth preferences and straw management requirements than dabbling ducks (e.g. Sánchez-Guzmán *et al.* 2007, Sesser *et al.* 2016). Thus, the management implications for migratory dabbling ducks of our study must be integrated into a more general management plan when other groups of waterbirds are included.

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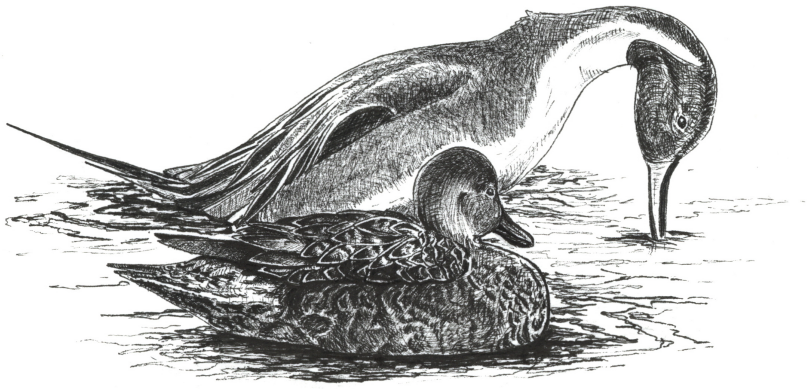
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4

Body mass and plasma metabolite changes in overwintering northern pintail *Anas acuta* in the South of Europe

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Abstract

It is assumed that long-distance migratory dabbling ducks overwintering in south or western Europe prepare for migration by storing large amounts of fat and, to a lesser extent, proteins as fuel for successful migration. However, although body mass at departure from wintering sites is an essential parameter in the study of bird migration, the physiological changes of dabbling ducks at wintering or stopover sites in relation to sex and their next non-stop flights have seldom been studied. Here, we studied body mass changes in male and female northern pintails *Anas acuta* overwintering in the rice fields of Extremadura (Spain), a key wintering site located in southern Europe. We also measured changes in the levels of plasma triglycerides and total proteins as indices of lipid and protein metabolism, respectively. Although males were considerably heavier than females at any given period, both sexes increased their body mass in late winter (pre-migration period) and showed a similar pattern of body mass increase. Levels of plasma triglycerides and proteins showed a similar pattern to that of body mass, albeit not statistically significant. The body mass increase pattern did not follow the general pattern described by the ‘wintering strategy’ for migratory dabbling-ducks wintering in western Europe, which predicts the highest values of body mass in mid-winter. This was most likely due to the milder environmental conditions (i.e. weather and food availability) in southern Europe compared to wintering areas at northern latitudes.

Introduction

Long-distance migratory movements of birds are governed by a chain of individual decisions, such as when to leave a site, how much energy to acquire before departure, and what distance to fly before stopping again (Newton 2008). Before setting off on their journeys, they store large amounts of fat and, to a lesser extent, proteins as fuel for migratory movements (Guglielmo 2010). Birds undertaking long-distance movements by powered flight are a remarkable example, since many species may double their weight while they store reserves to fuel their long journeys (Piersma 1998). Thus, mass at departure from wintering sites is an essential parameter in the study of long-distance migration of birds (e.g. Zwarts *et al.* 1990, Alerstam *et al.* 2003).

Many European dabbling ducks (genus *Anas*) fly each year several thousands of kilometres between their arctic or northern temperate breeding grounds in Fennoscandia, Russia and Siberia and their wintering areas in south or western Europe and north or western Africa (e.g. Clausen *et al.* 2002, Zwarts *et al.* 2009, Parejo *et al.* 2015). There is a substantial amount of research focused on *Anatidae* ecology due to their importance as a hunting resource (Green and Elmberg 2014, Petrie *et al.* 2014). Specifically, body mass changes during winter have been assessed widely from a range of perspectives (e.g. Moon *et al.* 2007, Guillemain *et al.* 2010, Fleskes *et al.* 2016). Body mass and lipid stores at departure from wintering grounds, for example, have been related to breeding success in some dabbling ducks species such as the Eurasian teal *Anas crecca* (Guillemain *et al.* 2008). However, studies on how long-distance migratory dabbling ducks adjust pre-migratory physiological changes in the wintering or stopover sites in relation to their next non-stop flights are very scarce (Guillemain *et al.* 2004, Zwarts *et al.* 2009).

In dabbling ducks, body mass changes throughout the boreal winter have been considered as the consequence of their “wintering strategy” (Tamisier *et al.* 1995, Elmberg *et al.* 2005, Guillemain *et al.* 2005). According this wintering strategy, the lowest and highest body mass of dabbling ducks occur in early- and mid-winter, just after migration and restoring period, respectively (Guillemain *et al.* 2005). It also predicts that body mass decreases again in late winter because of the high energetic demands of the pairing period (Guillemain *et al.* 2005). It is therefore expected that conspicuous shifts in energy substrates and body mass occur across these successive periods of the wintering season.

Many overwintering dabbling ducks rely on rice fields as feeding grounds worldwide, where rice kernels are a fundamental component of their diet (e.g. Navedo *et al.* 2015). Understanding the role of these man-made wetlands in providing energy stores for successful migration is key for the design of conservation programs (Guillemain *et al.* 2010, Fleskes *et al.* 2016). Here, we examined body mass changes in northern pintails *Anas acuta*, the most widely distributed dabbling duck species (Fox 2005), at Extremadura, southern Spain, throughout the wintering season, including the pre-migratory period. We also measured changes in the plasma levels of triglycerides and total proteins as indices of lipid and protein metabolism (e.g. Albano *et*

al. 2016), respectively, since the physiological changes underlying the wintering strategy are largely unexplored in long-distance migratory dabbling ducks. This study contributes significantly to the body of knowledge regarding the role of rice fields as foraging grounds for migratory waterbirds.

Methods

Study Area, species and capture

The study area was located at Extremadura, in the middle basin of the Guadiana river (SW Spain; 39°N 6°W), where several reservoirs together with adjacent rice fields (25,000 – 30,000 ha) support several thousands of waterbirds, including more than 45,000 migratory dabbling ducks (Navedo *et al.* 2012; 2015). These rice fields have emerged as a new wintering area of international importance for several dabbling duck species, supporting on average 7,000 northern pintails overwintering during the last decade (Navedo *et al.* 2012; see Figure 1).

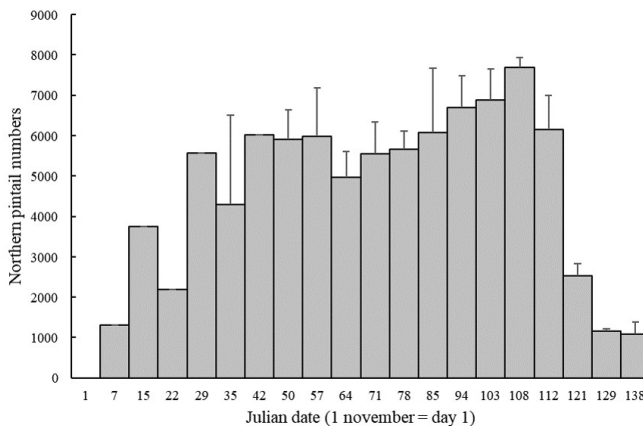


Figure 1: Numbers (mean \pm SE) of northern pintails in the study area throughout the wintering seasons 2012-2015.

A total of 188 northern pintails were cannon-netted during daylight at the shores of the main reservoir used as roosting area (Parejo *et al.* 2015), between early November and late February 2008 - 2013. All birds were individually measured (culmen and tarsus length, accuracy \pm 0.01 mm; wing length both flattened and straightened \pm 0.5 mm), weighed (\pm 0.01 g), and aged according to plumage characteristics (Baker 1993). Upon captures, a subsample of birds ($n = 94$) were blood sampled by brachial vein-puncture with a 26G needle. Blood samples were collected into heparinized one-step collection-centrifuge tubes (Microvette CB 300; Sarstedt AG & Co., Germany) and centrifuged (10,000 g for 10 min) in the field within 1 hour after collection.

Separated plasma and red blood cells were transported at 4°C in a portable cooler to the laboratory, where they were stored at - 80°C until analysis.

Although most birds were sexed using plumage characteristics, sex was confirmed through molecular sexing from blood samples. DNA was extracted from red blood cells using Chelex (Bio-Rad, Hercules, CA), following the manufacturer's protocol and sex was determined by PCR amplifications of the CHD genes with primers 2550F and 2718R (Fridolfsson and Ellegren 1999).

Scaled Mass Index and plasma metabolites assays

Size-corrected body mass was assessed on the basis of the Scaled Mass Index (SMI, g), a method that normalizes body mass to a fixed value of body size based on the scaling relationship between mass and length measures (Peig and Green 2009). Northern pintails are sexually dimorphic in size, so we calculated SMI separately for males and females. The fixed value of body size was the mean value of wing length for the study population: 276.39 ± 0.76 mm ($n = 87$) for males and 256.02 ± 0.67 mm ($n = 101$) for females (data from northern pintails caught in Extremadura from 2008 to 2013).

Plasma total triglycerides (triglycerides plus free glycerol), free glycerol and total proteins were measured by standard colorimetric endpoint assay kits adapted to small sample volumes in 400 μ L flat-bottom microplates (Greiner Bio-One, Germany) using a microplate spectrophotometer (BioTek Powerwave) (see Albano *et al.* 2011 for details). All measurements were made in duplicate and control reference serum samples (Menagent; Menarini Diagnostics) were run together with plasma samples. True triglyceride levels were calculated by subtracting free glycerol from total triglyceride levels.

Statistical Analyses

General linear models (GLMs) were used to examine potential effects of sex, period and their interaction on SMI (g). We included period as a fixed factor with three levels (early-, mid- and late-winter) to make comparable our results with previous studies (e.g. Guillemain *et al.* 2005). Periods of wintering season were classified as follow: early- (November), mid- (December) and late- (January–February) winter (Tamisier *et al.* 1995, Guillemain *et al.* 2005).

We also used GLMs to examine potential effects of period on plasma metabolite levels (log-transformed). Because of low sample size in early winter, males and females were analysed together, so we excluded sex as a fixed factor in these models. Plasma metabolite concentrations may vary with handling time, time of day, time elapsed from capture or body mass (e.g. Albano *et al.* 2016). For this reason, we performed regression analyses to determine whether both triglyceride ($\text{mmol}\cdot\text{L}^{-1}$) and total protein levels ($\text{g}\cdot\text{L}^{-1}$) varied with these variables. Plasma triglycerides were significantly correlated with elapsed time ($r = - 0.23$, $P = 0.03$), so we included elapsed time as

covariate in the model. By contrast, plasma proteins were not correlated with any of these variables ($r < 0.20$, $P > 0.1$, in all cases), so the model did not include any covariate.

Analyses were performed using the `glm` function in R3.3.3 software (R Core Team, 2016). Data are shown as mean \pm SE, and post-hoc Tukey test was performed when GLM results showed significance.

Results

SMI increased significantly in late winter in relation to both early and mid-winter (period: $F_{2,181} = 3.82$, $P = 0.02$; post-hoc Tukey test: $P < 0.01$), and it was greater in males than in females (sex: $F_{1,181} = 123.80$, $P < 0.0001$; Figure 2). The pattern of variation in SMI through the winter was similar in males and females (sex \times period: $F_{2,181} = 0.81$, $P = 0.44$; Figure 2).

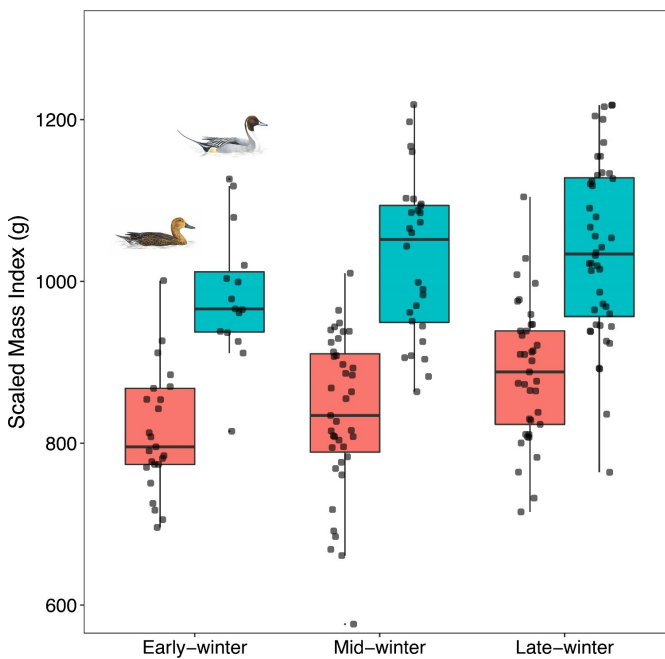


Figure 2: Variation in size-corrected body mass (Scaled Mass Index; SMI) in female and male northern pintails through the winter period. *Box- and whisker plots* denote medians (*horizontal line* within plot), interquartile ranges (*box*), and ranges (*bars*).

We did not find significant differences in plasma levels of triglycerides (period: $F_{2,90} = 0.30$, $P = 0.73$, elapsed time: $F_{1,90} = 5.37$, $P = 0.02$; Figure 3a) or total proteins throughout the winter ($F_{2,66} = 1.46$, $P = 0.24$; Figure 3b).

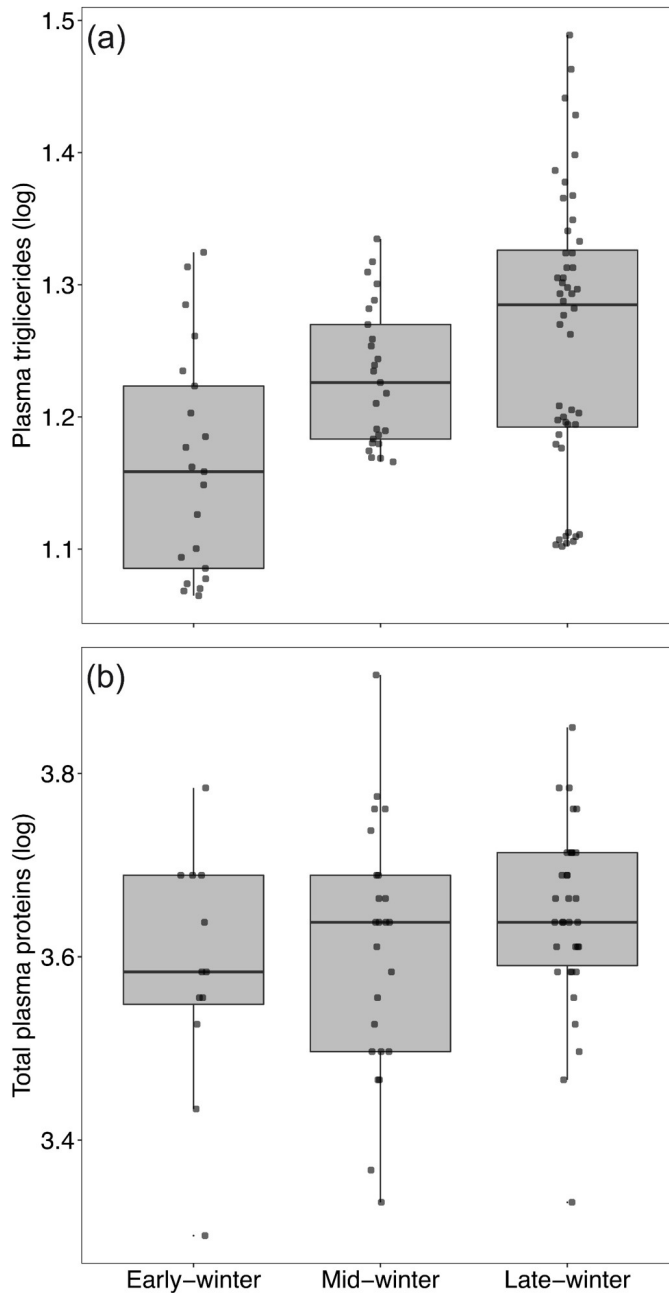


Figure 3: Variation in plasma levels of triglycerides (a) and total proteins (b) in northern pintails through the winter period. *Box- and whisker plots* denote medians (*horizontal line* within plot), interquartile ranges (*box*), and ranges (*bars*).

Discussion

Our study adds significantly to previous knowledge of physiological adjustments in long-distance migratory dabbling ducks overwintering in western and southern Europe. Contrary to the ‘wintering strategy’ of dabbling ducks (Guillemain *et al.* 2005), northern pintails showed the highest values of body mass in late winter (fattening period), instead of during mid-winter (pairing period). This pattern was paralleled by an increase in plasma triglycerides and proteins, albeit not statistically significant.

Overall, northern pintails may select different migration strategies, travelling long distances with non-stop flights or a series of shorter flights to staging sites (Miller *et al.* 2005). In our study area, most northern pintails leaving Extremadura have to fly 2,600 – 5,600 km to reach their breeding grounds (Parejo *et al.* 2015). Data from northern pintails equipped with GPS-GSM transmitters leaving Extremadura showed that they use four or five staging sites during their northward migration (Parejo *et al.* 2015). Most of them flew uninterruptedly about 900 km from Extremadura to the next staging sites located in France (estimates using data from Parejo *et al.* 2015). These individuals seem to follow a conservative migratory strategy, which would lead them to spend less time refueling and carry smaller fat stores than populations that engage in longer migratory flights (e.g. Warnock 2010).

The average body mass increase in males and females in late winter was 1.4% and 6.7%, respectively, with respect to mid-winter, an increase that should be enough to fuel the energy cost necessary to cover that distances by powered flight. If the body mass increase is not closely synchronized during the pre-migratory period, the average increase in body mass is always less than the rate at which individual birds gain body mass (Zwarts *et al.* 1990). At Extremadura there was a large variation in body mass in the late winter period, supporting that the body mass increase of northern pintails is not synchronized. Our estimate of the average body mass increase in the population, therefore, would reflect this asynchrony and underestimate individual mass gain, which should thus be considered as a minimum.

The plasma metabolite are increasingly being used to assess fattening rates of birds with diverse migration strategies (Albano *et al.* 2016). Because northern pintails foraged at night and arrived in the roosting site about 30 min before sunrise (authors unpubl. data from tracked individuals), blood samples were taken after several hours of diurnal fasting (most of them were caught and bled in the roosting site in the afternoon). Given that food intake prior to blood sampling play a significant role in the relationship between metabolite levels and body mass changes (Smith *et al.* 2007, Albano *et al.* 2016), the fasting period elapsed between sunrise and afternoon could have affected the recorded levels of both metabolites in our study.

The ‘wintering strategy’ of dabbling ducks predicts the highest body mass in mid-winter (Guillemain *et al.* 2005). This hypothesis was elaborated based on dabbling duck studies in the Camargue (France), and it also predict that most species decrease their body mass during the last period of the winter, when climatic conditions are usually less favourable and food resources are limiting (Tamisier *et al.* 1995, Guillemain *et al.* 2005). To date, empirical studies have shown no evidence of increasing

body mass of dabbling ducks in late winter with respect to mid-winter (Guillemain *et al.* 2005, Fleskes *et al.* 2016). In contrast, we found that northern pintails overwintering in the rice fields of Extremadura showed the highest body mass in late winter (fattening period), before leaving to the breeding grounds. A possible explanation for this discrepancy is that climatic conditions at Extremadura during winter are milder than those of the Camargue, and food (rice seeds) is not a limiting resource in the study area (Navedo *et al.* 2015), as observed in other American and European rice fields (Fleskes *et al.* 2012, Pernollet *et al.* 2016). Another potential factor affecting these body mass differences in late winter could be the sampling period considered as ‘late winter’. For example, Fleskes *et al.* (2016) included only body masses from January as ‘Late winter period’, which does not include the pre-migration or fattening period. Besides, different basal energetic requirements associated with body size and landscape features (e.g. Gutiérrez *et al.* 2012) could also have driven the observed differences. Either way, our results clearly show that northern pintails attained their highest body masses in late winter, just before leaving the wintering grounds.

Globally, rice kernels left on the ground after harvest have become a fundamental component of waterbird diet, including northern pintails and other dabbling ducks overwintering at Extremadura (Navedo *et al.* 2015). Although rice kernels consist mostly of starch and fiber, and contain a much lower lipid content than animal prey items, a recent study showed that black-tailed godwits *Limosa limosa* (a long-distance migratory waterbird) feeding on rice kernels can convert carbohydrate into fat by increasing *de novo* lipogenesis activity (Viegas *et al.* 2017). This finding provides strong evidence for metabolic plasticity in fat accumulation by long-distance migratory waterbirds feeding on rice kernels. Thus, northern pintails storing fat reserves for migration may also alter their lipid metabolism efficiently to compensate for a poorer dietary lipid contribution from rice.

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5

Unravelling trophic subsidies of agroecosystems for biodiversity conservation: Food consumption and nutrient recycling by waterbirds in Mediterranean rice fields

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Abstract

Waterbirds can reallocate a considerable amount of nutrients within agricultural fields and between agriculture sites and wetlands. However their effects on biogeochemical cycles have rarely been quantified. We estimated bird numbers, diet (from stable isotope analysis), food supply, and the food consumption on rice fields by overwintering waterbirds in one of the most important areas for rice production in southwestern Europe and a key area for various migrating and resident waterbird species. Herein, we modelled the nutrient (N and P) recycling in rice fields, and their transport to reservoirs. The energy consumption by waterbirds ($96,605 \pm 18,311$ individuals) on rice fields during winter averaged at $89.9 \pm 39.0 \text{ kJ}\cdot\text{m}^{-2}$, with its majority (89.9%) belonging to foraging on rice seeds. Thus, the birds removed about 26% of rice seeds leftover after harvest (estimated in $932.5 \pm 504.7 \text{ seeds}\cdot\text{m}^{-2}$ in early winter) wherein common cranes and dabbling ducks (four species) were the most important consumers. Waterbirds foraging and roosting in the rice fields recycled more than 24.1 ($1.0 \text{ kg}\cdot\text{ha}^{-1}$) of N and an additional 5.0 tons ($0.2 \text{ kg}\cdot\text{ha}^{-1}$) of P in the Extremadura's rice fields during winter. Additionally, we estimated that 2.3 tons of N and 550 kg of P were removed from rice fields and transported to reservoirs. The seasonal foraging of wildlife should result in a direct benefit for rice farmers by improving nutrient recycling through defecation by waterbirds with respect to artificial fertilisation. Additionally, rice fields located in the cranes' core wintering areas can provide sufficient food supply to induce habitat shift from their traditional wintering habitat in 'dehesas' to rice fields, which causes indirect socioeconomic benefit through reduced acorn consumption by cranes. Our modelling approach may thus be especially helpful for management decisions regarding rice agroecosystems in areas which are also important for the conservation of migratory waterbirds.

Introduction

Agriculture can have significant implications for wild animal and plant species, and is thus relevant for biodiversity conservation (Liang *et al.* 2001, Liu *et al.* 2013). The biodiversity differs between agroecosystems wherein two components are often recognised: ‘planned’ biodiversity, which relates to the crops and livestock intentionally included; and ‘associated’ biodiversity, which encompasses all flora and fauna colonising the agroecosystem from surrounding environments (Vandermeer and Perfecto 1995). The abilities of such associated diversity to thrive depend upon the management and structure of the agroecosystem (Altieri 1999). Thus, agroecosystem management is crucial to improve economic and ecological sustainability, and the final result of agroecological ‘design’ should be to use the proposed management systems in ways that are specifically in tune with local biodiversity, as well as existing environmental and socio-economic conditions (Altieri 1995, Campbell 2006). Despite the well-documented role of the remains of agriculture production after crop harvesting (e.g. Rand and Louda 2006), and the associated detritus as energetic subsidies for invertebrate predators like arachnids and insects (e.g. Halaj and Wise 2002, Birkhofer *et al.* 2008), the potential role of agroecosystems regarding vertebrate predators such as waterbirds has so far received little attention (Elphick *et al.* 2010).

Waterbirds play an important role in mass and energy fluxes within wetland food webs (e.g. Moreira 1997, Post *et al.* 1998, Hahn *et al.* 2008), and often provide essential ecosystem services (reviewed by Green and Elmberg 2014). Herein, waterbirds may remove a substantial proportion of the annual production of plants (e.g. Stafford *et al.* 2010) and macroinvertebrates (e.g. Moreira 1997), and their excrements are in turn a natural source of nitrogen and phosphorus (e.g. Frost *et al.* 2009). During recent decades, many herbivorous waterbird species have increased in numbers in the western Palearctic (Wetlands International 2012). An important driving force for these population growths might be the current agricultural practices, which provide high-quality food nearly year-round, thereby enlarging the carrying capacities of terrestrial habitats for herbivorous waterbirds (van Eerden *et al.* 1996, Toral and Figuerola 2010, Navedo *et al.* 2012). At sites where non-breeding waterbirds are numerous, their excrements can represent a major but local nutrient input of N and P (Portnoy 1990, Manny *et al.* 1994). On the other hand, some waterbirds show commuting behaviour, foraging in agricultural crops and resting in neighbouring wetlands (e.g. Mayes 1991, Gill 1996). They may therefore be responsible for a considerable reallocation of nutrients within agricultural fields (Green and Elmberg 2014), and between agriculture sites and wetlands, including inland waterbodies (Hahn *et al.* 2008). To date, waterbirds’ effects on nutrient and other biogeochemical cycles are yet poorly understood, so they are currently the subject of ongoing research (see review in Green and Elmberg 2014).

Recently, rice *Oryza sativa* has become the world’s most important crop in continental areas (Elphick 2010), and rice fields occupy over 1% of the Earth’s ice-free land surface (Maclean *et al.* 2002). Many migratory waterbirds use rice fields as foraging grounds outside the breeding season (e.g. Elphick 2010, Masero *et al.* 2011, Santiago-Quesada *et al.* 2014). In temperate regions like the Mediterranean, most ri-

ce is grown under flood during the warm summer period, and fields are left fallow during winter (Maclean *et al.* 2002). Waterbird abundances peak during this winter season (Sánchez-Guzmán *et al.* 2007, Eadie *et al.* 2008, Rendón *et al.* 2008), and predation pressure on rice fields by non-breeding waterbirds is expected to be high (Remsen *et al.* 1991, Shuford *et al.* 1998, Eadie *et al.* 2008, Amano 2009, Toral and Figuerola 2010). Overall, waterbirds mainly rely on spilled grain (Stafford *et al.* 2010, Toral *et al.* 2012, Santiago-Quesada *et al.* 2014) and, to a minor extent, on macroinvertebrates (e.g. Brochet *et al.* 2012). The high abundance of waterbirds during the non-breeding periods often lasts several months, and thus their increasing number will presumably cause a parallel increase in nutrient flux to rice fields via defecation (Bird *et al.* 2002, Liu *et al.* 2014). Despite this obvious potential of waterbirds to mediate nutrient inputs (Post *et al.* 1998, Hahn *et al.* 2008, Frost *et al.* 2009), data on nutrient recycling by waterbirds in rice fields are still scarce (Stafford *et al.* 2006, Elphick 2010).

Here, we studied diet, food consumption and nutrient recycling by overwintering waterbirds in Mediterranean rice fields located in the Extremadura (SW Spain), which is one of the most important areas for rice production in Western Europe. Extremadura's rice fields are of international importance for several migratory waterbirds, including common crane *Grus grus* (Sánchez-Guzmán *et al.* 2007), black-tailed godwit *Limosa limosa* (Masero *et al.* 2011) and several dabbling duck species (*Anas* spp.) (Navedo *et al.* 2012). Some species, especially dabbling ducks, use rice fields as foraging grounds during the night and commute to adjacent freshwater reservoirs to roost during the day (Navedo *et al.* 2012), whereas a proportion of overwintering cranes forage in the rice fields during daylight and fly to roost in adjacent reservoirs at dusk (Sánchez *et al.* 1999, Prieta and Del Moral 2008), and thus may transport nutrients from the rice fields to the surrounding reservoirs. The aims of this study were (1) to estimate the trophic subsidy of the agroecosystem as the total amount of energy removed by waterbirds through consumption of rice seeds and macroinvertebrates; (2) to quantify the recycling of local nutrients by defecation of waterbirds in rice fields; (3) to estimate the allochthonous nutrient loading via excreta by waterbirds to adjacent reservoirs.

Methods

Study area

Extremadura's rice fields (24,207 ha on average during 2005–2010 period) are located in the Guadiana river basin (SW Spain; 38°N 6°W) (Figure 1). The cycle of rice production starts with preparation of the fields in March, followed by flooding and sowing until the end of May. Rice growth is commenced in September and harvesting starts in October. At the end of November, many fields are rolled and flooded again, thus providing large areas of shallow water throughout the winter.

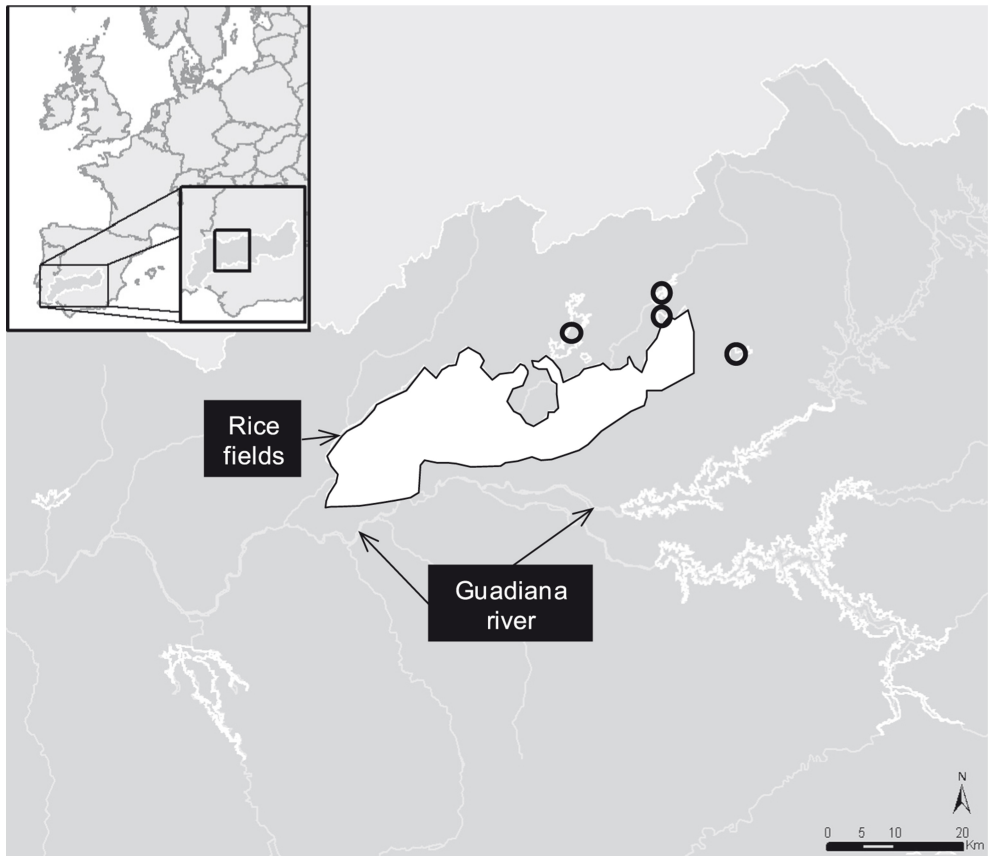


Figure 1: Map of the middle Guadiana river basin (Extremadura, SW Spain) indicating the location of the rice fields (white polygon) and most important reservoirs (open circles) for waterbirds within the study area.

Waterbird abundance and local food supply

We carried out monthly counts of waterbirds overwintering in the Extremadura rice fields (November–February 2004–2005 and 2007–2008), using the methodology described by Sánchez-Guzmán *et al.* (2007). Briefly, the total study area was divided into four counting sectors where different teams performed simultaneous daylight counts on each sector, using binoculars and telescopes. The number of dabbling ducks counted monthly (November–February 2007–2010) in the adjacent reservoirs was assumed to forage at night in the rice fields of the study area (data from Navedo *et al.* 2012, unpublished data from northern pintails *Anas acuta* and Eurasian teals *Anas crecca* equipped with radio- and GPS/GSM-transmitters).

The majority of waterbirds overwintering in the study area are herbivorous species that rely on rice seeds left over on the ground after harvest (see results). We

quantified the potential availability of rice seeds at the beginning of the wintering season (November 2009) by collecting soil samples (3-5 replicates each) in harvested fields, using a core of 6.6 cm in diameter and 12 cm in depth. The samples ($n = 37$) were taken randomly from five sectors of different sizes (range: 2,075-8,300 ha) which harboured the highest numbers of waterbirds. The areas included rolled as well as unrolled fields. Samples were stored in plastic bags and frozen until further processing. After thawing, the soil samples were sieved (mesh size: 1.0 mm) and all rice seeds counted to estimate the density of rice seeds per sample. We used a conversion factor of 0.02 g of dry mass per rice seed (average dry mass of a rice seed in the study area in November; $n = 30$) to estimate the biomass of rice seeds available for foraging waterbirds.

Diet composition

We used stable carbon isotopes ($\delta^{13}\text{C}$) and stable nitrogen isotopes ($\delta^{15}\text{N}$) of whole blood to determine the diet composition of waterbirds foraging in the rice fields. Whole blood typically archives the isotopic composition of diet over the last 20 days before tissue sampling (Hahn *et al.* 2012). We focused on species with significant numbers in the study area and potential mixed diets (i.e. rice seeds and animal prey). Between November and February we caught overwintering northern pintails ($n = 101$), Eurasian teals ($n = 23$), black-tailed godwits ($n = 9$) and ruffs (*Philomachus pugnax*) ($n = 5$), using mist and cannon nets. Blood samples (200–300 μl) were collected from the brachial vein, and the whole blood was stored in tubes at $-20\text{ }^{\circ}\text{C}$ until further analyses. Contrasting with other Mediterranean but coastal rice field areas where the seeds of various weed species are also important (e.g. Brochet *et al.* 2009; 2012 in the Camargue, Mateo *et al.* 2000 in the Ebro delta), the main potential food items of these waterbirds species at the Extremadura's rice fields were rice seeds, oligochaetes, and diptera larvae, as previously stated by Santiago-Quesada *et al.* (2014) using a 0.5 mm sieve. All these food items were simultaneously collected in the rice fields for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. Stable-isotope analyses were performed at the Iso-Analytical Laboratory (Cheshire, UK). We fitted a Bayesian mixing model to calculate diet composition (SIAR; Parnell *et al.* 2008), for which the isotopic values of potential food were adjusted by discrimination factors ($\delta^{15}\text{N}$: 2.2 ± 0.2 ; $\delta^{13}\text{C}$: 1.13 ± 0.12 according to Caut *et al.* 2009). For the laboratory standard material, we used Iso-Analytical Working Reference Standard IA-R042 (powdered bovine liver) with a $\delta^{13}\text{C}$ value of 21.60‰ vs Vienna-Peedee Belemnite, and a $\delta^{15}\text{N}$ value of 7.65‰ vs air. Standard deviations of laboratory standard bovine liver run along with blood samples and food items were estimated to vary between ± 0.01 and $\pm 0.05\text{‰}$ for carbon, and between ± 0.05 and $\pm 0.11\text{‰}$ for nitrogen.

Unfortunately, we could not capture northern shoveler *Anas clypeata*, mallard *Anas platyrhynchos*, or greylag goose *Anser anser* to perform stable isotope analyses. Thus, for these species we assumed a similar diet composition to the dabbling ducks and northern pintail (see Mateo *et al.* 2000), since they show similar foraging behaviour and also fed in the rice fields at night (unpublished data from birds equipped with radio transmitters and pers. obs.). Although geese foraged in the rice fields during

daylight, we also assumed for them a similar diet to the northern pintail, since they foraged in the same areas and food remains in faeces were mainly constituted of rice seeds. For common cranes foraging in the Extremadura rice fields, we used data on diet composition from a former study carried out in the same area, in which the diet comprised 90 % of rice seeds and 10 % of animal prey (Avilés *et al.* 2002). Small-medium shorebirds, little egret *Egretta garzetta*, grey heron *Ardea cinerea*, white stork *Ciconia ciconia* and gulls (Fam. *Laridae*) were assumed to feed on macroinvertebrates (pers. obs. during studies of shorebird foraging behaviour performed in the study area; e.g. Santiago-Quesada *et al.* 2012). Although gulls could also eat some rice seeds (Calvino-Cancela 2011), it is unlikely to be its main diet due to the high availability of invertebrates. For all further species where diet analysis by stable isotopes could not be performed (see Annex), we used data from bibliography (e.g. Cramp and Simmons 1977; 1983).

Food consumption

To estimate the total biomass removed by each species, we assumed that the wintering season lasted for 120 days. The average number of individuals of each species during November–February was assumed to be the average number of overwintering individuals in the study area. We calculated the seasonal food consumption in rice fields (FC_{rice}) using species-specific daily energy requirements (DER; $\text{kJ}\cdot\text{bird}^{-1}\cdot\text{day}^{-1}$), the proportion of food gathered in rice fields (f_{rice}), the average energy content of the main diets (E ; $\text{kJ}\cdot\text{g}^{-1}$), their apparent metabolisable energy coefficient (AM), the ratio of rice to invertebrates (Diet; see above), and the duration of non-breeding season (time: 120 days).

$$FC_{\text{rice}} = f_{\text{rice}} \times \text{DER} / (E_{\text{diet}} \times \text{AM}_{\text{diet}}) \times \text{Diet} \times \text{time}$$

The estimates of daily energy requirement of various waterbird species were calculated using the general allometric relationship of body mass and field metabolic rate in birds (Nagy *et al.* 1999). Data of average body mass were collected from overwintering individuals caught during ringing activities in the study area (17 species; Annex). Nevertheless, for seven species, site-specific body mass data were not available, so we used data from Cramp and Simmons (1977; 1983) (Annex). The energy density (E) of Extremadura’s rice seeds was estimated at 16.51 kJ per gramme dry mass (Santiago-Quesada *et al.* 2009), while the energy density of macroinvertebrates averaged at 23 kJ per gramme dry mass (Caudell and Conover 2006). Additionally, we used 0.80 for AM of cultivated seed (i.e. rice), and 0.77 for invertebrates (Karasov 1990). The relative amount of food (f_{rice}) gathered in the rice fields was assumed to vary depending on the species (Annex). We estimated that dabbling ducks, geese, cranes, storks, and godwits foraged exclusively ($f_{\text{rice}} = 1$) on rice fields. Shorebirds other than godwits foraged almost exclusively ($f_{\text{rice}} = 0.9$) on rice fields, whereas herons and gulls were expected to meet only about 50 % of their DER by foraging in this habitat (J.G. Navedo pers obs).

Nutrient recycling at rice fields

Using the intake model approach developed by Hahn *et al.* (2007; 2008), we calculated the nitrogen (N) and phosphorous (P) recycling by waterbird species in rice fields. We assumed all birds to be in a steady state with respect to N and P; that is, for all birds, the daily amount of N and P defecated corresponded to the amount ingested. Hence, defecation of N and P in the rice fields depended on daily food intake and its elemental concentration (X_{food} ; $\text{mg}\cdot\text{g}^{-1}$) minus the fraction of food in the digestive tract of commuting birds exported to the roost (i.e. the allochthonous nutrient load, see below). The daily food intake (DFI_t ; $\text{g}\cdot\text{day}^{-1}$) was calculated as described for food consumption, and the proportions of ingested food exported by commuters were estimated using relationships of digestive tract architecture and daily foraging time (for details, see section on nutrient loading).

Finally, we measured the elemental concentration (X_{food} ; $\text{mg}\cdot\text{g}^{-1}$) of N and P in rice seeds from the study area (Elemental and Molecular Analysis Laboratory, Universidad de Extremadura). The seeds contained, on average, $1.3 \pm 0.3\%$ N and $0.4 \pm 0.0\%$ P ($n = 115$); thus, X_{food} was estimated at $12.5 \text{ mg}\cdot\text{g}^{-1}$ and $3.7 \text{ mg}\cdot\text{g}^{-1}$ for N and P, respectively. The dry mass of a rice seed averaged at 0.02 g ($n = 80$ seeds collected in mid-winter). The N and P contents of an invertebrate diet averaged at 88.5 and $9.1 \text{ mg}\cdot\text{g}^{-1}$ (Hahn *et al.* 2007).

Nutrient loading at reservoirs by commuting waterbirds

The nutrient loading at reservoirs depends on the number of birds that commute between foraging in rice fields and roosting at reservoirs, and on the proportion of food transported between sites. To quantify the N and P loads, we assumed the digestive tract of waterbirds to be completely filled when feeding ceases and birds fly to the roost. The fraction of N and P in faeces produced at the roost (X_i) can then be estimated as the ratio of retention time (RT) and total foraging time (Tf), where RT is defined as the average time for food to pass a bird's digestive tract (Hahn *et al.* 2008), and Tf is related to diurnal or nocturnal foraging in rice fields. Combining RT/Tf with food intake and N and P contents in the food, the ratio of rice to invertebrates in the diet (Diet) yields the daily nutrient loading at the roost:

$$X_i = (\text{RT}/\text{Tf}) \times \text{DFI}_t \times X_{\text{food}} \times \text{Diet}.$$

We estimated Tf for each species, varying from 4.2 h (moorhen *Gallinula chloropus*) to 13.2 h (Eurasian teal), depending on the proportion of foraging activity (see references in Annex) and their diurnal and nocturnal activity in the rice fields (Sánchez-Guzmán *et al.* 2007, Santiago-Quesada *et al.* 2012, Navedo *et al.* 2012). Daily activity period commenced at dawn and finished at dusk for diurnal foragers, and the opposite for nocturnal foragers. We estimated the total activity period at 14.5 h for nocturnal foragers (i.e. dabbling ducks; Navedo *et al.* 2012) and at 9.5 h for diurnal foragers.

Although the majority of cranes and geese roost in the rice fields, a significant percentage of both species commutes between daylight foraging in the rice fields and nocturnal roosting at the reservoirs. We assumed that 20% of the non-breeding population of cranes and geese performed commuting behaviour (Prieta and Del Moral 2008), and that all dabbling ducks commuted between nocturnal foraging grounds and diurnal roosting at the reservoirs.

Model sensitivity test

We checked for the influence of the following parameters on the model output, which had been influenced by observational error or by assumption in our study: the total number of birds per species, the length of non-breeding period (time), the proportion of food from rice fields (f_{rice}), the proportion of diet category (diet), total foraging time (Tf), and the proportion of the population with commuting behaviour (commute).

We varied the species-specific parameter estimates successively by $\pm 10\%$, and calculated a general sensitivity coefficient across all species by relating changes in the model output to the changes in the focal input parameter [$SC = (R_{-10\%} - R_{+10\%}) / R / (P_{-10\%} - P_{+10\%}) / P$] with R the model output and P the focal parameter; Hamby 1994]. The direction and magnitude of the resulting output changes were given by the local sensitivity coefficient (SC): values of $SC > 1$ indicated disproportionately high changes, and values of $SC = 0$ indicated no effect of the considered parameter on model output (Hamby 1994). We did not test the model sensitivity with regard to variation in the input parameters of metabolic and digestive performances in waterbirds, and of the nutrient concentration in diets, because this has already been done in similar studies (Hahn *et al.* 2007; 2008).

All results are given by means \pm SE, except when indicated otherwise.

Results

Waterbird numbers and diet composition

A mean of $96,605 \pm 18,311$ waterbirds were present in the study area throughout the winter season. Common crane was the most abundant species, with a mean estimate of $24,196 \pm 2,960$ birds, followed by the four dabbling duck species (Table 1). These five species accounted for 70% of total mean waterbird abundance.

Stable isotope analyses revealed that pintails and teals (dabbling ducks), as well as godwits (shorebird) fed almost exclusively on rice seeds (0.99 ± 0.39 , 0.92 ± 0.47 , 0.94 ± 0.77 , respective proportions) (Figure 2). In contrast, the proportion of rice seeds in the diet of ruffs (shorebird) averaged at $0.77 \pm 0.69\%$ (Figure 2).

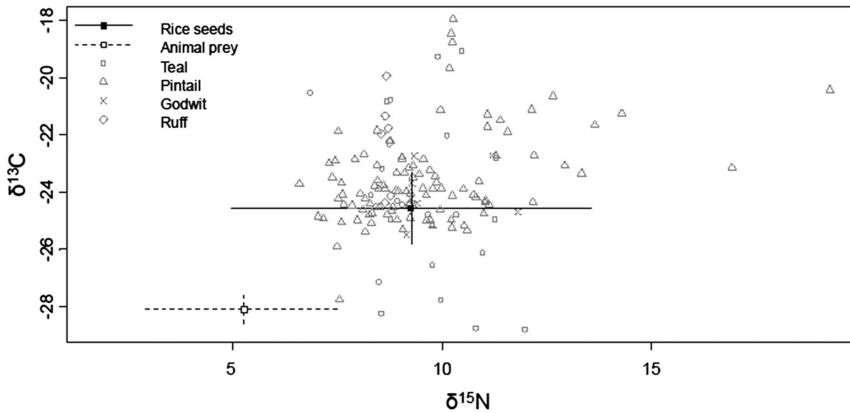


Figure 2: Stable isotope ratios (mean \pm SD) of carbon and nitrogen for potential food sources (rice seeds and animal prey) and for whole blood of Eurasian teal, northern pintail, black-tailed godwit and ruff. Values were adjusted with trophic enrichment factor of 1.13‰ for $\delta^{13}\text{C}$ and 2.25‰ for $\delta^{15}\text{N}$.

Food supply and food consumption of rice seeds

The mean density of leftover rice seeds in November was 932.5 ± 504.7 seeds $\cdot\text{m}^{-2}$ (307.9 ± 166.6 kJ $\cdot\text{m}^{-2}$). This is equivalent to 186.5 ± 101 kg of dry mass of rice seeds per hectare ($3.1 \cdot 10^6 \pm 1.7$ kJ $\cdot\text{ha}^{-1}$) available for waterbirds. Seven species accounted for 94% of total food consumption: common crane, dabbling ducks (four species), greylag goose and black-tailed godwit (Figure 3). The gross energy consumption by waterbirds during winter was 89.9 ± 39.0 kJ $\cdot\text{m}^{-2}$, with the majority (89.9%) belonging to consumption on rice seeds. Thus, the total consumption of rice seeds by waterbirds in the Extremadura rice fields throughout the wintering season is estimated at $1,184.8 \pm 501.4$ tons (48.9 ± 20.7 kg $\cdot\text{ha}^{-1}$).

Nutrient recycling in rice fields

Waterbirds recycled, in total, 24,108 kg of N (12,964 – 35,602) and 5,025 kg of P (2,839 – 7,294) during the total wintering season in Extremadura's rice fields (Table 1), wherein 55% of N and 78% of P originated from rice seeds. The most important species for recycling was the common crane which contributed to 64% of recycling of rice seeds and 44% of recycling of invertebrates, followed by mallards (15% of rice seeds) as well as white storks and lapwings *Vanellus vanellus* with 13% and 12% respectively of recycling of invertebrates (see Annex).

Nutrient loading at reservoirs by commuting waterbirds

Waterbirds with commuting behaviour transported/exported about 2,280 kg of organic N (1,410–3,156) and about 550 kg of organic P (338–762) during the winter

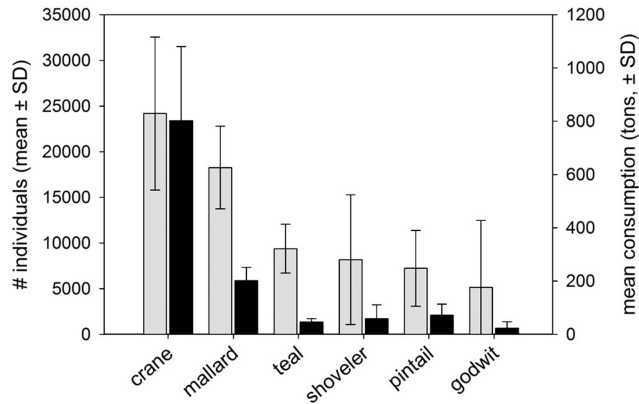


Figure 3: Mean waterbird abundance (only the six most abundant species are shown; grey bars, left Y-axis) and mean estimated food consumption (black bars, right Y-axis) throughout the wintering season in the Extremadura rice fields (SW Spain), extended along 24,207 ha.

season from the rice fields to the reservoirs when roosting (Table 1). The majority of the loading originated from rice seed foraging (72 % in N and 88 % in P). Herein, again cranes were the main contributor to this allocation of nutrients between habitats (53 % and 64 % of N and P, respectively).

Sensitivity test

The estimates of the number of birds and the duration of the winter period proportionally affected all models (subsidy, nutrient recycling and loading models) in a similar fashion (Table 2). For the subsidy model, the diet composition (the proportion of rice and invertebrates) and the proportion of food from rice seeds were of minor importance. However, any variation of the proportion of rice seeds in the diet composition was crucial for the results of invertebrate consumption in both the recycling and the loading model: a higher proportion of rice seeds in the diet would drastically reduce the effect of nutrients originating from invertebrates (Table 2), due to the significantly different energy and N and P contents in rice seeds and invertebrates (see material and methods). The total foraging time and the estimates of the proportion of birds with commuting behaviour had minor effects on the recycling model output, but impacted the loading model proportionally.

Discussion

Extremadura's rice fields provided an important trophic subsidy for overwintering waterbirds through consumption of rice seeds, especially for common cranes, dabbling ducks, greylag geese and black-tailed godwits. This trophic subsidy is comparable with

Table 1
 Estimated trophic subsidy (i.e. consumption), nutrient recycling and nutrient loading, indicating the percentage of the total N and P from rice (the rest is estimated to come from invertebrates) which is attributable to that bird species (% Rice), throughout the non-breeding season at rice fields in Extremadura.

Species	Waterbirds		Subsidy		Recycling N		Recycling P		Loading N		Loading P					
	Mean	SD	(kg m ⁻² season ⁻¹)	Range(±SD)	(kg season ⁻¹)	Range(±SD)	%Rice	(kg season ⁻¹)	Range(±SD)	(kg season ⁻¹)	%Rice	(kg season ⁻¹)	Range(±SD)	%Rice		
<i>Grua grus</i>	24196	8373	54.76	35.81-73.70	13190.6	8025.9-17755.3	35.0	2984.8	1951.9-4017.8	49.7	1353.7	88.5-1822.2	38.0	306.3	200.3-412.3	46.7
<i>Anas platyrhynchos</i>	18270	4524	13.76	10.35-17.16	2461.4	1851.9-3070.8	8.4	645.5	485.7-805.3	12	592.6	378.2-627.1	18.2	131.8	99.2-164.4	22.4
<i>Anas crecca</i>	9389	2664	3.15	2.26-4.04	599.1	429.1-769.1	2.1	157.1	112.5-201.7	2.9	79.6	57.0-102.2	2.9	20.9	15.0-26.8	3.5
<i>Anas platyrhynchos</i>	8187	7093	4.05	0.54-7.57	749.9	100.2-1399.7	2.6	196.7	26.3-367.1	3.6	123.0	16.4-229.6	4.5	32.3	4.3-60.2	5.5
<i>Anas acuta</i>	7235	4147	4.92	2.10-7.74	891.0	380.3-1401.7	3	233.7	99.7-367.6	4.3	170.4	72.8-298.1	6.2	44.7	19.1-70.3	7.6
<i>Vandellia vanellus</i>	5482	2743	0.97	0.49-1.46	1262.7	630.9-1894.4	1.2	129.8	64.9-194.8	1.7	129.8	64.9-194.8	1.7	129.8	64.9-194.8	1.7
<i>Limosa limosa</i>	5161	7309	1.62	0-3.91	375.2	0-906.6	1.2	93.3	0-225.5	1.7	93.3	0-225.5	1.7	93.3	0-225.5	1.7
<i>Chroicocephalus ridibundus</i>	4009	2811	0.42	0.13-0.72	552.0	165.0-939.0	1.2	56.8	17.0-96.5	1.7	56.8	17.0-96.5	1.7	56.8	17.0-96.5	1.7
<i>Gallinago gallinago</i>	3048	2819	0.34	0.03-0.66	446.7	38.5-859.9	4.6	45.9	3.4-88.4	4.6	45.9	3.4-88.4	4.6	45.9	3.4-88.4	4.6
<i>Anser anser</i>	2348	2882	3.35	0-7.46	673.3	0-1099.7	2.3	176.6	0-393.3	3.3	48.1	0-107.2	1.7	12.6	0-28.1	2.1
<i>Colaptes auratus</i>	2141	838	0.13	0.08-0.18	18.9	11.5-26.3	1.9	1.9	1.2-2.7	1.9	1.9	1.2-2.7	1.9	1.9	1.2-2.7	1.9
<i>Bubulcus ibis</i>	2044	1051	0.48	0.23-0.73	625.7	304.0-947.4	64.3	64.3	31.3-97.4	64.3	64.3	31.3-97.4	64.3	64.3	31.3-97.4	64.3
<i>Larus fuscus</i>	1932	1503	0.45	0.10-0.81	587.8	130.6-1045.1	60.4	60.4	13.4-107.5	60.4	60.4	13.4-107.5	60.4	60.4	13.4-107.5	60.4
<i>Ciconia ciconia</i>	906	734	1.12	0.21-2.03	1455.5	276.0-2635.0	0.1	149.7	28.4-270.9	0.1	149.7	28.4-270.9	0.1	149.7	28.4-270.9	0.1
<i>Gallinula chloropus</i>	465	396	0.13	0.02-0.24	28.1	4.2-52.1	0.1	7.4	1.1-13.7	0.1	7.4	1.1-13.7	0.1	7.4	1.1-13.7	0.1
<i>Pluvialis apricaria</i>	275	324	0.05	0-0.11	64.0	0-139.5	0	6.6	0-14.3	0	6.6	0-14.3	0	6.6	0-14.3	0
<i>Philomachus pugnax</i>	247	224	0.05	0-0.09	11.3	1.0-21.6	0	2.8	0.3-5.4	0.1	2.8	0.3-5.4	0.1	2.8	0.3-5.4	0.1
<i>Tringa ochropus</i>	239	430	0.02	0-0.05	25.0	0-70.0	0	2.6	0-7.2	0	2.6	0-7.2	0	2.6	0-7.2	0
<i>Colaptes auratus</i>	227	209	0.01	0-0.02	1.3	0.1-2.4	0.1	0.1	0-0.3	0.1	0.1	0-0.3	0.1	0.1	0-0.3	0.1
<i>Himantopus himantopus</i>	196	131	0.03	0.01-0.05	37.4	12.4-62.5	3.8	3.8	1.3-6.4	3.8	3.8	1.3-6.4	3.8	3.8	1.3-6.4	3.8
<i>Egretta garzetta</i>	176	206	0.03	0-0.06	6.8	0-14.7	0.7	0.7	0-1.5	0.7	0.7	0-1.5	0.7	0.7	0-1.5	0.7
<i>Ardea cinerea</i>	122	82	0.04	0.01-0.07	11.1	3.6-18.6	1.1	1.1	0.4-1.9	1.1	1.1	0.4-1.9	1.1	1.1	0.4-1.9	1.1
<i>Charadrius dubius</i>	169	82	0.01	0-0.01	0.8	0.2-1.4	0	0	0-0.1	0	0	0-0.1	0	0	0-0.1	0
<i>Tringa erythropus</i>	37	28	0.00	0-0.01	6.3	1.5-11.0	0.6	0.6	0.2-1.1	0.6	0.6	0.2-1.1	0.6	0.6	0.2-1.1	0.6
<i>Charadrius alexandrinus</i>	31	26	0.00	0-0.01	0.2	0-0.4	0.0	0.0	0-0.1	0.0	0.0	0-0.1	0.0	0.0	0-0.1	0.0
<i>Charadrius hiaticula</i>	31	37	0.00	0-0.01	0.4	0-0.8	0.0	0.0	0-0.1	0.0	0.0	0-0.1	0.0	0.0	0-0.1	0.0
<i>Tringa totanus</i>	28	42	0.00	0-0.01	4.2	0-10.5	0.4	0.4	0-1.1	0.4	0.4	0-1.1	0.4	0.4	0-1.1	0.4
<i>Tringa nebulosa</i>	27	21	0.00	0-0.01	5.6	1.2-10.1	0.6	0.6	0-1.0	0.6	0.6	0-1.0	0.6	0.6	0-1.0	0.6
<i>Burhinus oedicnemus</i>	22	36	0.01	0-0.02	9.5	0-24.8	1.0	1.0	0-2.5	1.0	1.0	0-2.5	1.0	1.0	0-2.5	1.0
<i>Recurvirostra aesculapii</i>	17	16	0.00	0-0.01	5.0	0.3-9.7	0.5	0.5	0-1.0	0.5	0.5	0-1.0	0.5	0.5	0-1.0	0.5
<i>Actitis hypoleucos</i>	9	9	0.00	0-0.01	0.9	0-1.7	0.1	0.1	0-0.2	0.1	0.1	0-0.2	0.1	0.1	0-0.2	0.1

Table 2

Results of the model sensitivity test indicating the influence of each parameter in each model output. Values over ± 1 indicate a high influence and values near 0 indicate no effect.

Parameter	Subsidy model	Recycling model		Loading model	
		Rice	Invert.	Rice	Invert.
#Birds of per species	1	1	1	1	1
Duration winter period (time)	1	1	1	1	1
Proportion food from rice field (f_{rice})	0.7	0.74	0.87	0.74	0.74
Proportion rice seed diet	0.3	1.18	-7.21	1.13	-14.39
Proportion invertebrate diet	-0.06	-0.17	1.5	-0.15	1.96
Total foraging time (Tf)	n.a.	0.13	0.06	-1.01	-1.01
Commuting behaviour	n.a.	-0.12	-0.06	1	1

the food supply provided by natural wetlands throughout the Western Palearctic (Figure 4), despite the fact that the food supply at those natural areas is based on invertebrates that, overall, have a higher energy density than rice seeds. The available (leftover) rice for waterbirds in the Extremadura rice fields at the start of the wintering season was 41% and 24–30% lower than values reported in North America ($315 \pm 133 \text{ kg}\cdot\text{ha}^{-1}$; see review in Eadie *et al.* 2008) and some areas in Japan (e.g. $245\text{--}267 \text{ kg}\cdot\text{ha}^{-1}$ reported by Amano *et al.* 2004; 2006), respectively. However, the food supply of rice seeds in our study region of South Europe was significantly higher than in other regions of Japan with estimations of $84\text{--}103 \text{ kg}\cdot\text{ha}^{-1}$ (Shimada 1999), $69\text{--}88 \text{ kg}\cdot\text{ha}^{-1}$ (Shimada 2002), and $56\text{--}78 \text{ kg}\cdot\text{ha}^{-1}$ in 2007 (Shimada and Mizota 2008). This large inter-regional variation on the availability of food in rice fields may be caused primarily by region-specific management techniques (Stafford *et al.* 2010).

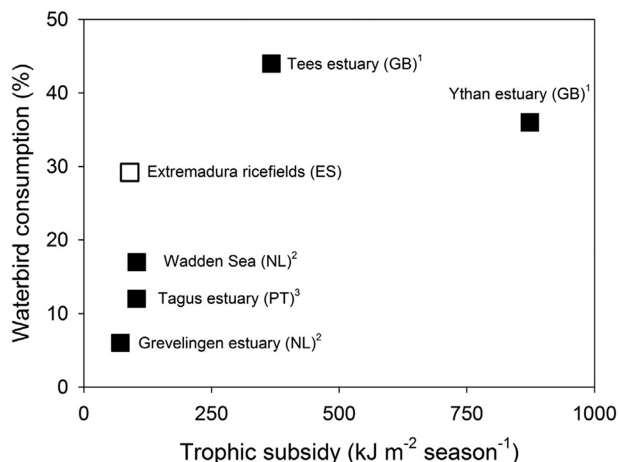


Figure 4: Trophic subsidy and rice consumption by waterbirds in the Extremadura rice fields (this study; empty square) and some important natural wetlands for waterbirds in the western Palearctic (filled squares). Sources: ¹ Baird *et al.* (1985); ² Wolff (1989); ³ Moreira (1997).

Total food consumption by waterbirds in the Extremadura reached about 26 % of rice seeds potentially available at the start of the wintering season. This value was significantly lower than the range of 75–95 % reported in Japan and North America (Shimada and Mizota 2008, Stafford *et al.* 2010). However, this figure would be treated as a minimum since the decomposition of rice grains throughout the season (Stafford *et al.* 2005, Greer *et al.* 2009, Fogliatto *et al.* 2010) will increase the number of rice grains needed to get the DER of birds, thus increasing to some extent the percentage consumed at the end of the season. Moreover, although waterbirds dispersed for foraging through the whole study region, certain areas were favoured by seed foragers such as common cranes, dabbling ducks and greylag goose (unpubl. data) resulting in a spatially non-uniform consumer/loader effect at the landscape level. Most of these species probably increased their DER during the last weeks of the wintering season, due to extra energy requirements for pre-migratory fattening (e.g. Masero and Pérez-Hurtado 2001). In addition, DER could also have increased substantially as a function of the thermoregulatory demands in mid-winter (Gutiérrez *et al.* 2011). This implies that the consumption of available rice would probably be higher, especially in some sectors often close to roosting sites and particularly in areas used heavily by foraging cranes, since this species exert more than 60 % of the total food consumption reported in this study.

Waterbirds foraging and roosting in the rice fields recycle more than 24.1 tons of N and an additional 5.0 tons of P during winter. They will thus improve nutrient recycling by an increase in decomposition rate of rice seeds and invertebrates in comparison with areas where seeds and invertebrates are not consumed (Hutchinson 1950, Liu *et al.* 2014). This should also result in a direct benefit from wildlife to rice farmers by rapid nutrient recycling within affected areas with respect to artificial fertilisation (Green and ElMBERG 2014). Since common cranes are responsible for the greatest proportion of nutrient recycling, areas used heavily by this species will receive a high level of organic fertilisation. Overall, the eastern part of the whole study area (about 9,400 ha of rice fields) was used by waterbirds much more heavily than the rest of the area, concentrating about 70 % of the total crane population (Prieta and Del Moral 2008), as well as ca. 90 % of geese and dabbling ducks (data from waterbird counts). Thus, waterbirds using the eastern part of the study area would fertilise these rice fields at a rate of 1.50 kg·ha⁻¹ and 0.3 kg·ha⁻¹ organic N and P, respectively, per wintering season.

Additionally, specific areas used as roosting sites for cranes within these heavily used rice fields would receive peak fertilisation rates. Commuting dabbling ducks and, to a lesser extent, geese and cranes, loaded a certain amount of N and P to reservoirs where they roosted. When considering the differential release of various nutrient contents from droppings into the water column (Liu *et al.* 2014), an additional 2.3 tons of N and 550 kg of P were loaded to reservoirs, which were also located in the eastern part of the study area. Commuting waterbirds, therefore, could affect water quality or productivity within the reservoirs where they roost. For instance, resident waterbirds are known to change states in local pond systems by eutrophication (Chaichana *et al.* 2010; 2011). However the large surface of reservoirs at the study area (i.e. the smallest reservoir covers 142 ha) and the discontinuous seasonal loading of nutrients exerted

by migratory waterbirds may diminish effects of nutrient enrichment, though further studies should accurately assess their ecological consequences.

The crucial parameters in our modelling approach are the number of birds, the duration of the winter period and the proportion of rice in the consumer's diet. The latter might be less variable within a season and between shorter periods, because diet preferences in birds are rather stable (e.g. Nagy *et al.* 1999). However, further studies should accurately estimate the proportion of rice in diet, especially in other areas where weed seeds are also important (Brochet *et al.* 2009). Because the winter period will not change so much with seasonally different weather conditions or long-term climatic conditions, the number of birds remains the most important factor. Many waterbirds are highly versatile and quickly adapt their foraging behaviour according to temporal environmental conditions, such as the level of disturbance (Klaassen *et al.* 2006), spatial food availability (Jia *et al.* 2013) and local weather conditions (Rippe and Dierschke 1997). This flexible behaviour is already mirrored in our input data set, because this parameter showed the largest standard deviation ('waterbirds'; Table 1). Thus, any long-term conclusions or adaptation to other study areas should pay special attention to obtaining the most precise determination of the number of birds involved within a particular season and area. Nevertheless, although our calculations may misrepresent some processes, we believe that the results were robust and are reliable estimates of minimum nutrient recycling by waterbirds within rice fields of the Extremadura region.

The presence of rice fields from the 1960s, and their extension from the 1990s within the Guadiana basin in Extremadura, had been proposed as key landscape features modifying the wintering and/or foraging sites of various waterbird species (Sánchez-Guzmán *et al.* 2007). In fact, prior to the 1990s, the typical wintering habitats used by cranes were the pasture lands covered by holm *Quercus ilex* and/or cork *Quercus suber* oaks (the so-called 'dehesas'), where the species forage primarily on bulbs and acorns (Díaz *et al.* 1997). Since the latter resource is crucial for extensive pig-farming and thus the ham industry, crane use of 'dehesas' appeared as a considerable damaging factor to the agriculture of the zone (Sánchez 1993). Although cranes continued to use 'dehesas' to forage during the 1990s (e.g. Avilés *et al.* 2002), the further extension of rice fields from the 1990s diminished their use of these areas of conflict (Sánchez *et al.* 1999). Specifically, one important benefit for cranes is the availability of roosting areas within rice fields, which allows for saving considerable energy by skipping the daily flights of some 30–40 km between the foraging and roosting sites (Sánchez *et al.* 1999). Furthermore, this commuting behaviour has virtually disappeared during recent years, and today, cranes regularly roost within rice fields. Our results show that rice fields, at least those in the cranes' core wintering area in the Extremadura, can provide sufficient food supplies to induce a marked disappearance of wintering cranes from the 'dehesas' (Prieta and Del Moral 2008). Therefore, we argue that the increasing temporal availability of rice fields for waterbirds in this Mediterranean region can cause indirect socioeconomic benefits by reducing the acorn consumption by cranes, thus decreasing the damages caused to a crucial industry within the area.

To sum up, our results may be especially helpful for future management decisions

regarding these rice agroecosystems, tidily geared with the conservation of migratory waterbird populations, and modelling the bird-driven nutrient recycling and fertilisation of rice fields and thus the ecosystem services provided (Green and Elmberg 2014). The whole agroecosystem of ca. 25,000 ha is currently crucial for the conservation of several species using the East Atlantic Flyway. Despite the current status of the western part of this rice field area as a Special Protection Area for Birds (ES0000400; 13,324.4 ha), our results give additional confidence for the necessity to effectively protect the whole rice field area by means of legal mechanisms (Sánchez-Guzmán *et al.* 2007, Masero *et al.* 2011, Navedo *et al.* 2012). Therefore, further development and adoption of a management plan emerge as urgent issues to ensure that this agroecosystem continues to provide an important trophic subsidy for migratory waterbirds.

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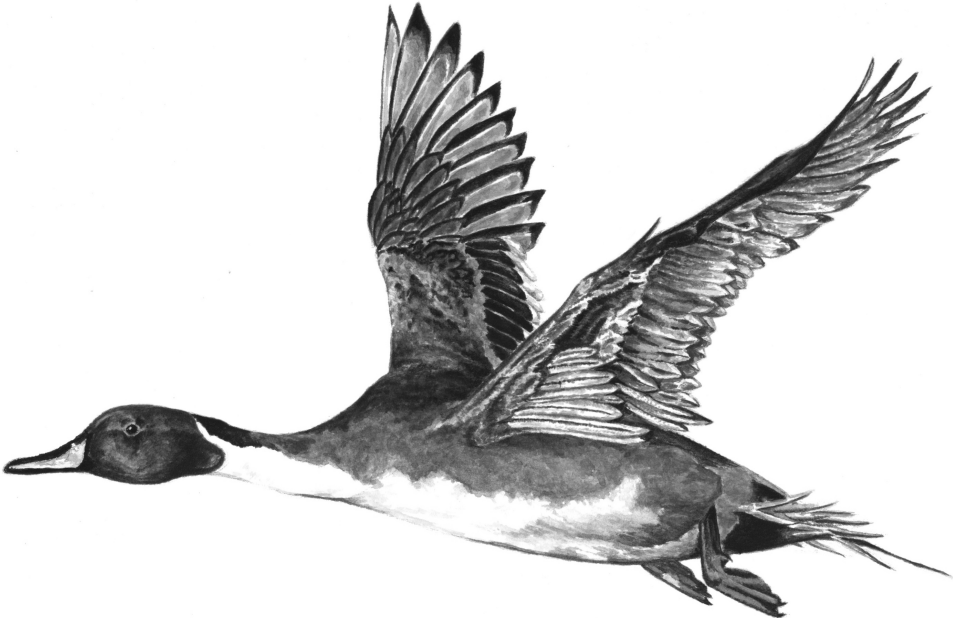
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Annex

Detailed parameters used in calculations of nutrient recycling within rice fields and nutrient loading to reservoirs via waterbird excretions throughout the non-breeding season in the Extremadura rice fields. BM = Body Mass; DER = Daily Energy Requirements; Rice = proportion of rice in diet; f_{rice} = proportion of food obtained in rice fields; DFL Rice = Daily Food Intake from rice seeds; DFL Invert. = Daily Food Intake from invertebrates; RT = Retention Time; Tf = Total daily foraging time (see text for more details).

Species	DER		DFL Rice		DFL Invert.		Recycling		Loading		BM source	Foraging activity source	
	BM(g)	(kJbird ⁻¹ day ⁻¹)	Rice	(gday ⁻¹)	f _{rice}	(gday ⁻¹)	RT(h)	Tf(h)	% Rice	% Invert.			% Rice
<i>Grua grus</i>	5625.0	3758.6	0.90	1.0	256.1	20.4	2.7	5.9	64.0	48.6	53.2	75.2	* Abaso and Alonso 1992
<i>Anas platyrhynchos</i>	1088.3	1228.0	0.96	1.0	89.3	2.7	2.0	11.6	15.4	3.9	25.5	13.5	This study
<i>Anas crecca</i>	332.1	547.2	0.96	1.0	39.8	1.2	1.5	13.2	3.8	1.0	4.0	2.1	This study Guillemin <i>et al.</i> 2002
<i>Anas clypeata</i>	587.6	807.1	0.96	1.0	58.7	1.8	1.7	12.3	4.7	1.2	6.2	3.3	This study Estimated after Guillemin <i>et al.</i> 2002
<i>Anas acuta</i>	938.8	1110.5	0.96	1.0	80.7	2.4	1.9	11.9	5.6	1.4	8.6	4.6	This study Estimated after Guillemin <i>et al.</i> 2002
<i>Vandellia vanellus</i>	197.5	384.1	1.0	1.0	21.7	0.0	1.9	11.9	5.6	1.4	8.6	4.6	This study
<i>Limosa limosa</i>	303.1	514.2	0.94	1.0	36.6	1.7	1.5	6.2	2.1	0.8	11.6	0.0	This study Santiago-Quesada <i>et al.</i> 2012
<i>Chroicocephalus ridibundus</i>	256.7	459.2	0.5	0.5	13.0	0.0	0.0	5.1	0.0	0.0	5.1	0.0	This study
<i>Gallinago gallinago</i>	101.7	244.4	1.0	1.0	13.8	0.0	0.0	0.0	4.1	0.0	4.1	0.0	This stud
<i>Anser anser</i>	2780.0	2325.9	0.96	1.0	169.1	5.1	2.4	7.1	4.2	1.1	2.4	1.3	* Clausen <i>et al.</i> 2013
<i>Colinus alpinus</i>	48.2	147.0	0.1	0.1	0.8	0.0	0.0	0.2	0.0	0.0	0.2	0.0	This study
<i>Bubulcus ibis</i>	350.0	567.2	0.9	0.9	28.8	0.0	0.0	5.7	0.0	0.0	5.7	0.0	*
<i>Larus fuscus</i>	822.5	1014.8	0.5	0.5	28.7	0.0	0.0	5.4	0.0	0.0	5.4	0.0	This study
<i>Coturnix coturnix</i>	3421.2	2679.0	1.0	1.0	151.3	0.0	0.0	13.3	0.0	0.0	13.3	0.0	*
<i>Gallinula chloropus</i>	255.9	458.2	0.96	1.0	33.3	1.0	1.5	4.2	0.2	0.0	0.0	0.0	This study Acquarone <i>et al.</i> 2001
<i>Platalea apricaria</i>	200.6	388.2	1.0	1.0	21.9	0.0	0.0	0.6	0.0	0.0	0.6	0.0	This study
<i>Phalacrocorax pugnax</i>	153.4	323.4	0.77	1.0	23.0	1.1	1.3	8.1	0.1	0.0	0.0	0.0	This study estimated after Santiago-Quesada <i>et al.</i> 2012
<i>Tringa ochropus</i>	72.4	193.9	0.9	0.9	9.9	0.0	0.0	0.2	0.0	0.0	0.2	0.0	*
<i>Colinus minima</i>	24.8	93.5	0.1	0.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study
<i>Himantopus himantopus</i>	175.0	353.8	0.9	0.9	18.0	0.0	0.0	0.3	0.0	0.0	0.3	0.0	This study
<i>Egretta garzetta</i>	420.8	643.0	0.1	0.1	3.6	0.0	0.0	0.1	0.0	0.0	0.1	0.0	*
<i>Ardea cinerea</i>	1489.7	1520.8	0.1	0.1	8.6	0.0	0.0	0.1	0.0	0.0	0.1	0.0	*
<i>Charadrius dubius</i>	36.6	121.9	0.1	0.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study
<i>Tringa erythropus</i>	146.4	313.3	0.9	0.9	15.9	0.0	0.0	0.1	0.0	0.0	0.1	0.0	This study
<i>Charadrius alexandrinus</i>	39.2	127.7	0.1	0.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study
<i>Charadrius hiaticula</i>	76.0	200.5	0.1	0.1	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study
<i>Tringa totanus</i>	124.2	280.1	0.9	0.9	14.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study
<i>Tringa nebularia</i>	200.0	387.4	0.9	0.9	19.7	0.0	0.0	0.1	0.0	0.0	0.1	0.0	This study
<i>Burhinus oedipinus</i>	493.7	716.9	1.0	1.0	40.5	0.0	0.0	0.1	0.0	0.0	0.1	0.0	**
<i>Recurvirostra amasetta</i>	332.4	547.6	0.9	0.9	27.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study
<i>Actitis hypoleucos</i>	56.9	164.6	1.0	1.0	9.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	This study

*Crump and Simmons 1997, **Gutiérrez *et al.* 2012.



6

Conclusiones generales

1.- Los valores de ^2H en plumas ($\delta^2\text{H}_p$) sugieren que más del 70 % de los ánades rabudos *Anas acuta* invernantes en Extremadura proceden de latitudes superiores a los 55°N . Las áreas de reproducción se localizan principalmente en la península de Fenoscandia y el norte-centro de Rusia hasta, por lo que deben desplazarse entre 2600 y 5600 km hasta Extremadura. Los desplazamientos de individuos equipados con transmisores GPS-GSM confirmaron estos movimientos migratorios de largas distancias.

2.- Existieron diferencias en el origen geográfico de machos y hembras juveniles de ánades rabudos que invernan en Extremadura. Los machos proceden de áreas situadas más al norte que las hembras, de modo que el emparejamiento durante el invierno contribuiría a incrementar la variabilidad genética de la población.

3.- Los valores de ^2H en plumas ($\delta^2\text{H}_p$) indican que más del 70 % de las cercetas comunes *Anas crecca* invernantes en Extremadura provienen de la región biogeográfica localizada entre los 48° y los 60°N . Esta región abarcaría desde el centro de Europa a los montes Urales, por lo que deben viajar entre 1500 y 4500 km hasta llegar a Extremadura. Aunque no existieron diferencias entre ambos sexos, la potencial área geográfica de procedencia de las hembras fue menos amplia que la de los machos.

4.- Los datos proporcionados por ánades rabudos equipados con transmisores GPS-GSM, confirmaron que estos ánades descansan durante el período de luz en los embalses y que utilizan exclusivamente los campos de arroz como áreas de forrajeo, siempre durante la noche.

5.- La distancia máxima que los ánades rabudos se desplazan para forrajear, así como su área de campeo nocturno, aumentaron a medida que la disponibilidad de tablas de arroz inundadas fue menor. Ambas variables también estuvieron relacionadas positivamente con la iluminación procedente de la luna. Estos hallazgos sugieren que los arrozales secos pierden su funcionalidad como áreas de forrajeo para los ánades de superficie, y que la luz de la luna incrementa su actividad exploratoria.

6.- Durante la invernada los ánades rabudos seleccionaron como áreas de forrajeo nocturno tablas de arroz inundadas, con un nivel de agua de entre 9 y 21 cm, con rastrojo y cuyo sustrato contiene grava de menos de 0,5 cm de diámetro. La abundancia de alimento (semillas de arroz) y las variables paisajísticas no fueron predictores significativos de la selección de las áreas de forrajeo por los ánades rabudos.

7.- Dentro de los arrozales utilizados por los ánades de superficie la presencia de tablas de arroz inundadas, con rastrojo y partículas finas en el sustrato debe ser priorizada con el fin de proporcionar áreas de forrajeo favorables a estas especies. Estas prácticas de manejo no afectarían al rendimiento económico ni productivo del cultivo de arroz y podrían ser aplicadas para la conservación de los ánades de superficie en todo el mundo.

8.- Los ánades rabudos invernantes en los arrozales de Extremadura incrementaron significativamente su masa corporal a través del invierno. Este incremento fue del 1,4 % y 6,7 % en machos y hembras, respectivamente, en el periodo pre-migratorio en relación a mediados del invierno. Nuestra estimación del aumento promedio de la masa corporal en la población debería considerarse como una estima conservativa, ya

que parece existir una falta de sincronía en el aumento de la masa corporal, lo que conllevaría una subestima de la ganancia individual de dicha masa corporal.

9.- El patrón de incremento de los niveles plasmáticos de triglicéridos y proteínas fue paralelo al de la ganancia de masa corporal, aunque no estadísticamente significativo. Ello fue probablemente debido al gran período de ayuno transcurrido entre el amanecer y la captura de los individuos, lo cual afectaría negativamente a los niveles de ambos metabolitos.

10.- Los ánades rabudos alcanzaron los mayores valores de masa corporal a finales del invierno, justo antes de abandonar el área de invernada. Las condiciones ambientales benignas de Extremadura en la parte final del invierno podrían haber condicionado este patrón de ganancia de masa corporal, el cual difiere del descrito por la “estrategia de invernada” para ánades de superficie invernantes en el oeste de Europa.

11.- Durante su estancia en los arrozales de Extremadura, las poblaciones de aves acuáticas invernantes consumieron el 26 % del total de semillas disponibles al inicio de la invernada. Los principales consumidores fueron las grullas comunes *Grus grus* y los ánades de superficie. Las aves acuáticas reciclaron más de 24 toneladas de N y 5 toneladas de P durante el invierno. Este aporte de nutrientes supone un beneficio directo para la agricultura con respecto a la fertilización artificial.

12.- Las especies que utilizan los embalses como áreas de descanso aportaron a estos, a través de sus excrementos, 2,3 toneladas de N y 550 kg de P. Este aporte no disminuye la calidad del agua por eutrofización, debido a la gran superficie de los embalses del área de estudio, y al uso estacional de estos por las aves acuáticas.

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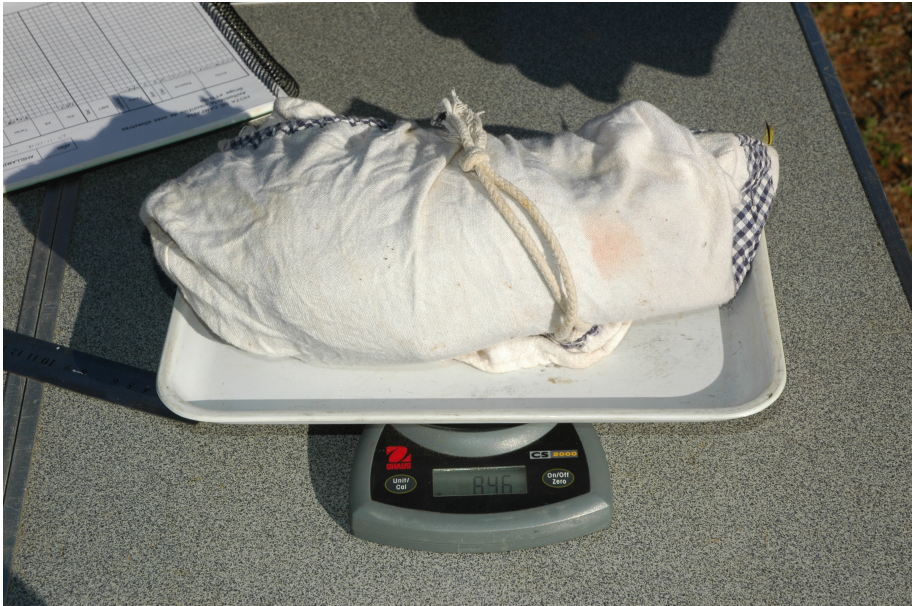
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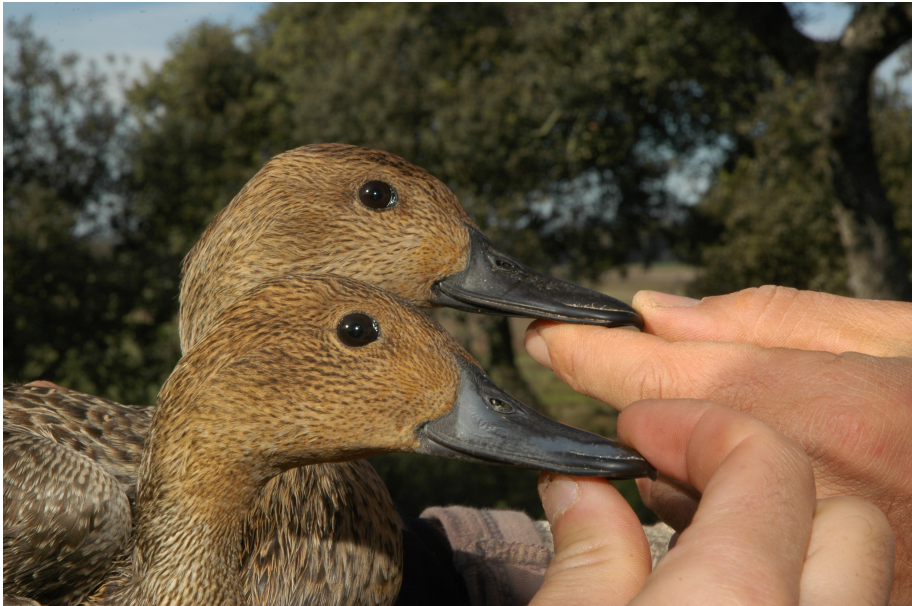






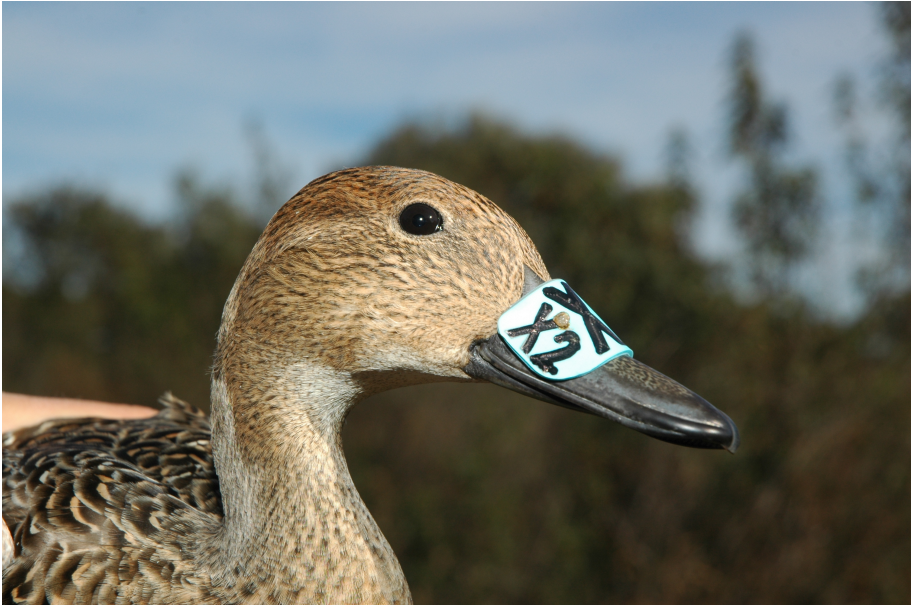














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