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“Aplicaciones de la ecología trófica en la conservación de poblaciones periféricas de Tetraónidas”

“A trophic ecology approach to the conservation of peripheral grouse populations”

TESIS DOCTORAL

Beatriz Blanco Fontao

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A mi familia:

mis padres Julio y Guadalupe,

mis hermanos Carolina y Alfonso

mi tía Gema,

mis güelas Guadalupe y Bernarda

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Resumen

La ecología trófica es un aspecto clave de la habilidad de los animales para sobrevivir, que varía a lo largo de su rango de distribución. Desde el centro hasta los márgenes del área de distribución de una especie, las condiciones bióticas y abióticas varían, determinando diferencias ecológicas notables entre las poblaciones centrales y periféricas de una misma especie. En particular, las poblaciones periféricas se encuentran en los límites de tolerancia de las especies; son susceptibles, por tanto, de presentar notables adaptaciones locales en su relación con el medio, así como distintas interacciones con otras especies. Aquellas especies en que la adquisición de recursos puede constituir un factor limitante, como el caso de aves herbívoras como las tetraónidas, serán especialmente susceptibles a los efectos negativos de la competencia por los recursos tróficos (interacciones competitivas). Esto es debido a que los sistemas digestivos de las tetraónidas se sitúan en el límite inferior de tamaño entre los herbívoros endotermos y, por lo tanto, condicionan la satisfacción de los requerimientos nutricionales. Asimismo, las especies de esta familia de aves de distribución holártica han sufrido declives generalizados en las últimas décadas, siendo más acusados en las poblaciones periféricas situadas en los márgenes meridionales de la distribución.

En este contexto, evaluar aspectos clave de la ecología de las especies como: la selección de dieta y la diferenciación trófica de poblaciones periféricas, las relaciones tróficas con potenciales competidores y la variación trófica dentro de las poblaciones,

es fundamental para asistir la toma de medidas de conservación efectivas que reviertan las tendencias actuales de las poblaciones. Mediante dos aproximaciones metodológicas complementarias, el análisis microhistológico de los excrementos y el análisis de isótopos estables de plumas, uñas y sangre, se evaluaron los patrones de selección de dieta, la variabilidad trófica inter e intrapoblacional, y las relaciones con otros herbívoros. Para ello, utilizamos como modelo dos poblaciones periféricas de tetraónidas, situadas en el límite meridional de la distribución de la familia: el Urogallo Cantábrico (*Tetrao urogallus cantabricus)* y el Gallo de las Praderas Grande (*Tympanuchus cupido*); ambas amenazadas.

En el **Capítulo I**, se abordó la selección de dieta y de hábitat para el Urogallo Cantábrico, así como las peculiaridades tróficas de esta población periférica respecto a poblaciones más centrales. La selección positiva en la dieta del haya (*Fagus sylvatica*), el acebo (*Ilex aquifolium*), el arándano (*Vaccinium myrtillus*) y los helechos, y la negativa de recursos muy abundantes en la Cordillera Cantábrica como los robles albares (*Quercus petraea*), abedules (*Betula pubescens*) y brezos (*Erica* spp.), condicionó la selección de hábitat a pequeña escala. La importancia del arándano tanto en la selección de dieta como de hábitat resultó ser una característica común entre poblaciones centrales, del Norte de Europa y Rusia, y periféricas de Urogallo. Por el contrario, el Urogallo Cantábrico mostró una acusada diferenciación ecológica relacionada con la mayor dependencia trófica de esta subespecie de recursos del sotobosque que del dosel arbóreo, así como con presentar, a nivel de población, un carácter más generalista (es decir, esta población utilizó una mayor variedad de recursos en la dieta).

En el **Capítulo II** se evalúo si el marcado dimorfismo sexual del Urogallo está asociado con una diferenciación trófica entre sexos. También se analizó la fidelidad a los sitios de muda y su relación con la selección de un tipo de bosque concreto. Para ello se analizaron los ratios de $\delta^{13}C$ y $\delta^{15}N$ en plumas mudadas de la población cantábrica de urogallos. Se encontraron diferencias en los valores isotópicos medios tanto entre machos y hembras cómo entre plumas recogidas en robledales, hayedos y abedulares, indicando que los urogallos seleccionan con una alta fidelidad determinados tipos de bosque durante el periodo de muda. Además, los resultados indican que las hembras ocupan un nicho trófico más amplio, basado en una mayor variabilidad trófica individual. Los patrones encontrados apoyan una segregación sexual en la época de muda, asociada con el uso de las hembras del límite del bosque, a priori con mayor diversidad de microhábitats.

En el **Capítulo III** se evalúo el potencial competitivo entre herbívoros forestales alejados filogenéticamente. En concreto, se abordó la superposición trófica del Urogallo con ciervos (*Cervus elaphus*), corzos (*Capreolus capreolus*) y vacas (*Bos taurus*) en la Cordillera Cantábrica. Asimismo, se relacionaron las abundancias relativas de ungulados con la herbivoría sobre el arándano, a priori un recurso importante para los grandes herbívoros del bosque cantábrico. Se encontró que el arándano fue efectivamente un recurso trófico importante para todas las especies, y especialmente para el Urogallo. El porcentaje de brotes de arándano dañados estuvo relacionado positivamente con las densidades de grandes herbívoros. Los ungulados y el Urogallo mostraron una elevada superposición en la dieta, pero esta superposición fue asimétrica. Es decir, el nicho trófico más especializado del Urogallo estuvo contenido dentro del más generalista de los ungulados, y por lo tanto, la superposición del nicho del Urogallo en el de los ungulados fue prácticamente total, pero no *viceversa*. Además, en el área en el que la presión de herbivoría fue mayor, y por tanto también la competencia potencial, la superposición trófica entre ungulados y urogallos fue menor, el nicho trófico del Urogallo fue más amplio, y su dependencia del arándano, menor. Todo lo anterior sugiere un desplazamiento del nicho del Urogallo cuando la presión competitiva es alta. Por lo tanto, los patrones de superposición trófica, así como la diferente dependencia del arándano, sugieren que el Urogallo es más susceptible de sufrir las consecuencias negativas de un incremento en la intensidad de la competencia interespecífica, derivadas del sobrepastoreo.

El **Capítulo IV** complementa al capítulo III ya que está dirigido a evaluar la evolución de las densidades de la cabaña ganadera bovina en régimen extensivo en la Cordillera Cantábrica (especie que representa la mayoría de la biomasa de ungulados en este sistema), y su posible relación con el declive de la ocupación de los leks de Urogallo. Las densidades de ganado bovino aumentaron en este sistema montañoso en los últimos 20 años y estuvieron relacionadas negativamente con la presencia del Urogallo, *especie paraguas* o *bioindicadora* de la diversidad de aves forestales y funcionamiento del ecosistema en bosques de montaña. Por lo tanto, nuestros resultados no apoyan ni la disminución generalizada y ampliamente aceptada de las densidades ganaderas en los sistemas montañosos europeos, ni el supuesto papel beneficioso del ganado en régimen extensivo en la conservación de la biodiversidad. Se cuestiona, por tanto, la política conservacionista de la Red Natura 2000 que centra su preocupación en los supuestos efectos negativos del abandono de los usos tradicionales; el pensamiento tipológico en la relación entre los cambios socio-económicos y la conservación de la biodiversidad debe ser reemplazado por datos rigurosos y por la consideración de la naturalidad de los ecosistemas.

El último capítulo (**Capítulo V)** está dirigido a evaluar los patrones de variación trófica intrapoblacional, centrándose en la variación sexual y en la especialización individual a lo largo del ciclo anual. El trabajo se desarrolla sobre dos poblaciones de Gallo de las Praderas Grande que ocupan distintos paisajes: praderas nativas poco fragmentadas, y mosaicos de tierras agrícolas y parches remanentes del hábitat original. Con este objetivo, se analizó el ratio de isótopos estables ($\delta^{13}C$ y $\delta^{15}N$) en tres tejidos (plumas, sangre y uñas) que integran información trófica de diferentes periodos del ciclo anual. Tanto las hembras como las poblaciones en praderas nativas poco fragmentadas mostraron nichos tróficos más amplios basados en una mayor variabilidad individual en otoño y en invierno. Sin embargo, las diferencias sexuales se diluyeron en primavera, periodo en el que la convergencia de machos y hembras en los leks determina comportamientos tróficos similares. La mayor diversidad de estrategias tróficas encontradas en paisajes continuos, poco fragmentados refleja la mayor diversidad específica y estructural de los hábitats nativos, frente a los mosaicos de campos agrícolas y remanentes del hábitat original.

A modo de síntesis, las poblaciones de Urogallo Cantábrico y de Gallo de las Praderas Grande en el límite meridional de la distribución de la familia Tetraonidae mostraron una marcada diferenciación trófica, relacionada, en el caso de los primeros, con su carácter periférico (**Capítulo I**), y con los cambios en la composición del hábitat en los segundos (**Capítulo V**). Esta diferenciación trófica en el Urogallo Cantábrico, mediada por una elevada dependencia de los recursos del sotobosque, parece estar relacionada con una mayor susceptibilidad a los efectos negativos de un incremento en la intensidad competitiva con los grandes mamíferos herbívoros (**Capítulo III y IV**). Asimismo, en un nivel de estudio inferior, dentro de las poblaciones, machos y hembras, e incluso individuos dentro de las poblaciones, presentaron variabilidad trófica a pesar de que el grado de dimorfismo sexual en el tamaño de las especies de estudio es notablemente diferente (**Capítulos II y V**)

Como aportaciones principales de esta Tesis Doctoral se evaluaron las hipótesis de (i) la diferenciación trófica de poblaciones periféricas, (ii) el dimorfismo sexual en la variabilidad trófica y (iii) la superposición trófica entre especies alejadas filogenéticamente. Asimismo la utilización del análisis de isótopos estables para la medida del nicho trófico en herbívoros constituye una aproximación metodológica novedosa que permite o facilita la evaluación de la partición de hábitat entre sexos y de la variación trófica individual en especies poco abundantes y amenazadas. De forma complementaria y como aplicación a la conservación, nuestros resultados ponen en relevancia la necesidad de estrategias de conservación específicas, que tengan en

cuenta las características locales de las poblaciones a conservar, así como las de los diferentes segmentos de la población (ej. machos y hembras) para que éstas sean efectivas.

Introducción general

El rango de distribución de las especies: ¿Son todas las poblaciones ecológicamente equivalentes?

El nicho ecológico de una especie (*sensu* Hutchinson 1957) puede variar sustancialmente a lo largo de su rango de distribución, especialmente cuando éste es amplio, dando lugar a diferentes nichos efectivos en cuanto a las características demográficas y ecológicas de las distintas poblaciones locales (Chase y Leibold 2003; Gaston 2003; Guo el al. 2005). Es decir, las diferentes poblaciones responden a las condiciones locales mostrando una variabilidad ecológica a lo largo del área de distribución de la especie. Esta variabilidad desvía a las diferentes poblaciones de la descripción tipológica de la ecología de la especie; las poblaciones no deberían, por tanto, ser tratadas como ecológicamente equivalentes.

Quizá el ejemplo más claro de diferenciación entre poblaciones de la misma especie lo constituyen los márgenes de la distribución de la misma; es esperable que las poblaciones periféricas interaccionen con el medio abiótico y biótico de diferente manera que las que ocupan el centro del área de distribución (Chase y Leibold 2003). Entre las poblaciones periféricas, las que ocupan la "retaguardia" del área de distribución de la especie (*sensu* Hampe y Petit 2005), además de diferir en aspectos ecológicos, etológicos y demográficos de otras poblaciones, son desproporcionadamente importantes para la supervivencia y la evolución de las especies (Lesica y Allendorf 1995; Hampe y Petit 2005).

Por otro lado, la fragmentación está relacionada con los cambios en la composición del paisaje, procesos ambos que varían localmente a lo largo del rango de distribución de una especie y que ejercen una importante influencia en numerosos aspectos ecológicos (Turner 1989; Pulliam et al. 1992). Una de las causas principales de cambio en la composición del paisaje a nivel global es la conversión del hábitat nativo en cultivos agrícolas (Saunders et al. 1991). Como consecuencia, el paisaje original se transforma en un mosaico de tierras agrícolas y parches de hábitat nativo (Primack y Ralls 1995; Laurence 2010). Estos cambios en el paisaje modifican la dinámica de los ecosistemas (p. ej. Herkert 1994; Terborgh et al. 2001) incluyendo, entre otros, cambios en la ecología trófica de las poblaciones como respuesta a variaciones en la disponibilidad de recursos tróficos (p. ej. Layman et al. 2007b; Abbas et al. 2011).

Variabilidad dentro de poblaciones ¿Son todos los individuos ecológicamente equivalentes?

Las adaptaciones locales de las poblaciones son básicas en ecología. Sin embargo, la variabilidad intrapoblacional entre segmentos (sexos, clases de edad) o entre individuos dentro de una población es una importante fuente de variación, mucho menos estudiada (Bolnick et al. 2003). En aspectos como la selección de dieta, una elevada variabilidad intrapoblacional representa la especialización de individuos o segmentos de la población en uno u otro recurso dependiendo de las diferencias individuales en el uso del hábitat o en las estrategias tróficas (Durell 2000; Catry et al. 2005; Bearhop et al. 2006).

Los machos y las hembras son segmentos de la población, susceptibles de estar sometidos a diferentes limitaciones ecológicas. En concreto, las diferencias sexuales en los requerimientos energéticos y/o tasas de ingesta (Isaac 2005; Bulte et al. 2008) resultan en una diferenciación trófica entre sexos (p. ej. Mysterud 2000; Bolnick et al. 2003; Ruckstuhl 2007). Esta diferenciación conlleva segregación sexual en el uso del hábitat, al menos en algunos momentos del ciclo anual. Específicamente, en especies dimórficas en cuanto al tamaño, el grado de dimorfismo sexual está positivamente relacionado con la segregación de nicho entre sexos (Mysterud 2000; Phillips et al. 2009).

Tanto la variación intrapoblacional relacionada con determinados segmentos de la población como la interindividual *per se*, deberían tenerse en cuenta en la toma de decisiones de gestión; en caso contrario, el diseño de medidas de gestión encaminadas a la protección de valores promedio de una población podría excluir a una parte importante de la misma.

Interacciones interespecíficas en el límite de distribución ¿Competencia entre especies alejadas filogenéticamente?

Las interacciones interespecíficas, como la competencia, ganan importancia relativa como factores limitantes a medida que nos acercamos a los límites de distribución de una especie (Grant y Antonovics 1978; Guo et al. 2005); y pueden modificar la viabilidad de una especie amenazada, provocando incluso su declive o desaparición de un hábitat aparentemente adecuado.

La abundancia y los rangos de distribución de ungulados silvestres y domésticos han aumentado en el Hemisferio Norte en las últimas décadas (Gill 1990; Putman 1994; Trimble y Mendel 1995). Este incremento lleva asociados efectos negativos sobre los productores primarios extensibles al resto de la red trófica (Weisberg y Bugmann 2003; Côté et al 2004; Allombert et al 2005a; Allombert et al 2005b). Por ejemplo, el sobrepastoreo - consecuencia de densidades elevadas de ungulados - podría modificar el resultado de las interacciones competitivas con otros herbívoros (Latham 1999; Dolman y Waber 2008). La evaluación de estas interacciones competitivas entre ungulados simpátricos ha sido el objeto de numerosos estudios (revisado en Latham 1999). Sin embargo, pocos han intentado cuantificar la intensidad de esta interacción entre especies que no estén tan estrechamente relacionadas filogenéticamente; en cuyo caso, un efecto asimétrico es esperable (Schoener 1983; Aikio 2004; Abrams et al.

2008). Es decir, la susceptibilidad de las especies implicadas respecto a los efectos negativos de la competencia no es equivalente (p.ej. Weiner 1990).

¿Cómo evaluar la variabilidad y las interacciones? Ecología trófica en herbívoros

La ecología trófica de las poblaciones es un aspecto clave de la habilidad de los animales para enfrentarse a su medio, y es fundamental para entender los requerimientos ecológicos de una especie (Sutherland 2000; Sutherland 2004). Por ello, constituye una aproximación apropiada para evaluar la divergencia de poblaciones periféricas respecto a las tendencias ecológicas y etológicas centrales; permite además evaluar respuestas ante cambios en la composición del hábitat, la variación entre sexos e individuos o el potencial competitivo en poblaciones en el límite de distribución. Esto es especialmente cierto en el caso de aves herbívoras, ya que debido a sus bajas tasas de ingesta y pequeños tractos digestivos en el marco de los herbívoros endotermos, necesitan dedicar mucho tiempo a la adquisición de recursos tróficos (Sedinger 1997; Van Gils et al. 2007).

El estudio de la ecología trófica de animales salvajes se puede llevar a cabo de forma directa controlando individuos (p. ej. mediante radio-seguimiento), o bien indirectamente, utilizando marcadores biológicos o biogeoquímicos intrínsecos (Rubenstein y Hobson 2004). Los métodos indirectos pueden permitir un muestreo menos invasivo, especialmente relevante en el caso de poblaciones amenazadas, con comportamientos esquivos o que vivan en hábitats poco accesibles (Figura 1). Entre los métodos poco invasivos, el análisis microhistológico de los excrementos y el análisis de isótopos estables de carbono y nitrógeno en tejidos inertes (Peterson y Fry 1987), constituyen dos aproximaciones complementarias que nos proporcionan información trófica a lo largo de diferentes intervalos temporales.

El análisis microhistológico de excrementos de herbívoros se basa en la resistencia de la epidermis de las plantas a la digestión, permitiendo identificar el recurso ingerido a partir de los fragmentos presentes en las heces (Holechek 1982; Alipayo et al. 1992; Figura 1). Esta técnica utilizada con frecuencia en el estudio de la selección de dieta de aves herbívoras (Owen 1975; Madsen y Mortensen 1987), proporciona una alta resolución y muestra una "foto estática" de la dieta referida a un único evento de alimentación (Holechek 1982).

Los isótopos estables se utilizan como marcadores intrínsecos en ecología trófica porque proporcionan una visión de las interacciones basada en los flujos de energía y recursos (Peterson y Fry 1987); su análisis en tejidos animales se ha mostrado como una aproximación muy potente en el estudio de la ecología trófica de las especies, poblaciones o individuos (West et al. 2006). Concretamente, la combinación de $\delta^{13}C$ y $\delta^{15}N$ junto con la aplicación de técnicas cuantitativas de ecomorfología a los valores de estos dos isótopos (p. ej. Layman et al. 2007a), permite evaluar aspectos como la variabilidad trófica intrapoblacional; es decir diferencias en la amplitud de nicho entre segmentos poblacionales y grado de especialización individual. Asimismo, y en contraposición al análisis microhistológico de los excrementos, esta técnica proporciona una medida de la dieta asimilada durante el periodo de la síntesis del tejido analizado (Hobson y Clark 1992; Bearhop et al. 2002), integrando información de la dieta a lo largo de periodos temporales más largos (West et al. 2006; Inger y Bearhop 2008). Por ejemplo, tejidos inertes como las plumas y las uñas de las aves almacenan de forma permanente la señal de los isótopos estables correspondiente al periodo de síntesis del tejido, es decir el periodo de muda en las plumas y el periodo de formación de la uñas (Hobson y Clark 1992; Bearhop et al. 2002; Bearhop et al. 2003). En cambio, tejidos activos con tasas de recambio rápidas como la sangre, integrarían un periodo máximo de dos meses previo al muestreo (Carleton y Martínez del Rio 2005).

Figura 1: Excrementos (A) y pluma de hembra de Urogallo Cantábrico (B). Epidermis de tallos de arándano (C) y de hojas de gramíneas (D) encontrados en excrementos de Urogallo y analizados mediante microhistología.

Tetraónidas periféricas y sus hábitats: Especies y áreas de estudio

Las tetraónidas son una familia de aves de distribución holártica que ocupan desde ecosistemas subárticos como la tundra y la taiga, hasta templados como los bosques montanos holárticos y las praderas americanas (Johnsgard 1983; del Hoyo et al. 1994). Todos estos hábitats presentan una marcada estacionalidad para la que las tetraónidas poseen adaptaciones morfológicas, fisiológicas y etológicas (Johnsgard 1983; del Hoyo et al. 1994; Watson y Moss 2008). Una de las adaptaciones más notables es el comportamiento trófico de unas aves mayoritariamente herbívoras que adoptan dietas extremadamente monótonas en épocas invernales - basadas en una o unas pocas especies disponibles - y más variadas cuando la desaparición de la nieve permite el acceso a los recursos del sotobosque (del Hoyo et al. 1994).

En esta Tesis Doctoral se utilizaron dos poblaciones modelo de tetraónidas que se distribuyen en dos ecosistemas muy diferentes estructuralmente, pero con la característica común de que ambas se sitúan en el límite sur de distribución de la familia: el Urogallo Cantábrico (*Tetrao urogallus cantabricus)* que ocupa los bosques montanos caducifolios de la Cordillera Cantábrica, y la población de Gallo de las Praderas Grande (*Tympanuchus cupido*) del estado de Kansas (EE.UU.), cuyo hábitat original corresponde a las praderas de hierba alta (*tallgrass prairies;* Figura 2).

El Urogallo (*Tetrao urogallus*) en la Cordillera Cantábrica constituye una subespecie endémica situada en el límite suroccidental de la distribución de la especie (Castroviejo 1975; Figura 2). En contraste con la mayoría de las poblaciones de Urogallo que viven en bosques de coníferas (Storch 2007), la población Cantábrica es la única que habita en bosques caducifolios a lo largo de todo el ciclo anual, lo que sugiere diferenciación ecológica y etológica. Tal diferenciación forma parte de la consideración del Urogallo Cantábrico como Unidad Evolutiva Significativa, parte de un linaje meridional de la especie (Duriez et al. 2006; Rodríguez-Muñoz et al. 2007). Por otra parte, en la población cantábrica, machos y hembras presentan diferencias en el uso del hábitat, posiblemente relacionadas con el marcado dimorfismo sexual y la diferente implicación en la cría propios de la especie (Bañuelos et al. 2008); ese dimorfismo sexual podría también reflejarse en la dieta.

Figura 2: Área de distribución de la familia Tetraonidae (gris claro), del Urogallo (gris oscuro) y del Gallo de las Praderas Grande (gris medio) según del Hoyo et al. (1994). Las poblaciones de estudio están señaladas con flechas.

El Urogallo Cantábrico está amenazado y ha experimentado un declive muy pronunciado desde hace al menos tres décadas, quedando en la actualidad restringido a un área de ocupación de unos 1700 Km^2 (Storch et al. 2006). En los últimos años se ha realizado un esfuerzo por definir los factores que han llevado a la población al borde de la extinción (p. ej. Obeso y Bañuelos 2003; Quevedo et al. 2006a; Quevedo et al. 2006b; Bañuelos et al. enviado). No obstante, existen muchas lagunas tanto en el conocimiento de la ecología de esta subespecie como de las razones de su declive. Esta Tesis Doctoral pretende responder a algunas de estas cuestiones básicas de la ecología del Urogallo Cantábrico como: ¿Qué recursos son importantes en la dieta de la población?, ¿Existe diferenciación trófica entre machos y hembras? ó ¿Cómo interacciona el Urogallo con otros grandes herbívoros por los recursos tróficos?

Por otro lado, el Gallo de las Praderas Grande (*Tympanuchus cupido*) es una especie nativa de las praderas neárticas. Con anterioridad a la llegada de los europeos, la especie se distribuía ampliamente por todas las praderas de hierba alta de Norte América (Schroeder y Robb 1993). Sin embargo, las transformaciones agrícolas a gran escala desde comienzos del siglo XX, han fragmentado y modificado la composición original de su hábitat, restringiendo su distribución a aproximadamente el 20 % de su rango histórico, y provocando declives en torno al 50% en los últimos 40 años (Schroeder y Robb 1993; Svedarsky et al. 2000). En la actualidad, algunos de los núcleos poblacionales más importantes se encuentran en los Flint y Smoky Hills (estado de Kansas), en el límite sur de distribución de las tetraónidas (Schroeder y Robb 1993; Figura 2), ocupando tanto paisajes de praderas nativas poco fragmentadas como mosaicos de cultivos y praderas nativas. Las poblaciones responden a la composición de su hábitat (praderas nativas *vs* mosaico agrícola) mostrando diferencias en sus parámetros demográficos y genéticos (Gregory 2011; McNew 2011); es decir, las poblaciones en praderas nativas muestran una supervivencia anual más alta y una fecundidad más baja que las poblaciones en mosaicos agrícolas (McNew 2011); además, los mosaicos agrícolas son menos permeables a los movimientos que las praderas nativas, limitando la dispersión de los individuos (Gregory 2011). Teniendo en cuenta la variación anterior, también es probable que las diferencias en la composición del hábitat se vean reflejadas en una diferenciación trófica de las poblaciones (diferencias en los valores promedio, preferencias o variabilidad de la dieta entre las poblaciones; Johnson et al. 1992), ya que la composición del hábitat determina la disponibilidad de recursos tróficos para un ave que se alimenta principalmente de hojas, yemas y de semillas, tanto de especies nativas de las praderas, como de especies cultivadas (Yeatter 1943; Mohler 1952; Korschgen 1962; Jones 1963; Rumble et al. 1988).

En otro orden de cosas y al igual que el Urogallo, el Gallo de las Praderas Grande presenta un sistema de emparejamiento tipo lek en el que los machos no participan en el cuidado y alimentación de los pollos (del Hoyo et al. 1994). Sin embargo, al contrario que el Urogallo, esta especie presenta un dimorfismo sexual moderado; los machos sólo son un 17% más pesados que las hembras (Schroeder y Robb 1993). Por un lado y de acuerdo con el escaso dimorfismo sexual en el tamaño, no es esperable encontrar partición de recursos - dieta y hábitat - entre machos y hembras; sin embargo, por otro lado, la marcada diferencia en el cuidado parental sugiere una partición de nicho entre sexos. Por último, resaltar que esta población constituye una población modelo adecuada para evaluar tanto la diferenciación sexual en el comportamiento trófico, como la respuesta trófica a la fragmentación del hábitat en tetraónidas periféricas. A pesar de haber sufrido declives importantes en las últimas décadas, las densidades de esta población son todavía elevadas (Svedarsky et al. 2000). Esto permite su captura y el muestreo de plumas, uñas y sangre para análisis isotópicos, y así obtener información trófica individualizada de diferentes periodos del ciclo anual.

Objetivos de la Tesis Doctoral y estructura en capítulos

Los objetivos generales de la presente Tesis Doctoral son cuantificar la variabilidad inter e intrapoblacional y el potencial competitivo en poblaciones periféricas y amenazadas de tetraónidas. Para ello, nos centramos en un aspecto clave y que puede ser limitante de la ecología de aves herbívoras: la adquisición de recursos tróficos (Sedinger 1997; Van Gils et al. 2007). Por lo tanto, la ecología trófica proporciona una aproximación adecuada para la evaluación de toda esta variabilidad; siendo además, fundamental en la biología de la conservación de estas especies.

Las diferentes facetas de esta Tesis Doctoral se abordan en los siguientes capítulos, cada uno de ellos con unos objetivos específicos:

Capítulo I. Objetivo: Evaluar la diferenciación trófica de la población de Urogallo Cantábrico respecto a poblaciones situadas en zonas centrales del rango de distribución. Para alcanzar este objetivo se utilizó el análisis microhistológico de los excrementos y se evaluaron la selección de dieta y su papel en la selección de hábitat a pequeña escala, la amplitud de nicho trófico y la especialización de los eventos de alimentación en la población cantábrica. Por último, estos resultados se compararon con los datos de otras poblaciones.

Capítulo II. Objetivos: Determinar el grado de diferenciación entre sexos en el comportamiento trófico de la población cantábrica de Urogallo, así cómo analizar si la fidelidad individual a los sitios de muda está relacionada con la selección de un tipo de bosque concreto. Para tal fin se caracterizó el nicho trófico de machos y hembras en los diferentes hábitats forestales a partir de los valores de $\delta^{13}C$ y $\delta^{15}N$ en plumas mudadas de machos y hembras de Urogallo.

Capítulo III. Objetivo: Determinar el potencial competitivo asimétrico entre urogallos y ciervos, corzos y vacas, especies muy alejadas filogenéticamente. Asimismo se evalúa el impacto producido sobre el arándano, una especie a priori importante para los grandes herbívoros cantábricos y clave para el Urogallo, por los ungulados, dependiendo de la densidad de estos últimos. Las dietas anuales de las especies de estudio se determinaron mediante análisis microhistológico de grupos fecales en dos zonas adyacentes que diferían en la carga de grandes herbívoros. A partir de esto se valora el efecto de la densidad de ungulados sobre el arándano y sobre el nicho trófico del Urogallo Cantábrico.

Capítulo IV. Objetivo: Discutir el supuesto papel de los usos tradicionales (ganadería extensiva en ecosistemas de montaña) en la conservación de la biodiversidad. Para ello se analizó la evolución de la cabaña ganadera bovina en régimen extensivo en la Cordillera Cantábrica (como especie que representa la mayoría de la biomasa de ungulados en este sistema; Rodríguez et al. 2007) en los últimos 20 años y su relación con el declive de la ocupación de los leks de Urogallo.

Capítulo V. Objetivo: Valorar si machos y hembras de Gallo Grande de las Praderas presentan diferentes comportamientos tróficos y determinar la amplitud de nicho trófico y el grado de especialización individual de dos poblaciones que difieren en la fragmentación y composición del hábitat (praderas nativas de hierba alta *vs* mosaicos de cultivos y pradera). Para esto se utilizó el análisis de isótopos estables ($\delta^{13}C$ y $\delta^{15}N$) en diferentes tejidos (plumas, sangre y uñas) que integran información de la dieta a lo largo de diferentes periodos del ciclo anual.

Los resultados obtenidos en este trabajo permitirán una mejor comprensión de los patrones de variabilidad tanto interespecífica a lo largo de los rangos de distribución, como intrapoblacional, y de las potenciales relaciones competitivas asimétricas entre especies alejadas filogenéticamente. Las dos poblaciones de estudio se encuentran amenazadas (Storch 2007) y en el límite sur de distribución de una familia holártica (del Hoyo et al. 1994) en el contexto de cambio global actual. Los conocimientos derivados de esta Tesis Doctoral serán de gran valor a la hora de elaborar planes de conservación y/o recuperación que puedan revertir las tendencias actuales de estas poblaciones.

Capítulo I

Diet and habitat selection in Cantabrian Capercaillie: ecological differentiation of a rear-edge population

Beatriz Blanco-Fontao[1], Alberto Fernández-Gil[2], José Ramón Obeso[1], Mario Quevedo[1]

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[1] *Unidad Mixta de Investigación en Biodiversidad (CSIC/UO/PA), Dpto. de Biología de Organismos y Sistemas, Área de Ecología, Universidad de Oviedo*

[2] *Dpto. de Biología de la Conservación. Estación Biológica de Doñana (CSIC)*

Abstract. Cantabrian Capercaillie *Tetrao urogallus cantabricus* is a peripheral population with distinctive phenotypic, biogeographic and genetic characteristics. Hence, the population may also show substantial ecological differentiation associated with its habitat in purely deciduous forests. We assessed seasonal diet selection, small scale habitat selection, and patterns of trophic niche width in Cantabrian Capercaillie over two years. Diet was found to be a driver of small-scale habitat selection, a result consistent with previous studies of stand-scale habitat selection. Diet and habitat selection showed the importance of beech *Fagus sylvatica*, holly *Ilex aquifolium,* bilberry *Vaccinium myrtillus* and ferns in Cantabrian Capercaillie's resource selection. Conversely, the abundant oaks *Quercus petraea*, birches *Betula pubescens* and heaths *Erica* spp. were used below their availability. The reliance on bilberry appears as a unifying characteristic between central and peripheral Capercaillie populations. Cantabrian Capercaillie showed stronger reliance on understory resources than range-central populations. It also showed wider trophic niche and higher specialization of feeding events. Trophic niche patterns and reliance on ground resources indicated a marked ecological differentiation, which stresses the need of local data and specific conservation actions.

INTRODUCTION

The ecological niche of a species (*sensu* Hutchinson 1957) can be quite variable across distribution ranges, leading to different realized niches and variability in the demographic and behavioral characteristics of local populations (e.g. Chase and Leibold 2003). Peripheral populations, closer to the limits of tolerance of a species, are embedded in a set of community interactions that differs, both in quality and strength, from that at the central parts of their species range (Gaston 2003). In this regard, conservation measures based on information from the central part of a species' range may be of limited use, or even counterproductive, at the edges of the range (Hampe and Petit 2005).

Not only can the realized niche of a species vary among populations across geographic ranges - intrapopulation variability in features such as diet and habitat selection is another potentially important source of variation (Smith and Skulanson 1996; Bolnick et al. 2003). Conservation plans that protect an average population trait (for instance, a folivorous bird species said to obtain 60% of its diet from trees) might fail when a population is built up of substantially different sex, age-class or individual components (Durell 2000; Bolnick et al. 2003). That said, both the conservation consequences of variation within populations and the ecological characteristics of populations at the rear edge of distribution have been understudied (Durell 2000; Bolnick et al. 2003; Hampe and Petit 2005).

Capercaillie, *Tetrao urogallus* (Tetraonidae), in the Cantabrian Mountains of NW Spain is an endemic, rear edge population that lives at the southwestern edge of the species' range (Castroviejo 1975), and occupies a particularly southerly location within Palearctic grouse distribution (Storch 2007). Cantabrian Capercaillie *Tetrao urogallus cantabricus* lives in purely deciduous forest in contrast to the vast majority of

Capercaillie populations that inhabit coniferous forests (Storch 2007). Hence, the population may be expected to show marked ecological and behavioral differentiation related to its distinct habitat. Although the population is known to be an Evolutionary Significant Unit and may be part of a distinct southern Capercaillie lineage (Duriez et al. 2006; Rodríguez-Muñoz et al. 2007), its potential ecological peculiarities remain largely unknown (e.g. Storch 2007). Unfortunately, the population has been declining sharply at least in the last three decades, and hence is also unique in terms of conservation status (Storch et al. 2006).

The trophic ecology of a population may provide an appropriate evaluation of divergence from central ecological and behavioral trends because resource selection is a key aspect of the ability of animals to cope with their environment. This is especially true in the case of herbivorous birds, which need to devote much time to foraging, because of their low intake rate and relatively small gut (Sedinger 1997; van Gils et al. 2007). Grouse specialize on different food resources depending on local conditions, although usually only a few plant species are important throughout the entire range (Sedinger 1997). Capercaillie are mostly folivores; however, diet and habitat selection probably vary substantially from the well-known habitat in boreal forests to the purely deciduous Atlantic montane forests. Bilberry may be a major exception to such differentiation (Storch 1993; Quevedo et al. 2006b). Hence, diet selection could be an important mechanism to explain patterns of habitat selection in birds like Capercaillie on the scale of individual daily ranges.

Another biogeographic peculiarity is that Capercaillie is the only extant grouse species in the Cantabrian Mountains; hence it does not compete for resources with any closely related species. Furthermore, in winter and early spring, deciduous forests lack the permanent food and shelter supplied by the needles of coniferous forests, which could be a key environmental constraint driving ecological differentiation. These peculiarities lead us to expect higher diversification in the diet of Cantabrian

Capercaillie and wider trophic niche than in conifer-dwelling populations. Previous studies have indeed shown that the diet of Cantabrian Capercaillie might be varied (Castroviejo 1975; Martínez 1993; Rodríguez and Obeso 2000). However, these studies were based on opportunistic sampling schemes, and did not address diet selection. Nonetheless, they have provided several hypotheses along the interface of diet and habitat selection for further investigation. For instance, the widely assumed importance of holly *Ilex aquifolium* for Cantabrian Capercaillie (Castroviejo 1975) or the paradoxical minor importance in the diet of sessile oak *Quercus petraea* (Martínez 1993; Rodríguez and Obeso 2000), a canopy species that dominates large forest patches with Capercaillie presence in the Cantabrian Mountains (Quevedo et al. 2006b).

In this study, we evaluated year-round diet selection, small-scale (daily-range) habitat selection and trophic niche width in an area of presumed good habitat quality for Cantabrian Capercaillie (Quevedo et al. 2006a). Our specific objectives were to assess the potential relationship between diet and small-scale habitat selection in the population, and to see how this related to previous stand-scale studies (Quevedo et al. 2006b). We also evaluated the extent of diet-related ecological differentiation of this peripheral population compared with other range-central Capercaillie populations.

METHODS

Study area and survey design

The fieldwork was conducted over a 10-km^2 tract of forested habitat on the northern slope of the western Cantabrian Mountains (NW Spain), centered at 42.94º N – 6.48ºW, between August 2002 and April 2004. Altitude in the study area ranges from 900 to 1900 m a.s.l., and the average slope is 21%, resulting in a rugged landscape. Siliceous soils are the substrate of a mixed forest mostly composed of mountain birch *Betula pubescens* (39%), sessile oak *Quercus petraea* (30%), and beech *Fagus sylvatica* (14%). Isolated trees or small groups of holly *Ilex aquifolium* and rowan *Sorbus aucuparia* also occur scattered through the forest. The treeline lies at about 1600 m a.s.l., and is a fine-grained mixture of birch thicket, tree heaths *Erica arborea*, common heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus*, broom formations (*Genista florida, Cytisus scoparius*), grazing meadows, and talus.

The study area held at least three display areas occupied in 2001. Previous observations by forest rangers and the authors showed that the area included also Capercaillie brooding, moulting and wintering areas. The study area was also chosen because of its relatively stable lek occupancy compared to the overall population (M. Quevedo unpubl. data), its overall habitat quality for Capercaillie in a previous model (habitat suitability values > 0.60, Quevedo et al. 2006a), and the negligible presence of domestic ungulates (cattle and horses).

Sampling units were 10 plots of 1 km^2 each, based on the UTM grid, which covered the complete surface of the study area. All plots were surveyed bimonthly, from August 2002 to April 2004. The same observer surveyed all the plots, devoting a sampling effort of three hours per plot and zigzagging within its boundaries. Signs of Capercaillie presence, such as direct sightings, fresh droppings, feathers, and footprints, were used to determine habitat use by recording vegetation composition and cover (to the nearest 5%). These variables were visually estimated for both canopy and understory within a circle of 25 m radius (2000 m^2) centered on the sign of Capercaillie presence. The minimum distance to consider signs as independent samples was 50 m. All signs were collected (droppings, feathers) or erased (footprints) in each survey to ensure that they were recorded only once. Droppings were stored for posterior diet analysis. Additionally, to collect identical information on resource and habitat availability, control spots were selected randomly by taking one every 30 min of survey in each of the ten sampling plots.

Diet analyses

We used microhistological methods to identify plant remains in the droppings of Capercaillie; these were then compared to reference material in a library. Although these methods may lead to some bias (reviewed in Holechek et al. 1982), they are non-intrusive, thus allowing study of diet in secretive and endangered populations (Holechek et al. 1982). Moreover, fecal analysis has been widely and successfully applied in the study of diet selection in herbivorous birds (e.g. Owen 1975; Madsen and Mortensen 1987; Prop and Deerenberg 1991). The technique relies on the resistance of plant epidermis to herbivore digestion, which leaves plant fragments undigested and identifiable in the droppings (Holechek 1982; Alipayo et al. 1992). The reference material was prepared from 28 potential food sources, determined from previous studies of Capercaillie diet in the Cantabrian Mountains (Castroviejo 1975; Martínez 1993; Rodríguez and Obeso 2000) and plant availability in the particular study area. To do this, samples were dried at 60ºC for 48 h, ground with a Retsch MM200 ball mill and rinsed with NaOCl to improve clarity (Holechek 1982). Samples were then centrifuged to eliminate the supernatant fluid, and subsequently rinsed and centrifuged twice with distilled water. The resulting material was sieved through 1 and 0.2 mm pore–size filters, and the intermediate fraction was kept for analysis. Approximately 30 mg of the sieved material was mounted on a slide with a hydrophilic mounting medium (Jung Tissue Freezing Medium). These reference slides were studied carefully before proceeding with diet slides, and the specific features of the epidermis (cells shape, hairs and trichomes, stomas) were digitally photographed under a 100× microscope.

Previous tests had been carried out to determine the asymptote of the relationship between the diversity of plant remains and fragments counted. As a result the number of plant remains identified per sample was fixed at 50 along two transects, i.e. the first 25 non-overlapping fragments intercepted per transect/scale line under a 100x microscope. Samples were classified into spring (March-June), summer-autumn (July-October) and winter (November-February), on the basis of Capercaillie life cycle and plant phenology. Diet composition was used to calculate the proportion of understory resources in the diet and to compare it with that of other Capercaillie populations.

Diet and habitat selection

Diet selection was analyzed on the basis of 11 plant categories, split into canopy and understory. Canopy categories consisted of the main tree species in the study area: beech, sessile oak, birch, holly and rowan. Diet selection on understory plants was analyzed using the following categories: broom, bilberry leaves, berries and shoots, heaths, heather, ferns and grasses. These categories were chosen to represent microhabitats that were to some extent different, and to maintain a balance between a too coarse-grained scheme that would underestimate selection, and a too fine-grained one that would merely reflect the natural patchiness of resources.

Diet and habitat selection were determined using *design I* (population level) selection ratios (Manly et al. 2002). These ratios are proportional to the probability of each category being used, assuming unrestricted access to available resources. Selection ratios range from 0 (null selection) to infinite (maximum positive selection), where 1 indicates that resources are used according to availability. Vegetation composition and cover data, in both used and control spots, was pooled, and the mean over the whole study area was used as an estimate of habitat and food availability (Sutherland and

Green 2004) of perennial resources. Availability of ferns and grasses was estimated on a seasonal basis.

Niche width

Total trophic niche width and specialization of feeding events were estimated by following metrics that use the total diet of the population to define resource availability. These metrics have been reviewed and updated by Bolnick et al. (2002), who provided the companion software *IndSpec1* that facilitates metric calculations and provides resampling routines. To estimate total niche width (TNW) we used an index adapted to discrete data (Bolnick et al. 2002):

$$TNW = -\sum_j q_j \ln q_j$$

where q_j is the proportion of the j^{th} food category in the population's niche. The degree of specialization in feeding events for the population was estimated by means of the mean proportional similarity index (IS, Bolnick et al. 2002):

$$IS = \frac{\sum_i^n \sum_j \min\left(p_{ij}, q_j\right)}{n}$$

where p_{ij} is the proportion of the j^{th} food category in each dropping or feeding event i, and q_j are the same as above. Then, proportions of the different categories in the diet of the population are calculated as the average proportion of each food category. This similarity index estimates the degree of overlap between a given sample and the population. It approaches 0 for fully specialized feeding events (monodiet), and 1 for those with a generalist pattern. The main advantages of this metric over others available are that it estimates specialization for each sample, it is not too sensitive to artifacts due to the presence of purely monophagous samples, and it makes no assumption about particular distributions of resources (Bolnick et al. 2002). *IndSpec1* provides a Monte Carlo routine to test the significance of the IS index against a null model of a fully generalized diet. We compared overall, generalized and seasonal IS values by means of one–way ANOVAs and post-hoc Tukey tests. All analyses were performed with freeware (R Development Core Team 2010).

Last, we calculated TNW (as described above) and the proportion of understory resource use for other published studies on Capercaillie diet (Jacob 1988; Storch et al. 1991; Picozzi and Catt 1996; Saniga 1998; Summers et al. 2004). To enable comparison with our population, we only considered the studies that (1) showed year-round quantitative data for adult animals; and (2) at least had the same taxonomic resolution as our data. Additionally, diet categories in these studies were grouped according to categories from our data, that is: all tree and shrub species appearing in the diet, animal material, ferns, grasses, mosses and unidentified plant remains.

RESULTS

Sampling surveys over the two-year period yielded 146 signs of Capercaillie presence in the 10 km^2 study area. Most of these signs were droppings (122), although feathers, footprints, and direct sightings were also included in the analyses of habitat selection. Signs of presence were balanced across seasons (spring 46, summer–autumn 57, winter 43).

Diet and habitat selection

The 122 diet samples analyzed yielded only two monodiets, both consisting of holly leaves in winter and early spring. In spring, diet was dominated by beech buds, bilberry shoots and fern fronds, at 28%, 19% and 16%, respectively (n = 43). In summer-autumn, the major diet items were 54% bilberry and 10% fern fronds (n= 49). Most bilberry consumption in this period consisted of berries (63%). In winter (n= 30), holly leaves accounted for 33% of the diet, and beech buds, bilberry shoots and fern fronds accounted for 13% each. Details of proportional use and availability are given in Appendix A.

The diet selection index for tree species showed that beech and holly were preferred, whereas birch, oak and rowan were consumed below availability. Results in spring and winter mirrored the overall trend except for beech in winter, which was consumed according to its availability (Fig. I. 1a). In summer-autumn, only rowan, which was not consumed at all, departed from availability (Fig. I. 1a). Among understory species, bilberry and ferns were important in the diet selection. Bilberry was strongly selected in summer-autumn, whereas ferns were strongly selected in spring and winter (Fig. I. 1a). Heaths and brooms, the former a particularly abundant resource, were always used below availability (Fig. I. 1a). Cantabrian Capercaillie obtained much higher percentages of understory or ground-based resources than other populations, averaging 65%, with maximum in summer-autumn (83%) and minimum in winter (50%, Table I.1).

Habitat selection for tree species did not show a clear pattern. In spring, beech-dominated areas were used above availability whereas oak-dominated areas were used below availability. In summer-autumn, holly was used below availability (Fig. I. 1b). Habitat selection for understory vegetation showed that areas rich in bilberry and grasses were preferred in winter and spring, whereas areas rich in ferns were used below availability in spring, and brooms or common heather were used below availability all year round (Fig. I. 1b).

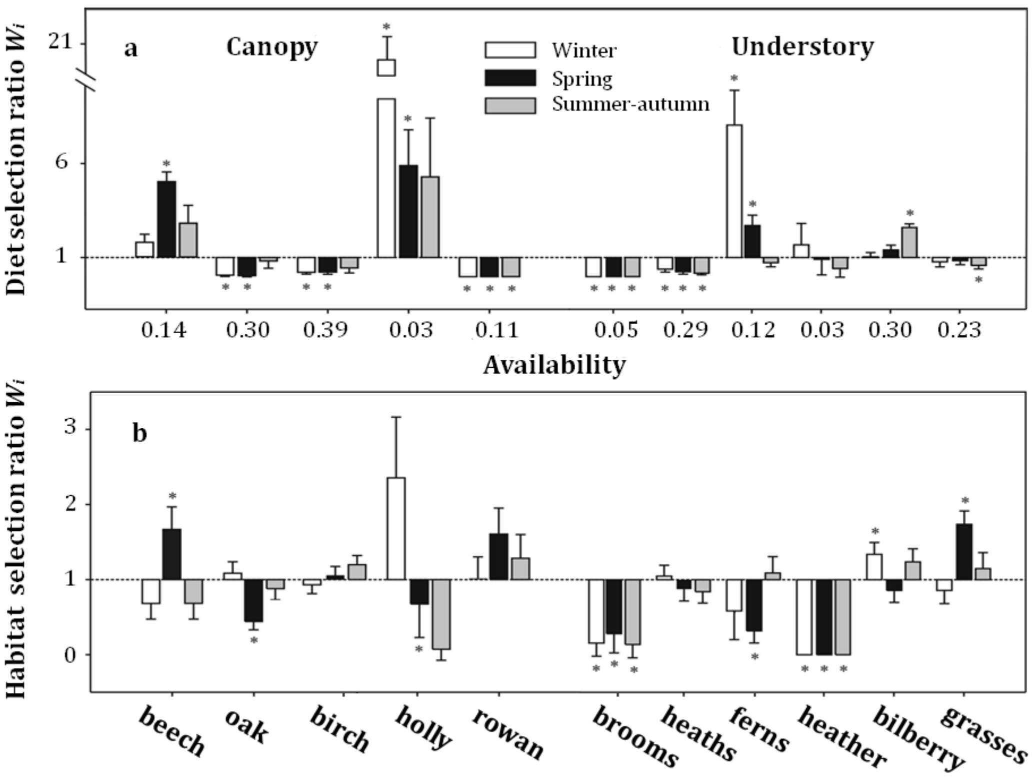

Figure I .1: Diet and habitat selectivity indexes for canopy and understory species, calculated from the average use of each resource category, and resource availability. a) Diet selection ratio W_i. This equals 1 when resources are used according to availability. The *dashed line* at 1 separates resource used above or below availability. *Asterisks* indicates W_i was significant after controlling for multiple comparisons (note that significance of W_i is calculated on a seasonal basis). *Error bars* indicate the standard error of W_i. The numbers on the X axis correspond to the mean proportional abundance of the canopy and understory species written below them in the X axis of Fig. I. 1b. Canopy and understory proportions do not add up to 1 as species with less than 1% cover were not included in the analysis. For seasonal resources such as ferns and grasses, we show the seasonal average. b) Habitat selection ratio *Wi*. Notation and interpretation as above.

Niche width and diet similarity index

We found that TNW in Cantabrian Capercaillie was wider than in any other Capercaillie population analyzed (Table I. 1). Both overall and seasonal values of the similarity index (IS) for our study population were significantly different from a generalized resource use (Table I. 2). In addition IS varied between seasons ($F_{2,\ 119}$ = 11.3, $p < 0.0001$, Fig. I. 2) indicating that specialization of feeding events was higher in winter than in spring and summer-autumn ($p = 0.016$ and $p < 0.001$ in Tukey HSD tests, respectively).

	TNW	UD overall	UD spring	UD summer	UD winter
This study	2.11	0.65	0.62	0.83	0.50
Scotland 1[1]	1.36	0.14	0.02	0.29	0
Scotland 2[2]	0.73	0.21	0.14	0.47	0.08
Slovakia[3]	1.50	0.43	0.44	0.78	0.08
Jura Mountains[4]	1.69	0.43	0.10	0.85	0.35
Bavarian Alps[5]	1.63	0.36	0.14	0.81	0.07

Table I.1. Total trophic niche width (TNW) and average proportion of understory-based diet (UD) for different Capercaillie populations. Sources: 1- Picozzi et al. 1996; 2- Summers et al. 2004; 3- Saniga 1998; 4- Jacob 1988; 5- Storch et al. 1991.

	n	TNW	IS	P_{IS}
Pooled dataset	122	2.11	0.47 ± 0.01	< 0.001
Winter	30	2.08	0.45 ± 0.02	< 0.001
Spring	43	2.10	0.54 ± 0.02	< 0.001
Summer / autumn	49	1.74	0.61 ± 0.02	< 0.001

Table I. 2: Total niche width (TNW) and mean proportional similarity index (IS ± standard error) for this study. IS varies between 0 and 1, where diets departing strongly from the population overall approach 0 whereas diets similar to the population average approach 1. P_{IS} indicates the probability of IS being equal to that of a fully generalized overall diet.

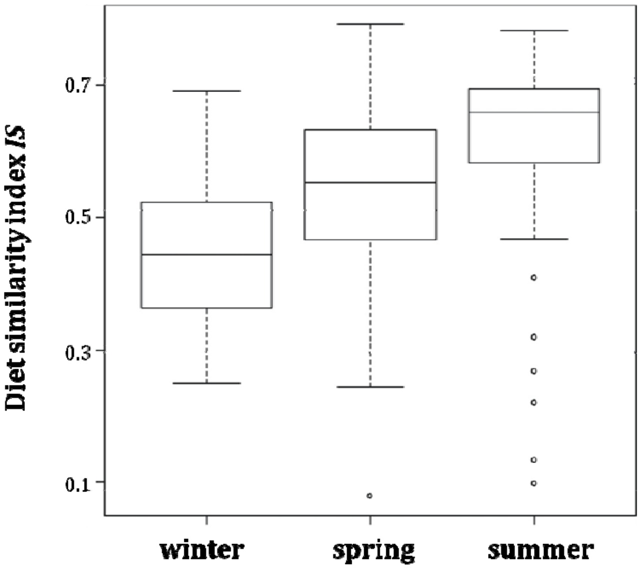

Figure I. 2: Box plots showing the seasonal distribution of the proportional similarity index IS. This is an index of specialization of feeding events that approaches 0 for fully specialized feeding events (monodiet), and 1 for those with a generalist pattern. *Boxes* indicate the interquartile range of the data and the position of the median; *error bars* extend to non-outlier data within 1.5 times the interquartile range.

DISCUSSION

Ecological singularity

In this study we confirmed that living in purely deciduous forests has trophic and possibly behavioral consequences for Capercaillie. Cantabrian birds obtained, annually, 65% of their resources on the ground, whereas for other populations this ranged between 14 and 43%, averaging 34%. This contrast appears particularly marked in winter, arguably the season with more pronounced structural differences between deciduous and conifer forests. The differences may be because of the lack of foliage in winter and early spring in deciduous forests, together with the rugged terrain where plants protrude above the snow in ridges, whereas the availability of conifer needles in most populations allows the birds to use trees as their primary food source. This result is a mechanistic example of differential interactions with both biotic and abiotic components of the environment, predicted for peripheral populations (e.g. Gaston 2003). Several consequences could result from this behavioral peculiarity. For instance, we speculate that higher reliance on understory resources may imply that Cantabrian birds are more susceptible than boreal birds to the overall unfavorable competition with large mammalian herbivores (Van Gils et al. 2007).

In other Capercaillie populations and forest grouse species, foraging is often concentrated on individual food items, and includes perching in individual trees for days or even weeks (Bergerud and Gratson 1988; Sedinger 1997). We found almost no such monodiet feeding events. In addition, diet and habitat preference showed several contrasting results, especially for holly and ferns, which were preferred as winter diet but were not especially common as part of winter habitat. All in all, we interpret this as a markedly distinct foraging behavior in which Cantabrian Capercaillie moved more often and farther while foraging, departing from the usual overlap between food and cover found in other Capercaillie populations and forest grouse species (reviewed in Bergerud and Gratson 1988).

Mechanisms of habitat selection

The high proportion of understory resources in the diet of Capercaillie may partially explain the results of previous, larger-scale studies, which showed that stand-scale forest composition was not a key factor for habitat selection in Cantabrian Capercaillie (Quevedo et al. 2006b). In addition, previous studies of stand-scale habitat selection also suggested a preference for areas richer in bilberry (Quevedo et al. 2006b), a trend which our diet analyses confirmed. Bilberry appears in high proportion in the diet all year round, and the birds positively selected it in summer-autumn. Leaves, shoots and, mostly, berries were consumed. Therefore, bilberry reliance seems to be a general characteristic of both central and peripheral Capercaillie populations (Martínez 1993; Storch 1993; Rodríguez and Obeso 2000, Selås 2000). It also seems that bilberry, a major source of food and shelter for adults and chicks (e.g. Storch 1994, Wegge et al. 2005), is the only major diet resource shared with birds from the conifer domain.

Diet selection and trophic niche width

The phenology of deciduous forests determines the availability of resources for herbivores. This may explain the highly positive selection of holly and ferns in winter and spring. Holly is the only evergreen tree species in the study area, although it appears highly scattered within the forest; it was present only in 82 of 429 surveyed plots, averaging 3% availability. Hence, as suggested in previous studies (Castroviejo 1975, Martínez 1993, Rodríguez and Obeso 2000), holly is a key winter food resource for Cantabrian Capercaillie that may also provide shelter. Also important in the winter diet were beech buds, the first to appear in the season in these forests (B. Blanco-Fontao, personal observation). Diet preferences shifted markedly in summer-autumn, when Cantabrian Capercaillie converged with other populations and selected bilberry. Conversely, the abundant oak and birch (taken together, representing a total of 69% of the canopy) and heaths (29% of understory), were consumed below availability. The low consumption of oak and birch may be related to the phenology of beech and bilberry, because the former is the first tree species to produce buds in winter, and the latter provides widespread supply of fresh leaves before oak and birch unfold theirs. This idea is supported by the use of beech as both a diet and habitat resource beyond its availability (Fig. I. 1). Nonetheless, accurately explaining such diet shifts would require higher sampling frequency than in this study, and chemical determinations. Overall, we found stronger patterns of diet and habitat selection in spring (Fig. I. 1), perhaps reflecting the fact that resources are still scarce in early spring, the season that marks the onset of the energy-demanding reproductive period for Capercaillie.

We found that Cantabrian Capercaillie showed a broader TNW than the other Capercaillie populations studied. This result confirms our expectations based on both the strong seasonality of resource availability in deciduous forests, and the lack of interspecific competition with other grouse species that may lead to niche expansion (Van Valen 1965; MacArthur et al. 1972; Costa et al. 2008). Interestingly, TNW of Cantabrian Capercaillie was closest to that of those Capercaillie populations living in montane habitats, for example the Jura Mountains and Bavarian Alps.

There were substantial seasonal differences in niche patterns. Niche width was narrower and the specialization of feeding events was lower in summer-autumn, as the population foraged on the preferred bilberry fruits. In winter we found the opposite: more food items were included in the diet, but single feeding events were less similar to those for the population overall. We interpret this as a consequence of the lack of an abundant, widespread resource for folivores in winter and early spring in deciduous forests, compensated for by a broader niche than other Capercaillie populations. This result is also consistent with previous, larger scale results indicating more varied winter habitat use in Cantabrian Capercaillie (Quevedo et al. 2006b).

Final remarks

Our study revealed substantial ecological differences between Cantabrian and range-central Capercaillie populations, and strong reliance on bilberry as a common feature among them. Our results stress the need for specific, local data to develop sound conservation plans, and suggest that bilberry, an important ground resource for Cantabrian Capercaillie, should be specifically protected in Capercaillie recovery plans. Most extant Capercaillie areas in the Cantabrian range are protected (Quevedo et al. 2006a), but such protection does not prevent overgrazing on bilberry and other resources. Free-ranging livestock, though extensive and considered ‘‘traditional’’, attain densities up to an order of magnitude larger than those of wild ungulates in some areas. Moreover, they double the highest densities of native ungulates in protected areas where overgrazing has long been discussed, for example the Northern Range of Yellowstone National Park (Rodríguez et al. 2007). Reducing the season and range over which cattle herds graze and trample freely within sensitive areas has already been suggested for protecting the habitat of brown bears *Ursus arctos* in the Cantabrian range (Naves et al. 2006). We suggest that limiting overgrazing by livestock may also help Capercaillie directly by reducing competition, and indirectly by improving bilberry productivity (Tolvanen 1994).

In this study we did not attempt to discriminate between hen and cock droppings because the overlap between them may be sometimes substantial, adding too much uncertainty to our quantitative approach. We considered that visual discrimination of sex from Capercaillie droppings may be hampered by individual diet variation and seasonal diet shifts, which may be particularly important in our fine-grained study area. Nonetheless, sexual dimorphism and individual variation are potential sources of variability that could affect understanding of Capercaillie ecology and management plans (Bañuelos et al. 2008). Intrapopulation variability in the use of resources should be addressed by specific studies that assign diet unequivocally to individuals, perhaps combining microhistological and molecular techniques.

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Capítulo II

Habitat partitioning and molting site fidelity in *Tetrao urogallus cantabricus* revealed through stable isotopes analysis

Beatriz Blanco-Fontao, José Ramón Obeso, María José Bañuelos,
Mario Quevedo

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Unidad Mixta de Investigación en Biodiversidad (CSIC/UO/PA), Dpto. de Biología de Organismos y Sistemas, Área de Ecología, Universidad de Oviedo

Abstract. Sexual dimorphism is often associated with different feeding strategies between sexes because of distinct nutritional demands or intake rates. Capercaillie is the most sexually dimorphic grouse, thus sexual segregation in resource use is likely. This study assessed intrapopulation variation in the diet related to habitat use, focusing on differential feeding behaviors between Capercaillie females and males. We used stable isotopes analyses in feathers of Cantabrian Capercaillie, a population living at the southern edge of the range in purely deciduous forests. We analyzed feathers of females and males, and sorted them according to the dominant tree species in the patch where they were found. Mean isotopic values differed both between sexes and among forest types. The latter explained most of the isotopic variance, suggesting that birds consistently selected certain forest types to molt. Capercaillie females showed wider trophic niche and seemingly more intra-gender diversity in resource use than males. The differences between sexes in the trophic variability support the sexual segregation reported in previous studies which is associated with females using the more micro-habitat diverse treeline areas, while males mainly use the inner areas of the forests. Stable isotope analysis proved very useful to assess intersexual niche partitioning in rare species living in rugged terrains where it is logistically difficult to rely on direct approaches (i.e. direct observation, capture and radio-tracking).

INTRODUCTION

Adaptations to local resources at the population level are widely acknowledged in wildlife ecology. However, at a finer level of organization individuals or sectors within a population (i.e. age or sex-classes) might specialize on different food resources, depending on differences in habitat use and feeding behaviors (Durell 2000; Catry et al. 2005; Bearhop et al. 2006). Males and females are often subjected to different ecological constraints, and in turn, likely to show distinct feeding behaviors (Mysterud 2000; Bolnick et al. 2003; Ruckstuhl 2007). Differential ecological constraints can be driven by distinct nutritional demands (Isaac 2005; Bulte et al. 2008), and are frequently related to sexual segregation, i.e. seasonal, distinct habitat use by males and females. This is especially true in highly sexually dimorphic species as the degree of sexual size dimorphism and the level of inter-sex niche segregation are positively correlated (Mysterud 2000; Phillips et al. 2009).

Capercaillie (*Tetrao urogallus*) is the most sexually dimorphic grouse species. Males may almost double females in weight (i.e. males: 3.3-6.5 Kg, females: 1.5-2.5 Kg; Madge et al. 2002), and sexes differ in various other morphological, physiological and ecological aspects (e.g. Rintamaki et al. 1984; Borchtchevski 1987). Moreover, Capercaillie is a large, herbivorous bird, with a relatively simple digestive tract, and low intake rates (Sedinger 1997; Van Gils et al. 2007); as such, diet is an environmental constraint, likely to be reflected in sexual dimorphism. Diet differences between sexes can be either the result of differences in mean diet composition and preferences, or otherwise related to the diet variance, i.e. generalist or specialist character of each sex, or degree of intra-gender diversity in resource use. Regarding the latter aspect and following the predictions of the niche variation hypothesis, more generalized populations are likely to exhibit more intrapopulation niche variation (Van Valen 1965; Bolnick et al. 2007). We studied the Cantabrian population of Western

Capercaillie (*Tetrao urogallus cantabricus*), the only population that inhabits all year round purely deciduous forests (Quevedo et al. 2006a, b). Previous studies on Cantabrian Capercaillie showed that habitat partitioning exists during summer in this population, related to sex and reproductive status, and associated with the females' stronger reliance on more heterogeneous treeline habitats while males remain in more homogeneous inner areas of the forests (Bañuelos et al. 2008). These previous studies on the Cantabrian range, altogether with studies on northern Capercaillie populations that report more generalized diets for females (Storch et al. 1991; Borchtchevski 2009) are hinting possible sexual dimorphism in the diet and feeding behaviors. In addition, molting is a period of the annual cycle that determines reduced home ranges and high site fidelity in other Capercaillie populations (Rolstad et al. 1988; Martínez 1993). In the highly fragmented and heterogeneous Cantabrian landscape - result of a long-term process of both natural fragmentation and historical deforestation by humans (García et al. 2005) - molting site fidelity may be related to the selection of specific forest patches and, thus, it could be studied through analysis of habitat-related diet differentiation.

Stable isotope analysis can provide estimates of resource use over longer time periods than conventional diet analyses, which are often based on single feeding events (West et al. 2006; Inger and Bearhop 2008). For instance, the isotopic values in feathers, which are metabolically inert, reflect the resources assimilated by birds during feather formation (Hobson and Clark 1992; Bearhop et al. 2002). Hence, feathers provide valuable information on resource use during the cryptic, molting period, when energy demands are highest for Capercaillie (Lindén et al. 1984). Stable isotope analysis of molted feathers of Cantabrian Capercaillie is an indirect approach that allows evaluation of sex-related trophic ecology in a sparse population living in a rugged landscape. Specifically, we used stable isotope analysis to, 1) assess intra-specific dietary variation between females and males and, 2) evaluate fidelity to microhabitats during the molting. Our hypothesis is that Capercaillie's marked sexual dimorphism would imply distinct dietary variation of each sex. Therefore, based on previous studies on habitat partitioning for this population (Bañuelos et al. 2008), we predict broader trophic niche in females.

MATERIAL AND METHODS

Study area and sample collection

Our study area includes the entire Cantabrian Capercaillie (*Tetrao urogallus cantabricus)* range in the Cantabrian Mountains (provinces of Asturies and León, NW Spain, Fig. II. 1). This rugged landscape contains the largest portion of the remnant Atlantic deciduous forest on the Iberian Peninsula, at the southernmost boundaries of this vegetation type (Polunin and Walters 1985; García et al. 2005). These are mostly semi-natural forests with a long history of human use that resulted in a highly fragmented pattern, with highly interspersed patches dominated by different tree species (García et al. 2005). Beech *Fagus sylvatica*, mountain birch *Betula pubescens* and sessile oak *Quercus petraea* are the dominant canopy species in the Cantabrian forests. The treeline lies at about 1600 m a.s.l., and is a mixture of forest, tree heaths *Erica arborea*, common heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus*, broom formations (*Genista florida*, *Cytisus scoparius*), grazing meadows, and scree slopes.

A total of 125 different areas of aprox. 1 Km^2 in the vicinity of leks and known molting sites were surveyed during three consecutive molting seasons (2005-2007). These surveys consisted of drives conducted from 15th July to 15th September, in areas where Capercaillie was present according to spring surveys of lek occupancy, and summer survey of reproductive success. In the Cantabrian Mountains, Capercaillie reproduction appears to occur 3–4 weeks later than in northern populations (Martínez

1993; Moss et al. 2001; Wegge et al. 2005), and thus, molting is also delayed. See Bañuelos et al. (2008) for details on those surveys.

The feathers of Capercaillie females and males are easily differentiated by color and pattern. All feathers found in these surveys were positioned with a GPS and stored in paper envelopes. We collected Capercaillie feathers in 533 different points. We arbitrarily set a minimum distance of 500 m between feathers of the same sex to minimize the use of feathers from the same individuals, up to a total of 126 analyzed feathers (Fig. II. 1).

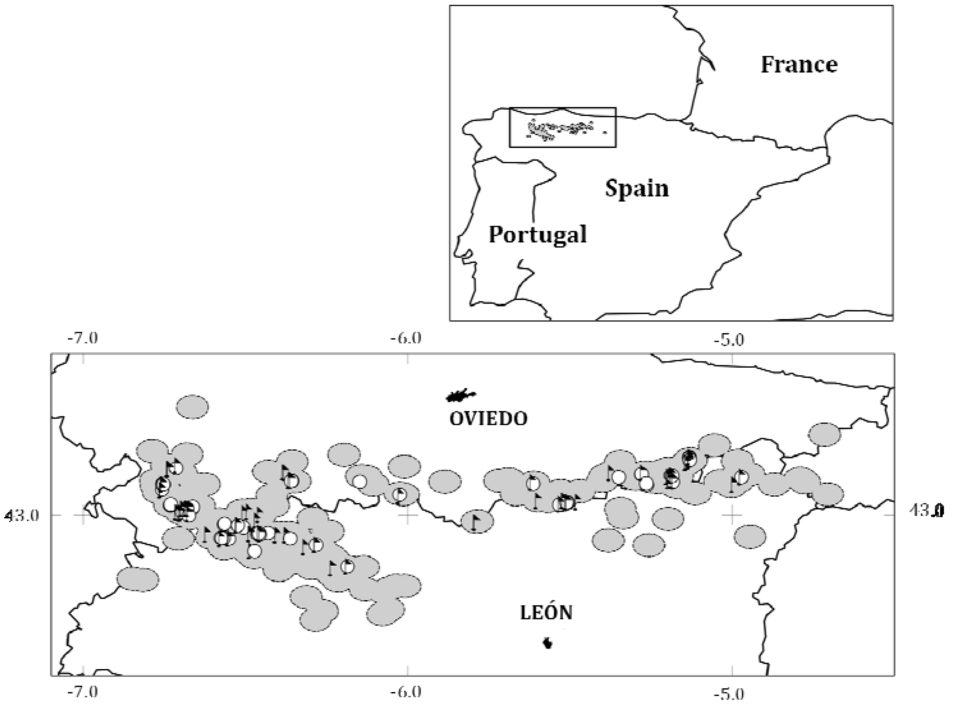

Figure II. 1: Study area and approximate area of occupancy of Cantabrian Capercaillie (in grey), mapped by plotting buffer areas of 2-km radius around display grounds occupied in 2007 (see Storch 2007, for criteria). Flags correspond to feather collection points for males (n = 74) and white dots for females.

To evaluate microhabitat fidelity during the molt, we grouped feathers according to the dominant tree species in the patch were they were found - birch, beech or sessile oak - in a 500 m radius buffer around each feather. Each major canopy species roughly defines an array of accompanying plants. Thus, we used them as proxies to distinguish forest patches. Information on canopy species was extracted from a 1:25.000 GIS database (see Quevedo et al. 2006a, b, for details).

Feathers were split into six subsets for analysis: female feathers in birch (n = 18), beech (n = 21) and oak patches (n = 13) and male feathers in birch (n = 15), beech (n = 37) and oak patches (n = 22).

Stable isotope analysis

We measured $\delta^{13}C$ and $\delta^{15}N$ ratios in feathers to evaluate sexual- and habitat-mediated differences in trophic variability of the Cantabrian Capercaille population. The $\delta^{13}C$ ratio traces the importance of different carbon pools to a consumer, whilst $\delta^{15}N$ is an effective tracer of the origin of nitrogen in plants (Kelly 2000; Inger and Bearhop 2008). Therefore, the combination of both isotopes, together with the application of quantitative metrics (Layman et al. 2007a) is a powerful approach to assess both the origin of resources and the trophic variability of populations (Newsome et al. 2007; Inger and Bearhop 2008). Only body-covert feathers were analysed to ensure that all feathers had a similar growing period. Feather samples were cleaned to remove oils and debris by rinsing in a 2:1 chloroform-methanol solution for 24 hours, then dried in an oven at 60ºC to constant weight (e.g. Hobson and Bairlein 2003; Symes and Woodborne 2009). Subsequently, feathers were frozen in liquid nitrogen and immediately ground to fine powder using a MM200 ball mill. Subsamples of 1 mg (± 0.2 mg) were packed into 6 × 4 mm tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analyses, which were performed using a continuous-flow isotope ratio mass spectrometer at UC Davis Stable

Isotope Facility (USA). Stable isotopes ratios are expressed in δ notation, as part per thousand deviation from standard material, Pee Dee belemnite limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$ according to the equation:

δX = [(Rsample / Rstandard) − 1] × 1000 where X is ^{15}N or ^{13}C and R is the corresponding ratio ^{15}N:^{14}N or ^{13}C:^{12}C.

To discard a spatial structure of the isotopic values in feathers we compared the standardized Euclidian geographical distance and isotopic distance matrices. We standardized the geographical and isotopic values by subtracting the mean of all elements in the matrix from each observation and then dividing by the SD (Fortin and Gurevitch 2001). The significance of the relationship was assessed using a simple Mantel test with 1000 randomizations with the software *zt* provided by Bonnet and Van de Peer (2002).

Trophic niche breadth and population specialization

To calculate trophic niche breadth and trophic variability we used quantitative metrics based on the position of individuals in the $\delta^{13}C$-$\delta^{15}N$ space, and Euclidean distances (Layman et al. 2007) We applied those metrics to the six subsets of the population (see above), using individuals as measurement units. The individuals of each subset were plotted in a $\delta^{13}C$-$\delta^{15}N$ niche space. To estimate the total niche of each subset we measured the total area of the convex hull (TA) that included the isotopic values of all individuals. To obtain null distributions of TA and test the significance of differences between subsets, we randomized the empirical data set of isotopic signatures 1000 times and calculated TA in each resampled data set. *P* values were approximated as the proportion of resampled data sets that exceeded the observed differences; for forest patch comparisons, false discovery rate was controlled using the FDR adjustment (Benjamini and Hochberg 1995).

To estimate the trophic variability within each subset of the population we calculated Euclidean distances among individuals in the $\delta^{13}C$-$\delta^{15}N$ bi-plot. First, we calculated the distance of each individual to the isotopic centroid of its subset (CD), providing an index of the trophic diversity in females and males. Then we calculated the coefficient of variation of the distances from each individual to its same-sex neighbors in the isotopic space (CVND), which gives a measure of the clustering of values and trophic redundancy (Quevedo et al. 2009).

Two-way ANOVAs and post hoc Tukey tests were used to test for differences among forest patches and between sexes regarding mean $\delta^{13}C$ and $\delta^{15}N$ values, CD (square root transformed to achieve normality) and CVND.

CD and CVND were calculated in a GIS. Convex hulls and TA were calculated using package Adehabitat (Calenge 2006), an extension to R statistical environment (R Development Core Team 2010), which we used for all the statistical analyses.

RESULTS

Mean $\delta^{13}C$ and $\delta^{15}N$ isotopic values significantly differed between males and females and among forest patches (Table II. 1, Fig. II. 2). Forest patch explained the majority of $\delta^{13}C$ (75 %) and $\delta^{15}N$ variance (40%; the rest of $\delta^{15}N$ variance was equally distributed between sex and residual variance). Capercaillie feathers in oak patches showed higher values of $\delta^{13}C$ than in birch and beech patches whereas birch patches showed higher values of $\delta^{15}N$ than beech and oak ones (Tukey HSD tests, Table II. 2, Fig. II. 2). Males showed higher values for both isotopes (Tukey HSD tests, Table II. 2, Fig. II. 2).

Variable	**$\delta^{13}C$**	**$\delta^{15}N$**
Sex	$F_{1,122} = 4.56$; $p = 0.034$	$F_{1,122} = 5.56$; $p = 0.019$
Forest	$F_{2,122} = 10.30$; $p < 0.001$	$F_{2,122} = 3.49$; $p = 0.033$
Sex*Forest	$F_{2,122} = 3.03$; $p = 0.052$	$F_{2,122} = 0.7974$; $p = 0.453$

Table II. 1: ANOVA table comparing the effects of sex and forest patch on the isotopic signatures of Capercaillie feathers.

Sex	**$\delta^{13}C$**	**$\delta^{15}N$**
Male	-24.1 ± 0.6^{a}	1.5 ± 1.0^{a}
Female	-24.4 ± 0.5^{b}	1.1 ± 1.3^{b}
Forest		
Birch	-24.3 ± 0.5^{a}	1.85 ± 1.4^{a}
Beech	-24.5 ± 0.6^{a}	1.2 ± 1.1^{b}
Oak	-23.9 ± 0.5^{b}	1.1 ± 1.0^{b}

Table II. 2: $\delta^{13}C$ and $\delta^{15}N$ isotopic values (mean ± SD) in feathers of Capercaillie for sex and forest patch. Different superscripts indicate significant differences among groups after Tukey tests ($p < 0.05$).

Capercaillie total niche space (TA) varied among forest patches and between sexes. TA was significantly bigger in beech and birch patches than in oak ones (Table II. 3). Females showed significantly larger values than males (Table II. 3).

CD and CVND were significantly different among forest patches and CD was marginally larger for females (Table II. 3). Neither CVND between sexes nor both interactions significantly differed. CD was significantly shorter in oak patches than in birch ones (*p* = 0.013 in Tukey HSD tests) whereas the significant differences in CVND among forest patches were determined by lower values for oak patches than for birch and beech patches (*p* = 0.006 and *p* = 0.002 in Tukey HSD tests, respectively, Table II. 3).

There was no spatial structure in the isotopic values, i.e. no significant correlation was found between the standardized Euclidian geographical distance and the isotopic distance matrices (Mantel test: r = 0.004, p = 0.42).

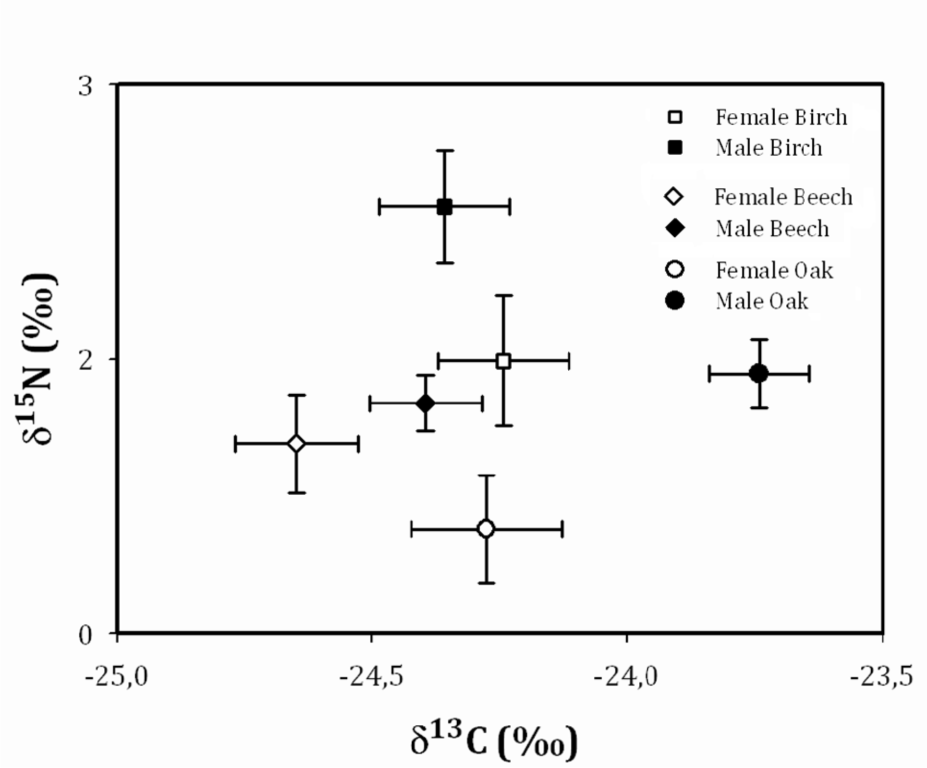

Figure II. 2: $\delta^{13}C$ and $\delta^{15}N$ isotopic values (mean ± SE) for males and females of Cantabrian Capercaillie in birch, beech and oak forest patches.

	TA		**CD**		**CVND**	
Forest	Male	Female	Male	Female	Male	Female
Birch	4.37	8.38	1.3 ± 0.75	1.53 ± 0.78	0.54 ± 0.12	0.54 ± 0.09
Beech	7.36	7.82	1.03 ± 0.55	1.16 ± 0.82	0.52 ± 0.13	0.56 ± 0.12
Oak	3.48	4.08	0.88 ± 0.41	1.06 ± 0.47	0.46 ± 0.06	0.45 ± 0.11
Variable						
Sex	p = 0.012		$F_{1,122} = 3.84$; p = 0.052		$F_{1,122} = 1.09$; p = 0.29	
Forest	p = 0.22; p = 0.050; p = 0.012		$F_{2,122} = 4.88$; p = 0.013		$F_{2,122} = 7.09$; p < 0.001	
Sex*Forest	-		$F_{2,122} = 0.06$; p = 0.94		$F_{2,122} = 0.73$; p = 0.48	

Table II. 3: Summary of trophic niche metrics (mean ± SD) and comparisons among birch, beech and oak forests and between males and females. TA represents the total area of the convex hulls that included $\delta^{13}C$-$\delta^{15}N$ isotopic values of each of the subsets; CD shows the distance of each individual to the isotopic centroid of its subpopulation; CVND is the coefficient of variation of distances from each individual to its neighbors in the isotopic space. *P* values for TA were estimated as the proportion of resampled data sets that exceeded the observed difference; for the forest variable, *p* values correspond to birch-beech, birch-oak and beech-oak forest patch comparisons after controlling for false discovery rate (FDR). *F* values correspond to two-way ANOVAs.

DISCUSSION

Trophic sexual dimorphism

A stable isotope analysis of molted feathers is a valuable, unintrusive tool to study the trophic ecology of an endangered, elusive bird, the Cantabrian Capercaillie. We found that females and males of this Capercaillie population showed differences in their average isotopic signatures, which could be related to distinct habitat use; females and males also showed distinct trophic variability, both results consistent with a sexually dimorphic species with marked separation of reproductive roles. Such differences suggest relevant dietary segregation within the population among individuals from different sexes, likely related to spatial segregation of females and males during the molt.

Using stable isotopes to study resource selection by herbivores has difficulties because of the wide variability of isotopic signatures in primary producers; intrinsic variances in plant signatures in pure C3 environments could have been expected to yield statistically undetectable differences between herbivore individuals, whereas carnivores in a similar system should render simpler interpretations because the variability of primary producers is averaged up the successive trophic levels (e.g. Fry 2008). Despite to the presumed difficulties, we found marked differences between sexes within the different microhabitats. Males and females differed in average isotopic values, with males showing higher $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures (Fig. II. 2); they also differed in the trophic niche breadth and variability, reflecting distinct dietary variation of each sex. Regardless of the smaller sample size for females, their overall trophic niche (TA) was wider (Table II. 3) suggesting a more generalized diet (Storch et al. 1991; Borchtchevski 2009). In addition, longer distances to the isotopic centroid (CD; Table II. 3) indicated higher trophic diversity, i.e., females showed greater variability in resource use. Overall, differential trophic variability for each sex is apparent; females show a wider niche, with a higher level of intra-gender diversity compared to males that had more specialized diets with less intra-gender variability in resource use. These results thus lend support to the niche variation hypothesis (Van Valen 1965; Bolnick et al. 2007).

Our results suggest distinct trophic variability for each gender, which may be related to spatial separation in foraging; females use the more diverse and less homogeneous treeline forests, while males mainly use the inner areas of the forests during molting (Rolstad et al. 1988; Ménoni 1990; Bañuelos et al. 2008). Our main contribution to previous knowledge of Capercaillie feeding ecology (Storch et al. 1991; Borchtchevski 2009) is to reveal sex-related trophic variability in Capercaillie by means of stable isotope analysis, and trophic differences likely driven by habitat segregation. Using radio-tracking data, summer spatial sexual segregation is also found in Scandinavian Capercaillie populations related to differential sexual constraints of both predation and nutritional requirements (Rolstad et al. 1988), but not in the Alps where both sexes were reported to overlap in habitat use, converging in old forests with a well developed understory (Storch 1993).

From the viewpoint of conservation biology, results indicated sex-biased vulnerability to habitat change and likely differential responsiveness to habitat management. Thus, it should be again stressed that conservation measures should take into account for sex-related variation (e.g. Durell 2000; Bolnick et al. 2003).

Site fidelity during the molting season

The kind of forest patch explained most variance for both isotopes. This is a very interesting result considering (i) the montane forest structure in the Cantabrian Mountains, (ii) our sampling design and (iii) the ecology of Capercaillie. First, our study area included the montane forests within the entire Cantabrian Capercaillie distribution range (Fig. II. 1). These forests show a highly fragmented pattern, where different canopy species often build small, interspersed patches (García et al. 2005). Second, feathers sampled in a given year and sorted to the dominant patch type where they were found, were actually formed during the previous molting season, i.e. one year before collection. Third, Capercaillie is an herbivorous bird that needs to devote extra-time to foraging (Sedinger 1997; Van Gils et al. 2007), and it is likely to use income resources to grow feathers (Thomas 1988; Meijer and Drent 1999). On the basis of these previous studies, Capercaillie molting and foraging activities are likely to overlap in time and space, and hence feathers are likely to reflect the trophic resources used in the forest patches where molt and growth occur. Thus, the striking differences found among average isotopic signatures of feathers collected in patches dominated by distinct tree species suggest that birds consistently selected certain forest types to molt. These differences might also indicate reduced home ranges during this period of the annual cycle due to fragmentation and small patch size. These findings agree with the smaller summer home ranges and with the observed return to summer molting places in consecutive years in other Capercaillie populations (Rolstad et al. 1988; Storch 1993). It is worth noting that the high site fidelity suggested here is microhabitat-related, i.e. individuals are seemingly returning to the same kind of forest patch during the molting period.

The isotopic approach in terrestrial systems has been widely used to assess predator diets or to evaluate the relative contribution of C3 and C4 plants to herbivore diets in tropical areas (reviewed in Kelly 2000, for birds and mammals). However, its application to study the feeding ecology of terrestrial herbivores inhabiting pure C3 plant environments is quite challenging (Herrera et al. 2003; Stewart et al. 2003; Feranec 2007; Symes and Woodborne 2009). In this study, we have found distinct average isotopic values in the feathers found in each forest type, which might be a consequence of the set of particular conditions that determine the dominance of one species or the other in the canopy of the forest patches. For instance, $\delta^{13}C$ indicates differences in moisture regimes; hence the higher $\delta^{13}C$ values in oak patches may reflect more xeric conditions in this kind of forest (Heaton 1999). However, this study was not designed to find a mechanistic proximate explanation for the isotopic signature of each subset of the population and further research on fractionation and isotopic routing for exclusively C3-plant consumers would greatly improve the possibilities of this approach and, therefore, the knowledge of the feeding ecology of terrestrial herbivores inhabiting these environments.

Isotopic applications and caveats

Stable isotope analyses do have several advantages over traditional techniques (reviewed in West et al. 2006; Inger and Bearhop 2008). However, the approach is indirect; it does not have the resolution required to capture subtle, yet meaningful, differences in resource use that could be derived from analyses of stomach content or droppings, approaches more directly related to birds' natural history. Hence, future research combining both isotopic and microhistological analysis of inert tissues and droppings, respectively, may provide more robust dietary information spanning different time-scales (e.g. Hobson and Clark 1992; Bearhop et al. 2002). This would be particularly useful to study the trophic ecology of elusive species (i.e. sexual or age-class trophic partitioning, population trophic structure; Post 2003; Newsome et al. 2007). Furthermore, unintrusive studies using droppings to obtain data on population structure and stress levels (e.g. Thiel et al. 2005; Jacob et al. 2010), combined with isotopic information may provide mechanistic insights into the feeding ecology of animals and open new research paths in trophic ecology.

Other caveats that could affect our results are related to the intrinsic isotopic variance in resources, and to different metabolic routing of distinct diet components (Matthews and Mazumder 2004; Araújo et al. 2007; Martínez del Rio and Anderson-Sprecher 2008). In our study we minimized potential biases due to intrinsic resource variance by including microhabitat (patch type) as a variable in the analyses. In addition, our goal was mainly to get comparative measures of trophic niche, rather than estimating the proportion of diet items; although the lack of baseline suggests a cautious interpretation of the results, we considered that baseline isotopic variance is unlikely to obscure the clear patterns identified here.

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Capítulo III

Asymmetric niche overlap between distantly related species: Capercaillie and forest ungulates


Foto: Héctor Ruíz

Beatriz Blanco-Fontao, Mario Quevedo, José Ramón Obeso,

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Unidad Mixta de Investigación en Biodiversidad (CSIC/UO/PA), Dpto. de Biología de Organismos y Sistemas, Área de Ecología, Universidad de Oviedo

Abstract. Theory predicts high resource overlap in closely related taxa. However, distantly related taxa may also show high overlap in resource use, which may be affecting the outcome of biotic interactions. Differences in size, metabolism or abundance between distantly related taxa are expected to result in asymmetric interspecific competition. We evaluated trophic overlap patterns between several, distantly related taxa: an endangered grouse, Cantabrian Capercaillie *Tetrao urogallus cantabricus*, and the assemblage of sympatric forest ungulates in two adjacent areas that differed in ungulate abundances. We focused on bilberry *Vaccinium myrtillus* as a potentially important resource for forest herbivores. We found that bilberry was indeed a key, shared resource, especially important for Capercaillie. Herbivory damage to bilberry was positively correlated to ungulate densities. Such distantly related taxa as ungulates and Capercaillie highly overlapped in diet during the year. However, Capercaillie trophic niche was contained within the niche of wild ungulates. The overlap between Capercaillie and wild ungulates was lower when the intensity of resource competition was potentially higher (winter and intensively browsed area). Wider Capercaillie niche breadth, together with Capercaillie lower reliance on bilberry in areas with higher ungulate pressure, suggests niche shift. This pattern of resource overlap and bilberry reliance is expected to entail dissimilar consequences in the performance of these herbivores, with Capercaillie being the more susceptible to the negative consequences in case of heavy overbrowsing or interspecific competition. The reported, widespread increase of ungulate densities puts in focus the potential importance of competition and niche shift among distantly related herbivores, especially in the case of endemisms and threatened species.

INTRODUCTION

Patterns of resource overlap among sympatric species hint at the structure of the community; they reflect similarities among coexisting species indicating the degree of resource partitioning and potential for competition (*sensu* Keddy 1989; Putman 1994). Theory predicts that resource overlap should be stronger in assemblages of closely related species that share similar digestive systems and feeding behaviors (Schoener 1974, 1983; Underwood 1986). However, resource overlap between distantly related species has also been reported (e.g. Hulbert and Andersen 2001), although it has received much less attention. Large differences in body size, energy requirements, life history characteristics or even abundances, may yield highly asymmetric competition and nested niches (Aikio 2004; Abrams et al. 2008; Araújo et al. 2010), especially when species differ in specialization and the niche of the specialist species is likely to be contained inside the wider niche of a generalist. Hence, competitive interactions between distantly related species may also play an important role in community structuring.

The assessment of resource overlap and partitioning between species is the first step in the evaluation of competition for resources. It demonstrates that competition affects community structure when the prerequisite of limiting resources is met (Keddy 1989). Such is the case when two species show a high degree of overlap in resource utilization in allopatry, and low overlap in sympatry (Schoener 1970; Putman 1994) due to niche shift (Schoener 1974). The same can be argued in the case of low/high competitor densities (Latham 1999; Bonesi et al. 2004) or periods of resource abundance/scarcity (i.e. summer/winter in seasonal environments; Gordon and Illius 1989). However, the final definitive proof of an increase in competition intensity is the reduction in fitness of the outcompeted species.

There is a widespread increase in the abundance and range of both wild and domestic ungulates (Gill 1990). This increase has profound, negative effects on primary producers, thereby indirectly affecting the rest of the food web (Côté et al. 2004). For instance, the browsing effects of this increase in ungulate activity may alter patterns of resource overlap between herbivores and, therefore, the outcome of competition (Latham 1999; Dolman and Waber 2008). The assessment of patterns of resource overlap among wild and domestic ungulates has been the object of numerous studies (reviewed in Latham 1999), but few have attempted to address this subject between species that are not so closely related.

Our study area, the Atlantic forest in the Cantabrian range of NW Spain, is no exception to the increase in wild and domestic ungulates. Ungulates in the area may affect resource availability for smaller, rarer herbivores like Cantabrian Capercaillie *Tetrao urogallus cantabricus*, an endemic and endangered population comprising the southwestern limit of the species' range (Quevedo et al. 2006b). Cantabrian Capercaillie shows phenotypic, genetic and ecological differences from its conspecifics that inhabit the coniferous woodland (e.g. Blanco-Fontao et al. 2010). It lives in purely deciduous forests, facing a shortage of arboreal food resources in winter, which results in a strong diet reliance on understory plants (Blanco-Fontao et al. 2010). Such trophic behavior could render this population more susceptible to suffer negative effects of competition with large, wide-ranging ungulates, which have larger, more complex digestive tracts, and higher intake rates (Sedinger 1997; Van Gils et al. 2007).

Bilberry *Vaccinium myrtillus*, a dwarf shrub of forest understory, is a key resource for Capercaillie (Storch 1993; Blanco-Fontao et al. 2010), and an important diet resource for red deer *Cervus elaphus,* and roe deer *Capreolus capreolus* (reviewed in Cornelis et al. 1999; Gebert and Verheyden-Tixier 2001). It may also be consumed by free-ranging cattle in spring and summer. Bilberry performance significantly decrease after prolonged ungulate herbivory (Tolvanen 1994), being thus a likely candidate for overbrowsing. It is worth noting that it is much less abundant in the Cantabrian Mountains (its southern distribution limit) than in boreal areas. Hence, bilberry may be a shared resource for ungulates and Capercaillie and contribute to a potential niche overlap between these distantly related species in the Cantabrian Mountains. However, Capercaillie low numbers and sparse distribution (Storch et al. 2006) hints at an asymmetric effect on resources, where this bird is likely to have a relatively little impact on resources for ungulates but not vice versa.

In this context, we predicted a key role of bilberry in the diets of both Capercaillie and ungulates and a significant reduction of the availability of this resource for large herbivores when high ungulate densities are reached. In addition, we expected a high resource overlap between coexisting distantly related taxa (Capercaillie and ungulates) that may result in Capercaillie niche shift due to asymmetric exploitation competition (Aikio 2004). To test these predictions we investigate the patterns of trophic overlap between these distantly related taxa. Specifically, we assessed (1) seasonal red deer, roe deer, cattle and Capercaillie diets, (2) bilberry availability as a consequence of ungulate herbivory and (3) seasonal patterns of trophic niche overlap, niche breadth and trophic niche shifts for the same three ungulate species and Cantabrian Capercaillie in two adjacent areas differing in ungulate density.

MATERIAL AND METHODS

Study site

Our study area includes the Atlantic montane deciduous forests and treeline of the present Cantabrian Capercaillie distribution range, on the northern slopes of the

Cantabrian Mountains (Asturias province, northwestern Spain, Fig. III. 1). This mountain range contains the largest portion of the remnant Atlantic deciduous forest on the Iberian Peninsula and constitutes one of the southernmost boundaries of this habitat (García et al. 2005). Beech *Fagus sylvatica,* sessile oak *Quercus petraea* and birch *Betula pubescens* forests are dominant, but isolated trees or small groups of holly *Ilex aquifolium* and rowan *Sorbus aucuparia* also occur scattered through the forest. The understory is mainly composed of bilberry *Vaccinium myrtillus*, tree heaths *Erica arborea*, common heather *Calluna vulgaris* and broom formations (*Genista florida*, *Cytisus scoparius*), although herbaceous understory is also quite frequent. The treeline lies at about 1600 m a.s.l., and is a fine-grained mixture of birch thicket, tree heaths, common heather and bilberry, broom formations, grazing meadows, and talus.

The wild ungulates present in Cantabrian forests are red deer, roe deer, chamois *Rupicapra pyrenaica* and wild boar *Sus scrofa*. Additionally, when considering the effect of ungulates in the Cantabrian forests, the large number of livestock in the area (mostly cattle) should not be ignored, as they dominate ungulate biomass in a substantial part of the range (Rodríguez et al. 2007; Blanco-Fontao et al. 2011) and spend at least 6 months of the year (from early spring to late autumn) in the upland summer pastures, frequently using the adjacent forests (B. Blanco-Fontao personal observation).

Based on previous knowledge of ungulate densities in the Cantabrian Mountains (Asturian Environmental Agency, unpublished data), and on the distribution range of Cantabrian Capercaillie, the study area was divided into two adjacent subareas: the western part of the range with *a priori* lower ungulate biomass density and the eastern side which supports higher densities (Table III. 1, Fig. 1). The division of these subareas also corresponds to the incipient gap between the eastern and western Capercaillie populations.

	Western Subarea	Eastern Subarea
Approx. area (km^2)	520	330
Cattle density (2008 census)	11.13	19.93
Red deer density	3.75	5.26
Roe deer density	7.38	6.35
Capercaillie lek occupancy rate (2005-2007 census)	44.14%	26.75%
Capercaillie productivity (chicks per hen, census 2006-2007)	0.93	0.75

Table III. 1: Ungulate density (individuals/km^2) and Cantabrian Capercaillie population characteristics in the two study subareas. Roe and red deer approximate densities are estimated on the basis of hunting data for the 2008/2009 hunting season.

Sampling design and ungulate abundances

Sampling units were 10 plots of 1 km^2, based on the UTM grid, distributed across the study area, 5 in each of the subareas (Fig. III. 1). The plots were regularly spaced over the study area to represent its variability, the only condition being forested plots with bilberry cover of over 30% of the understory surface (i.e. rich in bilberry) to control for this species abundance.

Each plot was surveyed bimonthly, from May 2007 to March 2008, in a two-hour zigzag sampling effort conducted by the same individual observer. The observer counted the fecal pellet groups of red deer, roe deer and cattle in a 1 m wide strip, and used a GPS to obtain the total distance walked in each plot (mean area ± SD covered per plot and survey: 2176 m^2 ± 424). We considered fecal pellet counts as appropriate estimates of ungulate abundances in our study area, as neither habitat nor diet differences are likely to occur among plots or subareas and bias the results: all the plots were included within the same habitat type (Atlantic montane deciduous forests) and diet differences are not expected on the basis of previous diet studies (e.g. Fandos et al. 1987). We focused on these three ungulate species as they overlap in habitat use with Capercaillie and are the most likely to show a high trophic overlap with them in the Cantabrian range. Moreover, they account for the vast majority of herbivore biomass in the study area (Rodríguez et al. 2007).

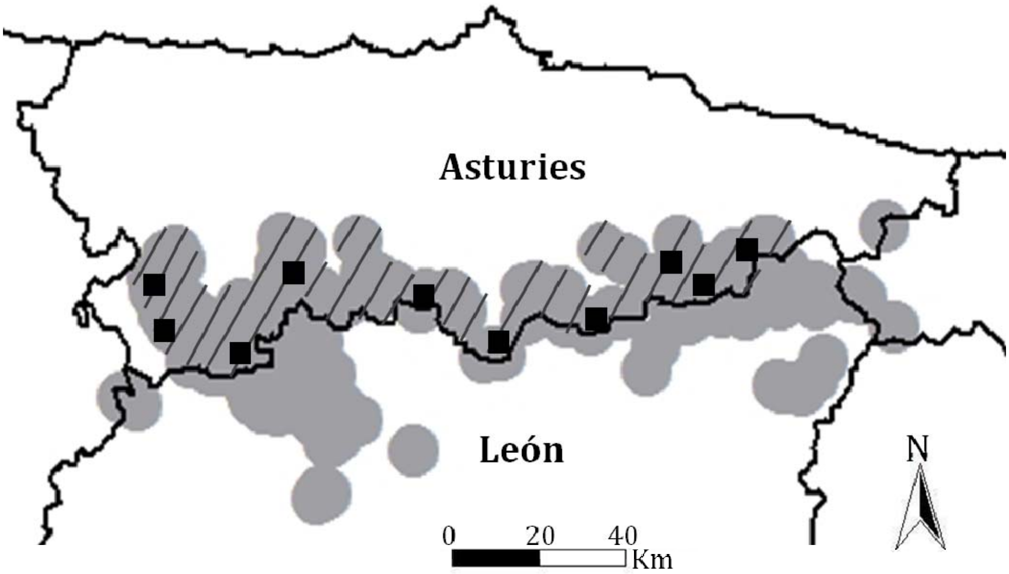

Figure III. 1: Study area (striped area) inside the area of occupancy of Cantabrian Capercaillie (in grey), mapped by plotting buffer areas of 2-km radius around display grounds occupied in 2007 (see Storch 2007, for criteria). Black rectangles represent the survey plots. The discontinuous line divides the western and eastern subareas.

In spite of the variability of fecal pellet decay rates (Mayle and Peace 1998; Laing et al. 2003), we considered the time lapse of two months between sampling periods as appropriate in our study area to avoid resampling fecal pellet groups (B. Blanco-Fontao, personal observation.) and to allow the evaluation of seasonal changes. We used fecal pellet group counts as a relative index of ungulate abundances in order to infer herbivory pressure (Harkonen and Heikkila 1999). Yearly average ungulate species abundances on the plots expressed as number of fecal groups per ha were transformed to calculate a weighted index of ungulate herbivory pressure, assuming the average body masses and defecation rates shown in Appendix B and also assuming metabolic needs in herbivores scale with weight (W) as $W^{0.75}$ (Demment and Vansoest 1985). The values for the different species (red deer, roe deer and cattle) were added to give an average value for each plot. Finally, we used a one-way ANOVA to evaluate differences in ungulate herbivory pressure between the two adjacent subareas.

Herbivory damage to bilberry by ungulates

We measured the damage caused to bilberry by browsing ungulates in 100 subplots. In each of the 10 1-Km^2 plots, we selected 10 circular subplots (10-meter radius), randomly distributed and spread across the plots. The first 100 annual bilberry shoots visually contacted in each subplot were evaluated as browsed or not to obtain a percentage of damaged bilberry shoots. Although ungulates browsing is undistinguishable from Capercaillie browsing, the vast majority of this damage can be attributed to ungulates, as Capercaillie density and biomass is negligible compared to ungulates one; being its effect insignificant. For instance, Capercaillie density in the Cantabrian range averages 0.29 ind./km^2 (Storch et al. 2006) whereas cattle densities alone in the same area are approx 100-fold those of Capercaillie (23.4 ind./km^2; Blanco-Fontao et al. 2011). Only the current annual shoots were taken into account as they are those preferred by herbivores, and thus most often consumed, due to their higher dietary quality (González-Hernández and Silva-Pando 1996). Annual shoots are not lignified, allowing them to be distinguished from the previous year's shoots, hence this measurement avoided recording herbivory from previous years. These measurements were taken twice, in May 2007 and March 2008. Although the measurement dates differ by two months in the two different years, both dates give an indication of bilberry damage occurring before the start of the growing season in each year. This is due to the very different climatic conditions in the years studied, whereby the start of the growing season was considerably delayed in 2007. As current annual bilberry shoots are those preferred by herbivores (González-Hernández and Silva-Pando 1996), the measurement of the percentage of predated annual shoots provide a proxy of the remaining bilberry availability as diet resource for large herbivores in the two subareas.

The relationship between the average damage to annual bilberry shoots and the weighted index of ungulate herbivory (averaged across the year for each plot) was analyzed by means of GLMs, with a Gaussian distribution of errors for the response variable (bilberry damage). To account for differences between the two sampling periods, year (2006 and 2007) was also entered in the model as a predictor variable.

Diet

In each of the ten plots, we collected 5 fresh fecal pellet groups per ungulate species (roe and red deer) every two months from May 2007 to March 2008. Four of the plots showed no sign at all of red deer in the year. Feces from free-ranging cattle were found and collected in 6 of the plots during the sampling periods of July, September and November, which corresponds to the cattle grazing period in the study area. A minimum distance of 200 m between collected fecal pellet groups was considered to represent collection of feces from different feeding events and therefore to avoid pseudoreplication. A single sample was obtained per sampling period and plot by mixing all the samples collected within each period and plot making a total of 55 composite samples for roe deer, 36 for red deer and 18 for cattle, all of them above the minimum recommended number (N = 15 according to Anthony and Smith 1974). In our study, composite samples provide an evaluation of the three ungulate diets throughout the year as well as a comparison for Capercaillie diet. Finally, all fresh Capercaillie droppings found in the surveys were collected. We arbitrarily set a minimum distance of 50 m between droppings to minimize the use of droppings from the same feeding event. This smaller area chosen for considering a Capercaillie single feeding event is justified by the Capercaillie's smaller daily home ranges (Eliassen and Wegge 2007), the extra-time they have to devote to feeding to reach their energy requirements as herbivorous birds (Sedinger 1997; Van Gils et al. 2007) and their higher defecation rates compared to ungulates (Appendix B).

We used microhistological methods to identify plant remains in ungulate fecal pellets and Capercaillie droppings. This technique relies on the resistance of plant epidermis to herbivore digestion, which leaves plant fragments undigested and identifiable in the droppings (Alipayo et al. 1992). A reference library was prepared from potential food sources, determined from the available previous studies on red deer, roe deer, cattle and Capercaillie diets in the Cantabrian Mountains (e.g. Blanco-Fontao et al. 2010) and plant availability in the particular study area. See Blanco-Fontao et al. (2010) for details of sample preparation for microhistological analysis. The number of plant remains identified per ungulate fecal sample was set at 200 along eight transects (two transects on each of the four slides) i.e., the first 25 fragments intercepted per transect/scale line under a 100x microscope were counted. Thus we identified a total of 11,000, 7,200 and 3,600 fragments for roe deer, red deer and cattle, respectively. As the number of Capercaillie droppings found in these surveys was very small (n = 29), we also analyzed samples from previous surveys collected in the same areas and in the same fashion from October 1999 to April 2004 (n = 202). Including droppings from several years in the analysis is justified by an insignificant variation in (i) Cantabrian Capercaillie diet among years (Rodríguez and Obeso 2000; Blanco-Fontao et al. 2010) and (ii) also in ungulate abundances which numbers remained very high during all the study period (e.g. Rodríguez et al. 2007; Blanco-Fontao et al. 2011). The samples were balanced both for season and subarea. The number of fragments identified per Capercaillie sample was fixed at 50 (Blanco-Fontao et al. 2010), resulting in a total of 11,550 fragments identified. The fragments were identified to species level for trees and shrubs and assigned to one of the following categories for the herbaceous fragments: forbs, grasses, ferns, or mosses (Appendix C).

We grouped diet results in two periods according to the phenology of the Cantabrian forests and to the annual cycle of the study species: non-growing (November-April) and growing (May-October) seasons. Seasonal differences between eastern and western Capercaillie populations for the main diet categories were assessed by means of non-parametric Wilcoxon rank sum test.

Diet overlap and niche breadth

The indices of dietary overlap provide an objective measure of diet similarity and potential niche overlap between animals that occupy sympatric ranges (Anthony and Smith 1974). Overlap in diet between Capercaillie and the species of the ungulate assemblage was assessed using an asymmetrical overlap index (MacArthur and Levins 1967; Pianka 1973; Mishra et al. 2004).

$$O_{jk} = \frac{\sum \left(p_{ij} p_{ik} \right)}{\sum p_{ij}^2}$$

where O_{jk} is the niche overlap of species *k* on species *j*, and p_{ij} and p_{ik} represent the proportion that a diet category *i* contributes to the diets of herbivores *j* and *k.* This index separately estimates the extent to which the diet of one species overlaps with the other and vice versa. Thus, it shows the direction of most intense competition between pairs of species. For instance, it takes into account the fact that, if the diet of the first species of a pair of herbivores is a subset or is nested inside the trophic niche of the second (i.e. show a narrower niche), then, from the point of view of the former, overlap is total, but only partial from that of the second. We found this index to be superior to any other overlap index because we expected asymmetrical overlaps, due to differences in size, physiology, and specialization; Capercaillie trophic niche is expected to be nested in the ungulate niche. We also used this index to calculate the overlap between Capercaillie and roe deer in the two subareas with different ungulate herbivory pressure. We did not calculate this same index for the Capercaillie-red deer and Capercaillie-cattle pairs, due to the small sample sizes of these ungulates in the western subarea.

Additionally, we used a symmetric overlap index (Pianka 1973) to calculate the seasonal diet overlap between western and eastern populations (overlap within each species, between populations) and assess a possible niche shift. This is a geometric mean of the two values of the asymmetrical index that characterize any given pair:

$$O_{jk} = \frac{\sum\left(p_{ij}\,p_{ik}\right)}{\sqrt{\sum p_{ij}^{2}\sum p_{ik}^{2}}}$$

The notation is the same as above. As before, this index was only calculated for the Capercaillie-roe deer pair. Dietary overlap for both indices can range from 0 (no overlap) to 1 (complete overlap; Anthony and Smith 1974), and significant overlap (that one that implies high competition potential) was judged at values of O_{jk} over 0.54

(MacArthur and Levins 1967; Putman 1994) for both asymmetrical and symmetrical overlap indexes.

The seasonal niche breadth of different species, representing diet diversity per fecal sample, was assessed as follows,

$$B = \frac{1}{\sum p_i^2}$$

where *pi* is the proportion of diet contributed by diet category *i* (Levins 1968). This was standardized in order to compare between species on a scale of 0–1 following (Hurlbert 1978), $Bs = (B - 1)/(n - 1)$ where *n* is the total number of plant species. For Capercaillie, niche breadth was also assessed separately for the eastern and western populations.

Differences in niche breadth in relation to species and season, as well as differences in Capercaillie niche breadth between subareas and seasons, were tested using a two-factor ANOVA and post-hoc Tukey tests. Cattle were excluded from the former analysis as only summer samples were available.

RESULTS

Ungulate abundances and bilberry availability

We found significant differences in the yearly-averaged index of herbivory by ungulates between subareas ($F_{1,8} = 8.8$; $p = 0.018$). The index averaged 3.0 kg.day^{-1}ha^{-1} and 1.0 kg. day^{-1}ha^{-1} for the eastern and western subareas respectively (hereafter referred to as intensively browsed and moderately browsed). Roe deer numbers did not differ between the intensively and the moderately browsed subareas ($F_{1,8} = 0.4$, $p = 0.6$), whereas both red deer and cattle numbers were marginally significant (i.e. $p<0.1$) higher in the intensively browsed subarea ($F_{1,8} = 4.4$, $p = 0.068$; $F_{1,8} = 3.9$; $p = 0.091$, respectively) suggesting that the difference in the index of ungulate herbivory pressure is due to red deer and cattle numbers.

The proportion of damaged bilberry shoots was higher in the intensively browsed subarea (mean ± SD: 69.3 ± 9.8 *vs* 47.4 ± 17.7; $F_{1,8} = 13.0$; $p = 0.007$). The proportion of damaged shoots at the end of the growing season was positively associated with the weighted index of ungulate herbivory, averaged across the year for each plot (GLM: $Z = 3.5$, $p = 0.002$, $n = 20$, function = identity, index of ungulate pressure log-transformed).

Diets

Capercaillie diet in the winter period ($n = 113$) was almost equally distributed between beech buds, holly leaves and bilberry shoots. All three items together accounted for 56% of winter diet. Ferns and grasses were also important, accounting for 13% and 8.5% respectively of the diet in this season. In the reproductive season ($n = 118$), bilberry was the major diet item (32 %), followed by beech, fern fronds, and grasses at 18%, 12% and 11%, respectively. However, significant differences were found between Capercaillie populations in summer, when beech leaves replaced bilberry as the major summer diet item in the intensively browsed subarea (Wilcoxon sum rank tests for beech and bilberry in summer: $W = 759.5$, $p< 0.001$ and $W = 2336$, $p< 0.001$, respectively; Fig. III. 2).

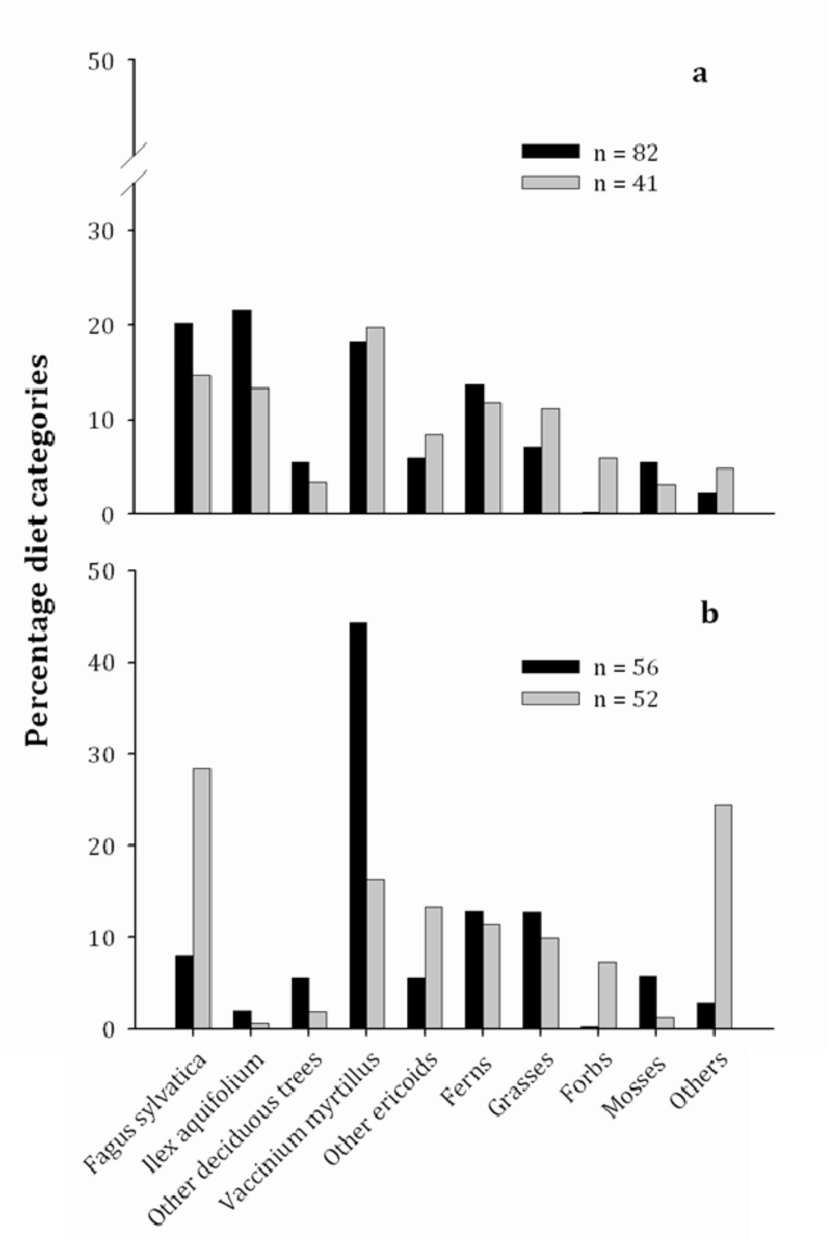

Figure III. 2: Capercaillie percentage diet categories in the moderately browsed (black columns) and intensively browsed subareas (grey columns) in winter (a) and summer (b).

Both bilberry and grasses were important for roe deer over the whole year and each accounted for approximately 20% of the diet. Additionally, in winter, ferns (12%) and holly leaves (10%), followed by heather, beech and heaths at 7 % each complete the bulk of roe deer diet. With respect to summer, roe deer diet is completed by ferns, accounting for 18% of the diet, and beech and forbs at 8% each (Appendix C).

The bulk of red deer diet was grasses, especially in summer (32%) but also in winter (26%). Bilberry, bramble, heaths and holly each accounted for approximately 7% of the winter diet. Bilberry was also important in summer (9%), as well as heather (8%). The other main items of summer diet were ferns and forbs, each accounting for 7% of the diet. Grasses accounted for 73% of cattle diet. The rest of their summer diet was mainly composed of mosses, forbs, ferns and bilberry but always in proportions under 5% (Appendix C).

Diet overlap and niche breadth

The highest mean asymmetrical overlap was observed between the two species of wild ungulates both in winter and summer (mean O_{jk} for both seasons = 0.85). Cattle trophic niche in summer was completely embedded (O_{jk} =1) in the niches of roe and red deer, but not vice versa (O_{jk} = 0.32 and 0.47 for roe and red deer, respectively). The overlap of Capercaillie diet with roe and red deer was stronger than its converse, both in summer and winter, indicating that Capercaillie diet was a subset of the diet of red and roe deer (Fig. III. 3). Capercaillie showed strongest overlap with roe deer, especially in summer (O_{jk} = 0.95, Fig. III. 3). At the other extreme, the overlap of Capercaillie on cattle diet was limited (O_{jk} = 0.19, Fig. III. 3).

The asymmetrical overlap index for Capercaillie diet on roe deer diet in the moderately browsed subarea was complete in summer (O_{jk} = 1) and very high in winter (O_{jk} =

0.84). The values of overlap in the intensively browsed subarea were also high but less than in the other subarea, although, in contrast, winter showed higher values (O_{jk} = 0.88) than summer (O_{jk} = 0.69). Roe deer niche in both seasons and Capercaillie niche in winter showed a high overlap between the two subareas (O_{jk} = 0.89, O_{jk} = 0.93 and O_{jk} = 0.92, respectively). However, in summer Capercaillie niche overlap between the intensively and moderately browsed subareas markedly decreased (O_{jk} = 0.67).

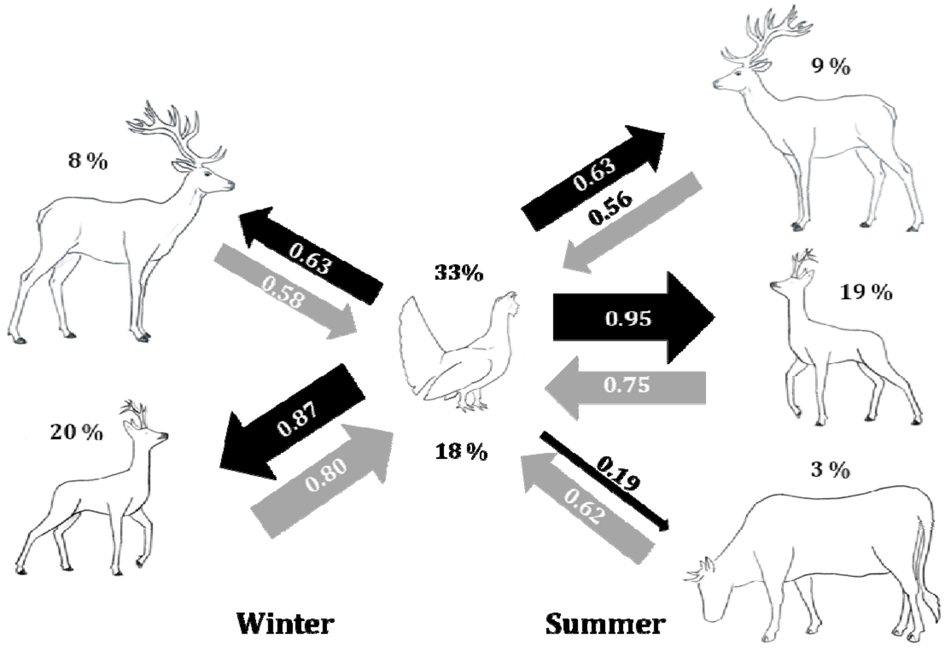

Figure III. 3: Overall index of asymmetric overlap for the whole study area. Values range from 0 (no overlap) to 1 (total overlap). Black arrows represent the overlap of Capercaillie diet with ungulates, whereas grey arrows show the overlap of ungulates with Capercaillie. Arrows are scaled according to the values. Percentages indicate the importance of bilberry in the diets; in the case of Capercaillie, summer is the upper value.

Niche breadth varied between species ($F_{2,313}$ = 47.4, p < 0.001, Fig. III. 4), with roe and red deer niches being wider than Capercaillie niche (p < 0.001 in both Tukey HSD tests), and also between seasons, with smaller summer values ($F_{1,313}$ = 5.5, p = 0.019). Focusing on Capercaillie, niche was wider in the intensively browsed subarea ($F_{1, 227}$ = 32.7, p < 0.001) and in winter ($F_{1,227}$ = 5.6, p = 0.019). Cattle in summer showed the narrowest niche breadth (Fig. III. 4).

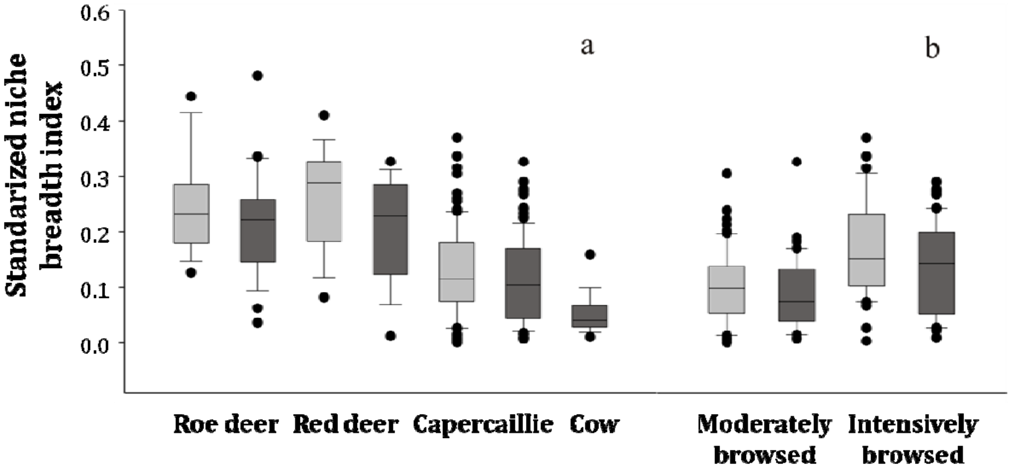

Figure III. 4 : Box plots showing seasonal niche breadth values (mean ± 1 SE) a) for the ungulate assemblage and Cantabrian Capercaillie in the Cantabrian Mountains and b) Cantabrian Capercaillie in the moderately and intensively browsed subareas. Light grey and dark grey columns represent winter and summer, respectively.

DISCUSSION

Resource overlap and potential for competition

The application of the morphological niche in studies of species packing and competition potential has led to studies of resource overlap and competition mostly focusing on closely related species (Schoener 1983; Hurlbert et al. 1986; Morin et al. 1988). Conversely, interactions between distantly related taxa have received much less attention, although they may be strong and their effect on the species' performance is likely to be different from that between closely related species.

In this study, we report strong resource overlap between distant species (mammals and a bird). The overlap was asymmetric, following a nested niche pattern: the bird's niche was contained within the broader niche of the ungulates. This fact suggests dissimilar consequences in the case of competition in the performance of the overlapping taxa, with the species with the embedded niche being more highly susceptible to the negative effects of competition (Aikio 2004; Abrams et al. 2008).

Patterns of resource overlap are a tool to assess the potential of exploitative competition when the rarity of endangered populations prevents manipulative studies (e.g. Mac Nally 1983; Schoener 1983). However, some assumptions are necessarily required to definitely evaluate the effect of competition in a population: 1) two or more species share a resource whose demand with respect to supply is high, and one of the species must negatively affect the acquisition of this key resource by the other 2) high resource overlap is found in allopatry but is reduced in sympatry due to niche shift, 3) reductions in resources availability are translated into a poorer performance of the study population (Mac Nally 1983; Keddy 1989; Petren and Case 1996). In this sense, our study makes an important contribution as we assessed the evidence of potential for asymmetric exploitative competition between two distantly related taxa: Capercaillie and the sympatric guild of ungulates. We provide some evidence for each of the previous assumptions.

First, we found an important reduction in the availability of annual bilberry shoots between the moderately and intensively browsed subareas – reduction in bilberry availability being likely to imply limitation of this key resource for large herbivores in some parts of the range, at least in winter (<30% undamaged bilberry shoots) . This condition is easily met when there are high deer densities (Gordon et al. 2004), especially taking into account that only a small fraction of the available preferred resources are suitable for large herbivores (Putman 1994).

Additionally, bilberry performance is lower in the case of intensive browsing (Tolvanen 1994). The reduction in bilberry availability, with its synergistic reduction in performance, may be related to the niche shift observed in summer in the eastern Capercaillie populations. That is, in the intensively browsed subarea, Capercaillie did not shift to the highly preferred, and expected, bilberry-based summer diet (Blanco-Fontao et al. 2010), whereas it did in the moderately browsed subarea, where bilberry availability was greater. The lack of preferred resources may explain the reported shift, and it is also in accordance with the broader niche found in the eastern Capercaillie population. In this regard, when a species or an individual is outcompeted from preferred resources, it is likely to broaden its trophic niche by increasing its consumption of less suitable forage (e.g. Gordon and Illius 1989; Agashe and Bolnick 2010).

Second, we showed high overlap between Capercaillie and wild ungulates. This overlap was not symmetrical: the narrower Capercaillie niche was a subset of the wild ungulates' niche. Therefore, Capercaillie seems prone to being negatively affected by these ungulates in the case of strong competition. It could be argued that this is also the case for cattle, whose narrow niche is embedded in that of the wild ungulates. However, cattle diet is supplemented with fodder, thereby departing from the natural regime.

High overlap of resource use demonstrates potential for competition between species; it does not prove that competition is strong enough to affect individual species performance (Goldberg and Barton 1992). However, an increase in the intensity of competition is evidenced when a decrease in resource availability is followed by a reduction in resource overlap between species (Schoener 1970, 1982; Putman 1994). In other words, when competition for resources increases, resource partitioning or niche shift diminishes interspecific diet overlap (Hespenheide 1975; Gordon and Illius 1989). For instance, reductions in interspecific overlap from allopatry to simpatry, from summer to winter, or in areas with higher competitor densities (Bonesi et al. 2004) clearly point towards an increase in competition for resources. In accordance with these predictions, we found smaller diet overlap between Capercaillie and roe deer in the intensively browsed subarea than in the moderately browsed one, and also a slightly smaller overlap in winter than in summer.

Lastly, the final step to prove the negative effects of competition on Capercaillie populations would relate the depletion in bilberry availability with a loss of performance in Capercaillie populations. Although this information is missing, there is some evidence of higher decline rates and lower productivity (see table III. 1) in the eastern Capercaillie populations. We speculate that the niche shift observed regarding summer bilberry consumption in the eastern populations, may be influencing female nutrition in the energy-demanding breeding season, which in turn, is known to affect grouse fecundity and breeding success (Sedinger 1997).

All in all, niche and overlap measures may provide useful insights into potential for competition (*sensu* Putman 1994) in rare, endangered populations living in rugged landscapes. However no such interaction may be in fact occurring yet and the definite proof of the negative effects of competition in the performance of a population should be addressed through manipulative experiments (Schoener 1983).

Bilberry: focus on shared resources

Bilberry constitutes an important component of the understory in holarctic montane and taiga forests; it is a key resource for both vertebrate and invertebrate herbivores (Hancock et al. 2010). The importance of this dwarf shrub in the diet of Capercaillie is a unifying feature of different populations of the species, which otherwise show a large distribution range and face distinct conditions (Blanco-Fontao et al. 2010).

Wild ungulates have also found a stable, year-round resource in bilberry that drives a significant reduction in bilberry shoot availability (<30% undamaged at the end of the growing season) in the area supporting higher levels of herbivory. The proportion of bilberry in the diet of red deer and cattle are smaller than those of roe deer. However, the two former ungulates showed higher abundances in the intensively browsed subarea, whilst roe deer numbers remained similar in both subareas. Thus, red deer and cattle are likely to account for the difference in bilberry damage between subareas. Moreover, maximum intake rates for red deer and cattle are, respectively, 2.35 and 5.3 times those of roe deer (average values for red deer and cattle reviewed in Shipley et al. (1994); we did not find maximum intake rates for roe deer, and we used the values provided by Gross et al. (1993) for white-tailed deer *Odocoileus virginianus*). Hence, the additive effect of all the ungulate species resulted in a high overall bilberry consumption. If these high levels of bilberry consumption are prolonged over time, herbivory can have long-lasting, dramatic effects on bilberry performance, leading to a decrease in its biomass and nutritive value (Tolvanen 1994). This fact may have negative consequences for all the large herbivore community. In particular, the greater reliance of Capercaillie on bilberry suggests that Capercaillie would be most negatively affected by a decrease in bilberry availability.

Finally, reductions in bilberry cover may lead to indirect effects in the performance of Capercaillie by means of a reduction in ground nest site quality (Allombert et al. 2005a), decreasing shelter against predation, and weakening the assemblage of invertebrates associated to the plant, which are an important resource for birds in general and specifically for the broods of Capercaillie (Baines et al. 1994; Fuller 2001).

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Capítulo IV

Abandonment of traditional uses in mountain areas: typological thinking *versus* hard data in the Cantabrian Mountains (NW Spain)

Beatriz Blanco-Fontao, Mario Quevedo, José Ramón Obeso

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Unidad Mixta de Investigación en Biodiversidad (CSIC/UO/PA), Dpto. de Biología de Organismos y Sistemas, Área de Ecología, Universidad de Oviedo

Abstract. Conservation policies of the European Nature 2000 network reflect an overarching concern about alleged negative effects of abandonment of traditional uses. In particular, the abandonment of livestock herding is widely assumed to be responsible of biodiversity decreases through habitat homogenization. However, those negative effects of land abandonment on biodiversity are neither straightforward nor the repeatedly assumed land abandonment has been always supported by hard data. We analyzed the evolution of cattle densities in the Cantabrian Mountains (NW Spain) in the past 20 years, and its relation with the decline in the occupancy of Capercaillie leks. Instead of the widely-assumed decrease of livestock numbers, which has been already incorporated into landscape and wildlife management, we found an actual increase in cattle numbers. Those cattle numbers were negatively related to the presence of an endangered, distinctive population of Capercaillie, a bird considered an umbrella species in mountain forest ecosystems. Thus our data do not support the alleged role of free-ranging livestock in the conservation of biodiversity. We consider that typological thinking in the relationship of socio-economic changes and biodiversity conservation should be replaced by hard data and consideration of ecosystem naturalness.

INTRODUCTION

Trends in European land use have taken two opposing directions in the last decades: either agricultural intensification or land abandonment (Meeus 1995). Surprisingly, both of them have been claimed as determinants of biodiversity decreases through landscape and habitat homogenization (Ostermann 1998; Benton et al. 2003). Agricultural intensification has negative effects on biodiversity because it leads to highly simplified communities, a consequent disruption of food chains, and declines in many farmland species (reviewed in Stoate et al. 2001). On the other hand, the results of previous studies on the effects of land abandonment on biodiversity are ambiguous, and depend on the temporal and spatial scales considered (MacDonald et al. 2000); those results are also subjective, depending on the relative importance assigned to mere species richness vs. functional diversity or even considerations of ecosystem naturalness.

In particular, the abandonment of certain land uses like livestock herding in mountain areas is frequently regarded as a conservation problem, leading to overall decreases in biodiversity (West 1993). The assumed negative effects of land abandonment are reflected in the European conservation policies, which appear to aim at maintaining the so-called traditional land uses, claiming that they benefit certain species (Larsson and Spyropoulou 2006). For instance, these policies consider farmed environments as part of the European Natura 2000 network, and prescribe active management to maintain the attributes of the above-mentioned environments (Tucker and Evans 1997; Ostermann 1998; Ludwig 2001). However, the effects of abandonment of certain land uses on biodiversity showed complex, contrasting results in several studies (West 1993; Suárez-Seoane et al. 2002; Laiolo et al. 2004). Moreover, the abandonment of land uses, incorporated into management advice even at the European scale, has not always been supported by hard data. Conversely, the numbers of free-ranging cattle have experienced increases in many ranges in the last century (Putman 1994; Trimble and Mendel 1995), and globally account for the majority of ungulate biomass in ranges (Schwartz and Ellis 1981).

Perhaps then concerns should be raised about the effects on ecosystems of high densities of free-ranging livestock. Those effects may range from changes in the plant community through overgrazing and trampling to modifications in the herbivore interactions and changes in the ecosystem processes and functioning (Côté et al. 2004). In addition, two major biases may be perceived in European policies that advice the protection of farming landscapes by preventing the abandonment of land use. First, the centuries of human influence in the landscape seem trivial compared to the time scale at which evolution operates in ecosystems. A long-term perspective is necessary to establish the natural attributes of ecosystems and, based on those natural attributes, to set the goals of biodiversity conservation (Willis and Birks 2006). Second, high levels of biodiversity are the adduced reason for the protection of many extensive farming landscapes (e.g. Suárez-Seoane et al. 2002; Laiolo et al. 2004; Spiegelberger et al. 2006). However, biodiversity per se does not guarantee the naturalness of the ecosystem (*sensu* Angermeier 2000), and says nothing about its functioning. Naturalness and stability of ecosystem functioning are more holistic conservation objectives (Noss 1990; Angermeier 2000; Petchey and Gaston 2006). They set the baseline on how much diversity should be conserved to maintain the natural attributes of the ecosystem, which elements should contribute to that diversity, and where those elements should occur to ensure a certain degree of naturalness and guarantee the ecosystem functioning (Anderson 1991; Angermeier 2000).

We present a case study, conducted in the Cantabrian Mountains of NW Spain, a semi-natural landscape result of centuries of human influence. The landscape shows a fine-grained mosaic of forests, heathlands and pastures (García et al. 2005), partly maintained by ungulate grazing. This mountain range still holds an assemblage of habitats and species remarkable in the context of the highly developed Western Europe; it is readily perceived considering the extant array of habitat- or resource-demanding vertebrates: wolves, brown bears, black and middle-spotted woodpecker, golden eagles, and Capercaillie. However, some concerns have been raised about the effects of changes in livestock-related practices and the conservation of this ecosystem (Serrano et al. 2006). For instance, an assumed decline in extensive cattle herding has been related to scarcity of suitable habitat for broom hare *Lepus castroviejoi* and Pyrenean grey partridge *Perdix perdix hispaniensis* (Acevedo et al. 2007). As a result, there is a widely assumed idea that cattle numbers in the upland pastures have been declining in recent decades, leading to overall decreases in biodiversity. We contend that none of these assumptions have been supported by hard data. We question the widely accepted positive relation between livestock densities and biodiversity with data on cattle densities in the habitat of Cantabrian Capercaillie (*Tetrao urogallus cantabricus*), a distinctive and endangered population of an umbrella species (Suter et al. 2002) whose response to cattle densities may be indicative of the overall effect on the montane forest ecosystem. However, we do not aim at discussing here those situations in which traditional uses are the sole alternatives to heavy anthropogenic disturbance (reviewed in Norris 2008).

METHODS

Between 2005 and 2007 a survey of Capercaillie lek occupancy was performed in the northern watershed of the Cantabrian Mountains (NW Spain, Asturias, Fig. IV. 1), over a territory that comprises more than 50% of the bird's population (Bañuelos and Quevedo 2008). Almost all known and occupied display areas in a census performed in the 80's (N=364; Del Campo and García-Gaona 1983) were repeatedly surveyed during the lekking season (April-May). Surveys were performed during the day, looking for signs such as feathers, fresh droppings or footprints, so that results were mainly presence-absence data. Occupancy surveys during the day were mostly chosen over more traditional lek counts at dawn to minimize disturbances, but also because the previous survey (2000/2001) showed that less than 10% of the occupied sites had more than one cock (Obeso and Bañuelos 2003).

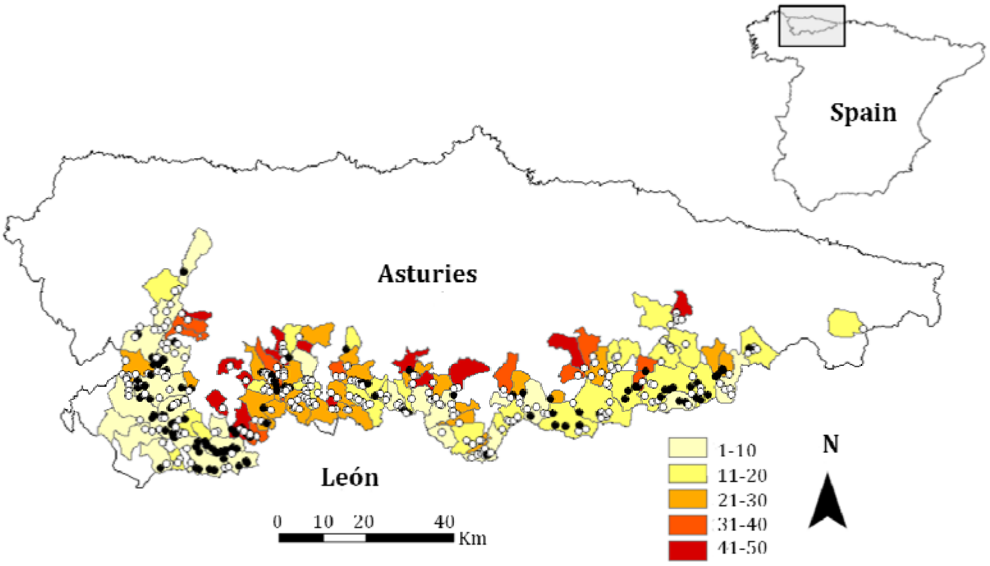

Figure IV. 1: Combined free-ranging horse and cattle densities (heads × km^{-2}) in the Asturian parishes within Capercaillie distribution range. Filled and clear circles represent occupied and empty Capercaillie leks, respectively, according to last occupation survey (2005-2007).

To relate the probability of lek abandonment to cattle and horse densities, we obtained the numbers of free-ranging cattle and horses for 2007 from the Department of Agriculture of the Asturias government at the administrative level of parishes, a subdivision within municipalities with average surface of 27 Km^2. We calculated mean biomass livestock density in the study area considering available mean body mass values for cattle (Llaneza et al. 1996; Rodríguez et al. 2007). Additionally, the evolution of free-ranging cattle numbers in the northern watershed of the Cantabrian range was evaluated from 1986 to 2007 at the administrative level of municipalities (data on cattle densities were available for 1986, 1998, 2003 and 2007).

To relate cattle densities to the probability of lek abandonment, we used logistic regression. We considered that a parish was either occupied (1) when at least one of the leks remained active according to the last census, or abandoned (0) when all leks showed no activity. Cattle densities were log-transformed.

RESULTS

Cattle and horse densities in the upland summer pastures of the northern watershed of the Cantabrian Range averaged 23. 4 (±18.9) heads Km^{-2} in 2007 (range 0.2 to 100 heads Km^{-2} (Fig. 1). 29% of the parishes showed cattle densities above 30 heads Km^{-2}. Cattle represent the bulk of livestock biomass within the Capercaillie distribution area in the Asturias province (89%) followed by horses (8%), both together summing a mean biomass density of 3.734 Kg Km $^{-2}$.

The overall cattle densities in the northern watershed of the Cantabrian Mountains experienced a significant 28 % increase from 1986 to 2007 (paired t-test for 1986 and 2007 cattle densities across municipalities: t_{16} = -5.18, p < 0.001; Fig. IV. 2). 14 out of the 16 municipalities of the study area showed increases in cattle numbers, while the remaining two showed slight decreases.

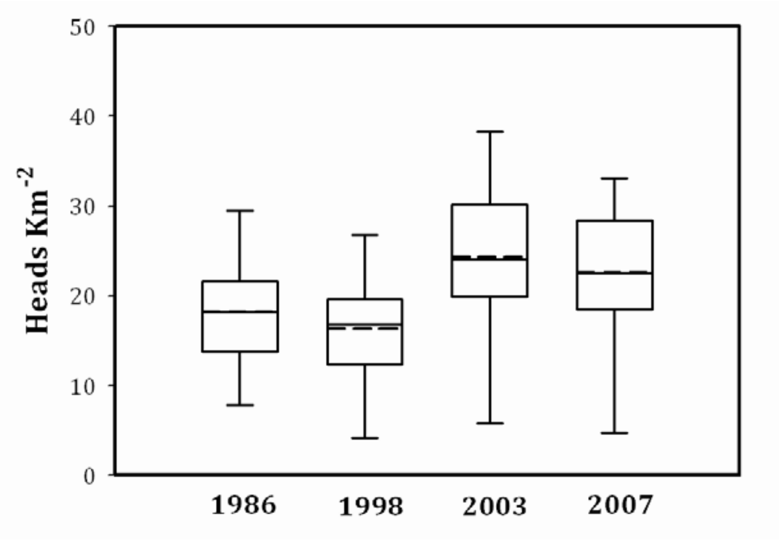

Figure IV. 2: Box and whisker plot showing the evolution of mean cattle densities from 1986 to 2007 (1986, 1998, 2003, 2007) across municipalities within Cantabrian Capercaillie distribution range in the northern watershed of the Cantabrian Range. *Boxes* indicate the interquartile range of the data and the position of the median (*continuous line*); *error bars* extend to non-outlier data within 1.5 times the interquartile range; *dots* represent the 5th/95th percentile. *Dashed lines* represent mean cattle and horse densities.

Lek occupancy was negatively related with the density of cattle and horses ($\chi^2_{1,\,104} = -2.355$, $p = 0.018$, Fig. IV. 1 and IV. 3). In 67% of the parishes that showed densities above 20 heads Km^{-2}, all the leks were abandoned.

DISCUSSION

One idea that has percolated the practice of researchers and wildlife managers in Europe, not always based on hard data, is that upland terrain is being abandoned due to a decline in livestock numbers and the so-called traditional uses (Tucker and Evans 1997). We discussed this issue with a case-study carried out in uplands of NW Spain, an area where cattle herding is a major, so-called traditional, economic activity (Sociedad Asturiana de Estudios Económicos e Industriales, 2010).

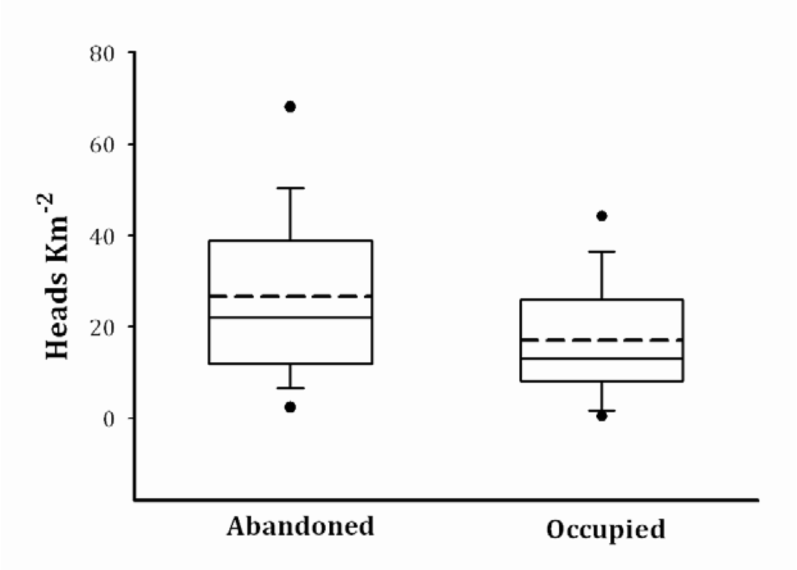

Figure IV. 3: Box and whisker plot showing combined cattle and horse density in areas that harbor either abandoned or occupied Capercaillie leks in the Cantabrian Range. Notation as for figure IV. 2.

Despite of likely decreasing permanent human presence in the mountains (Instituto Nacional de Estadística 2005), cattle numbers in the northern watershed of the Cantabrian Mountains have increased by 30% in the last 20 years. The trend is similar in the southern watershed of the mountain range, which showed increases up to 300% in the same period (Serrano et al. 2004; Olea and Mateo-Tomás 2009). Although we cannot draw excessive conclusions from our simple, correlative data, we found that cattle numbers showed a negative correlation to the occupancy of Capercaillie leks in spring. Coincidentally, Capercaillie in the recent decades showed an inverse trend, which led to its listing as Endangered (Quevedo et al. 2006a; Storch et al. 2006).

Besides considerations of what is natural or traditional, it is worth considering the sheer numbers: cattle account for the vast majority of ungulate biomass in the Cantabrian range. Their densities are one order of magnitude higher than those of wild ungulates; together with the latter, they attain biomass densities two times higher than the highest densities of native ungulates in temperate ecosystems (Mattson 1997; Rodríguez et al. 2007). But the issue that we raise with our case study is not solely local; free ranging cattle increased in many ranges in the last century (Putman 1994; Trimble and Mendel 1995), and presently account for the vast majority of ungulate biomass (Schwartz and Ellis 1981). At high densities, cattle may act as geomorphologic agents or ecosystem engineers (Trimble and Mendel 1995, Derner et al. 2009). They maintain open areas, altering ecological succession, and change nutrient cycling. Consequently, excessive, subsidized cattle densities may affect ecosystem processes directly by modifying pathways of energy and material flow, or indirectly by modifying the abundances of other species.

As noted before, cattle herding is often associated to the term *traditional* (e.g. López 2002; Lobo et al. 2006), which appears in the ecological and conservation literature loosely referring to long-term, low to moderate transformation of natural ecosystems due to human activities. We argue that its use needs careful consideration when it comes to present-day cattle herding: recent changes in extensive livestock practices actually approach intensive use modes in areas with easy access (MacDonald et al. 2000); cattle spend longer periods at summer upland pastures, and use adjacent forests more intensively (e.g. Ménoni 1994; Timmins 2002). Other departures from *tradition* in present-day cattle herding are supplemental feeding instead of reliance on available pastures and transhumance, and machinery-aided slashing of the natural upland vegetation, a common practice in the Cantabrian Mountains to favour pastures. Thus, cattle herding is not submitted to the carrying capacity of the ecosystem; its consideration as a traditional activity and a “conservation asset” (e.g. Hancock et al. 2010) for other species seems highly questionable.

Most current European mountain systems are semi-natural landscapes; consequence of a long history of low-intensity land uses (Birks 2005). However, such long history of human influence in the landscape is recent from an evolutionary perspective. The Cantabrian Mountains experienced the first pulse of deforestation associated to human activities only a couple of thousand years ago (Sobrino et al. 1997). Since then, deforestation took its toll on the closed, deciduous forests where Cantabrian Capercaillie and other native vertebrates live (Quevedo et al. 2006a). Were it not for the human impact, forest would presently be the dominant vegetation (Svenning 2002). Instead, landscape in the Cantabrian Mountains is highly fragmented, forest cover is less than 25%, and showed a likely indirect role in Capercaillie decline (García et al. 2005; Quevedo et al. 2006b). Hence, it is hard to see how could the reported cattle densities, which arguably suppress the ecological succession back to a forested landscape, be beneficial for any montane forest-dwelling vertebrate.

Underneath these considerations lays the question of what is natural, how far back should we go to find conservation goals (Willis and Birks 2006), and whether to preserve cultural landscapes (*sensu* UNESCO 1974) or the naturalness and integrity of ecosystems (*sensu* Anderson 1991; Angermeier 2000). We feel that these considerations, together with more hard data at appropriate spatial scales, should replace typological thinking and assumptions about negative ecological effects of land abandonment in mountain areas. Preserving traditional uses of the landscape and helping local human communities are legitimate policy options. The aesthetic and social values of these modified mountain landscapes, while subjective, are not discussed here. Instead, we argue that such goals should not be disguised under the term of nature conservation. Instead, they should be named according to their main objective, e.g. preservation of cultural landscapes or economic activities.

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Capítulo V

Niche segregation in a lek-mating species despite moderate sexual size dimorphism

Foto: Lance McNew

Beatriz Blanco-Fontao[1], Mario Quevedo[1], José Ramón Obeso[1],
Lance B. McNew[2], Brett K. Sandercock[2]
[1]Unidad Mixta de Investigación en Biodiversidad (CSIC/UO/PA), Dpto. de Biología de Organismos y Sistemas, Área de Ecología, Universidad de Oviedo
[2] Division of Biology, Kansas State University

Abstract. Niche segregation is expected in lek-mating species with marked sexual size dimorphism, as a consequence of sex-specific ecological constraints. However, within lekking species, sexual dimorphism may be moderate and its consequences in sexual segregation uncertain. In addition, the niche of a species is context-dependent and may respond to changes in landscape composition. In particular, agricultural fragmentation may influence the trophic behavior of herbivores, even at population level. Sex-class differences and individual specialization may be important sources of variation of trophic behavior. Greater Prairie-Chickens are moderate sexually dimorphic grouse native to tallgrass prairies of North America, although they persist in less natural mosaics of agricultural crops and native habitats. We assessed differences in the trophic variability (trophic niche breadth and individual specialization) between male and female Greater Prairie-Chickens, in both fragmented and continuous native habitat. We used stable isotope analysis of carbon and nitrogen in three tissues (feathers, claws and blood) that integrated autumn, winter and spring diet. We found sexual niche segregation in Greater Prairie-Chickens. Females showed broader niches and a higher degree of individual specialization in winter and autumn; differences between males and females were smaller in spring, when birds converge in leks and may thus exhibit similar feeding behaviors. The marked distinct reproductive roles of males and females may explain the niche segregation found here. We also found higher trophic variability in continuous, native prairies than in agricultural mosaic landscapes throughout the annual cycle. Native habitats seem to provide greater dietary diversity that is reflected in a greater diversity of feeding strategies.

INTRODUCTION

Size dimorphism in vertebrates is usually associated with polygamy and large differences between the sexes in parental care (Owens and Hartley 1998). Lek-mating species tipically exhibit a polygynous mating system where males are the larger sex - presumably because of sexual selection for larger body size (Payne 1984; Björklund 1990) and take no part in parental care (Andersson 1994). The marked size differences between dimorphic males and females are frequently related to sexual niche segregation (Mysterud 2000; Phillips et al. 2009; Blanco-Fontao et al. in press). For instance, each sex in size dimorphic species shows specific nutritional requirements (Isaac 2005; Bulte et al. 2008), which, in turn, are likely to be reflected in distinct trophic niche variability (i.e. differences in overall niche breadth and individual specialization; Mysterud 2000; Bolnick et al. 2003; Ruckstuhl 2007). However, within lek-mating species, the degree of size dimorphism covaries with body size (Fairbairn 1997); thus large-bodied species show the greatest dimorphism and smaller species may be nearly sexually monomorphic (Höglund 1989). Based on sexual differences in size, monomorphic lekking species are not expected to show niche segregation; yet males and females may partition their niche as a result of their distinct reproductive roles.

In addition, the niche of the distinct populations of a species is context-dependent (Pulliam 2000) and expected to vary within the distribution of the species. Landscape composition in altered landscapes usually varies within the distribution range of a species and has been recognized as an important influence in key ecological processes (Turner 1989; Pulliam et al. 1992), such as the trophic ecology of herbivores inhabiting heterogeneous landscapes (Johnson et al. 1992). Fragmentation of native habitats due to conversion to agricultural crops is one of the main causes of landscape composition change worldwide (Saunders et al. 1991); unfragmented native habitats have been transformed to mosaics of agricultural lands and native habitat (Saunders et al. 1991; Laurence 2010). The associated landscape changes are expected to influence ecosystem dynamics (e.g. Herkert 1994; Terborgh et al. 2001), including the trophic niche modifications due to changes in the availability of resources throughout the annual cycle (e.g. Layman et al. 2007b; Abbas et al. 2011).

Within lekking grouse (Tetraonidae), Capercaillie (*Tetrao urogallus*) is the most sexually dimorphic species whith male mass nearly twice that of females (Madge et al. 2002). Previous work has shown the species to exhibit niche segregation (Blanco-Fontao et al. in press; Bañuelos et al. 2008). In contrast, Greater Prairie-Chicken (*Tympanuchus cupido;* hereafter "prairie-chicken") show moderate size differences between males and females (17%; Schroeder and Robb 1993); a difference in mass similar to that found in most monogamous birds (10-15%; Andersson 1994). Nevertheless, reproductive roles in this lek-mating species are sex-specific (del Hoyo et al. 1994). Prairie-chickens are native to the prairies of central North America. Prior to European settlement, prairie-chickens were widely distributed across all areas occupied by tallgrass prairie in North America (Schroeder and Robb 1993). However, cropland expansion and large-scale agricultural transformations largely fragmented the landscape (Svedarsky et al. 2000). Currently, the core range of prairie-chickens extends from South Dakota to Oklahoma (Schroeder and Robb 1993), inhabiting both areas that are dominated by native grasslands and fragmented areas. Recent research suggests that variability in landscape composition and human land use has resulted in large differences in demography, genetic structure, and population viability of prairie-chickens (Gregory 2011; McNew et al. 2011a, b, in press). Hence, niche differences between environments might be expected due to differences in the habitat structure and the availability in quantity and kind of diet resources throughout the annual cycle.

Trophic ecology is a central aspect of the niche of a species. It plays an important role in the ability of animals to cope with their environment, influencing their behavior, habitat selection, and demography (Sutherland 2004). Populations respond to the biotic and abiotic conditions of their local environment and, consequently, show different trophic behaviors (Chase and Leibold 2003; Blanco-Fontao et al. 2010). Different aspects of variation in trophic behavior among populations may be perceived in differences in average diet composition, and diet variance (Durell 2000; Catry et al. 2005; Bearhop et al. 2006). For instance, an important source of variation of the trophic ecology of a species across its range is how much individuals vary their food resources (Bearhop et al. 2006). Interindividual variation can be attributed to sex or age-class differences or to individual specialization *per se* (Bolnick et al. 2003). In particular, prairie-chickens are at the lower end of the size range of endothermic herbivores; accordingly, diet is an environmental constraint and they have to devote extra time to feeding to meet their energy requirements (Sedinger 1997; Van Gils et al. 2007). Adults eat mostly leaves, buds and seeds of native prairie species and cultivated grains, whereas chicks may eat a substantial amount of invertebrates during their growth (Yeatter 1943; Mohler 1952; Korschgen 1962; Jones 1963; Rumble et al. 1988).

Stable isotope analysis of consumer tissues is a powerful approach in the study of trophic ecology of species, populations or individuals (West et al. 2006), allowing the assessment of intersexual niche partitioning and intrapopulation trophic variability (Kelly 2000; Newsome et al. 2007). The value of stable isotopes in a given tissue provides a measure of the assimilated diet integrated throughout the period of tissue synthesis (Hobson and Clark 1992; Bearhop et al. 2002). Hence, analyzing tissues with distinct growth rates gives diet information that spans several temporal scales. Whole blood has rapid turnover and integrates diet during the 3-6 wk prior to sampling (Carleton and Martínez del Rio 2005). Claws and feathers are metabolically inert tissues that preserve diet information at the time of their synthesis. Claws integrate winter diet over the 2-5 month period before sample collection, whereas feathers integrate information from the molting and synthesis period of the previous year (Hobson and Clark 1992; Bearhop et al. 2002; Bearhop et al. 2003). We used stable isotope analyses of feathers, claws and whole blood sampled in spring, to gain insight into autumn, winter and spring diets, respectively. Specifically, we aimed to (1) evaluate intra-specific dietary variation between females and males throughout the annual cycle and (2) compare prairie-chicken feeding behavior in two populations differing in the degree of native habitat reduction. From such, we show context-dependent sexual niche segregation in a lekking species with moderate sexual size dimorphism.

METHODS

Study sites

Our field study was conducted at two study sites in north central Kansas that differed in land cover, land use and prairie fragmentation; one site located in the northern Flint Hills ecoregion and one site in the Smoky Hills ecoregion (Fig. V. 1). The two study areas were ≥ 112 km apart. The Flint Hills study site (hereafter *native prairie*; 533 km^2; 39°00’27”N 96°26’41”W) had land cover of 81% grassland and 10% cropland, a mean grassland patch size of 51 ha, and a road density of 0.57 km per km^2. The Smoky Hills site (hereafter *agricultural mosaic*; 1,295 km^2; 39°25’20”N 97°34’04”W) was more fragmented with landcover of 53% grassland and 38% cropland, a mean grassland patch size of 15 ha, and a higher road density of 1.4 km per km^2. Cultivated crops include sorghum, corn, wheat, and soybeans. Indices of prairie-chicken densities were 0.19 and 0.17 birds km^{-2} for native prairie and the agricultural mosaic, respectively.

Tissue collection

Prairie-chickens were captured at 20 lek sites with walk-in traps and drop-nets during March-May, 2009, following the methodology of Silvy et al. (1990); Schroeder and

Braun (1991). At first capture, we collected samples of three tissues: blood, claw and feather samples. We clipped 3 mm of the distal part of the toenail on one claw and collected the clipped toenail into a sterile envelope. Cutting the toenail allowed us to collect 1 ml of blood from the toe vein in an Eppendorf tube for preservation in 1.5 ml of 70% ethanol. Last, a chest covert feather was cut and stored in a paper envelope.

Stable isotope analysis

We measured $\delta^{13}C$ and $\delta^{15}N$ ratios in feathers, claws and blood to examine sexual and habitat-related population differences in the trophic variability of prairie-chickens. Each of the three tissues integrates dietary information from different periods of the annual cycle. Whole blood has rapid turnover and integrates diet during the 3-6 wk prior to sampling, according to Carleton and Martínez del Rio (2005) equations, and considering an average prairie-chicken weight of 1 kg (McNew, unpublished data). Hence, whole blood integrates prairie-chicken spring diet. Claws are a metabolically inert tissue that grows continuously integrating longer periods; the tip of them integrates dietary information of a 2-5 month period before sample collection, which corresponds, in this study, to winter diet (Bearhop et al. 2003). Finally, feathers are also metabolically inert tissues that preserve diet information at the time of their synthesis; this corresponds to the autumn diet of the previous year when molting and synthesis of new feathers occurs (Hobson and Clark 1992; Bearhop et al. 2002; Bearhop et al. 2003).

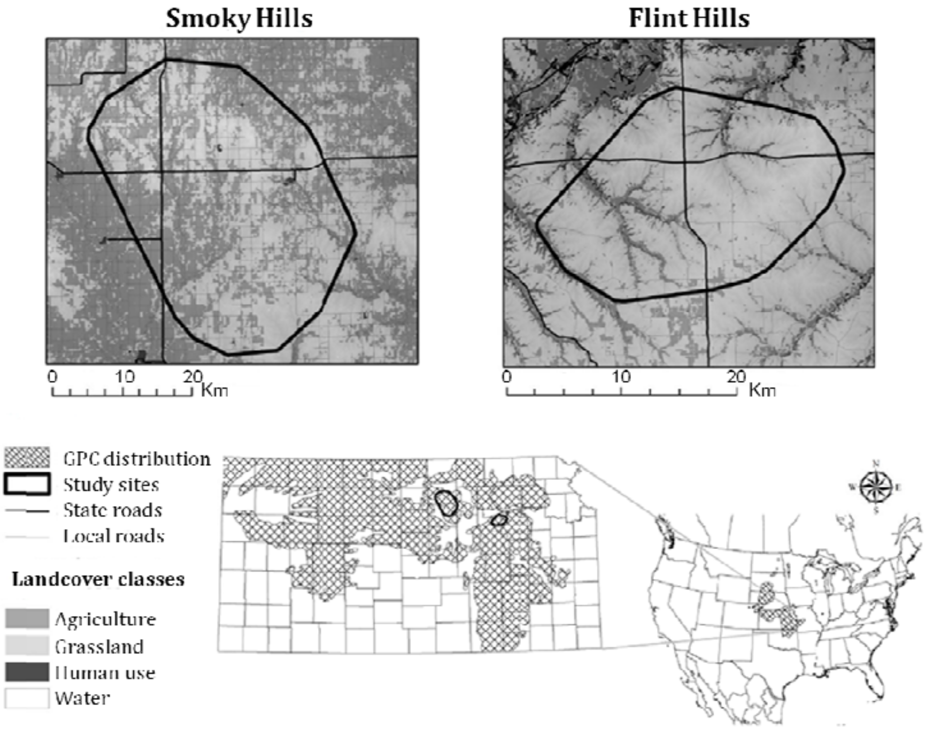

Figure V. 1: Greater Prairie-Chicken distribution and landcover of the study sites in Kansas showing differences in grassland fragamentation. The Smoky Hills study site is a mosaic of agricultural fields and native prairie. Native tallgrass prairie is relatively unfragmented at the Flint Hills site.

Blood samples were dried in an oven at 60ºC until the mass stabilized and then refrigerated until isotopic analysis. Feather and claw samples were cleaned to remove oils and debris by rinsing in a 2:1 chloroform-methanol solution for 24 hours and, and then dried in an oven at 60ºC to a constant mass. Feathers were frozen in liquid nitrogen and immediately ground to a fine powder using a MM200 ball mill. Approximately 1 mg (1 ± 0.2 mg) of each of the tissues was subsampled and packed into a 4 × 6 mm tin capsules for δ^{13}C and δ^{15}N analyses using a continuous-flow isotope ratio mass spectrometer at the University of California Davis Stable Isotope Facility

(USA). Stable isotopes ratios are expressed in δ notation, as parts per thousand deviation from a standard (‰). We used Pee Dee belemnite limestone as a standard for δ^{13} C and atmospheric nitrogen as a standard for δ^{15}N according to the equation:

δX = [(Rsample / Rstandard) − 1] × 1000 where X is ^{15}N or ^{13}C and R is the corresponding ratio of stable isotopes for ^{15}N:^{14}N or ^{13}C:^{12}C.

A random quarter of the samples were analyzed in duplicate, and the analytical error was minimal at 0.13‰ (± 0.14) for δ^{15}N and 0.18‰ (± 0.24) for δ^{13} C.

Trophic niche breadth and variability

To calculate trophic niche breadth and trophic variability, we used quantitative metrics based on the position of individuals in the δ^{13}C-δ^{15}N space, and Euclidean distances (Layman et al. 2007a). We applied those metrics to populations at our two study sites and to males and females within each population, using individuals as measurement units. The individuals of each subset (populations and sex-classes) were graphed in a δ^{13}C-δ^{15}N niche space. To estimate the total niche of each subset we measured the total area of the convex hull (TA) that included the isotopic values of all individuals. To obtain null distributions of TA and test the significance of differences between sexes and study sites, we randomized the empirical data set of isotopic signatures 1000 times and calculated TA in each resampled data set. P values were approximated as the proportion of resampled data sets that exceeded the observed differences.

To estimate the trophic variability within each sex and population we calculated Euclidean distances among individuals in the δ^{13}C-δ^{15}N biplot. First, we calculated the distance of each individual to the isotopic centroid of its subset (CD), providing an index of the trophic diversity within each segment of the population. Second, we calculated the coefficient of variation of the distances from each individual to its neighbors in the isotopic space (CVND), which yields a measure of the clustering of values and trophic redundancy within the subset of the population (Quevedo et al. 2009). Populations or subsets of the population with a large proportion of individuals characterized by similar trophic ecologies will exhibit a smaller CVND (increased trophic redundancy) than a population in which individuals are, on average, more divergent in terms of their trophic niche (Layman et al. 2007a; Quevedo et al. 2009).

We used factorial ANOVAs (type II SS) to determine whether study site or sex explained variation in $\delta^{13}C$ and $\delta^{15}N$ isotopic values of feathers, claws and blood The absolute isotopic values of claws ($\delta^{13}C$) and feathers (both isotopes) were log10-transformed to achieve normality and homogeneity of variances. Factorial ANOVAs were also used to test for differences between the fixed effects of study site and sex-class regarding CD (square root transformed to achieve normality and homocedasticity) and CVND. Significance was established at *alpha* levels ≤0.05. Means are presented ± 1SD. CD, CVND were calculated with QuantumGis 1.6.0. All statistical analyses were conducted in R Statistical Environment (R Development Core Team 2010), including package Adehabitat (Calenge 2006) for convex hulls and TA.

RESULTS

We captured 156 prairie-chickens at 20 leks during 6 March – 6 May, 2009; 8 located in native prairie and 12 located in the agricultural mosaic. In the isotopic analyses we used samples from all birds captured in the native prairie, from all the females captured in the agricultural mosaic, and a random selection of half the males captured in the agricultural mosaic to balance sample sizes. The selection totaled 100 feather samples, 55 claw samples and 96 blood samples distributed across sex-classes and study sites as shown in Fig. V. 2.

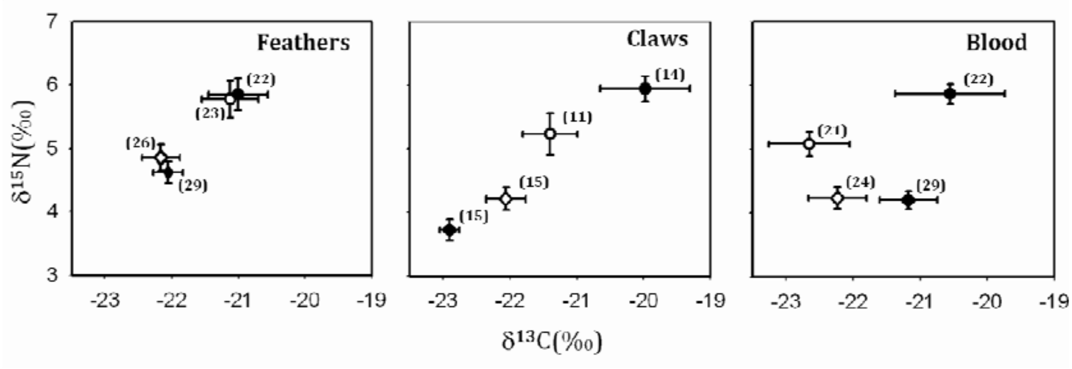

Figure V. 2: Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$, mean ± SD) for feathers (autumn), claws (winter) and blood (spring) of Greater Prairie-Chickens in Kansas, 2009. Symbols as follows: filled symbols = males, open symbols = females, diamonds = agricultural mosaic, circles = native prairie. Sample sizes for each category are given in parentheses.

Sexual dimorphism

$\delta^{13}C$ and $\delta^{15}N$ values in blood were higher in males. We did not find significant differences in isotopic values of feathers and claws (Table V. 1; Fig. V. 2). In the ANOVA model we found that the interaction term site:sex was significant for the isotopic values of claws and $\delta^{15}N$ blood values (Table V. 1; Fig. V. 2).

Nonparametric permutation tests of total niche space (TA) showed that the TA of female prairie-chickens was 23 and 27 % wider than males for feathers (autumn) and claws (winter), respectively. We observed no difference in isotopic values of blood (spring) between the sexes (Fig. V. 3).

	Feathers		**Claws**		**Blood**	
Variables	Log(δ^{13}C)	Log(δ^{15}N)	Log(δ^{13}C)	δ^{15}N	δ^{13}C	δ^{15}N
Study site	9.66 **	22.28 ***	26.32***	61.11 ***	0.05	60.91 ***
Sex	0.08	0.15	0.03	0.30	7.13 **	4.18 *
Study site *Sex	0.01	0.59	9.79 **	7.69 **	0.82	6.24 *
df	1, 96	1, 96	1, 51	1, 51	1, 92	1, 92

Table V. 1: Results of the ANOVA models (*F* values) comparing the effects of site, sex, and an interaction on the isotopic signatures of three tissues of Greater Prairie-Chickens (*Tympanuchus cupido*). Significance of *F* values: *** p< 0.001; ** p<0.01; * p<0.05. See Fig. V. 2 for sample size.

The distance of each individual value to the isotopic centroid (CD) of the population was higher in female feathers (autumn) than in males, and so was the coefficient of variation of the distances from each individual to its neighbors in the isotopic space (CVND). Males showed higher CVND than females in claws (winter; Fig. V. 3). CD and CVND did not differ between sexes in blood isotopic values (spring). We found a marginally significant interaction ($p< 0.1$) between study site and sex for CD for claws and blood isotopic values and significant interaction for CVND for the three tissues (Fig. V. 3).

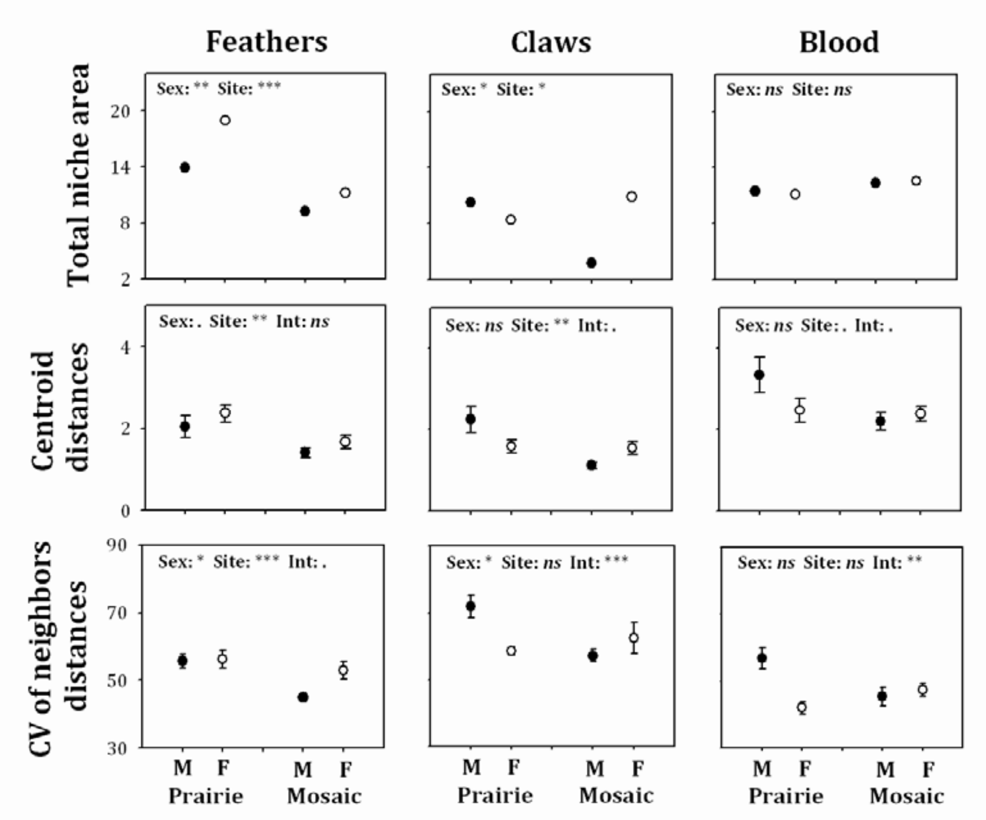

Figure V. 3: Trophic niche metrics (mean ± SD) and comparisons between Greater Prairie-Chicken populations occurring in native prairies (Prairie) and in an agricultural mosaic (Mosaic) and between males (M; black dots) and females (F; white dots). Total niche area (TA) was the area of the convex hulls that included $\delta^{13}C$-$\delta^{15}N$ isotopic values of each of the subsets; Centroid distance (CD) was the mean distance of each individual to the isotopic centroid of its subpopulation; and the CV of the neighbors distances (CVND) was the coefficient of variation of distances from each individual to its neighbors in the isotopic space. *P* values of the differences between males and females and populations in native prairie and agricultural mosaic habitats in TA were estimated as the proportion of resampled data sets that exceeded the observed difference. Significance codes: *** p< 0.001; ** p<0.01; * p<0.05; • p<0.1

Landscape differences

Prairie-chickens showed higher isotopic values in the native prairie than in the agricultural mosaic in all analyses except $\delta^{13}C$ in blood (Table V. 1; Fig. V. 2).

Total niche space (TA) was broader in the native prairie than in the agricultural mosaic when derived from feather samples (38%) and claws (22%), whereas no differences were found in blood-derived TA (Fig. V. 3).

The distance of each individual to the isotopic centroid (CD) and the coefficient of variation of the distances from each individual to its neighbors in the isotopic space (CVND) were significantly higher for prairie-chickens in the native prairie than in the agricultural mosaic in most comparisons of the three tissues (Fig. V. 3). Birds in the native prairie had higher values of CD in feathers (autumn), claws (winter) and blood (spring; Fig. V. 3). The CVND for blood (spring) and claws (autumn) did not show significant differences between populations (Fig. V. 3).

DISCUSSION

In this study we found intrapopulation partitioning of trophic niche in Greater Prairie-Chicken, particularly outside the breeding season. Stable isotope analysis in three tissues suggested that males and females use partially different resources in autumn and winter, and also present distinct patterns of resource use with wider variability in females; indicating sexual niche segregation in this moderate dimorphic lekking species. In addition, we found wider trophic variability in the population inhabiting a native prairie landscape, compared to birds inhabiting an agricultural mosaic.

Trophic sexual dimorphism

Ours is the first study to find sexual niche partitioning in North American prairie-grouse and our results are consistent with patterns observed in old world forest grouse (Blanco-Fontao et al. in press). These trophic differences are likely driven by habitat segregation during some seasons of the annual cycle. We found that females and males showed striking distinct trophic variability in autumn that was diluted as spring approached (Fig. V. 3). Such seasonal differences suggest similar short-term trophic behavior during the lekking season, when males and females converge in the leks (Robel et al. 1970; McNew et al. in press), and substantial dietary segregation among individuals from different sexes in the other seasons; the latter may be interpreted as sexual spatial segregation.

In autumn, the wider niches (TA), higher trophic diversity (CD) and smaller trophic redundancy (CVND, Fig. V. 3) of females are consistent with a more generalized diet, based on greater individual variability of feeding strategies. In turn, this result is consistent with the known natural history of this species. Prairie-chickens tend to gather in flocks in autumn, in particular in feeding grounds, but females are more prone to solitary behavior (Robel et al. 1970). Thus the latter may individually use different feeding grounds and dietary resources. In addition, during this season females may be a more heterogeneous segment of the population as females with broods may preferentially use habitats with good access to arthropods for developing young, whereas failed breeders may use different habitats that minimize their predation risk (Robel et al. 1970). Hence, the solitary behavior and the differences in the breeding status of individuals in this sex-class may lead to a more diverse use of feeding grounds and in turn, to a greater diversity of feeding strategies.

In winter, we found that differences between sexes were site-specific: females showed wider niches (TA) in the agricultural mosaic but not in the native prairie landscape, where males showed wider niches and less trophic redundancy (CVND). We speculate that the reduced availability of diet resources in this season may favor opportunistic behaviors. In the agricultural mosaic landscape, different kinds of cultivated grains become available at different times of the season (Robel et al. 1970). Females, which show longer movements during this season (Robel et al. 1970), may be taking advantage of a greater variability of grains in the agricultural mosaic. Conversely, males show shorter movements and remain closer to leks (Robel et al. 1970); thus, the bigger niche width showed by males in the native prairie may reflect a higher variety of native tallgrass seeds around leks (Svedarsky et al. 2003).

Last, during the lekking season (spring) the convergence of males and females in the leks (Robel et al. 1970; McNew et al. in press) limits the sexual spatial segregation and this, in turn, may imply similar diet resource use. Notwithstanding, stable isotope studies in herbivores may render difficult interpretations as the variability of primary producers is integrated over a single trophic level, which makes difficult to detect significant differences (Fry 2008).

Generally, we reported that wider niches were attained via an increase of intra-sex individual diversity. This result supports the *niche variation hypothesis* that states that more generalized populations are expected to be more heterogeneous (Van Valen 1965; Bolnick et al. 2007).

In the Tetraonidae family, sexual differences in trophic strategies have been found for the most sexually dimorphic grouse species (i.e. Capercaillie; Blanco-Fontao et al. in press). Although prairie-chickens are among the least sexually size dimorphic lek-mating grouses, males and females show marked distinct reproductive roles (del Hoyo et al. 1994).

Prairie fragmentation as a driver of feeding behavior

Prairie-chicken populations showed distinct foraging strategies in two landscapes differing in the degree of native habitat reduction and fragmentation. Generally, the population in the native prairie landscape showed a more generalist behavior as a whole, and a higher individual trophic diversity than prairie-chickens occurring in the agricultural mosaic. Differences in trophic diversity among study sites with distinct landscape composition support the *niche variation hypothesis* (Van Valen 1965; Bolnick et al. 2007).

Landscape composition and the reduction of native habitat influence availability of food resources for herbivores. Hence, the higher trophic variability found in the native prairie landscape likely reflects the greater specific and microhabitat structural diversity of the less fragmented native habitats (Fahrig 2003; Cousins et al. 2007). Conversely, the individuals of the population in the agricultural mosaic landscape may converge on the highly available resources provided by crops in autumn and winter (Robb and Schroeder 2005), showing thus, smaller population niches and individual generalist behaviors.

The populations of a species may adapt to local conditions and show different trophic behaviors departing from central tendencies (Chase and Leibold 2003; Gaston 2003; Guo et al. 2005). Our results are an example of differences between populations in the trophic behavior, as a response to distinct local landscape composition, in a species within a family (i.e. tetraonids) where each species is considered specialist in an specific diet resource (Storch 2007). Nonetheless the lack of replication suggests a cautious interpretation of the results and opens new research paths aimed at examining whether the same trophic niche patterns hold for prairie-chickens across a greater range of ecological conditions or for other species in landscapes differing in the degree of native habitat reduction.

Acknowledgements

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Discusión general y conclusiones

El estudio de la ecología trófica es fundamental para entender los requerimientos ecológicos de las especies y la variabilidad presente tanto dentro como entre sus poblaciones (Sutherland 2004); especialmente en el caso de aves herbívoras cuyos sistemas digestivos son relativamente pequeños entre los herbívoros endotermos (Sedinger 1997; Van Gils et al. 2007). La adquisición de recursos en aves herbívoras puede ser un factor limitante de la distribución y abundancia de sus poblaciones (Newton 1980; Martin 1987).

En esta Tesis Doctoral, la ecología trófica de tetraónidas ha servido para evaluar la diferenciación trófica de poblaciones periféricas, la variación dentro de las poblaciones - especialmente teniendo en cuenta el dimorfismo sexual y el hábitat ocupado por los individuos - y las relaciones tróficas con potenciales competidores.

Entre los principales resultados, se observa que las poblaciones de Urogallo Cantábrico y de Gallo de las Praderas Grande, ambas en el límite meridional de la distribución de la familia mostraron una marcada diferenciación trófica; es decir distintas preferencias y variabilidad de la dieta respecto a otras poblaciones. Esta diferenciación estuvo relacionada, con el carácter periférico de los primeros (Capítulo I), y con los cambios en la composición del paisaje, en los segundos (Capítulo V). Asimismo, la diferenciación trófica en el Urogallo Cantábrico, mediada por una selección positiva de recursos del sotobosque, puede implicar mayor susceptibilidad a los efectos negativos de la competencia con los grandes mamíferos herbívoros (Capítulos III y IV). En un nivel de estudio inferior, dentro de las poblaciones, machos y hembras de ambas especies de tetraónidas, e incluso individuos dentro de las poblaciones, presentaron diferentes estrategias tróficas (Capítulos II y V). A continuación se analizan más en detalle cada uno de los aspectos anteriores.

Diferenciación ecológica y respuesta local de poblaciones periféricas

La manera en que los organismos se enfrentan al medio biótico y abiótico varía a lo largo del rango de distribución de las especies (Chase y Leibold 2003). En esta Tesis Doctoral se constatan adaptaciones locales en el comportamiento trófico de dos especies de tetraónidas. Estos comportamientos tróficos difieren de la descripción tipológica de las especies, en una familia en la que las especies son supuestamente consideradas especialistas en un determinado recurso trófico (Storch 2007). En concreto, se observa una respuesta local mediada por el hábitat que ocupan las poblaciones de Urogallo y Gallo de las Praderas en los márgenes meridionales de distribución de la familia. Por una parte, el Urogallo Cantábrico mostró una diferenciación ecológica relacionada con su hábitat, que es singular para el conjunto de la especie (Quevedo et al. 2006b; Storch 2007; González et al. 2010) y, por otra parte, las poblaciones de Gallo de las Praderas Grande de Kansas (EE.UU.) mostraron diferentes comportamientos tróficos según el grado de reducción de su hábitat original.

La diferenciación trófica del Urogallo Cantábrico respecto a poblaciones de zonas centrales del rango de distribución se sustenta en i) la obtención de una mayor proporción de recursos alimenticios del sotobosque, especialmente en invierno, ii) un comportamiento trófico en el que los individuos se desplazan más frecuentemente y más lejos mientras se alimentan, en contraposición al uso prolongado de posaderos para alimentarse descrito para la especie (Bergerud y Gratson 1988; Sedinger 1997), y iii) en un nicho trófico más amplio. Los resultados anteriores son consistentes con las predicciones de los mecanismos determinantes de interacciones diferenciales con el ambiente en poblaciones periféricas (Gaston 2003). La fenología de los bosques caducifolios montanos parece explicar las diferencias. La estacionalidad de este hábitat determina cambios importantes en la disponibilidad de recursos a lo largo del ciclo anual y propicia una mayor variabilidad y diversidad de recursos en la dieta - un nicho más amplio. La propia naturaleza caducifolia del dosel arbóreo determina a su vez una mayor dependencia de los recursos del sotobosque, especialmente en el invierno. Por otra parte, la disponibilidad de recursos a lo largo del año parece dirigir los patrones estacionales de selección de dieta y explica la preferencia de esta población por el acebo en invierno, las yemas de haya en primavera y el arándano en verano-otoño (véase **Capítulo I**). Esta última especie es clave para el Urogallo a lo largo de todo su rango de distribución (Martínez 1993; Storch 1993; Rodríguez y Obeso 2000; Selås 2000), por lo que constituye una característica común y compartida por todas las poblaciones de la especie. Por último, cabría destacar que la elevada proporción de recursos del sotobosque en la dieta es consistente con estudios previos que mostraron que la composición del estrato arbóreo del bosque no era un determinante de la selección de hábitat en las poblaciones Cantábricas (Quevedo et al. 2006b). Por el contrario, la selección de recursos del sotobosque y, en concreto, de zonas ricas en arándano parece determinar la selección de hábitat del Urogallo Cantábrico.

En el caso del Gallo de las Praderas Grande, las poblaciones que ocupan praderas nativas mostraron un comportamiento más generalista, y una mayor diversidad trófica individual que las poblaciones que habitan en mosaicos agrícolas (véase **Capítulo V**). La composición del hábitat del Gallo de las Praderas Grande determina, como en el caso del Urogallo Cantábrico, la disponibilidad de recursos tróficos para un ave herbívora (Sedinger 1997; Van Gils et al. 2007). Esto, a su vez, modifica el comportamiento trófico de las poblaciones de estas aves según el grado de reducción de su hábitat original. En líneas generales, las poblaciones que ocupan hábitats nativos relativamente poco fragmentados tienen un comportamiento más generalista a nivel de población, con un nicho más amplio, pero basado en una mayor diversidad trófica de los individuos de la población - especialización individual- que las que viven en hábitats mosaico. Por lo tanto, la mayor diversidad específica y estructural a nivel de microhábitat de las praderas nativas poco fragmentadas (Fahrig 2003; Cousins et al. 2007) se refleja en una mayor variabilidad trófica.

Competencia asimétrica entre especies filogenéticamente alejadas

La importancia relativa de la interacción con otras especies como factor limitante de las poblaciones debería aumentar a medida que nos acercamos a los límites de distribución de una especie (Grant y Antonovics 1978; Guo et al. 2005). La diferenciación ecológica de las poblaciones situadas en esos límites de la distribución podría modificar la intensidad y el resultado de interacciones interespecíficas como la competencia. Los resultados de esta Tesis sugieren que la elevada dependencia de los recursos del sotobosque de la población Cantábrica de Urogallo determina que sea más susceptible que otras poblaciones más septentrionales a los efectos negativos de un incremento de la intensidad competitiva (véase también Baines 1996). Este incremento sería el resultado de un aumento de las densidades de grandes mamíferos herbívoros que tienen acceso a los mismos recursos del sotobosque que el Urogallo (Gill 1990; Putman 1994; Trimble y Mendel 1995; **Capítulo IV**).

La teoría ecológica predice que la superposición de nicho debería ser mayor entre especies filogenéticamente cercanas (Schoener 1974; Schoener 1983; Underwood 1986). Sin embargo, en la Cordillera Cantábrica, la elevada superposición entre el Urogallo y varias especies de ungulados (corzos, venados y ganado bovino) revela un alto potencial competitivo asimétrico (*sensu* Putman 1994) entre especies filogenéticamente poco relacionadas. Este elevado potencial competitivo no implica necesariamente que alguna de las especies esté sufriendo los efectos negativos de la interacción, pero sí que podría sufrirlos en el caso de que haya limitación de recursos (Mac Nally 1983; Keddy 1989; Petren y Case 1996).

En la Cordillera Cantábrica las densidades de ungulados se relacionaron negativamente con la disponibilidad del arándano. A su vez, esa relación negativa podría explicar el desplazamiento de nicho trófico del Urogallo, observado en la zona en la que las densidades de ungulados fueron mayores y la disponibilidad de arándano menor (véase **Capítulo III**). Esta ericácea fue importante en las dietas de todas las especies, pero especialmente en la del Urogallo que depende de ella como alimento y refugio a lo largo de todo su rango de distribución (esta Tesis Doctoral; Storch 1993; Storch 1994; Selås 2000; Wegge y Kastdalen 2008). En consecuencia, un incremento de la intensidad competitiva interespecífica entre ungulados y urogallos podría constituir un factor limitante para las poblaciones periféricas de este último. Estudios previos en otras poblaciones de tetraónidas europeas consideran que la competencia por el alimento es particularmente crítica en los casos en los que el recurso alimenticio es también refugio, como ocurre en esta familia de aves (Storch 1994; Baines 1996; Baines et al. 1996).

Variación intrapoblacional: diferenciación sexual

Machos y hembras son segmentos de una población sobre los que pueden actuar diferentes limitaciones ecológicas. Por ejemplo, cada sexo puede presentar distintos requerimientos nutricionales o tasas de ingestión (Isaac 2005; Bulte et al. 2008) y por lo tanto, es probable que muestren diferentes estrategias tróficas (Mysterud 2000; Bolnick et al. 2003; Ruckstuhl 2007). De acuerdo con esta predicción, cada uno de los sexos, tanto de Urogallo Cantábrico como de Gallo de las Praderas Grande, presentó estrategias tróficas distintas (véanse **Capítulos II y V**). En líneas generales, para ambas especies, las hembras mostraron nichos tróficos más amplios y una mayor diversidad trófica individual, mientras que los machos en conjunto, estuvieron más especializados (nicho trófico más estrecho), aunque a nivel individual presentaron estrategias más generalistas (Figura 3). Estos patrones apoyan la *hipótesis de variación del nicho* que establece que las poblaciones (o en nuestro caso, segmentos de las poblaciones) más generalistas son más heterogéneas en cuanto a sus componentes (Van Valen 1965; Bolnick et al. 2007).

En la mayoría de las especies con un sistema de emparejamiento tipo lek, los machos son más grandes que las hembras - supuestamente como resultado de la selección sexual (Payne 1984; Björklund 1990) - y no participan en la cría y alimentación de los pollos (Andersson 1994). Sin embargo, las diferencias de tamaño entre machos y hembras covarían con el tamaño corporal en especies formadoras de leks (Fairbairn 1997); así, las especies de mayor tamaño son más dimórficas (Höglund 1989). Entre las tetraónidas formadoras de leks, el Urogallo es la especie más dimórfica - los machos doblan en tamaño a las hembras (del Hoyo et al. 1994)- mientras que el Gallo de las Praderas Grande se encuentra en el límite inferior de dimorfismo sexual (Schroeder and Robb 1993), presentando valores similares a los de la mayoría de las aves monógamas (machos 10-15% más grandes; Andersson 1994). A pesar de las diferencias en la magnitud del dimorfismo sexual, ambas especies mostraron una partición del nicho trófico entre sexos que sugiere una segregación en el uso del hábitat. Las diferencias en el cuidado parental entre machos y hembras podrían explicar la segregación sexual. Las hembras, encargadas de la cría de los pollos, podrían ser más restrictivas que los machos en cuanto a los requerimientos de hábitat. Por ejemplo, las hembras de Urogallo tienen una dieta más diversa que los machos (Storch et al. 1991; Borchtchevski 2009 y, en la Cordillera Cantábrica, usan con más frecuencia el límite superior del bosque, más diverso y heterogéneo (Bañuelos et al. 2008).

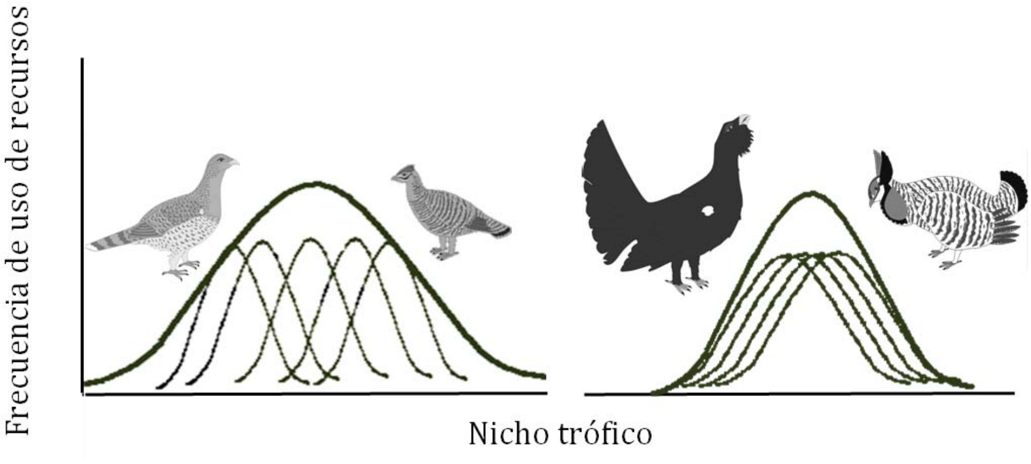

Figura 3: Esquema de la estructura del nicho trófico de los machos (dcha.) y las hembras (izq.) de Urogallo Cantábrico y Gallo Grande de las Praderas. La línea exterior representa el nicho total de cada segmento de la población mientras que las interiores muestran el nicho de cada individuo. Las hembras en conjunto presentan mayor amplitud de nicho, a partir de un comportamiento individual más especialista. El diagrama ha sido modificado a partir de Bolnick et al. (2003).

¿Es útil el análisis de isótopos estables en el estudio de la ecología trófica de tetraónidas?

El análisis de isótopos estables tiene varias ventajas frente a otras aproximaciones más convencionales (revisado por West et al. 2006; Inger y Bearhop 2008) y ha resultado ser un instrumento muy potente para la caracterización de la ecología trófica de las especies, poblaciones o individuos (West et al. 2006). En este caso, permitió evaluar la partición de nicho entre sexos y la variabilidad trófica intrapoblacional de dos poblaciones de tetraónidas amenazadas, difíciles de rastrear, y muy poco conspicuas en determinadas épocas de su ciclo anual. Las plumas mudadas de Urogallo Cantábrico proporcionaron información robusta y poco intrusiva de la segregación sexual y fidelidad al sitio de muda de esta población (**Capítulo II**). Por otra parte, en un único evento de muestreo y seleccionando diferentes tejidos (plumas, uñas y sangre) se evalúo la ecología trófica del Gallo Grande de las Praderas a lo largo de diferentes periodos de su ciclo anual (**Capítulo V**). Sin embargo, esta aproximación a la dieta y ecología trófica es indirecta, y no tiene la resolución de otras técnicas (ej.: análisis de contenidos estomacales o de excrementos) para reflejar diferencias más sutiles en el uso de los recursos. En esta Tesis, la combinación del análisis microhistológico y el análisis de isótopos estables proporcionó información trófica de alta resolución y a lo largo de diferentes escalas temporales.

La aproximación isotópica en ecosistemas terrestres ha sido ampliamente empleada para evaluar las dietas de predadores, o las contribuciones relativas de plantas C3 o C4 a las dietas de herbívoros en áreas tropicales (revisado en Kelly 2000). Sin embargo, su aplicación en el estudio de la ecología trófica de herbívoros terrestres que viven en hábitats en los que sólo hay plantas C3, como la Cordillera Cantábrica, es novedosa y podría facilitar el estudio de la ecología trófica de especies poco abundantes o amenazadas también en estos sistemas (véase Stewart et al. 2003; Feranec 2007). No obstante, se hace necesario un mejor conocimiento del fraccionamiento y enrutamiento isotópico de estas plantas en herbívoros para incrementar las posibilidades de esta técnica en hábitats templados dominados por plantas C3 (p. ej. Ben-David 2001).

Ecología trófica, tetraónidas periféricas y conservación

"In terms of conventional physics, the grouse represents only a millionth of either the mass or the energy of an acre. Yet subtract the grouse and the whole thing is dead". Aldo Leopold (1949)

Las poblaciones periféricas a menudo permanecen en sitios aislados y con escasas perturbaciones antropogénicas, proporcionando oportunidades excepcionales para la conservación de las especies amenazadas (Channell y Lomolino 2000). En concreto, las poblaciones en el límite inferior de latitud, son desproporcionadamente importantes para la supervivencia y el mantenimiento de los procesos evolutivos de las especies (Lesica y Allendorf 1995; Hampe y Petit 2005). Sus características ecológicas, dinámica de poblaciones y requerimientos de conservación suelen ser diferentes de los de otras poblaciones, por lo que las recomendaciones de gestión tipológicas para el conjunto de la especie, inferidas a partir de poblaciones más centrales, pueden ser contraproducentes en los márgenes de distribución de las especies (Gaston 2003).

Tanto el Urogallo Cantábrico como el Gallo de las Praderas Grande en el estado de Kansas se encuentran amenazados y en el límite sur de la distribución holártica de la familia Tetraonidae. El Urogallo Cantábrico ha recibido el rango taxonómico de subespecie bajo criterios morfológicos y biogeográficos (Castroviejo 1975; del Hoyo et al. 1994), se considera una Unidad Evolutiva Significativa dentro de un linaje diferenciado de urogallos meridionales (Duriez et al. 2006; Rodríguez-Muñoz et al. 2007) y, además, es singular en cuanto a su ecología (esta Tesis). Las poblaciones de Gallo de las Praderas Grande difieren en aspectos demográficos (McNew 2011), genéticos (Gregory 2011) y también ecológicos (esta Tesis) según habiten en praderas nativas o en mosaicos agrícolas.

Las adaptaciones locales al hábitat y la variabilidad entre poblaciones encontrada en esta Tesis, cuestionan la supuesta especialización de las especies de tetraónidas en uno o unos pocos recursos (Storch 2007) y hacen poco recomendables las estrategias de conservación basadas en la descripción tipológica de las especies. Por el contrario, las adaptaciones locales al hábitat hacen necesarias estrategias de conservación y seguimiento específicas, que tengan en cuenta las peculiaridades de las poblaciones a conservar para que sean efectivas y reviertan las tendencias de las poblaciones (Storch 1997; Sodhi y Ehrlich 2010).

El pronunciado declive que ha sufrido el Urogallo Cantábrico durante al menos las tres últimas décadas, ha llevado a su inclusión en el Catálogo Nacional de Especies Amenazadas bajo la categoría de "En peligro de extinción". Como tal precisa de un Plan de Recuperación basado en datos científicos rigurosos que busque revertir las tendencias poblacionales actuales. Según la diferenciación ecológica encontrada en esta Tesis, esos datos han de ser, además, específicos para esta población. Por ejemplo, la protección del sotobosque y en concreto del arándano es una medida de conservación recomendable en los bosques cantábricos que, sin embargo, no está contemplada en las estrategias para el conjunto de la especie (Storch 2007). Quizá el motivo de esa ausencia en las recomendaciones generales sea que el arándano, como ocurre con los urogallos, es más común en los bosques boreales y alpinos. El arándano fue clave en la selección de dieta y hábitat del Urogallo Cantábrico (**Capítulo I**) y también fue un recurso trófico importante para los ungulados salvajes y domésticos de la Cordillera Cantábrica (**Capítulo III**). Entre los últimos, el ganado bovino en régimen extensivo ha aumentado en este sistema montañoso en las últimas décadas, alcanzando densidades muy altas, un orden de magnitud superior a las de los ungulados silvestres (**Capítulo IV**; Rodríguez et al. 2007; Olea y Mateo-Tomás 2009). El sobrepastoreo por ganado bovino junto con el efecto aditivo de los ungulados salvajes, es probable que reduzcan la cobertura de las especies del sotobosque y la disponibilidad y productividad del arándano (Tolvanen 1994). Además, las densidades de ganado bovino estuvieron negativamente correlacionadas con la ocupación de los leks de la vertiente norte de la Cordillera Cantábrica **(Capítulo IV)**. Por lo tanto, la protección específica de arándano pasa por la reducción del sobrepastoreo, especialmente por ganado bovino, limitando tanto el tiempo como las zonas en las que pastorean. Esta medida además incrementaría la naturalidad (*sensu* Anderson 1991) de los bosques montanos Cantábricos y posiblemente sería beneficiosa para mantener la biodiversidad y el funcionamiento de este ecosistema, dado el carácter de *especie paraguas* o *bioindicadora* del Urogallo (Suter et al. 2002; Laiolo et al. 2011).

Por último, del mismo modo que en las estrategias de conservación es frecuente aplicar los valores tipológicos del conjunto de la especie a todas las poblaciones, también a nivel intrapoblacional es práctica común usar valores medios para la población, sin tener en cuenta la posible variabilidad entre segmentos de las poblaciones. Los resultados de esta Tesis para ambas poblaciones de estudio indican una importante variabilidad (especialmente relacionada con el sexo, pero también a nivel individual) que debe ser contemplada en los planes de conservación de las especies (Durell 2000; Bolnick et al. 2003). Por ejemplo, el dimorfismo trófico relacionado con una segregación de hábitat entre machos y hembras de Urogallo Cantábrico, subraya la necesidad no sólo de proteger los bosques Cantábricos como hábitat tipológico de la población sino también la heterogeneidad de hábitats que forman parte del dominio vital de algunos segmentos de la población, como los límites superiores del bosque y pastizales-brezales subalpinos que utilizan las hembras (**Capítulo II**; Bañuelos et al. 2008).

CONCLUSIONES

1. El Urogallo Cantábrico, como población periférica de la especie, presenta una elevada diferenciación ecológica respecto a poblaciones más centrales y que está relacionada con la selección de dieta. Esta diferenciación se basa en una mayor dependencia de los recursos del sotobosque de las poblaciones Cantábricas. Por el contrario, la importancia del arándano tanto en la selección de dieta como de hábitat constituye un carácter unificador y compartido por poblaciones centrales y periféricas de Urogallo.

2. La estacionalidad de los bosques caducifolios montanos dirige la selección de dieta del Urogallo Cantábrico. La disponibilidad de hojas de acebo en invierno, yemas de haya en primavera, frutos del arándano en verano-otoño y brotes de esta misma especie en invierno fue determinante tanto para la selección de hábitat a pequeña escala como para la de dieta en el Urogallo Cantábrico.

3. Los machos y las hembras de Urogallo Cantábrico mostraron diferente variabilidad trófica durante la época de muda, siendo las hembras las que presentaron un nicho trófico más amplio, basado en una mayor diversidad de estrategias tróficas individuales. Estos patrones están relacionados con una segregación sexual en el uso del hábitat, y ésta, a su vez, está asociada con la utilización de las hembras del límite del bosque que es más diverso a nivel de microhábitat.

4. El Urogallo Cantábrico presenta una elevada fidelidad a los sitios de muda, basada en la selección consistente, a nivel individual, de un determinado tipo de bosque durante el periodo de muda.

5. El arándano es un recurso trófico importante para los grandes herbívoros de la Cordillera Cantábrica, y clave para el Urogallo, cuya disponibilidad se reduce significativamente cuando las densidades de ungulados (salvajes y domésticos) son elevadas.

6. El nicho trófico de urogallos y ungulados (venados, corzos y ganado bovino) se superpone ampliamente en la Cordillera Cantábrica. Además, esta superposición es asimétrica, estando el nicho del Urogallo contenido dentro del de los ungulados. Todo lo anterior determina un elevado potencial competitivo entre estas especies alejadas filogenéticamente; siendo el Urogallo más susceptible de sufrir las consecuencias negativas del sobrepastoreo o de un incremento en la intensidad de la competencia interespecífica.

7. Las densidades de ganado bovino en régimen extensivo en la Cordillera Cantábrica aumentaron en un 28% en los últimos 20 años y estuvieron negativamente relacionadas con la ocupación de los leks de Urogallo Cantábrico.

8. Machos y hembras de Gallo de las Praderas Grande difieren en la variabilidad trófica durante el otoño y el invierno, pero no durante la primavera, periodo en el que la convergencia de ambos sexos en los leks determina comportamientos tróficos similares. Estas diferencias parecen estar relacionadas con una segregación del hábitat entre sexos, y se fundamentan en que las hembras muestran nichos tróficos más amplios y una mayor especialización individual que los machos.

9. Las poblaciones de Gallo de las Praderas Grande que ocupan praderas nativas poco fragmentadas presentan una mayor diversidad de estrategias tróficas que

las que viven en mosaicos de tierras de cultivo y praderas, reflejando la mayor diversidad estructural de los hábitats nativos poco fragmentados.

10. La utilización del análisis de isótopos estables en diferentes tejidos de aves para la medida del nicho trófico constituye una aproximación metodológica novedosa y poco intrusiva que permite la evaluación de la partición de hábitat entre sexos y de la variación trófica individual en especies poco abundantes y amenazadas.

11. Las estrategias de conservación de poblaciones periféricas de tetraónidas han de tener en cuenta las características locales de las poblaciones a conservar, así como a los diferentes segmentos de la población (ej. machos y hembras) para que sean efectivas y reviertan las tendencias de las poblaciones.

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Apéndices

APPENDIX A

Proportional abundance of resources and proportional use in the diet (mean ± 1 SD) of main canopy and understory species. For seasonal resources, for example, ferns and grasses, the average availability value is shown.

Species	Availability	Proportional diet use		
		Spring	Summer-autumn	Winter
Fagus sylvatica	13.6 ± 23.6	28.1 ± 20.8	5.3 ± 11.4	12.7 ± 20.2
Quercus petraea	29.7 ± 29.8	0.6 ± 1.0	3.5 ± 7.8	1.3 ± 2.4
Betula pubescens	39.3 ± 26.1	3.9 ± 5.2	2.5 ± 8.4	4.8 ± 11.8
Ilex aquifolium	3.2 ± 6.6	7.8 ± 21.0	2.4 ± 13.1	33.0 ± 37.8
Sorbus aucuparia	10.6 ± 10.4	0	0	0
Vaccinium myrtillus	27.8 ±16.1	19.1 ± 16.0	53.6 ± 27.7	13.3 ± 14.7
Erica spp.	29.2 ±19.5	3.7 ± 5.5	4.0 ± 6.4	5.4 ± 5.4
Calluna vulgaris	2.7 ± 11.9	1.2 ± 2.7	0.9 ± 1.7	2.1 ± 3.8
Cytisus / Genista spp.	4.5 ± 8.9	0	0	0
Ferns	11.6 ± 18.6	16.3 ± 20.8	10.3 ± 18.1	13.0 ± 20.4
Grasses	22.8 ± 20.4	4.1 ± 8.9	3.0 ± 5.1	2.3 ± 8.1
Mosses	-	6.0 ± 13.4	5.5 ± 8.8	4.2 ± 10.6
Unidentified	-	1.1 ± 1.95	2.6 ± 3.1	2.9 ± 5.7

APPENDIX B

Defecation rate (DF) and average adult weight (AW) for the study species

Ungulate species	DR	AW	References
Roe deer	20 pellets/day	27.2 kg.	(Mitchell et al. 1985, Mayle and Staines 1998, Loison et al. 1999)
Red deer	25 pellets/day	122.5 kg.	(Mayle and Staines 1998, Loison et al. 1999)
Cattle	11.5 pellets/day	159.6 kg.	(Wagnon 1963, Hafez and Bouissou 1975, Rodríguez et al. 2007)
Capercaillie	115 pellets/day	2.97 kg.	(Castroviejo 1975, Wallgren et al. 2009)

APPENDIX C

Seasonal proportional resource use in roe deer, red deer, cattle and Capercaillie diets.

	Capercaillie		Roe deer		Red deer		Cattle
	Winter	Summer	Winter	Summer	Winter	Summer	Summer
N	123	108	28	27	17	16	19
No. of fragments identified	6150	5400	5600	5400	3400	3200	3800
Fagus sylvatica	18.3 ± 19.7	17.6 ± 26.1	6.8 ± 5.1	8.3 ± 14.6	3.3 ± 3.0	5.3 ± 10.2	1.9 ± 2.1
Quercus petraea	0.8 ± 2.3	1.9 ± 5.6	0.6 ± 1.9	2.0 ± 7.7	0.1 ± 0.4	1.9 ± 2.8	0.1 ± 0.3
Betula pubescens	3.2 ± 7.1	1.5 ± 5.7	0.9 ± 2.1	1.1 ± 2.0	0.4 ± 1.1	0.6 ± 1.4	0
Ilex aquifolium	18.8 ± 28.4	1.4 ± 8.6	10.4 ± 12.9	2.1 ± 3.1	7.0 ± 7.3	0	<0.1 ±0.2
Sorbus aucuparia	0.6 ± 2.0	0.4 ± 1.5	1.6 ± 1.6	1.7 ± 1.7	0.8 ± 1.3	0.3 ± 0.7	0.7 ± 1.7
Alnus spp.	0	0	<0.1 ± 0.1	0	0	1.2 ± 1.4	0
Pinus spp.	0	0.4 ± 4.2	0	0	0	<0.1 ± 0.1	0
Corylus avellana	<0.1 ± 0.1	0	0	0	0	0	0
Vaccinium myrtillus	18.5 ± 16.7	31.7 ± 28.0	20.4 ± 8.9	18.5 ± 10.2	8.2 ± 6.2	9.3 ± 11.9	2.8 ± 2.7
Rubus spp.	<0.1 ± 0.1	1.2 ± 7.6	2.1 ± 2.9	8.1 ± 7.7	8.7 ± 9.3	4.8 ± 6.8	1.8 ± 4.7
Rosa spp.	0	0	0.1 ± 0.4	0	0.1 ± 0.4	0.1 ± 0.3	0
Daboecia cantabrica	0.2 ± 1.4	1.0 ± 7.0	1.6 ± 2.8	0.6 ± 1	3.1 ± 4.2	3.7 ± 5.8	0.1 ± 0.4
Erica spp.	3.1 ± 4.5	3.4 ± 6.5	6.5 ± 7.3	2.0 ± 2.3	7.1 ± 5.3	3.6 ± 3.6	1.3 ± 2.4
Calluna vulgaris	3.4 ± 7.6	4.4 ± 9.1	7.0 ± 6.6	3.7 ± 5.7	11.6 ± 7.2	7.9 ± 7.7	1.6 ± 3.1
Cytisus / Genista spp.	0.1 ± 0.7	0.2 ± 1.1	0.8 ± 1.0	0.9 ± 2.4	2.4 ± 2.7	3.1 ± 6.0	1.8 ± 6.5
Juniperus spp.	0.5 ± 4.7	0.1 ± 0.9	0	0	0.4 ± 1.2	0.8 ± 2.7	0.1 ± 0.2
Ferns	13.1 ± 17.4	12.2 ± 18.5	11.9 ± 11	18.0 ± 17.0	4.9 ± 5.0	6.7 ± 8.9	3.3 ± 3.6
Grasses	8.5 ± 12.2	11.5 ± 14.2	19.9 ± 12.1	20.7 ± 13.7	25.9 ± 16.8	32.5 ± 22.4	73.0 ± 13.9
Forbs	2.2 ± 4.9	3.4 ± 7.5	3.5 ± 3.4	8.0 ± 5.5	4.6 ± 3.9	6.6 ± 7.7	3.4 ± 2.3
Mosses	4.7 ± 10.9	3.6 ± 8.0	0.9 ± 0.9	1.1 ± 1.3	1.0 ± 2.0	1.9 ± 1.9	3.8 ± 4.2
Not recognised	3.9 ± 9.7	4.1 ± 4.6	4.9 ± 1.9	6.9 ± 2.8	10.4 ± 10.6	9.8 ± 6.7	4.3 ± 2.1

Anexo: publicaciones

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ORIGINAL ARTICLE

Diet and habitat selection in Cantabrian Capercaillie (*Tetrao urogallus cantabricus*): ecological differentiation of a rear-edge population

Beatriz Blanco-Fontao · Alberto Fernández-Gil ·
José Ramón Obeso · Mario Quevedo

Received: 19 March 2009 / Revised: 21 July 2009 / Accepted: 21 September 2009 / Published online: 11 October 2009

Abstract Cantabrian capercaillie *Tetrao urogallus cantabricus* is a peripheral population with distinctive phenotypic, biogeographic, and genetic characteristics. Hence, the population may also show substantial ecological differentiation associated with its habitat in purely deciduous forests. We assessed seasonal diet selection, small-scale habitat selection, and patterns of trophic niche width in Cantabrian capercaillie over two years. Diet was found to be a driver of small-scale habitat selection, a result consistent with previous studies of stand-scale habitat selection. Diet and habitat selection showed the importance of beech *Fagus sylvatica*, holly *Ilex aquifolium*, bilberry *Vaccinium myrtillus*, and ferns in Cantabrian capercaillie's resource selection. Conversely, the abundant oaks *Quercus petraea*, birches *Betula pubescens*, and heaths *Erica sp*. were used below their availability. The reliance on bilberry appears as a unifying characteristic between central and peripheral capercaillie populations. Cantabrian capercaillie showed stronger reliance on understory resources than range-central populations. It also showed wider trophic niche and higher specialization of feeding events. Trophic niche patterns and reliance on ground resources indicated a marked ecological differentiation, which stresses the need for local data and specific conservation actions.

Keywords Rear-edge populations · Ecological differentiation · Diet selection · Trophic niche · Deciduous forests · *Tetrao urogallus cantabricus*

Introduction

The ecological niche of a species (sensu Hutchinson 1957) can be quite variable across distribution ranges, leading to different realized niches and variability in the demographic and behavioral characteristics of local populations (Chase and Leibold 2003). Peripheral populations, closer to the limits of tolerance of a species, are embedded in a set of community interactions that differs, both in quality and strength, from that at the central parts of their species range (Gaston 2003). In this regard, conservation measures based on information from the central part of a species' range may be of limited use, or even counterproductive, at the edges of the range (Hampe and Petit 2005).

Not only can the realized niche of a species vary among populations across geographic ranges—intrapopulation variability in features such as diet and habitat selection is another potentially important source of variation (Smith and Skúlason 1996; Bolnick et al. 2003). Conservation plans that protect an average population trait (for instance, a folivorous bird species said to obtain 60% of its diet from trees) might fail when a population is built up of substantially different sex, age-class, or individual components (Durell 2000; Bolnick et al. 2003). That said, both the conservation consequences of variation within populations and the ecological characteristics of populations at the rear

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B. Blanco-Fontao · J. R. Obeso · M. Quevedo (✉)
Instituto Cantábrico de Biodiversidad (UO-PA-CSIC)/Ecology Unit, Department of Biology of Organisms and Systems, Oviedo University, Campus del Cristo, 33006 Oviedo, Spain
e-mail: quevedomario@uniovi.es

B. Blanco-Fontao
e-mail: bbfontao.uo@uniovi.es

A. Fernández-Gil
Department of Conservation Biology, Estación Biológica de Doñana (CSIC), Avenida de María Luisa s/n, Pabellón del Perú, 41013 Seville, Spain

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BRIEF COMMUNICATION

Abandonment of traditional uses in mountain areas: typological thinking versus hard data in the Cantabrian Mountains (NW Spain)

Beatriz Blanco-Fontao · Mario Quevedo · José Ramón Obeso

Received: 14 October 2010 / Accepted: 11 February 2011

Abstract Conservation policies of the European Nature 2,000 network reflect an overarching concern about alleged negative effects of abandonment of traditional uses. In particular, the abandonment of livestock herding is widely assumed to be responsible of biodiversity decreases through habitat homogenization. However, those negative effects of land abandonment on biodiversity are neither straightforward nor the repeatedly assumed land abandonment has been always supported by hard data. We analyzed the evolution of cattle densities in the Cantabrian Mountains (NW Spain) in the past 20 years, and its relation with the decline in the occupancy of capercaillie leks. Instead of the widely-assumed decrease of livestock numbers, which has been already incorporated into landscape and wildlife management, we found an actual increase in cattle numbers. Those cattle numbers were negatively related to the presence of an endangered, distinctive population of capercaillie, a bird considered an umbrella species in mountain forest ecosystems. Thus our data do not support the alleged role of free-ranging livestock in the conservation of biodiversity. We consider that typological thinking in the relationship of socio-economic changes and biodiversity conservation should be replaced by hard data and consideration of ecosystem naturalness.

Keywords Biodiversity · Ecosystem functioning · Free-ranging cattle · Land abandonment · Naturalness · *Tetrao urogallus cantabricus* · Traditional uses

Introduction

Trends in European land use have taken two opposing directions in the last decades: either agricultural intensification or land abandonment (Meeus 1995). Surprisingly, both of them have been claimed as determinants of biodiversity decreases through landscape and habitat homogenization (Ostermann 1998; Benton et al. 2003). Agricultural intensification has

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B. Blanco-Fontao (✉) · M. Quevedo · J. R. Obeso
Department of Biology of Organisms and Systems, Ecology Unit, Research Unit of Biodiversity (CSIC-UO-PA), Campus del Cristo, 33006 Oviedo, Spain
e-mail: bbfontao.uo@uniovi.es

Journal of
Ornithology

Acceptance letter for Chapter 2 in Journal of Ornithology

28 th September 2011

RE: JORN-D-11-00059R2 entitled "Habitat partitioning and molting site fidelity in Tetrao urogallus cantabricus revealed through stable isotopes analysis"

Dear Mrs. Blanco-Fontao,

It's my pleasure to inform you that your revised manuscript is now recommended for final acceptance.
Prior to final acceptance we have to add a German Summary which will be done by us but it will take a further few days.
In case, you could provide a German Zusammenfassung, please send it by e-mail as soon as possible.

Sincerely,
Franz Bairlein
Editor-in-Chief
Journal of Ornithology

Financiación

Durante el tiempo de realización de esta Tesis Doctoral he disfrutado de una beca del Programa Nacional de Formación de Profesorado Universitario del Ministerio de Educación y Ciencia (Ref. AP2005-3643) y de dos contratos a cargo de los proyectos IB08-158 de la Fundación para el Fomento en Asturias de la Investigación Científica Aplicada y la Tecnología (Ficyt) y CGL2010-15990 del Ministerio de Ciencia e Innovación. Este trabajo estuvo financiado por los proyectos CN-05-018 y CN-07-174 de la Consejería de Medio Ambiente del Principado de Asturias, UNOV-08-MB-2 de la Universidad de Oviedo, IB08-158 de la Fundación para el Fomento en Asturias de la Investigación Científica Aplicada y la Tecnología (Ficyt) y CGL2010-15990 del Ministerio de Ciencia e Innovación. La investigación presentada en esta Tesis Doctoral se ha realizado en el Área de Ecología del Departamento de Biología de Organismos y Sistemas de la Universidad de Oviedo/Instituto Cantábrico de Biodiversidad (UO/CSIC/PA) y en los Departamentos de Biología y de Ecología y Gestión de Recursos Naturales de, respectivamente, la Universidad Estatal de Kansas y la Universidad Noruega de Ciencias de la Vida (UMB), dónde realicé las dos estancias de esta Tesis Doctoral.

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Por fin llega este momento tan anhelado como difícil de agradecer el esfuerzo de todas las personas que de alguna manera se han implicado y han puesto su granito o su "pedrusco" de arena para que esto tenga un fin. Y es que son ya 5 años de ilusiones y frustraciones y mucha gente que ha compartido el camino. Espero no olvidarme de nadie y, si lo hago, gracias por adelantado a todos aquéllos que sabéis y sentís que tenéis una parte de esto.

Tres piedras angulares hay detrás de esta Tesis. Moncho como director depositó su confianza en mí y me dio la oportunidad de iniciarme en esto que llaman ciencia. Me sorprendió una y otra vez con una asombrosa clarividencia capaz de ver desde casi imperceptibles errores en los grados de libertad hasta encontrar la generalidad detrás de unos datos locales, transformando el manuscrito y haciéndolo mucho más interesante. Mario, fue mi director en el día a día, corrigió una y mil veces todos mis manuscritos hasta conseguir convertirlos en "publicables", aportó nuevas ideas y sobretodo me hizo pensar y buscar el placer de las cosas bien hechas. El tercer pilar de esta tesis es Mariajo, siempre con tiempo para echar una mano y con ese *buen rollo* que hace todo mucho más fácil en un mundo más bien de "hombres duros". Creo que mucho me habéis enseñado y algo he aprendido, gracias por vuestra paciencia.

Sin embargo, todo esto empezó una madrugada fascinante del mes de mayo hace ahora 8 años…esa mañana el feisán cantó en Currietsos y desde entonces no he dejado de compartir largas noches de chigre y tempranas mañanas de monte con todos esos palaciegos y tsacianiegos que resisten en la "aldea gala". Ellos me abrieron sus puertas y me enseñaron “El Vatse”, una joya demasiado preciosa como para dejarla en manos de la devastadora minería a cielo abierto. Óscar, Vero, Michel, las Anas, Eduardo… ¡muchas gracias! Andrés ¡Seguiremos filosofando en ése sitio telúrico en el que vives!

El trabajo de campo en los bosques de la Cordillera Cantábrica no es un bucólico paseo pastoril por el verde “paraíso natural” de Asturias. Y mucho menos con especies que por lo esquivas y poco abundantes, para algunos, ni existen (sí Carla y Alfonso, ésos sois vosotros). Un campo duro y poco generoso en cuanto a volumen de datos, aunque muy gratificante en cuanto a experiencias, y que no hubiese sido posible sin el esfuerzo de un montón de gente: Fernando Rodríguez Pérez, Fernando Rodríguez Álvarez, José Carral, José Luis Benito, Alberto Fernández Gil, Damián y Antonio Ramos fueron excelentes guías por las intricadas sendas del “salvaje oeste” transmontano. Andrés Gómez Merillas, Óscar Otero, Luis Robles y Manuel González hicieron lo equivalente en tierras astures cismontanas. María Cano fue testigo de la emoción de encontrar nuestras primeras plumas en aquel verano del 2006; su ayuda fue imprescindible en los inciertos comienzos. Mariajo, Mario, María Morán, Rolando, Paola, Mónica, Amalia, compañeros de fatigas, ¡gracias!

Tetxu me animó a que aprovechase las estancias de la beca y mucho me alegro de haberle hecho caso. En Manhattan, Kansas, en el medio de la inmensidad de las praderas americanas encontré a Brett, uno de esos científicos impecables que me ofreció mucho más de lo que yo podía esperar y se implicó de una manera poco común en conseguir que el último capítulo de esta tesis tuviese forma de manuscrito. Lance, Andy, Khara, Jasmine y Jorge fueron mis compañeros en el Avian Biology Lab; de ellos aprendí y con ellos rompí casi todos los tópicos americanos. Más al norte y en el viejo mundo, en la orilla del fiordo de Oslo (Aas, Noruega) descubrí que se podía trabajar menos horas y hacerlo mucho mejor, ¡viva la eficacia nórdica! Per Wegge fue el contacto, su experiencia y dilatada trayectoria trabajando con “wildlife” me aportaron conversaciones muy enriquecedoras; con los "oseros" descubrí (con gran satisfacción) que no era una utopía trabajar con grandes carnívoros, allí lo hacían y, ¡de qué manera! Especialmente Sam Steyaert y Andresito me hicieron la estancia muy agradable. Y cómo no, mis compañeros hippies, locos e idealistas de Tveter Sondra hicieron que Noruega ni siquiera me pareciese un país frío. Tusen takk!

El Departamento de Biología de Organismos y Sistemas ha sido prácticamente mi casa durante 5 años. En la sala de becarios "Cartografía", Ali, Magda, David, Su, Vane y sobretodo Carlina (que aunque no comparte sala, está muy presente) han sufrido más de cerca mis continuos despistes y dudas constantes. Pero no sólo ellos, también Nachu, Lucía, Isa, Fernando, Xurde, Jose, Joaquina, Emilie, Javi, Leti, Nere, Leandro, Paola, Jordi, María… Entre todos hemos resuelto problemas, aprendido y pasado muchos buenos momentos; todo esto al final queda reflejado en la Tesis.

La llegada de Amalia al departamento supuso un insufle de aire fresco. Siento haberte cargado con la tediosa tarea de moler-pesar-encapsular las muestras. El capítulo V no se hubiese podido iniciar sin su insistencia, que fue la única capaz de completar los trámites burocráticos para conseguir traer unas plumas, unas uñas y algo de sangre desde Estados Unidos a España.

Dani también merece un párrafo aparte. Él ha sido el primero en sufrir todos y cada uno de los capítulos de esta Tesis, se los ha leído a conciencia y no sólo ha aportado ideas y nuevas perspectivas, sino que además se ha encargado de dar el toque artístico necesario para intentar que lo que se escribe sea accesible e intuitivo y no pase a formar parte de la clásica "*consistently boring scientific litterature*". ¡Qué más se puede pedir!

Siri, Moli, Alvarito, aunque os suenen raras o incluso extravagantes palabras como ecología trófica o dimorfismo sexual, habéis compartido conmigo las dudas, inquietudes, desesperación, entusiasmo y hasta las “plantillas de Word” propias de todo estudiante de doctorado. ¡Ánimo que al final parece que las tesis se terminan!

Villabúrbula en la ribera del Porma y Lugueros en la montaña del Curueño fueron dos pequeños “paraísos en la otra orilla” que me sirvieron de retiro espiritual y de acercamiento a ese otro mundo rural en el que algunos todavía creemos. Gracias a todos esos ribereños y montañeses con los que llevo disfrutando desde hace ya varias décadas.

Creo que ni mis padres, ni las *güelas*, ni mi tía, ni mis hermanos entendieron nunca para que servía esto. A pesar de todo me apoyaron, y se tomaron con humor todo lo que esto se ha demorado. Por fin van a ver que “lo que me pagaba Zapatero” dio algún fruto. También sé que estarán orgullosos. ¡Gracias! Y qué decir de Manu… un fantástico compañero de casi todo lo que se puede compartir. Difícil no contagiarse de su entusiasmo y pasión por la Biología. En cierta medida él tiene gran parte de “culpa” en todo esto. ¡Ánimo que ya queda poco!

A todos, y a los que me puedan quedar, ¡***munches gracies!***

Gatsu, faisán, urogatso
nos rebotsares t'alcuentras
mátante al amanecere
cuandu rondas a la fema

Sos el ave más guapina
que vive nas nuesas sierras
¡cómu cantas a la pita
con celu na primavera!

Gatsu cantor ya formosu
dame muita muita pena
que queixándote d'amores
tiros tua vida rompieran

Eva González