Nicho trófico en *Falconidae* : heterogeneidad de hábitat, nutrición y reproducción

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Nicho trófico en Falconidae: heterogeneidad de hábitat, nutrición y reproducción

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RESUMEN TESIS
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La presente tesis examina desde distintas perspectivas la ecología trófica analizada por un lado en los falconidos como grupo de especies de rapaces depredadores con una distribución cosmopolita. Por un lado se analiza el hábitat (biomas) ocupado a escala global por el grupo de los falcónidos para investigar la relación entre la diversidad de dieta de las diferentes especies, la heterogeneidad del hábitat que ocupa y su área de distribución. Se predice que si la estrategia generalista en alimentación permite a las especies expandirse y colonizar nuevas áreas y hábitats, se obtendrá que tanto la diversidad como la riqueza trófica se relacionan de forma positiva con el tamaño del área de distribución y con el índice de especialización biómica. Por otro lado, la presente tesis se centra en una especie dentro del grupo de falcónidos, el cernícalo vulgar *Falco tinnunculus*, en la que se ha analizado el aprovisionamiento de alimento al nido, el hábitat así como la composición nutricional de sus principales especies-presa en una población mediterránea en la región de Campo Azálvaro, en Segovia. Se estudia si la amplitud del nicho trófico individual está asociada con la calidad individual usando componentes de la eficacia biológica, tales como la fecundidad o la viabilidad de la descendencia. Bajo la premisa de que el generalismo trófico es una estrategia seleccionada por los cernícalos, la diversidad de presas consumidas debe relacionarse positivamente con la calidad individual y la viabilidad la descendencia. Además se analiza el hábitat correspondiente al territorio de cría del cernícalo vulgar con el fin de investigar si territorios más heterogéneos aportan una mayor diversidad de especies-presa en la dieta como predice la hipótesis de la hetoregeneidad del hábitat LHH. Si los individuos de mejor calidad poseen una dieta más variada, se predice que los mejores territorios serán aquellos con una mayor heterogeneidad de paisaje que pueden proveer de una mayor diversidad de presas. Se analiza energéticamente y nutricionalmente la composición del alimento del cernícalo a través de la medición de calorías y macronutrientes (grasa, proteínas y amino ácidos) en las 11 principales presas del cernícalo. Bajo el enfoque de la OFT, se investiga si el tiempo que tarda el cernícalo en capturar una especie presa esta explicado por su tamaño, su dificultad de captura o su preferencia para determinar si la preferencia particular por una especie-presa es debido a su rentabilidad en términos energéticos y/o a su composición nutricional. También se investiga si el consumo de las especies-presa preferidas por el cernícalo promueve tiempos de aprovisionamiento más largos. Además, desde un enfoque nutricional se investiga la importancia tanto de la cantidad como de la diversidad de nutrientes en componentes de la eficacia biológica. Se predice bajo la Hipótesis de la Dieta Equilibrada que una mayor diversidad de especies-presa en la dieta aporta una mayor diversidad de nutrientes y por lo tanto una composición más equilibrada que beneficiaría a los individuos en términos de eficacia biológica. Finalmente, se estima la abundancia de especies-presa en el área de estudio y en la dieta y se calcula el índice de capturabilidad y preferencia de caza para cada especie.

Los hallazgos del Capítulo I revelaron que la dieta de las especies no es un buen predictor para el tamaño del área de distribución pero si lo es la heterogeneidad del hábitat. Especies más generalistas en dieta (valores medios y máximos) habitan significativamente en más biomas. Nuestros resultados también mostraron que la riqueza de la dieta mostró una sobreestimación en el número de especies generalistas en comparación con el índice de diversidad. Este estudio revela que la amplitud de la dieta es un rasgo ecológico importante que explica los patrones globales de ocupación de biomas para individuos, poblaciones y particularmente especies. En el Capítulo II los resultados obtenidos demuestran que la dieta de cernícalos varió significativamente entre los años y que los individuos de mejor calidad alimentaron a sus descendientes con una mayor diversidad de especies de presas y una mayor cantidad de alimentos. Además, la condición corporal y la respuesta inmune de los polluelos se correlacionaron positivamente con la diversidad de presas entregadas por los padres. Por otro lado el Capítulo III sugiere que en cernícalo vulgar las estrategias de forraje generalista de nichos se basan en una búsqueda activa de diferentes especies de presas dentro o entre hábitats en lugar de en la selección de territorios con alta diversidad de hábitats. En el contexto de la Optimal Foraging Theory el Capítulo IV reveló que en la población estudiada el tamaño de carga de las presas tiene un bajo poder explicativo para las especies de presas de mayor tamaño y que la capturabilidad de las presas juega un papel esencial en la descripción de las estrategias de forrajeo. En cuanto a los componentes energéticos y nutricionales de la dieta, nuestros resultados muestran que en nuestra población de cernícalos la selección de presas se basó en la rentabilidad energética de las presas, pero también en el contenido de proteínas de la presa. Por último, se mostró un alto valor de preferencia de cernícalos por los topillos comunes *Microtus arvalis* que no fue explicado por ninguna de las variables analizadas. Finalmente los resultados del Capítulo V muestran que los nutrientes encontrados en las dietas de animales tienen un claro potencial para explicar la variación en los rasgos de la historia de vida que median la eficacia biológica, como la condición corporal y la inmunocompetencia en cernícalo. Además, las dietas más diversas también contenían una mayor diversidad de aminoácidos y tenían diferentes perfiles de aminoácidos que los menos diversos.

A Pablo Vergara

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Introducción

El concepto de nicho ecológico, en su concepción moderna, fue definido por G. Evelin Hutchinson en 1957 cómo el conjunto de condiciones y recursos ambientales dentro de los cuales la población puede mantenerse viable. Se considera el nicho ecológico desde una perspectiva multidimensional en la cual la amplitud del nicho se refiere a la amplitud de la tolerancia de las poblaciones a lo largo de una o más dimensiones, es decir, la tolerancia dentro del rango de variación de factores ambientales (temperatura, humedad, etc.) o ecológicos (depredación, alimento, etc.) (Fox *et al.* 2001). Dentro de este concepto se diferencia el nicho ecológico fundamental, entendido éste como la amplitud máxima de una especie o población en ausencia de competidores y/o depredadores, mientras que nicho ecológico efectivo o real se considera al existente en presencia de estos (Begon *et al.* 2006). Un concepto derivado de nicho ecológico es el de nicho trófico, entendido éste como el lugar que ocupa un organismo en relación a su alimento y a sus depredadores (Silvertown 2004).

1. Especialización ecológica

La especialización ecológica se define como el proceso mediante el cual un organismo se adapta a un determinado conjunto de recursos dentro de la totalidad de recursos disponibles en su entorno (Futuyma & Moreno 1988; Poisot *et al.* 2011). Dicha especialización ecológica es promovida por varias presiones selectivas, siendo una de ellas la competencia por los recursos entre individuos de la misma o de distintas especies (Bolnick & Fitzpatrick 2007; Poisot *et al.* 2011). Los beneficios de una estrategia especialista destinada a reducir la amplitud de nicho consiste en la disminución de la competencia entre los individuos, las poblaciones o las especies mediante la segregación de los recursos (Futuyma & Moreno 1988; Araújo *et al.* 2011). Las estrategias pueden ser diferentes dependiendo de la predecibilidad de los recursos, tanto en el tiempo como en el espacio (Estes *et al.* 2003; Svanbäck & Bolnick 2007; Woo *et al.* 2008; Quevedo *et al.* 2009). Las estrategias especialistas, de nicho reducido, pueden ser favorecidas en ambientes estables y homogéneos donde los recursos son más predecibles debido a su menor fluctuación tanto en el tiempo como en el espacio. Por el contrario los ambientes heterogéneos e inestables promueven el desarrollo de estrategias generalistas, orientadas a ampliar el nicho de recursos utilizables y facilitar un cambio rápido en la explotación de los recursos cuando estos son fluctuantes e impredecibles (Estes *et al.* 2003; Svanbäck & Bolnick 2007; Woo *et al.* 2008; Quevedo *et al.* 2009). Esto ha llevado a la premisa de que las especies especialistas son más propensas a la extinción debido a que su dependencia de un número reducido de recursos induce una mayor vulnerabilidad frente a los cambios ambientales que afectan a la disponibilidad de recursos (Vrba 1987; Owens & Bennett 2000; Purvis *et al.* 2000). Contrariamente, los generalistas poseen una mayor capacidad para utilizar un amplio conjunto de recursos, disminuyendo su dependencia de un recurso determinado, lo que hace a su vez que los individuos sean menos vulnerables a los cambios ambientales que afecten a la disponibilidad de recursos (Vrba 1987; Owens & Bennett 2000; Purvis *et al.* 2000). Por tanto, la teoría predice que las estrategias especialistas pueden limitar la capacidad de los individuos a colonizar nuevos ambientes, mientras que el generalismo podría favorecerla.

1.1. Estrategias especialistas *vs*. generalistas

El papel del generalismo y el especialismo para explicar la especiación es un debate candente en ecología evolutiva, existiendo incluso algunos autores que niegan la existencia del generalismo en la naturaleza considerando a éste como una mera fase transitoria hacia el especialismo (Loxdale *et al.* 2011). De hecho, muchas de las especies consideradas generalistas a nivel trófico parecen estar compuestas en sus poblaciones por individuos especialistas generando así una falsa apreciación de lo que se considera generalismo a nivel de especie (Bolnick et al. 2003, Araujo et al. 2011). La existencia de especialización ecológica individual intrapoblacional de los recursos (por lo general de recursos tróficos) se sugiere como un mecanismo eficaz para evitar la competencia intraespecífica y aumentar la eficacia biológica y, por lo tanto, se predice que sea mayor en las especies depredadoras donde la competencia por los recursos alimenticios es más alta (Bolnick *et al.* 2003; Araujo *et al.* 2011). También se ha sugerido que la existencia de una especialización individual promueve la selección disruptiva a través de la competencia entre los individuos ecológicamente heterogéneos que ocupan diferentes nichos en la población generando procesos de especiación simpátrica, tipo de especiación que ha tenido en general más sustento teórico que empírico (Bolnick & Fitzpatrick 2007). El especialismo en la utilización de los recursos dentro de individuos de una misma población incrementa la heterogeneidad ecológica favoreciendo la emergencia de nuevas especies, y por tanto aumentando la tasa de especiación (Gavrilets 2006; Bolnick & Fitzpatrick 2007; Schluter 2009). Es por ello que se piensa, como se ha dicho arriba, que la reducción de la competencia debido a estrategias especialistas aumenta la eficacia biológica de los individuos produciendo a la larga fenotipos divergentes como resultado de las adaptaciones ecológicas (Gavrilets 2006; Bolnick & Fitzpatrick 2007). Estas divergencias fenotípicas pueden reducir la tasa de apareamiento como consecuencia de la desincronización y/o diferente localización de las parejas si los picos de los recursos están alejados tanto en el tiempo como en el espacio (Fry 2003; Bürger *et al.* 2006; Bolnick & Fitzpatrick 2007). También algunos rasgos seleccionados por la explotación de recursos determinados pueden estar unidos pleiotropicamente a los rasgos seleccionados por las hembras en los machos, por lo que a través de procesos de selección sexual puede promoverse también la especiación (Bolnick & Fitzpatrick 2007). Por tanto se piensa que la especialización ecológica promueve el especialismo y éste la especiación.

1.2. Distribución geográfica y ocupación de biomas

El mayor número de especies especialistas observado en la naturaleza (Eldredge & Cracraft 1980) podría ser originado, como se ha comentado anteriormente, por especiación simpátrica como consecuencia de la segregación de nicho (Bolnick & Fitzpatrick 2007). Una perspectiva diferente para explicar las altas tasas de especiación en especies especialistas puede ser a través de procesos de especiación no simpátrica. Estos procesos pueden ser originados por una mayor vulnerabilidad de las especies especialistas frente a la pérdida del hábitat o su fragmentación, aumentando así el aislamiento reproductor entre las poblaciones (Futuyma & Moreno 1988; Jocque *et al.* 2010). Por otra parte, existe otra idea para explicar la especiación a través de especies más generalistas basada en que estas especies al no depender de un conjunto tan pequeño de recursos cuentan con una mayor capacidad de expansión, pudiendo explotar una gama de recursos más diversos, aumentando su capacidad para colonizar nuevos ambientes y regiones (Thomas *et al.* 2001). Esta capacidad para colonizar nuevos entornos favorecería que el generalismo pueda ser una fuente de diversificación y de radiaciones adaptativas (West-Eberhard 2003; Phillimore *et al.* 2006).

Desde una perspectiva biogeográfica se considera que la mayor representación de especies especialistas podría estar favorecida por las condiciones ambientales propias de cada bioma. Siguiendo la misma argumentación, se piensa que los biomas más estables por sus condiciones ambientales menos variables, promueven a su vez que los recursos sean más estables y por lo tanto más predecibles favoreciendo la aparición y el mantenimiento de un elevado número de especies especialistas mientras que los biomas más inestables favorecerían la existencia de especies generalistas (Belmaker *et al.* 2011). Se ha sugerido que estas variaciones en las condiciones ambientales de los biomas pueden explicar el gradiente latitudinal de riqueza de especies ampliamente observado en diferentes taxones (Buckley *et al.* 2010; Belmaker *et al.* 2011; Davey *et al.* 2012; Salisbury *et al.* 2012). De la misma forma, la mayor capacidad de colonización de las especies generalistas permite a estas especies estar presentes en un mayor número de biomas. Así, el índice de especialización biómica (BSI en sus siglas anglosajonas), definido como el número de biomas en los que habita una especie (Hernández Fernández & Vrba 2005) puede ser considerado como un indicador fiable de la especialización ecológica, ya que describe la posición de una especie en el gradiente especialismo-generalismo a lo largo de la capacidad de la especie para la obtención de recursos en diferentes ambientes (Hernández Fernández & Vrba 2005; Cantalapiedra *et al.* 2011). Por lo tanto, si el generalismo está asociado con la capacidad de colonizar, se podría esperar que en general las especies más generalistas en la explotación de los recursos ocuparan un mayor número de biomas (mayor BSI) y tuvieran una mayor área de distribución (Hernández Fernández & Vrba 2005; Cantalapiedra *et al.* 2011).

1.3. Nicho trófico y heterogeneidad de paisaje

El nicho trófico también ha sido ampliamente usado para predecir el nicho ecológico de las especies, ya que por una parte, la abundancia y disponibilidad del alimento son importantes factores ambientales que modulan las estrategias adaptativas y los fenotipos de los organismos, y por otra parte, ambos factores van a depender a su vez del nicho ecológico de las especies que componen el alimento. Se ha observado en diferentes estudios una relación positiva entre la heterogeneidad de hábitat y de la dieta consumida en diferentes poblaciones de la misma especie, sugiriendo que el aumento de la heterogeneidad del hábitat puede favorecer el generalismo trófico (Abbas *et al.* 2011; Blanco-Fontao *et al.* 2013; Rosenblatt *et al.* 2015). Estos resultados concuerdan con la teoría clásica del nicho que predice una correlación positiva entre la diversidad / heterogeneidad de hábitats y la diversidad de especies (Simpson 1949; MacArthur & Wilson 1967; Lack 1969; Tews *et al.* 2004). Dicha relación es denominada como Hipótesis de la Heterogeneidad de Paisaje (LHH de su nombre anglosajón, Landscape Heterogeneity Hypothesis) (Simpson 1949; MacArthur & Wilson 1967). Se basa en la idea de que los paisajes más heterogéneos con una mayor diversidad de hábitats pueden proporcionar una mayor gama de formas para explotar los recursos ambientales (nichos) que los paisajes más homogéneos, por tanto permitiendo albergar una mayor diversidad de especies (Tews *et al.* 2004; Kadmon & Allouche 2007). De forma general se ha observado una correlación positiva entre la heterogeneidad del paisaje y el número de especie que lo habitan, sin embargo, existen casos en los que esta correlación no se ha observado o incluso se ha observado una correlación negativa (ver Tew *et al.* 2004). Teniendo en cuenta ambas ideas es posible predecir que los individuos, poblaciones o especies con una dieta más generalista (amplio nicho trófico) deben también utilizar los paisajes más heterogéneos, contrariamente a los especialistas (reducido nicho trófico). La relación encontrada en distintas especies entre heterogeneidad de hábitat y la dieta en los trabajos mencionados previamente parecen confirmar dicha predicción. Las discrepancias encontradas pueden deberse al grupo taxonómico estudiado en cada caso o en al tamaño del área efectiva para cada especie (Tews *et al.* 2004; Allouche *et al.* 2012).

Los estudios interespecíficos usan comúnmente índices generales como la riqueza de presas para cuantificar la especialización de la dieta (Phillimore *et al.* 2006; Belmaker *et al.* 2011). Por el contrario, muy pocos estudios han determinado con precisión la amplitud del nicho trófico (Williams *et al.* 2006), usando la dieta real y los índices de diversidad de dieta como el índice de Shanon - Wiener (SWI) o el índice de Evenness (Williams *et al.* 2006). Las mediciones de amplitud del nicho trófico usando la riqueza de dieta proporcionan igual importancia al consumo ocasional como al consumo preferente de especies (Colwell & Futuyma 1971), produciendo la sobrestimación de la capacidad generalista así como del número de especies generalistas, siendo dicha estima muy vulnerable al esfuerzo muestral (Hillebrand & Cardinale 2004). Por otro lado, la variación interpoblacional en el nicho trófico ha sido ampliamente omitida en los estudios comparativos interespecíficos (Korpimäki & Norrdahl 1991; Bolnick 2001; Martínez-Padilla & Fargallo 2008; Araujo *et al.* 2011; Terraube & Arroyo 2011; Evangelista *et al.* 2014; Terraube *et al.* 2014; Rosenblatt *et al.* 2015). Se hace necesario usar diferentes poblaciones para cada especie para obtener una imagen más precisa del nicho fundamental y efectivo de la especie que puede variar en distintas situaciones por la existencia de competencia intra– e interespecífica y/o abundancia del alimento. Además, el valor máximo de la diversidad de la dieta en un rango de poblaciones puede ser usado como un indicador de la capacidad de la especie para ampliar su nicho trófico y para habitar diferentes hábitats, pudiendo ser un valor más aproximado al nicho fundamental de la especie. Otro importante aspecto en los estudios que comparan nichos ecológicos entre especies es el nivel taxonómico usado en los recursos tróficos estudiados. Los consumidores pueden mostrar una preferencia o una capacidad especial para capturar especies de presas que comparten características ecológicas (hábitos alimentarios, periodos de actividad, hábitats preferidos, etc.) estos caracteres pueden estar determinados filogenéticamente, lo que produciría que la diversidad de la dieta pudiera depender del nivel taxonómico utilizado para cuantificar las especies presas (Jorge *et al.* 2014). Por ejemplo, una especie especializada en el consumo de muchas especies de presas pertenecientes a la misma familia puede ser especialista si la diversidad de la dieta se calcula a nivel de familia, pero puede ser considerada generalista si es calculada a nivel menor como género o especie.

2. Forrajeo óptimo

A nivel de individuo, las presiones selectivas que se derivan de la variación espacio-temporal en la abundancia, disponibilidad y diversidad del alimento han propiciado estrategias de forrajeo encaminadas a crear un balance óptimo entre el tiempo-energía empleado en buscar, capturar y manejar el alimento y la cantidad y calidad de los nutrientes aportados el mismo (Emlen 1966; MacArthur & Pianka 1966; Begon *et al.* 2006). Esta relación se estudia en el marco de lo que se conoce como Teoría de Forrajeo Óptimo (OFT, del inglés Optimal Foraging Theory; Charnov and Orians 1973) y constituye una de las teorías más modeladas matemáticamente en ecología y en la que se ha considerado una amplia gama de variables que van desde el comportamiento de depredadores y presas a nivel individual hasta la abundancia de presas o la dinámica poblacional a nivel poblacional (Stephens *et al.* 2007). Los modelos han mostrado que el éxito reproductor de los individuos está explicado en parte por la dieta y el esfuerzo dedicado a la obtención del alimento (MacArthur & Pianka 1966; Perry & Pianka 1997). Los individuos necesitan maximizar sus estrategias tróficas y de forrajeo a través de la optimización de la tasa de captura de presas o la energía obtenida y tiempo dedicados a cada presa (Stephens & Krebs 1986). Tanto el tiempo como la energía obtenida por maximización de la estrategia trófica podrían ser dedicados por el individuo a otras actividades relacionadas con la eficacia biológica como la búsqueda de pareja o la defensa del territorio, afectando la eficacia biológica del individuo (Fox *et al.* 2001).

2.1. Lugar central de forrajeo

Para el caso frecuente en que los individuos realizan viajes de forrajeo teniendo que regresar a un lugar fijo, como el nido, la despensa, el dormidero, etc, se han desarrollado modelos teóricos, sin perder el esquema de la OFT, dentro de lo que se llama el Lugar Central de Forrajeo (CPF, del inglés Central Place Foraging; Orians & Pearson 1979), siendo el aprovisionamiento de alimento en el nido en el grupo de las aves uno de los sistemas más estudiados (Orians & Pearson 1979; Kacelnik & Houston 1984; Stephens *et al.* 2007). Para los individuos reproductores el aprovisionamiento de alimento a su descendencia constituye un elevado gasto de energía, existiendo una fuerte selección por maximizar la eficiencia en la obtención de alimento ya que existe un mayor gasto energético por el hecho de tener que transportar el alimento hasta el lugar donde se encuentra. Al igual que otros modelos de comportamiento, estos modelos de aprovisionamiento enfatizan los costes y beneficios seleccionan para ciertos tipos de comportamientos de forrajeo. El forrajeo óptimo se logra, por un lado, minimizando la distancia y el tiempo de recorrido mediante la elección de parches de alimentación más cercanos al nido y, por otro lado, seleccionando el alimento que más energía aporta, es decir, el alimento con mayor contenido energético en el menor tiempo de forrajeo. En el caso de los depredadores, el tiempo de forrajeo es definido como el tiempo en la búsqueda, manipulación y transporte de una presa. El coste asociado a la caza de una presa estará relacionado con el tamaño de la misma (Griffiths 1980), debido a que las presas de mayor tamaño son más pesadas de transportar, más difíciles de cazar, tienen una mayor probabilidad de infringir daños físicos y suelen tener también una menor abundancia. Sin embargo, estas presas a su vez proporcionan una mayor cantidad de biomasa. Siguiendo los modelos, se necesitaría un mayor número de presas pequeñas para equiparar la biomasa aportada por una presa grande, aunque para las presas grandes. Numerosos estudios en diferentes especies han asociado positivamente el tamaño de la presa con el tiempo de dedicado a su caza (Werner & Hall 1974; Stein 1977; Elner & Hughes 1978; Griffiths 1980), obteniéndose dicha asociación también en especies de aves que alimentan a sus pollos (Kacelnik & Houston 1984). Incluyendo los tradicionales puntos de vista de selección de alimento y explotación de parches, los modelos se centran en predecir la carga óptima en los viajes de aprovisionamiento. La asunción básica es que los forrajeadores deberán elegir un mayor tamaño mínimo de presa cuando éstas son abundantes y/o cuando hay que recorrer una mayor distancia para su captura (Orians & Pearson 1979; Kacelnik & Houston 1984). Se han aplicado mejoras posteriores para comprender mejor cómo la predicción teórica sobre las tasas de aprovisionamiento de alimentos se ajusta a los datos empíricos. Así, la relación tiempo-energía se ha dividido en el tiempo dedicado a la búsqueda y manipulación del alimento, la alimentación propia, al descanso, etc. Por lo tanto, el tiempo de forrajeo dependerá de la eficiencia individual en la búsqueda, captura y manejo del alimento, que a su vez dependerá del comportamiento de forrajeo heredado-aprendido (revisado en Stephens *et al.,* 2007). En el caso de los depredadores, el forrajeo es el resultado de la coevolución de una carrera de armamentos entre las adaptaciones para la caza de los depredadores y las estrategias antidepredatorias de las especies-presa (Woodland *et al.* 1980; Brodie III & Brodie Jr 1999). El riesgo de depredación es una de las mayores fuerzas selectivas, siendo muchas de las características ecológicas y morfológicas de las especies (incluyendo tamaño) consecuencia de estrategias antidepredadotorias (Lima & Dill 1990; Abrams 2000; Dimitrova *et al.* 2009). Sin embargo, aunque aparentemente relevante, el potencial de capturabilidad de una presa ha sido raramente integrado en los modelos teóricos o considerado en los estudios en el campo de las estrategias de forrajeo (Abrams 1997).

2.2. Tiempo, energía y composición nutricional en el forrajeo óptimo

La energía (gasto y obtención) y el tiempo dedicado a la actividad de forrajeo han sido los pilares de la teoría del forrajeo óptimo desde su inicio (Emlen 1966; Schoener 1971). Sin embargo, muchos autores coinciden en la necesidad de dedicar más esfuerzos en la obtención de datos empíricos en el medio silvestre, ya que algunos supuestos teóricos se han revelado como erróneos cuando se prueban en el campo, estimulando críticas (Begon *et al.* 2006), e incluso duras críticas a la capacidad heurística de la teoría (Pierce & Ollason 1987). Por ejemplo, los modelos teóricos han fallado cuando se han aplicado a especies que se alimentaban de presas móviles o cuando se ha dado excesivo énfasis en la ingesta de energía en lugar de la composición nutricional (Sih & Christensen 2001; Kohl *et al.* 2015). Esto es particularmente relevante en el caso de los depredadores carnívoros, ya que se alimentan de presas móviles y se ha considerado que el equilibrio nutricional es innecesario para ellos (Kohl *et al.* 2015). El punto de vista tradicional para los carnívoros, en comparación con los herbívoros y los omnívoros, asume que el contenido nutricional es similar para las distintas especies de presas garantizando el equilibrio nutricional en relación con sus necesidades (Galef 1996; Kooijman *et al.* 2004; Kohl *et al.* 2015) . Se ha hipotetizado durante mucho tiempo que la energía aportada por la presa es la principal característica de la presa que influye en el comportamiento de alimentación de los depredadores (Stephens *et al.* 2007). Sin embargo, actualmente se ha observado que los nutrientes en la dieta también influyen en las decisiones para la búsqueda de alimento en especies depredadoras (Mayntz *et al.* 2005; Mayntz *et al.* 2009; Hewson-Hughes *et al.* 2011; Schmidt *et al.* 2012; Jensen *et al.* 2014). Una gran cantidad de biomasa (gran tamaño de la presa o gran cantidad de presas) no es garantía de la presencia de nutrientes esenciales para un desarrollo óptimo o para el auto-mantenimiento (Krebs & Avery 1984).

2.3. Nutrientes

Los nutrientes son sustancias químicas obtenidas a partir de los alimentos utilizadas para proporcionar no sólo energía sino también materiales estructurales y agentes de regulación química, que aseguran soporte al crecimiento, mantenimiento y reparación de los tejidos del cuerpo (Whitney & Rolfes 2007). Por lo tanto, la calidad nutricional de un alimento se reduce cuando las concentraciones de nutrientes disminuyen, así como cuando aumenta la dificultad para extraer los nutrientes (Barboza *et al.* 2008). El déficit de algún nutriente en la dieta, como amino ácidos, lípidos o proteínas, puede producir efectos adversos en la condición corporal, la tasa de crecimiento o en la salud (Krebs & Avery 1984; Mayntz & Toft 2001; Metcalfe & Monaghan 2001; Kitaysky *et al.* 2006; Jensen *et al.* 2012). Este hecho puede hacer que los individuos estén más limitados por el contenido nutricional del alimento que por la biomasa. Por tanto, los individuos podrían estar frente a un compromiso entre alimentarse de presas que aporten una mayor calidad nutricional o presas de mayor tamaño que aporten una mayor cantidad de biomasa (Wright *et al.* 1998; Wiebe & Slagsvold 2015), compromiso que puede afectar a largo plazo a los propios individuos o a sus descendientes.

2.3.1. Nitrógeno, proteínas y amino ácidos

Dentro de los principales nutrientes esenciales, el nitrógeno es considerado como uno de los mayores limitantes en las poblaciones naturales, en especial durante el crecimiento y la reproducción. Esta importancia es debida a que los compuestos nitrogenados son básicos para la creación de estructuras y del material genético, ADN y ARN, así como para la síntesis de numerosos metabolitos intermedios y vitaminas. La proteína contien la fracción más grande de nitrógeno en el cuerpo animal, con funciones muy versátiles que van desde producir la contracción de las fibras musculares hasta funciones hormonales, enzimáticas e inmunológicas (Li *et al.* 2007). Los individuos pueden usar la proteína almacenada para obtener energía durante la migración y la hibernación, así como en la producción de leche y huevos (Barboza *et al.* 2008). Las proteínas consumidas son catabolizadas en el intestino delgado por la acción de las peptidasas para extraer los aminoácidos que las conforman. Los amino ácidos se clasifican a nivel nutricional en relación a la capacidad de un organismo para sintetizarlos clasificándose como amino ácidos no esenciales cuando se puede sintetizar, o esenciales cuando por el contrario deben de ser ingeridos en la dieta para obtenerlos (Barboza *et al.* 2008). A nivel nutricional cuando la concentración de uno de estos aminoácidos esenciales se reduce por debajo de un umbral, se detiene la síntesis de proteínas produciendo una paralización en la maquinaria celular, produciendo graves consecuencias para el individuo. La concentración mínima de estos aminoácidos esenciales dependerá de la especie. El requerimiento de ciertos aminoácidos también pueden fluctuar temporalmente en función de la necesidad metabólica de ese aminoácido, por ejemplo, en aves durante la muda aumenta la necesidad de ciertos aminoácidos, en especial de la cisteína, para la formación de las plumas (Murphy & King 1984). Este aumento se debe a que las plumas son ricas en cisteína, siendo este aminoácido el responsable de los puentes que reticulan las fibras de proteína de la queratina. Los aminoácidos y las proteínas pueden ser desaminados para obtener energía, aunque el nitrógeno residual de este catabolismo puede ser tóxico. Esta generación de subproductos tóxico produce que el catabolismo de estos compuestos nitrogenados no sea la principal vía de obtención de energía para el individuo y su catabolismo se da sólo en ciertas circunstancias.

2.3.2. Lípidos

Otro grupo de nutrientes de gran importancia son los lípidos. La grasa corporal se ha visto relacionada con la supervivencia y la reproducción de muchas especies de aves debido a que la energía obtenida del tejido adiposo almacenado se utiliza durante los ayunos, la migración y la incubación (Carey 2012; Scanes 2015). Los ácidos grasos son la unidad estructural para todos los lípidos, especialmente los que constituyen los almacenamientos de grasa (triglicéridos) y las membranas (fosfolípidos). Al ser catabolizados se eliminan los enlaces éster produciendo una liberación de ácidos grasos, colesterol y glicerol que son absorbidos. Los ácidos grasos que se encuentran en los tejidos animales se incorporan en la dieta o son sintetizados de novo. En periodos de alto consumo de alimento, la energía se almacena en forma de ácidos grasos en el tejido adiposo que actúa como depósito de grasa (Scanes 2015). Los lípidos son los nutrientes con mayor densidad de energía en los tejidos de reserva, ya que contienen más carbono y el carbono en estos tejidos es más fácilmente reducible y por lo tanto produce una mayor cantidad de energía (Scanes 2015). La unidad de medida utilizada para expresar la cantidad de energía en los alimentos se define como caloría. Una caloría equivale a la cantidad de energía térmica equivalente a la cantidad de calor necesaria para elevar la temperatura de 1 gramo de agua en 1 grado, lo que equivale a 4,185 julios. Los depósitos de grasa pueden incluir una amplia variedad de ácidos grasos, estos son de gran importancia para la nutrición ya que algunos ácidos grasos polisaturados no pueden ser sintetizados y han de ser ingeridos en la alimentación (Barboza *et al.* 2008). La composición de ácidos grasos de la grasa corporal en las aves a menudo difiere tanto entre las especies de aves así como estacionalmente, los cambios en la dieta pueden ser responsables de esta variación. Se ha comprobado que el vireo ojirrojo *Vireo olivaceous* puede distinguir, limitar o incluso evitar el consumo de ciertos ácidos grasos que son menos digeribles como el ácido esteárico respecto a otros (Pierce *et al.* 2004). Algunas especies de aves pueden llegar a depender sustancialmente de la grasa durante vuelos migratorios, existiendo una relación directa entre la composición de los depósitos de grasa con el rendimiento del vuelo y otras actividades físicas (Price 2010). Sugiriéndose recientemente que los ácidos grasos más cortos y/o que tienen más dobles enlaces pueden aumentar el rendimiento máximo (Price 2010). Además de la importante función de los lípidos como fuente de energía también están relacionados con otras funciones en aves como el depósito de los ésteres de cera en las plumas así como los esteroles que son mensajeros hormonales entre los tejidos (Barboza *et al.* 2008).

2.3. Nutrientes en un contexto ecológico evolutivo

Todos estos nutrientes tienen una gran importancia en el estudio de la ecología trófica, ya que alteraciones en su concentración, así como en su composición son fundamentales para la supervivencia del individuo y por lo tanto han de estar sujetos a presiones selectivas. La alimentación óptima proporciona todos los nutrientes, pero su concentración variará en función de la dieta consumida por el individuo. Como se ha comentado previamente, el balance nutricional de las presas puede ser más importante en la dieta que la propia cantidad de alimento o biomasa obtenida, ya que el déficit en un nutriente determinado puede tener severos efectos negativos sobre los propios individuos o sus descendientes (Mayntz & Toft 2001; Metcalfe & Monaghan 2001; Kitaysky *et al.* 2006; Jensen *et al.* 2012). Cuando un nutriente es limitante en la composición de una presa o un conjunto de presas, los requerimientos nutricionales han de ser satisfechos mediante un mayor consumo de presas, lo que conlleva también un consumo elevado de otros nutrientes que deberán ser eliminados produciendo un coste a través del empleo de mecanismos para la eliminación (Scanes 2015). En cambio, el individuo puede contrarrestar el déficit de un nutriente consumiendo una combinación de presas nutricionalmente complementarias que aportarán una concentración adecuada de nutrientes (Begon *et al.* 2006). En los últimos años han proliferado investigaciones en distintas especies que demuestran que los individuos son capaces de regular de forma independiente la ingesta de múltiples nutrientes, evitando de esta forma un consumo excesivo de ciertos nutrientes mayoritarios en las presas así como los déficits en la abundancia de algún nutriente (Raubenheimer & Simpson 2003; Simpson *et al.* 2004; Mayntz *et al.* 2005; Raubenheimer *et al.* 2009; Kohl *et al.* 2015). Se ha observado que un consumo equilibrado de nutrientes tiene efectos positivos sobre rasgos que afectan la eficacia biológica de los individuos, como el funcionamiento del sistema inmunitario (Cotter *et al.* 2011), caracteres sexuales (Maklakov *et al.* 2008), tamaño corporal y tasa de crecimiento (Mayntz & Toft 2001; Simpson *et al.* 2004; Erlenbach *et al.* 2014). Estos resultados sugieren que los individuos habrían evolucionado bajo una presión de selección para equilibrar los nutrientes consumidos a través de la elección de presas con el fin de equilibrar los nutrientes ingeridos respecto a los requerimientos nutricionales o alimentarse de proporciones adecuadas de presas nutricionalmente complementarias mediante una dieta más variada (Hewson-Hughes *et al.* 2013). Además, las estrategias adaptativas para un crecimiento óptimo deben implicar la elección de determinados nutrientes sobre otros por parte de los padres a la hora de alimentar a la descendencia, teniendo en cuenta la dificultad para obtener alimentos de alto valor nutricional y la capacidad de los padres para obtenerlos en sus territorios (Ricklefs et al. 1998; Dmitriew 2011, Blanco et al. 2014). En este contexto la Hipótesis de la Dieta Equilibrada (Balanced-Diet Hypothesis; (Pulliam 1975; Lefcheck *et al.* 2013) postula que una amplio nicho trófico suministra una gama más completa de nutrientes, proporcionando beneficios para la eficacia biológica del consumidor (Lefcheck *et al.* 2013; Marques *et al.* 2015). Por lo tanto, sería lógico pensar que si los individuos son capaces de autorregularse nutricionalmente y además existe una presión selectiva para mantener una dieta nutricionalmente equilibrada, estos comportamientos alimenticios que desarrolla el propio individuo deberían de producirse también en los comportamientos dirigidos a alimentar a sus crías. Esta hipótesis se ve reforzada por un reciente meta análisis en el que se observó que los individuos que se alimentaban con una dieta generalista tenían significativamente una mayor eficacia biológica que la media de los individuos especialistas (Lefcheck *et al.* 2013). Aunque en más de la mitad de los estudios revisados, la dieta especialista fue tan buena o mejor que la dieta generalista (Lefcheck *et al.* 2013).

La presente tesis examina desde distintas perspectivas la ecología trófica analizada por un lado en los falconidos como grupo de especies de rapaces depredadores con una distribución cosmopolita. Por un lado se analiza el hábitat (biomas) ocupado a escala global por el grupo de los falcónidos para investigar la relación entre la diversidad de dieta de las diferentes especies, la heterogeneidad del hábitat que ocupa y su área de distribución. Se predice que si la estrategia generalista en alimentación permite a las especies expandirse y colonizar nuevas áreas y hábitats, se obtendrá que tanto la diversidad como la riqueza trófica se relacionan de forma positiva con el tamaño del área de distribución y con el índice de especialización biómica. Por otro lado, la presente tesis se centra en una especie dentro del grupo de falcónidos, el cernícalo vulgar *Falco tinnunculus*, en la que se ha analizado el aprovisionamiento de alimento al nido, el hábitat así como la composición nutricional de sus principales especies-presa en una población mediterránea en la región de Campo Azálvaro, en Segovia. Se estudia si la amplitud del nicho trófico individual está asociada con la calidad individual usando componentes de la eficacia biológica, tales como la fecundidad o la viabilidad de la descendencia. Bajo la premisa de que el generalismo trófico es una estrategia seleccionada por los cernícalos, la diversidad de presas consumidas debe relacionarse positivamente con la calidad individual y la viabilidad la descendencia. Además se analiza el hábitat correspondiente al territorio de cría del cernícalo vulgar con el fin de investigar si territorios más heterogéneos aportan una mayor diversidad de especies-presa en la dieta como predice la hipótesis de la hetoregeneidad del hábitat LHH. Si los individuos de mejor calidad poseen una dieta más variada, se predice que los mejores territorios serán aquellos con una mayor heterogeneidad de paisaje que pueden proveer de una mayor diversidad de presas. Se analiza energéticamente y nutricionalmente la composición del alimento del cernícalo a través de la medición de calorías y macronutrientes (grasa, proteínas y amino ácidos) en las 11 principales presas del cernícalo. Bajo el enfoque de la OFT, se investiga si el tiempo que tarda el cernícalo en capturar una especie presa esta explicado por su tamaño, su dificultad de captura o su preferencia para determinar si la preferencia particular por una especie-presa es debido a su rentabilidad en términos energéticos y/o a su composición nutricional. También se investiga si el consumo de las especies-presa preferidas por el cernícalo promueve tiempos de aprovisionamiento más largos. Además, desde un enfoque nutricional se investiga la importancia tanto de la cantidad como de la diversidad de nutrientes en componentes de la eficacia biológica. Se predice bajo la Hipótesis de la Dieta Equilibrada que una mayor diversidad de especies-presa en la dieta aporta una mayor diversidad de nutrientes y por lo tanto una composición más equilibrada que beneficiaría a los individuos en términos de eficacia biológica. Finalmente, se estima la abundancia de especies-presa en el área de estudio y en la dieta y se calcula el índice de capturabilidad y preferencia de caza para cada especie.

3. Bibliografía

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Objetivos

La presente tesis se enmarca en el contexto científico de la ecología evolutiva y su principal objetivo es incrementar el conocimiento desde una perspectiva evolutiva de las estrategias tróficas en las poblaciones silvestres. Este objetivo principal puede desglosarse en los siguientes objetivos concretos:

- Determinar si el nicho trófico identificado a través de la diversidad de la dieta puede predecir el tamaño del área de distribución y la heterogeneidad de paisaje a nivel interespecífico y a escala global (heterogeneidad de biomas; Capítulo I).

- Determinar si las diferentes estrategias de nicho trófico, especialismo *vs*. generalismo, a nivel intraespecífico se encuentran relacionadas con la calidad de los individuos y por lo tanto con componentes de la eficacia biológica, tales como éxito reproductor y viabilidad de la descendencia (Capítulo II).

- Determinar a nivel intraespecífico y escala poblacional si amplitud de nicho trófico está determinada por la heterogeneidad de paisaje en los territorios de cría (Capítulo III).

- Determinar si los modelos de forrajeo óptimo para una especie depredadora predicen la dificultad de captura y la composición nutricional de las especies que conforman la dieta (Capítulo IV).

- Determinar la relación entre la amplitud de nicho trófico y la composición nutricional de la dieta en una especie depredadora (capítulo V).

Material y métodos generales

1. Modelos de estudio

1.1. Familia *Falconidae*

Los falcónidos (*Falconidae*) son una familia de aves rapaces ampliamente distribuida en el planeta constituida a priori por 64 especies, variando su número según el estudio filogenético utilizado (Fuchs *et al.* 2015). Siguiendo a Fuchs y colaboradores (2015), las 64 especies de *Falconidae* se distribuyen en once géneros, siendo el género *Falco* el género que ha sufrido una mayor tasa de especiación. Existe una gran variedad ecológica entre las especies que componen esta familia, lo que se ha traducido en una gran variedad de nichos tróficos y de amplitud de los mismos, observándose desde especies muy especialistas en el consumo de presas pertenecientes a grupos taxonómicos concretos, como el caso de *Falco columbarius* muy especializada en el consumo de aves o el de *Spziapteryx circumcinctus* especializada en el consumo de insectos, hasta especies muy generalistas como *Falco tinnunculus* que consume una amplia gama de taxones o *Caracara plancus* que además de cazar es una gran consumidora de carroña. Esta variedad ecológica se asocia con un gran número de biomas ocupados, apareciendo en todos los terrestres a excepción de los desiertos helados de regiones polares, lo que genera una gran variación en ocupación de hábitats y en el tamaño del área de distribución, con especies muy cosmopolitas como *Falco peregrinus* que ocupa prácticamente todo el globo y está presente en 10 de los 11 biomas terrestres hasta especies que ocupan un único bioma como *Daptrius ater* presente solo en el bosque tropical o con áreas de distribución muy reducidas como *Falco punctatus* presente solo en ciertas partes de la Isla Mauricio o *Micrastur plumbeus* presente únicamente en una reducida región de la parte oriental de Colombia y norte de Ecuador. Sobre este grupo de aves existe también un aceptable número de estudios de alimentación lo que hace de este grupo taxonómico un buen modelo para investigar la relación entre nicho trófico, heterogeneidad de paisaje (a través de los diferentes biomas ocupados) y área de distribución.

1.2. Cernícalo vulgar *Falco tinnunculus*

El Cernícalo Vulgar *Falco tinnunculus* es un falcónido de pequeño-mediano tamaño con dimorfismo sexual invertido en tamaño, siendo las hembras aproximadamente un 20 % más pesadas que los machos y también en coloración siendo los machos de color más conspicuo que las hembras (Village 1990; Vergara & Fargallo 2011). Presenta una distribución paleártica, afrotropical e indomalaya (Village 1990). Es una especie común en multitud de hábitats ligados siempre a los espacios abiertos, por lo que es frecuente en medios humanizados, tales como áreas agrícolas y pastizales (Forsman 2007).

En Europa es una especie migradora en latitudes norteñas más frías, distribuyéndose por latitudes más templadas al sur fuera de la época de cría, pudiendo llegar al África subsahariana en época invernal (Cramp & Simmons 1980). Se le considera un migrador parcial en algunas regiones de la Península Ibérica, Gran Bretaña y Europa Central (Cavé 1968; Cramp & Simmons 1980). En el área de estudio, se comporta igualmente como migradora parcial con escasos efectivos invernales (Fargallo 1999), aunque con una alta filopatria (Vergara & Fargallo 2008). Los cernícalos vulgares crían en multitud de soportes naturales como repisas en cortados o agujeros y también usa nidos viejos de otras especies en árboles. También acepta soportes artificiales, como agujeros en paredes de edificios, torretas de líneas eléctricas, etc, por lo que es relativamente fácil que ocupen nidales artificiales (Fargallo *et al.* 2010). El patrón general de emparejamiento es la monogamia, aunque puede darse la poliginia en un 5-20% en años de alta abundancia de alimento (Korpimaki 1988). Los machos establecen los territorios que ofrecen a las hembras. Una vez elegido el lugar de nidificación, la hembra pone por lo general entre 3 y 6 huevos que incuba ella en la totalidad, aunque a veces el macho permanece echado sobre los huevos para evitar la pérdida de calor cuando la hembra sale del nido. El macho es el principal proveedor de alimento desde el cortejo hasta la independencia de los pollos (Village 1990; Sonerud *et al.* 2014). La hembra, por otra parte, permanece la mayor parte del tiempo en los alrededores del nido para defenderlo de los intrusos y depredadores, cazando esporádicamente (Village 1990). Estudios experimentales han encontrado que el grado de gasto energético, el esfuerzo de caza y el aprovisionamiento de presas que los machos pueden realizar durante el período de crianza de los pollos están explicados en gran parte por el tamaño de puesta (Masman *et al.* 1988; Korpimäki & Rita 1996; Wiehn & Korpimäki 1997; Fargallo *et al.* 2002), siendo reacios a modificar la inversión parental y la tasa de ceba por encima o por debajo del nivel establecido por el tamaño original de puesta (Korpimäki & Rita 1996; Tolonen & Korpimäki 1996; Fargallo *et al.* 2002), por lo que se considera que el tamaño de puesta es un indicador fiable de la calidad de los machos en esta especie.

La plasticidad encontrada en la variedad de hábitats ocupados por la especie se corresponde con una alta plasticidad en su nicho trófico observándose variaciones en la alimentación a lo largo de su distribución. La mayoría de los estudios realizados en las regiones frías y templadas del norte y centro de Europa han encontrado que las principales presas consumidas por el cernícalo son los mamíferos, especialmente los topillos diurnos del género *Microtus* (Village 1990). En estas poblaciones puede consumir otras especies, lo que le permite al cernícalo seguir habitando dichas zonas cuando la disponibilidad de topillos es escasa. La lista de presas alternativas en las zonas templadas es muy variada observándose el consumo de otras especies de mamíferos, así como aves, reptiles o invertebrados (Village 1990). Por otro lado, en las poblaciones situadas de la zona mediterránea y en el sur de la distribución de la especie, la dieta tiene un predominio de insectos y reptiles, aunque el consumo en términos de biomasa puede ser predominante de mamíferos (Aparicio 2000). La capacidad de la especie para alimentarse de un amplio rango de presas permite a los cernícalos colonizar nuevos hábitats, como los urbanos, donde se han especializado en el consumo de aves debido a su mayor densidad en este tipo de hábitats con respecto a otras presas como los mamíferos (Baziz *et al.* 2001; Aschwanden *et al.* 2005; Kubler *et al.* 2005; Souttou *et al.* 2007). También el consumo de aves puede ser de importancia en zonas mediterráneas cuando la disponibilidad de mamíferos es baja (Martínez-Padilla & Fargallo 2008).

2. Investigación en *Falconidae*

2.1. Literatura y análisis de la alimentación de *Falconidae*

Para el análisis de la dieta de las diferentes especies de falcónidos se obtuvieron datos de la bibliografía. La riqueza total de especies-presa en la dieta se calculó sumando el número de taxones distintos consumidos que se obtuvieron en el total de estudios usados para cada especie de falcónido. Para determinar la dieta tanto a nivel de orden como de clase, se usaron un total de 188 estudios para 61 especies de *Falconidae* en los que se pudieron encontrar datos sobre el número de presas consumidas. En algunos casos no se pudo estimar el esfuerzo muestral del estudio y debido a que la riqueza puede aumentar con el tamaño de la muestra, se intentó minimizar el error controlando el número de especies-presa encontrado en la dieta por el número de trabajos usados, tanto cuando la riqueza se calculó al nivel taxonómico de clase como de orden.

La diversidad media de especies-presa encontradas en la dieta se calculó mediante el Índice de Shannon-Wiener utilizando estudios donde aparecían datos cuantitativos de dieta. Así se pudieron obtener datos de las especies consumidas en un total de 161 poblaciones de 30 especies de falcónidos en 126 estudios al nivel taxonómico de Orden, mientras que se obtuvieron datos de 170 poblaciones de 31 especies en 133 estudios al nivel de Clase. Los valores de diversidad de la dieta se obtuvieron de estudios que informaban del número total de presas (86 estudios), el porcentaje de presas (116 estudios) o el porcentaje de biomasa aportada por cada especie-presa (32 estudios). La diversidad trófica media se calculó usando los índices Shanon-Wiener de cada población obtenidos para cada especie de falcónido. La diversidad máxima de la dieta se consideró como el mayor índice Shanon-Wiener registrado entre las poblaciones de cada especie. Dicho valor se correlacionó con el número de poblaciones estudiadas, por lo que se usaron los residuos del modelo de regresión entre ambas variables para corregir los datos por el esfuerzo muestral. Todos los estudios con un valor superior al 30 % de especies-presa indeterminadas fueron descartados.

Tanto la carroña como los alimentos de origen vegetal son tipos especiales de alimento difíciles de clasificar, ya que tienen características ecológicas muy diferentes a los animales vivos. En general los estudios centrados en ecología trófica incluyen a la carroña en una categoría independiente de clasificación taxonómica (Valdez 1996; McDonald *et al.* 2003; Donadio *et al.* 2007; Zhou *et al.* 2011). Para el estudio se usó este mismo criterio, no diferenciando las especies consumidas en forma de carroña y considerando que todas los individuos consumidos conformaban el mismo grupo taxonómico, carroña o vegetal, como dos grupos diferentes tanto a nivel de orden como a nivel de clase. La presas pertenecientes a *Lacertillia, Serpentes, Iguania* and *Gekkota*, fueron clasificados como ordenes independientes (Schwenk 2000).

2.2. Área de biogeografía de *Falconidae*

El área ocupada por cada especie fue estimada mediante el uso de mapas de distribución provenientes del "Handbook of the Birds of the World" (Hoyo *et al.* 1994). La determinación del área de ocupación se realizó mediante la herramienta "Wanda tool" del software Image J (Rasband 1997; Schneider *et al.* 2012). Los mapas se escalaron utilizando la distancia que cruzaban los continentes en los paralelos del Ecuador (latitud 0°) y del Trópico de Capricornio (23° 27' S). El Índice de Especialización Biómica (BSI de sus siglas en inglés se determinó como el número de biomas en los que cada especie estuvo presente (Hernández Fernández & Vrba 2005; Moreno Bofarull *et al.* 2008; Cantalapiedra *et al.* 2011).Como referencia en la clasificación de biomas se usó la propuesta por Walter y Box (Walter & Box 1976). Para controlar por el lastre filogenético en los análisis se siguió la filogenia más reciente propuesta para *Falconidae* (Fuchs *et al.* 2015).

3. Investigación en el cernícalo vulgar

3.1. Área de estudio

El trabajo de campo se realizó durante los meses de abril a julio de los años 2010 a 2014, en la comarca ganadera de Campo Azálvaro (Figura 1). En la presente tesis también se incluyen datos de años anteriores (2006 a 2009) tomados por J.A. Fargallo, P. Vergara, I. López-Rull y J. Martínez-Padilla. La región de Campo Azálvaro se localiza en la vertiente norte del Sistema Central en las provincias de Segovia y Ávila (40º40'N, 4º20'O). Se trata de un área dedicada a la ganadería extensiva con grandes extensiones de pastizal de montaña a una altitud de 1300 m.s.n.m (Fargallo et al. 2009). La cubierta arbórea está conformada principalmente por pequeños bosquetes de encina *Quercus ilex* y roble *Quercus pyrenaica,* además en las proximidades del área de estudio existen pequeñas repoblaciones de chopos *Populus sp*, junto con algún rodal disperso de pino *Pinus pinaster*. El clima de la región es Mediterráneo húmedo, con veranos templados y secos e inviernos húmedos y fríos. Desde 1994 se han ido instalando paulatinamente nidales artificiales en el área de estudio (Fargallo *et al.* 2001), hasta un total de 64 en 2005. La distancia media promediada entre los nidales es de 1.4 km con un rango que va de 0.11 a 6.28 km. El número de nidales ocupados durante los años de estudio fluctuó entre 25 y 44 en una área de of 23 km^2 (Fargallo *et al.* 2009).

3.2. Composición de la dieta del cernícalo vulgar

Para cuantificar la composición de la dieta en nuestra población se instalaron cámaras digitales de video en los nidales con el objeto de filmar las presas aportadas por los padres a los pollos a la edad de 12-14 días. El uso de este método nos permitió determinar las presas consumidas sin los sesgos observados en otros métodos como el análisis de egagrópilas o la recogida de presas en los nidos. Las grabaciones durante los años 2006 a 2008 se realizaron usando cámaras Cylinder SONY 1/3* Super HAD TM conectadas a un grabador digital ARCHOS AV500 100 Gb, mientras que en los años 2009 a 2011 se usaron cámaras digitales SONY HandyCam 60 Gb con un objetivo tipo ojo de pez, ambos sistemas fueron situados en la pared trasera del nidal con la lente dirigida hacia la entrada. Durante los años 2012 a 2014 se emplearon microcámaras CCD 1/3 Sharp conectadas a un gestor de vídeo AXIS Q7401. En este caso la micro cámara se situó en la pared lateral del nidal enfocando hacia la entrada. Todos los sistemas fueron alimentados a través de una batería SLI de 12 amperios (24 Ah 24 V) conectada a un convertidor de voltaje (12V).

Las grabaciones se hicieron durante periodos de 24 horas consecutivas o más, con el fin de grabar todas las presas aportadas desde el amanecer hasta el anochecer sin interferencias causadas por los investigadores. El periodo de luz en nuestra zona de estudio durante los meses de Junio y Julio, meses en los que se realizaron la mayoría de las grabaciones, fue aproximadamente de 15 horas. Las grabaciones se visionaron usando el software VLC Media Player (www.videolan.org).

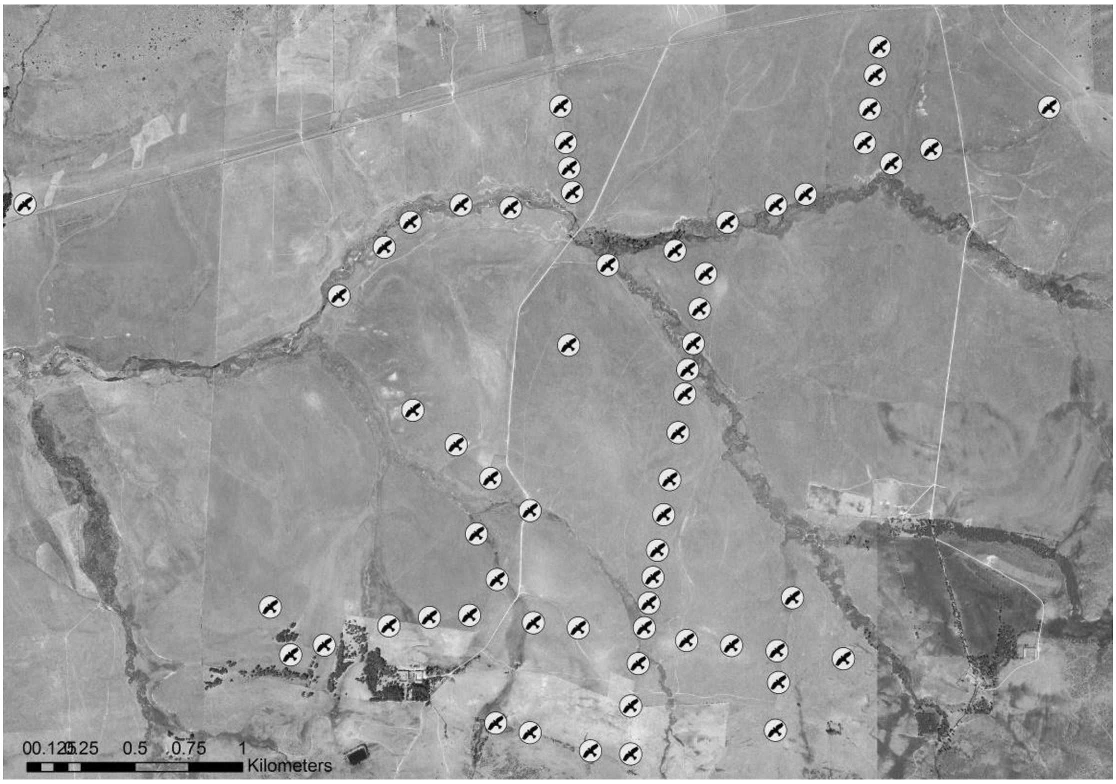

Figura 1. Mapa de la Zona de estudio. Foto aérea de la zona de estudio en donde se sitúan las cajas nido utilizadas para la realización de la presente tesis.

La determinación de las diferentes presas se realizó al menor nivel taxonómico posible. En anfibios, reptiles, aves y mamíferos se identificaron el 99% a nivel de especie (35 casos indeterminados de 9712 casos totales). La mayor dificultad para llegar a nivel de especie se encontró en el grupo de las aves (24 de los 35 casos indeterminados). Entre las especies de artrópodos consumidas, el grillo campestre *Gryllus campestris*, grillotopo *Gryllotalpa gryllotalpa* (*Insecta, Orthoptera*) y tarántula mediterránea o araña lobo *Lycosa tarentula* (*Arachnida*) fueron identificadas fácilmente en los vídeos, mientras que el resto de especies de artrópodos, debido a su pequeño tamaño no fue posible identificar de forma visual la especie a la que pertenecían, por lo que se identificaron al menor nivel taxonómico posible.

Para calcular la composición de la dieta en función de la biomasa consumida de cada presa usamos un único valor de biomasa por cada especie-presa. El valor de biomasa se calculó como la media de los pesos obtenidos de individuos de la misma especie. En las especies que pudieron ser capturadas en la zona de estudio se usó la media de todos los pesos de los individuos medidos. Mientras que en las especies que no se pudieron capturar en la zona de estudio (la mayoría aves), el valor promedio de biomasa se calculó usando la medía de los pesos obtenidos en la literatura científica, intentando usar poblaciones de las mismas características a la de nuestra zona de estudio. En algunas ocasiones, las presas de mayor tamaño son parcialmente consumidas por los padres antes de llegar al nido, por lo que para cuantificar la biomasa consumida, se calculó de forma visual la fracción de presa que había sido aportada. Para ello se usó la siguiente estimación con el fin de estandarizar todos los casos de mamíferos y reptiles: ¾ de la biomasa si a la presa le faltó la cabeza, ½ de la biomasa para presas sin cabeza ni extremidades anteriores y ¼ para presas que únicamente presentaban cola y extremidades posteriores. La biomasa en estos casos se calculó multiplicando el peso medio asignado a la especie por la fracción correspondiente a su estado (Fargallo *et al.* 2003). Cuándo la presa no pudo ser identificada al menor nivel taxonómico, se calculó su biomasa como la biomasa promedio teniendo en cuenta la frecuencia de consumo de cada especie en el nido.

La biomasa consumida por los pollos de un nido durante el tiempo de grabación se calculó como la suma de la biomasa aportada por todas las presas incluyendo la corrección para presas fraccionadas (Fargallo *et al.* 2003). Debido a que no todos los nidos se pudieron grabar durante el mismo periodo de tiempo, se calculó la tasa de ceba (número de presas consumidas / horas de filmación) y la biomasa consumida por hora (total biomasa consumida / horas de grabación) para poder hacer comparaciones entre nidos.

3.3. Amplitud del nicho trófico

En la presente tesis se usó la diversidad de presas consumidas como un indicador de la amplitud del nicho trófico (Bolnick *et al.* 2003). La diversidad de presas fue calculada usando el índice de Shannon-Wiener para cada nido, usando el menor nivel taxonómico en que las presas fueron identificadas en la totalidad de los datos, de esta forma se usó el nivel de especie en anfibios, reptiles, mamíferos, aves, tarántula mediterránea, grillo campestre y grillotopo, a nivel de familia los tetigónidos, acrídidos (*Orthoptera*) y mántidos (*Mantodea*)a nivel de orden los ortópteros y lepidópteros (orugas).

3.4. Reproducción

Desde los meses de marzo-abril se registraron de forma sistemática las cajas nidos de la población para determinar la fecha de puesta, el tamaño de puesta, fecha de eclosión y el número de pollos. Durante la incubación se capturó a la hembra para su identificación, además previamente a la instalación de las cámaras se capturaron a los dos progenitores para determinar su identidad tomar medidas morfológicas. A la edad de 26 días de los pollos se procedió a la toma de medidas morfológicas y a la extracción de sangre para su posterior sexado. Asimismo, durante los años 2006 a 2009 se utilizó un ensayo de inyección de fitohemaglutinina-P (PHA) para evaluar la inmunidad mediada por células T *in vivo* (CMI), uno de los tres componentes principales del sistema inmune. La PHA es un mitógeno comúnmente utilizado en estudios de aves, ya que se considera un método benigno y útil para evaluar la función dependiente del timo (Fargallo *et al.* 2002). A los 26 días de edad de los pollos se les inyectó intradérmicamente en el patagio del ala 0,3 mg de PHA disueltos en 0,1 mL de PBS. El grosor del patagio se midió tres veces con un calibre digital (0.01 mm) en el sitio de inyección antes y 24 horas después de la inyección. La repetibilidad de las medidas es alta (ver Fargallo *et al.* 2002), usándose los valores medios de las tres medidas. La diferencia entre el grosor inicial y final (24 h después) se usó como estimación de la respuesta inmunitaria.

3.5. Composición nutricional de las especies-presa

La determinación de la composición nutricional de las presas se realizó obteniendo especímenes de las principales especies-presa de cernícalo en la zona de estudio. Estas especies constituyen el 91% del total de especies consumidas por los cernícalos en nuestra zona de estudio. El valor nutricional para el grupo de aves fue determinado usando una muestra que combinaba individuos de estornino negro *Sturnus unicolor* y alondra común *Alauda arvensis.* Estas dos especies representan el 77% del consumo de aves en cernícalo en nuestra población. También el valor nutricional del grupo *Acrididae-Tettigoniidae* fue obtenido de una combinación de distintas especies de dos familias de Ortópteros, *Acrididae* y *Tettigoniidae.* Las especies de vertebrados fueron colectadas en los nidos de cernícalo, usando especímenes frescos recién cazados. La retirada de las presas de los nidos se compensó con una biomasa similar de pollos de gallina *Gallus gallus domesticus* muertos comercializados como alimento para rapaces. Por otro lado, debido a que los invertebrados (grillos, grillotopos, saltamontes y chicharras) son consumidos por los pollos rápidamente, estos rara vez se encuentran en los nidos de cernícalo, por lo que estas especies tuvieron que ser colectadas directamente en el campo bajo el pertinente permiso. Todas las presas fueron pesadas en el momento de la colecta, inmediatamente después congeladas a -21°C. Posteriormente se deshidrataron mediante liofilización antes de iniciarse los análisis de la composición nutricional en el laboratorio. Las plumas de mayor tamaño en las aves (rémiges y rectrices) no son consumidas por los cernícalos, por lo que dichas plumas no se incluyeron en los análisis de laboratorio. Para los análisis nutricionales fueron necesarios al menos 7 gramos de biomasa deshidratada por cada grupo de presas a estudiar. Todos los individuos de la misma especie o grupo de presas a analizar fueron homogenizadas conjuntamente antes de iniciar los análisis.

El nitrógeno total se determinó usando el método de Dumas, a través de la combustión de la muestra a una alta temperatura en una atmosfera de oxígeno. Para el proceso se usó el equipo TruSpec CN (Leco Corporación, USA). Para la cuantificar la energía bruta (calorías por gramo) de las especies-presa se usó una bomba calorimétrica (Parr Instrument CO., Moline, IL) en la que se realizó la combustión de la muestra. El contenido de grasa de las presas se obtuvo mediante saponificación de la muestra con 2N KOH en solución de etanol. Mientras que la fracción no saponificable se extrajo mediante éter de petróleo (b. p. 40-60°) y posterior evaporación y secado de la muestra a 103± 2 ºC hasta alcanzar un peso contante.

La composición de amino ácidos se determinó mediante hidrólisis de proteínas y posteriormente por cromatografía líquida de alta resolución (Pico Tag method; Waters, Milford, MA; Cohen et al., 1989) siguiendo el protocolo de Rivera-Ferre y colaboradores (2006). La cisteína y la metiona se determinaron como ácido cisteico y sulfona de metionina, respectivamente, obtenidos después de la oxidación con ácido perfórmico previa hidrólisis de HCl 6M. El triptófano no pudo ser determinado.

3.6. Capturabilidad de la presa

La capturabilidad potencial de las especies-presa se calculó asignando valores a ocho variables ecológicas relacionadas con la presumible dificultad de los cernícalos para la captura de la especie. Tres características ecológicas estuvieron relacionadas con el hábitat en donde la especie habita, otras dos lo están con la disponibilidad de la presa y las tres restantes reflejan el comportamiento antidepredatorio de la especie. Las variables relacionadas con protección ofrecida por el hábitat, la localización y la abundancia se estimaron en base a las observaciones realizadas en la zona estudio. Para todas variables se asignaron valores enteros comprendidos entre 1 y 3, siendo 3 el valor que expresa una mayor dificultad de captura. La dificultad de captura de una especie presa se calculó mediante la suma de los valores de las ocho variables, así valores mayores indican una mayor dificultad de captura para la especie.

3.7. Tiempo de aprovisionamiento, preferencia de presa y rentabilidad energética

Se definió el tiempo aprovisionamiento para cada especie-presa como la media del tiempo transcurrido entre la última presa aportada en el nido por los padres (el padre en más de un 90 % de los casos) hasta el siguiente aporte de la especie-presa objeto. Los tiempos medios de aprovisionamiento se calcularon usando un total de 12,779 registros. La preferencia de presa se calculó relacionando el número de veces que aparece la especie-presa en la dieta respecto a su abundancia en la zona. La preferencia se pudo estimar en un total de 15 grupos de especies-presa. La rentabilidad energética de la presa se estimó como calorías / tiempo de aprovisionamiento, considerando el número de calorías por gramo de peso seco. Además se calculó la "rentabilidad de la búsqueda de presas" definida como la biomasa proporcionada por una presa determinada en relación a su dificultad de captura y se calculó dividiendo el peso de la presa por índice de capturabilidad.

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Capítulo I:

Trophic niche breadth of Falconidae species predicts the number occupied biomes but not range size

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Abstract

Ecological specialization and trophic niche breadth concepts play a key role in our understanding of the biogeographic distribution patterns and the processes determining generation, extinction and diversification of species. Theory predicts that strategies aimed at reducing the niche (specialism) should limit the capacity of individuals to colonize new habitats, thus to expand its distribution area, which is favoured in more stable and homogeneous environments with temporally and spatially predictable resources. The opposite is predicted for strategies aimed at widening the niche (generalism). Applying this idea to trophic ecology, it is possible to forecast that those species with a wider/narrower trophic niche will have larger/smaller distribution areas and inhabit in higher/lower habitat heterogeneity at the global scale. This idea was assessed by analysing the relationships between indexes of trophic niche breadth (diet richness/diversity), generalism/specialism potential (maximum diet diversity), size of the distribution area and habitat heterogeneity measured as the biomic specialization index (BSI; number of biomes inhabited) for the different species of the family *Falconidae* (Aves, Falconiformes) at a global scale. Furthermore, in the analyses we used the maximum diet diversity (highest value of diet diversity among populations) as a measure of the potential of generalism/specialism in the species. Finally, we did two different approaches for calculating diet indexes attending to two different taxonomic levels (class and order) to know how this affects the trophic niche category assigned to the species and results of the study. Our findings revealed that species' diet was not a good predictor for range size but for habitat heterogeneity. Species more generalists in diet (mean and maximum values) inhabiting significantly more biomes. Our results also showed that diet richness index calculated at the superior taxonomic rank (class) showed an overestimation in the number of specialist species compared with the diversity index and with taxonomic level of order. This study reveals that diet breadth is an important ecological trait explaining global patterns of biome occupation for individuals, populations and particularly species.

Introduction

The knowledge about both the heterogeneity of consumed dietary resources (trophic niche breadth) and the process of adaptation to a subset of possible environments (ecological specialization) play a key role in our understanding of the global distribution patterns and of the generation, extinction, and diversification of species (Bolnick & Fitzpatrick 2007; Funk 2009; Nosil & Harmon 2009; Belmaker *et al.* 2011; Poisot *et al.* 2011). One of the proposed selective pressures that modulate trophic niche and promote ecological specialization is the competition for resources among individuals of the same or different species (Bolnick & Fitzpatrick 2007; Poisot *et al.* 2011). Thus the benefits of a strategy aimed at reducing the niche breadth consists in diminishing the competition among coexisting individuals, populations or species by segregating the areas and resources (Futuyma & Moreno 1988; Araújo *et al.* 2011). Strategies may be different depending on the predictability of resources in time and space (Estes *et al.* 2003; Svanbäck & Bolnick 2007; Woo *et al.* 2008; Quevedo *et al.*

2009). It is thought that specialism or niche narrowing may be favoured in stable and homogeneous environments where resources tend to be less variable in time and space, thus being more predictable. On the contrary, unstable and heterogeneous environments are considered to promote generalist or niche widening strategies aimed to expand the niche and facilitate rapid change in the exploitation of variable and unpredictable resources (Estes *et al.* 2003; Svanbäck & Bolnick 2007; Woo *et al.* 2008; Quevedo *et al.* 2009). This has led to the assumption that specialist species are more prone to extinction since a close dependence on a narrow range of resources make them more vulnerable against adverse environmental changes affecting resource availability, while the higher capacity of generalists to exploit a higher variety of resources makes them less vulnerable against unpredictable environmental changes affecting resource availability (Vrba 1987; Owens & Bennett 2000; Purvis *et al.* 2000).

The explanation of speciation under the context of niche narrowing *vs.* widening is a classical debate in evolutionary ecology. It has been suggested that disruptive selection caused by the frequency-dependent competition between ecologically heterogeneous individuals occupying different niches may trigger sympatric speciation processes (Bolnick & Fitzpatrick 2007). Specialism in the use of resources within a population increases ecological heterogeneity favouring the emergence of new species, thus increasing speciation rates (Gavrilets 2006; Bolnick & Fitzpatrick 2007; Schluter 2009). Furthermore, competition reduction by more specialist strategies increases fitness over the generalist individuals, allowing divergent phenotypes to result from ecological adaptations (Gavrilets 2006; Bolnick & Fitzpatrick 2007). This phenotypic divergence may reduce mating rate due to an increase in the difficulty of mate timing or location if the peaks of resources are distant in time and space (Fry 2003; Bürger *et al.* 2006; Bolnick & Fitzpatrick 2007). Also some ecological traits may be pleiotropically linked to sexually selected traits selected by the individuals, thus hindering the mating distance between phenotypes (Bolnick & Fitzpatrick 2007). A different perspective to account for high speciation rates in specialists may be due to a greater susceptibility of specialist species against habitat loss or fragmentation, increasing the reproductive isolation between populations, which decreases the time required for speciation (Futuyma & Moreno 1988; Jocque *et al.* 2010). On the other hand, generalist species have a greater potential of expansion due to its higher capacity to exploit more diverse resources and colonize new environments and regions (Thomas *et al.* 2001), that is why generalism is considered a source for adaptive radiation and diversification (West-Eberhard 2003; Phillimore *et al.* 2006; Gómez Cano *et al.* 2013).

From a biogeographic perspective it is considered that more stable biomes, such as those placed in equatorial regions, boost the emergence and maintenance of a higher number of specialist species (Belmaker *et al.* 2011), whereas in more variable biomes, such as temperate forests, where resources are more unpredictable, generalist species can be favoured. It has been suggested that these variations in the biome-related environmental conditions can explain the latitudinal gradient of species richness widely observed in many taxa (Buckley *et al.* 2010; Belmaker *et al.* 2011; Davey *et al.* 2012; Salisbury *et al.* 2012). On the other hand, due to the higher capacity of colonization of generalist species, it is expected these species to be present in a higher number of environments, habitats or biomes. The biomic specialisation index (BSI) as an indicator of habitat heterogeneity, is defined as the number of biomes inhabited by a given species (Hernández Fernández & Vrba 2005) and can be considered as a good indicator of ecological specialisation, since it describes the position of a species in the gradient specialism-generalism throughout the capacity of the species for obtaining resources in different environments (Hernández Fernández & Vrba 2005; Cantalapiedra *et al.* 2011). If generalist strategies are associated with the capacity of colonization, it would be expected that, in general, more generalist species occupy a higher number of biomes (higher BSI) and show a larger distribution area (Hernández Fernández & Vrba 2005). Trophic niche has been largely used as the basis for the study of ecological specialisation, as the availability of food resources is a major environmental force modulating adaptive strategies and phenotypes of the organisms. A positive correlation between heterogeneity of habitat and diet has been observed among populations of the same species, which suggests that increase of the habitat heterogeneity may produce trophic generalists or vice versa (Abbas *et al.* 2011; Blanco-Fontao *et al.* 2013; Rosenblatt *et al.* 2015). Another key aspect when comparing ecological niches of the species is the taxonomic scaling of the food resource to work with. Consumers can show a preference or a special capacity of preying species sharing ecological traits (feeding habits, activity periods, preferred habitats, etc.), these traits being philogenetically determined, for which the resulted diet diversity may depend on the taxonomic level used for the prey-species (Jorge *et al.* 2014). For example, a species specialised in the consumption of many prey-species belonging to a given family will behave as specialist if diet diversity is calculated at the family level, but as generalist if it is considered at the genus or species level.

In this study we explore whether diet diversity of organisms can predict habitat heterogeneity and size of the distribution area at a global scale. For this purpose, we calculated two different indexes of diet breadth (total richness and mean diversity) and BSI and recorded the size of the distribution area for all the bird species of the family *Falconidae*, since this group counts on broad knowledge on diet in different populations and exhibits a great variation in geographical range from local species with restricted distributions to cosmopolitan species. Relying with diet studies from different populations allowed us to estimate the maximum diet diversity considering this value as a measure of the potential for generalism of the species. Family *Falconidae* also counts on a good knowledge of its phylogenetic relationships (Fuchs *et al.* 2015), providing the opportunity of carrying out interspecific comparisons within this taxonomic group while correcting for phylogeny. We predict that if a more generalist strategy in obtaining food resources (higher diet richness/diversity) allows the species to expand and settle new areas and habitats we should find trophic niche breadth to be positively correlated with size of the distribution area and BSI. Finally, we analysed the influence of the diet breadth index chosen and the taxonomic level at which they were calculated (class and order) on the results.

Material and methods

Trophic niche

Interspecific studies typically quantify diet specialization as prey (food) richness, in order to increase the number of prey-species analysed (Phillimore *et al.* 2006; Belmaker *et al.* 2011). By contrast, very few studies have accurately determined the breadth of trophic niche (Williams *et al.* 2006), using indexes of diet diversity, such as the Shannon Wiener index (SWI) or the Evennes index (Williams *et al.* 2006). The measure of the breadth of trophic niche using the richness of prey consumed gives equal importance to both the occasional and preferential consumption of prey-species (Colwell & Futuyma 1971), which tend to overestimate the generalist capability and the number of generalist species depending of the effort in sampling (Hillebrand & Cardinale 2004). Moreover, the interpopulation variation in the trophic niche has been largely neglected in interspecific comparative studies (Korpimäki & Norrdahl 1991; Bolnick 2001; Martínez-Padilla & Fargallo 2008; Araujo *et al.* 2011; Terraube & Arroyo 2011; Evangelista *et al.* 2014; Terraube *et al.* 2014; Rosenblatt *et al.* 2015). Taking into account different populations for a given species allow us to offer a close picture about the fundamental niche (potential niche of the species according to its ecological characteristics) instead of the realised niche (obligate niche of the species according to the ecological characteristics of the environment), which may change in different situations of intra- and interspecific competition and food abundance. In addition, the maximum value of diet diversity in a range of populations may act as an indicator of the species potentiality to widen the trophic niche and to occupy different habitats.

In the present chapter, total diet richness (TDR) was calculated for *Falconidae* species summing the number of different prey taxa found 188 studies of all 61 *Falconidae* species. We estimated TDR at both class and order taxonomic level (Appendix 1.1 and Appendix 2.1). Information about diet recording procedures was dissimilar among studies, being those more general works (handbooks, atlas, etc) the ones that reported less detailed information. Thus, in some cases it was not possible to know the sampling effort, that is, the duration of the study period (years of study). Since TDR can increase with sampling effort, we tried to minimize its effect by controlling diet richness for the number of studies as both variables were significantly correlated at both class ($r=0.25$, $F_{1,61}=19.9$, $P<0.01$) and order ($r=0.53$, $F_{1,61}=65.5$, $P<0.01$) taxonomic levels. Therefore, in our analyses we used TDR residuals as an explanatory.

Mean diet diversity (MDD) was calculated as the mean Shannon-Wiener Index (SWI) of populations for each *Falconidae* species using PAST software (Hammer *et al.* 2001). We analysed diet diversity in 161 populations from 126 studies of 30 *Falconidae* species at the order taxonomic level and 170 populations in 133 studies of 31 species at the class taxonomic level (Appendix 1.1 and Appendix 1.2). For this purpose, we used studies in which the number of prey taxa (86 studies) and/or percentage (116 studies) and/or biomass percentage (32 studies) was reported. Those studies in which the fraction of undetermined prey taxa was over 30 % were excluded from the analyses. Carrion and vegetation are special food types difficult to classify as they have very different ecological characteristics to active living preys. In general diet studies do not classify them within taxonomic groups, but as different prey groups (Valdez 1996; McDonald *et al.* 2003; Donadio *et al.* 2007; Zhou *et al.* 2011). In this study the same procedure was followed by considering carrion and vegetation as two different classes or orders when present. *Lacertillia, Serpentes, Iguania* and *Gekkota*, were considered as separate orders (Schwenk 2000).

Maximum diet diversity (MaxDD) was estimated as the highest SWI value found within all populations studied for a given *Falconidae* species. MDD was not affected by the number of studied populations in any taxonomic level (class: r= 0.0, $F_{1,31}$= 0.0, P=0.94 ; order: r=0.0, $F_{1,30}$=0.1, P=0.90), while the value found for MaxDD was significantly higher when more populations were considered in the sample at both taxonomic levels (class: r=0.14, $F_{1,31}$= 5.2, P=0.03 ; order: r=0.25, $F_{1,30}$=9.5, P<0.01). Therefore, we used residuals of the regression in the case of MaxDD in order to control for sampling effort.

Geographic range size and biomic specialization

The geographic range size (occupied area) of each species was estimated using distribution maps (Hoyo *et al.* 1994), and the area was calculated through "*wanda tools*" in Image J software (Rasband 1997; Schneider *et al.* 2012). Maps were scaled using the distance of the Equator (latitude 0º) and the Tropic of Capricorn (23° 27' S) across the continents.

For each species, we followed the procedure described by Hernández Fernández and Vrba (2005) in order to determine the number of biomes inhabited and compute its biomic specialisation index (BSI) (Moreno Bofarull *et al.* 2008; Cantalapiedra *et al.* 2011). We used the classification of terrestrial biomes proposed by Walter and Box (Walter & Box 1976), summarized in Table 1.1.

Statistical procedures

The relationship between diet variables (TDR, MDD and MaxDD) and the number of populations shown above was analysed using phylogenetic generalized least squares (PGLS) regressions. We followed the recent *Falconidae* phylogeny suggested by Fuchs and co-workers in 2015 (Fuchs *et al.* 2015). In order to analyse the relationship between geographic range size and trophic niche breadth we did PGLS regressions for each taxonomic level. In these analyses the size of the distribution area was included as the dependent variable and diet variables (TDR, MDD and MaxDD) as the independent variables. To analyse the relationship between number of inhabited biomes and trophic niche breadth we did PGLS regressions with BSI as the dependent variable, while TDR, MDD and MaxDD were the explanatory variables. Since species occupying larger distribution areas are expected to inhabit a higher number of biomes (higher BSI), the area of the geographical distribution was also included as a covariate in these models.

Diet variables were highly intercorrelated, showing elevated variance inflation factors (all VIFs > 2) when included together in a model. Therefore, in order to avoid bias due to multicollinearity in the analyses (Zuur *et al.* 2007), we studied independently each trophic variable in regressions with geographic range size and BSI. Pagel's Lambda was estimated by *maximum* likelihood in all PGLS regressions. All analyses were done using R software, version 2.14.2 (CRAN 2012) and R package caper (CRAN 2013)(Orme 2013).

Table 1.1. Classification of biomes inhabited by *Falconidae*. Names and typology of biomes (modified from Walter 1970), number and percentage of species inhabiting each biome and number of specialist species in each biome are shown.

Biome	Typology	Number of species	Percentage of species	Specialist species (BSI = 1)
Evergreen tropical rainforest	I	26	40.6	5
Tropical deciduous woodland	II	38	59.4	2
Savannah	II/III	30	46.9	2
Sub-Tropical desert	III	21	32.8	2
Sclerophyllous woodland and shrubland	IV	18	28.1	1
Temperate evergreen forest	V	22	34.4	0
Broad-leaf deciduous forest	VI	17	26.6	0
Steppe/cold desert	VII	18	28.1	2
Boreal coniferous forest (taiga)	VIII	14	21.9	0
Tundra	IX	5	7.8	1

Results

Diet richness and diversity

Prey class most frequently consumed by *Falconidae* was Aves, consumed by 93.6% of species, followed by Insecta (87.1%), Mammalia (77.4%) and Reptilia (75.8%). At order level, however, the most frequently consumed was Lacertilia, consumed by 72.6% of species, followed by Passeriformes (59.6%), Rodentia (58.1%) and Orthoptera (46.8%).

At the class level, mean TDR was 5.77±2.51, ranging from 1 to 13 (Table 1.2) and its frequency distribution was slightly skewed to the right (skewness = 0.61; Fig. 1). At the order level, mean TDR for the *Falconidae* group was 11.08±9.80, ranging from 1 to 43 (Table 1.2) being its frequency distribution skewed to the right (skewness = 1.12; Fig. 1). This indicates a tendency towards specialism at this taxonomic level of the diet. The southern crested caracara *Caracara plancus* was the species showing the widest trophic breadth (13 classes and 43 orders), while the slaty-backed forest falcon *Micrastur mirandollei* showed the narrowest one (1 class and 1 order; Table 1.2).

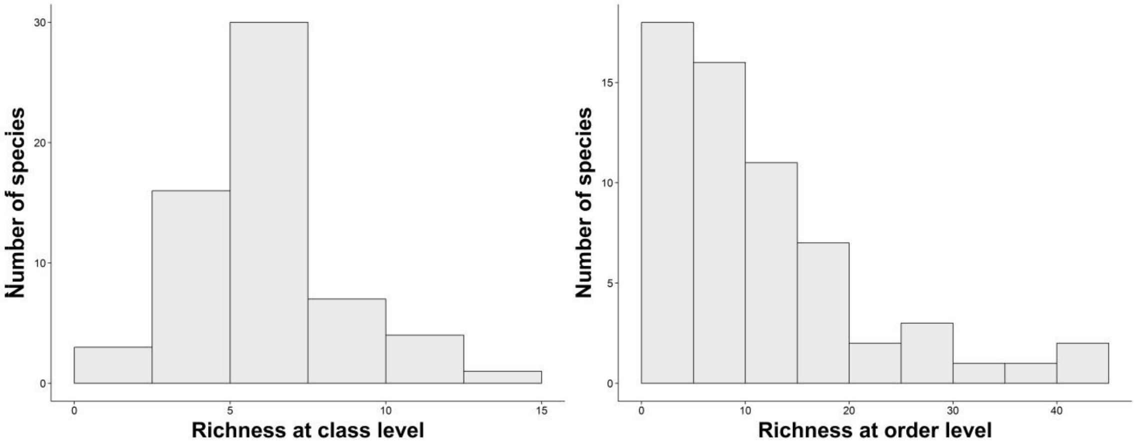

Figure 1.1. Frequency distribution of TDR, diet richness, in the *Falconidae* species at class (left) and order (right) taxonomic levels

At the class level, MDD was 0.61±0.37 ranging from 0 to 1.28 (Table 1.2) showing a more centred frequency distribution (skewness = 0.25; Fig. 2). At the order level, MDD for the *Falconidae* group was 1.12±0.46 ranging from 0 to 2.01 (Table 1.2) being its frequency distribution very slightly skewed to the left (skewness = -0.30; Fig. 1.2). MaxDDc was 1.37±0.52) showing a lightly skewness to the left (skewness = -0.81; Fig. 1.2). At the class level, MaxDD was 1.37±0.52 showing a lightly skewness to the left (skewness = -0.81; Fig. 1.2).

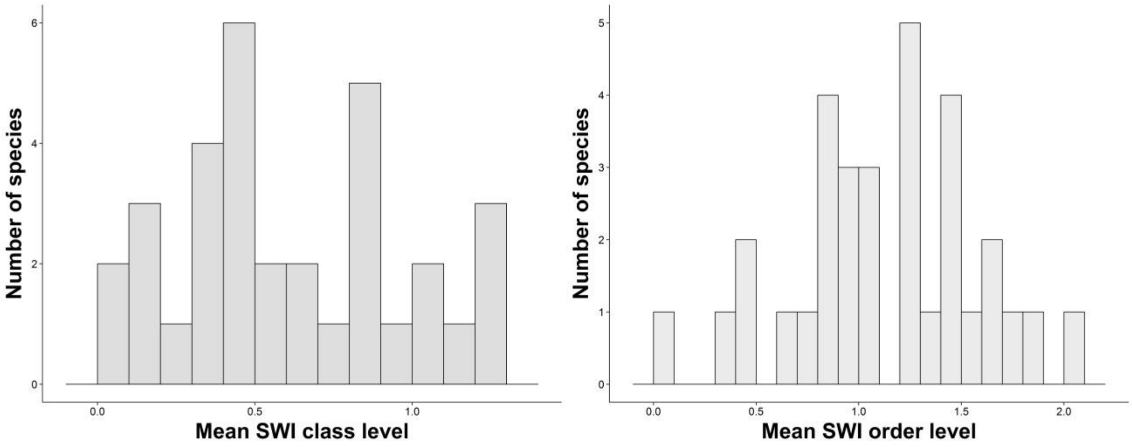

Figure 1.2. Frequency distribution of MDD, diet diversity (Shannon-Wiener Index), in the *Falconidae* species at class (left) and order (right) taxonomic levels.

Table 1.2. Habitat and diet indexes for *Falconidae* species. Biomic specialization index (BSI), total diet richness at class and order taxonomic levels, mean diet diversity (Shannon-Wiener Index; SWI) for diversity estimation for all populations at class and order taxonomic levels, maximum diet diversity found among considered populations and size of the distribution area are shown.

Species	**BSI**	**TDR (class)**	**TDR (order)**	**MDD (class)**	**MDD (order)**	**MaxDD (class)**	**MaxDD (order)**	**Distribution area size (Km^2 x 1000)**
Caracara plancus	9	13	43	1.276	1.853	1.721	2.009	21370.2
Daptrius albogularis	3	4	8	-	-	-	-	1001.6
Daptrius americanus	3	4	3	-	-	-	-	15495.8
Daptrius ater	2	8	10	-	-	-	-	8596.5
Daptrius australis	1	7	11	0.971	1.415	1.185	1.415	297.3
Daptrius carunculatus	1	7	12	1.161	1.471	1.161	1.471	403.6
Daptrius chimachima	4	9	11	-	-	-	-	16213.8
Daptrius chimango	6	12	28	0.354	1.430	0.538	1.582	5568.2
Daptrius megalopterus	1	5	9	0.858	0.997	1.275	1.329	1975.9
Falco alopex	3	5	4	-	-	-	-	5408.9
Falco amurensis	3	7	11	0.478	1.216	0.478	1.216	9821.4
Falco araea	1	5	7	0.883	1.289	1.000	1.337	0.9
Falco ardosiaceus	1	9	11	-	-	-	-	10655.5
Falco berigora	5	8	16	0.881	1.684	1.287	2.012	10226.8
Falco biarmicus	8	7	26	0.463	1.279	1.210	1.677	44527.4
Falco cenchroides	6	5	4	1.235	-	1.235	-	10210.3
Falco cherrug	4	6	8	-	-	-	-	27292.0
Falco chicquera	3	5	6	0.000	0.000	0.000	0.000	18207.1
Falco columbarius	4	7	24	0.176	0.462	0.351	1.161	77981.6
Falco concolor	1	5	15	0.316	0.840	0.462	1.333	2836.5
Falco cuvierii	2	3	2	-	-	-	-	10447.2
Falco deiroleucus	4	2	5	0.404	0.404	0.404	0.404	17721.3
Falco dickinsoni	1	8	9	-	-	-	-	4757.2
Falco eleonorae	1	3	20	0.000	0.749	0.000	0.749	2956.8
Falco fasciinucha	5	3	2	-	-	-	-	1807.5
Falco femoralis	8	7	25	0.433	1.321	0.779	1.767	19687.2
Falco hypoleucos	1	5	4	-	-	-	-	6636.1
Falco jugger	3	5	6	-	-	-	-	3185.6
Falco longipennis	6	4	10	0.587	1.617	0.587	1.617	8770.1
Falco mexicanus	5	7	17	0.679	0.990	1.025	1.450	7708.4
Falco moluccensis	2	5	4	-	-	-	-	769.5
Falco naumanni	3	7	18	0.430	0.802	1.077	1.720	34622.5
Falco newtoni	3	6	6	0.812	0.933	1.096	1.459	681.5
Falco novaeseelandiae	2	6	11	0.511	0.699	0.511	0.699	304.4

Species	BSI	TDR (class)	TDR (order)	MDD (class)	MDD (order)	MaxDD (class)	MaxDD (order)	Distribution area size (Km^2 x 1000)
Falco peregrinus	10	8	41	0.115	1.291	0.599	1.934	176850.1
Falco punctatus	1	5	5	0.395	0.395	0.395	0.395	78.3
Falco rufigularis	4	4	12	0.630	0.837	0.684	1.124	16560.7
Falco rupicoloides	3	6	5	-	-	-	-	4376.9
Falco rusticolus	2	5	11	0.407	1.085	0.669	1.325	108698.0
Falco severus	2	4	3	-	-	-	-	5729.1
Falco sparverius	8	11	34	1.060	1.574	1.427	2.146	38937.9
Falco subbuteo	6	5	19	0.185	1.216	0.374	1.508	76163.1
Falco subniger	2	6	12	0.823	1.734	0.823	1.734	7374.6
Falco tinnunculus	8	12	35	0.768	1.042	1.453	2.045	106347.0
Falco vespertinus	3	10	17	0.294	1.013	0.294	1.013	27295.3
Falco zoniventris	3	5	7	1.026	1.440	1.026	1.440	564.1
Herpetotheres cachinnans	3	5	7	0.346	0.815	0.580	0.921	15675.1
Micrastur buckleyi	1	2	2	-	-	-	-	1048.1
Micrastur gilvicollis	2	4	4	-	-	-	-	7871.2
Micrastur mirandollei	2	1	1	-	-	-	-	7916.0
Micrastur plumbeus	1	3	2	-	-	-	-	82.6
Micrastur ruficollis	4	9	17	-	-	-	-	15059.9
Micrastur semitorquatus	4	4	6	1.277	2.008	1.277	2.008	16165.4
Microhierax caerulescens	3	4	4	-	-	-	-	1813.3
Microhierax erythrogenys	2	3	2	-	-	-	-	391.4
Microhierax fringillarius	2	4	3	-	-	-	-	1055.7
Microhierax latifrons	1	3	2	-	-	-	-	69.5
Microhierax melanoleucos	2	5	6	-	-	-	-	2003.2
Neohierax insignis	2	6	5	-	-	-	-	893.9
Polihierax semitorquatus	1	5	4	-	-	-	-	2867.4
Spiziapteryx circumcincta	1	4	4	-	-	-	-	1863.4

Biomic specialization description

Mean BSI of the *Falconidae* group was 3.27 ± 2.23 ranging from 1 to 10 biomes (Table 1.3; Fig. 1.3). Family *Falconidae* occupied all 10 terrestrial biomes (Tables 1.1 and 3.1) with 15 species (24.59%) inhabiting only one, 26 species (42.62%) two or three and only six species (9.84 %) inhabiting eight or more biomes (Tables 1.1 and 1.3). One species, the peregrine falcon *Falco peregrinus* inhabited all 10 terrestrial biomes. The frequency distribution of BSI was skewed to the right (skewness = 0.96), indicating a trend towards an overrepresentation of biome specialist species (Fig. 1.3).

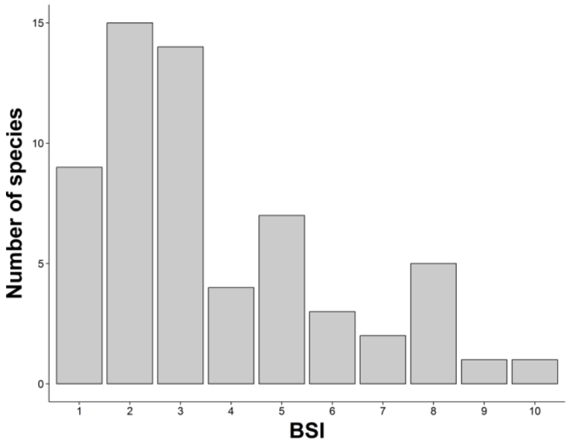

Figure 1.3. Frequency distribution of the biomic specialization index (BSI) in the *Falconidae* species.

Table 1.3. Values for the biomic specialization index (BSI), number of species and percentage of species within the *Falconidae* group.

BSI	Number of species	Percentage
1	15	23.4
2	14	21.9
3	13	20.3
4	8	12.5
5	4	6.3
6	4	6.3
7	0	0.0
8	4	6.3
9	1	1.6
10	1	1.6

The most frequently occupied biome was the tropical deciduous woodland (II) having 36 species (59.02 %), followed by savannah (II/III) having 28 species (45.90 %), while the least inhabited biome was the tundra (IX) having only five species (8.20 %). The biome having more specialist species was the evergreen tropical rainforest (I), with five species. *Caracara* (one species) was the most generalist genus (BSI = 9). Furthermore, the genus *Falco* (39 species), is the second genus with larger BSI (3.7± 2.4) biomes. On the other hand, *Polihierax* and *Spiziapteryx* are the most specialist genera (both BSI =1).

Diet, geographic range size and biomic specialization

Neither diet richness nor diet diversity predicted how large the geographic range size is in *Falconidae* species, as PLGS regression models showed no significant correlations between size of the distribution area and TDR, MDD or MaxDD either at the order nor class levels (Table 1.4).

Table 1.4. Results of phylogenetic generalized least squares (PGLS) models for the relationship between size of the distribution area and diet breadth indexes using both class and order taxonomic approaches.

Effect	R^2	λ	Estimate	*SE*	*t*	*F*	*P*	*95 % CI*
TDR (order)	0.03	0.001	0.060	0.043	1.385	1.92	0.171	(-0.03, 0.15)
TDR(class)	0.01	0.001	0.116	0.136	0.851	0.72	0.398	(-0.16, 0.39)
MDD (order)	0.01	0.001	0.041	1.118	0.036	0.01	0.971	(-2.20, 2.28)
MDD (class)	0.07	0.001	-2.084	1.295	-1.609	2.59	0.118	(-4.67, 0.51)
MaxDD (order)	0.01	0.001	0.328	1.132	0.289	0.84	0.774	(-1.94, 2.59)
MaxDD (class)	0.04	0.001	-1.446	1.204	-1.201	1.44	0.239	(-3.85,-0.96)

PGLS regression models showed a significant positive correlation between BSI and the geographic range size (Table 1.5), that is, *Falconidae* species showing larger distribution areas also occupied a higher number of biomes. Controlling for geographic range size, PGLS regression models showed a positive correlation between TDR and BSI at class and order levels. Species having higher diet richness also were present in more biomes (Table 1.5). BSI and MDD also were significantly and positively correlated at the order level. *Falconidae* species showing higher diversity of prey orders in their diet also inhabited a higher number of biomes. The correlation between BSI and MDD was not statistically significant at the class level (Table 1.5). PGLS regression models showed a significant positive correlation between BSI and MaxDD both at order and class level (Table 1.5). Values of lambda were close to zero for all these PGLS regressions (Tables 1.4 and 1.5), revealing a lack of phylogenetic influence in the models.

Table 1.5. Results of phylogenetic generalized least squares (PGLS) models for the relationship between biomic specialization index (BSI) and diet breadth indexes using both class and order taxonomic approaches. Size of the distribution area was included as covariate.

Effect	R^2	λ	Estimate	*SE*	*t*	*F*	*P*	*95 % CI*
TDR (order)	0.47	0.001	0.134	0.033	4.107	25.788	<0.001	(0.07,0.20)
Distribution area size	0.47	0.001	0.486	0.097	5.018	25.182	<0.001	(0.29,0.68)
TDR (class)	0.36	0.001	0.240	0.111	2.171	8.777	0.034	(0.02,0.46)
Distribution area size	0.36	0.001	0.522	0.105	4.950	24.5	<0.001	(0.31,0.73)
MDD (order)	0.45	0.001	2.013	0.799	2.519	6.49	0.018	(0.41,3.61)
Distribution area size	0.45	0.001	0.550	0.130	4.214	17.76	<0.001	(0.29,0.81)
MDD (class)	0.39	0.001	1.701	1.071	1.588	0.16	0.123	(-0.44,3.84)
Distribution area size	0.39	0.001	0.618	0.143	4.332	18.77	<0.001	(0.33,0.90)
Max.DD(order)	0.44	0.001	1.920	0.822	2.337	6.52	0.027	(0.28,3.56)
Distribution area size	0.44	0.001	0.536	0.132	4.049	16.39	<0.001	(0.27,0.80)
Max.DD (class)	0.42	0.001	1.917	0.939	2.042	1.25	0.050	(0.04,3.79)
Distribution area size	0.42	0.001	0.614	0.137	4.489	17.41	<0.001	(0.34,0.89)

Discussion

Geographic range size and habitat heterogeneity

Our results do not support our first prediction, as no correlation was found between trophic breadth of *Falconidae* species and size of the distribution area. This lack of relationship may be explained by i) those more generalist species have not higher capacity for spatial expansion, ii) spatial colonization is not a profitable strategy in this group and iii) variation in the size of the distribution area among *Falconidae* species may be accounted for ecological characteristics of the group different to trophic niche breadth or for other environmental or biogeographical factors, such as large-scale spatial distribution of resources and biome distribution and size (Hernández Fernández and Vrba 2005).

The frequency distribution of the BSI for the family *Falconidae* showed a high number of species using only a few biomes, similarly to that found in other taxonomic groups (Hernández Fernández & Vrba 2005; Moreno Bofarull *et al.* 2008), which coincides with the high representation of specialist species in nature (Eldredge & Cracraft 1980; Vrba 1987).

The most frequently inhabited terrestrial biome by *Falconidae* species is the tropical deciduous woodland. This result is similar to that found by Belmaker and co-workers (2011) who concluded that the geographical area occupied by this biome was the one showing the highest richness in bird species. Latitudinal gradients found for species richness and speciation also place its maximum in this tropical biome (Gaston & Blackburn 2008). Furthermore, the highest number of biomic specialists (BSI = 1) was found in other different tropical biome, the evergreen tropical rainforest, containing 20% of biomic specialist species. These results are in agreement with the idea that more stable environments, as those located in the tropics, are home for more specialist species that would be expected if such environments favour speciation (Belmaker *et al.* 2011).

In agreement with our second prediction, species showing a higher trophic breadth in terms of diet richness and diversity (higher TDR and MDD) occupied areas with higher habitat heterogeneity (higher BSI); maximum diet diversity could give some information about the potential for a given species to colonise new habitat due to its diet. The results similarly showed a positive correlation between diet and habitat heterogeneity, being more evident when working at the order than at the class level. These findings gives partial support to the hypothesis that a generalist trophic strategy allows the species a greater environmental plasticity to inhabit different or a greater variety of habitats or biomes.

Trophic niche of *Falconidae*

Our results shows that for the *Falconidae* family the trophic niche defining it varies depending on the taxonomic rank used to describe the preys consumed by each species. At the order level, falconids can be defined as mainly lizard consumers (*Lacertilia*), although passerine- (Passeriformes) and rodent-consumer species are also highly represented within the family, followed in importance by grasshopper consumers (Orthoptera). However, at the class level, *Falconidae* is mainly composed by bird-consumer species, with Insecta, Mammalia and Reptilia classes having a great representation in the diet as well. Differentiation of prey species at class or order levels affects the trophic breadth calculated for each species. The family was overrepresented by specialist species (right-skewed frequency distribution of species) when considering total diet richness at the order level, while it was not so at the class level (more centred frequency distribution of species). Clear examples for this discrepancy are the peregrine falcon and the Eleonora’s falcon *Falco eleonorae*, two bird-specialist consumers showing very low values of diet richness and diet diversity (closer to specialism) when working at the class level, but showing high values (closer to generalism) when estimating the trophic breadth at the order level. Resource-species share functional, habitat, spatial or phylogenetic ecological characteristics that can favour or hamper their consumption by a given consumer species (Chazdon *et al.* 2011; Junker *et al.* 2013; Jorge *et al.* 2014) therefore influencing the trophic specialisation category assigned to the species (Jorge *et al.* 2014). In agreement with this, our results highlight the importance of the taxonomic rank at which the diet study is done in the determination of the trophic niche of the species. Nevertheless, the use of mean diet diversity allowed use to overcame, at both taxonomic approaches, the overestimation of specialist species within the family found for total diet richness. This result also indicates, that not only the taxonomic approach at which the food resource is studied, but also the index used to calculate the trophic breadth of the consumer has an important influence in the assignation of a given trophic niche for a given species.

In conclusion, our study foregrounds the importance of the taxonomic approach used for categorising specialisation on trophic resources. Similarly, our results also point out the relevance of choosing different indexes for describing trophic niche breadth. In addition, our findings give support to the idea that more stable environments are more prone to generate and sustain more species and species showing narrower trophic niche breadths. More importantly, this study reveals that diet of species can predict the degree of heterogeneity of the habitats they occupy and give support to the idea that increasing trophic breadth (more generalist strategies) increase the capacity of the species to exploit different habitats. This reveals the importance of diet studies for the investigation of distribution patterns and habitat/biome occupation of species at a global scale.

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Appendix

Appendix 1.1. Number of studies (NS) used to calculate total diet richness and number of populations (NP) used to calculate mean diet diversity at order and class levels in each *Falconidae* species.

Species	NS richness	NP diversity (order)	NP diversity (class)
Caracara plancus	27	7	7
Daptrius albogularis	1	-	-
Daptrius americanus	2	-	-
Daptrius ater	4	-	-
Daptrius australis	3	1	2
Daptrius carunculatus	4	1	1
Daptrius chimachima	7	-	-
Daptrius chimango	10	2	2
Daptrius megalopterus	5	4	4
Falco alopex	1	-	-
Falco amurensis	5	1	1
Falco araea	2	2	2
Falco ardosiaceus	1	-	-
Falco berigora	11	5	5
Falco biarmicus	12	5	5
Falco cenchroides	3	-	1
Falco cherrug	3	-	-
Falco chicquera	2	1	1
Falco columbarius	10	5	5
Falco concolor	6	2	2
Falco cuvieri	1	-	-
Falco deiroleucus	2	1	1
Falco dickinsoni	1	-	-
Falco eleonorae	10	1	1
Falco fasciinucha	1	-	-
Falco femoralis	14	7	8
Falco hypoleucos	1	-	-
Falco jugger	1	-	-
Falco longipennis	3	1	1
Falco mexicanus	11	15	15
Falco moluccensis	1	-	-
Falco naumanni	30	21	21
Falco newtoni	4	3	3
Falco novaeseelandiae	4	1	1
Falco peregrinus	53	18	18

Species	NS richness	NP diversity (order)	NP diversity (class)
Falco punctatus	2	1	1
Falco rufigularis	6	2	3
Falco rupicoloides	1	-	-
Falco rusticolus	52	8	8
Falco severus	1	-	-
Falco sparverius	28	12	12
Falco subbuteo	10	2	2
Falco subniger	2	1	1
Falco tinnunculus	68	26	31
Falco vespertinus	7	1	1
Falco zoniventris	2	1	1
Herpetotheres cachinnans	9	2	2
Micrastur buckleyi	1	-	-
Micrastur gilvicollis	1	-	-
Micrastur mirandollei	1	-	-
Micrastur plumbeus	1	-	-
Micrastur ruficolis	6	-	-
Micrastur semitorquatus	4	1	1
Microhierax caerulescens	1	-	-
Microhierax erythrogenys	1	-	-
Microhierax fringillarius	1	-	-
Microhierax latifrons	1	-	-
Microhierax melanoleucos	1	-	-
Neohierax insignis	1	-	-
Polihierax semitorquatus	1	-	-
Spiziapteryx circumcincta	1	-	-

Appendix 1.2. Bibliographical list of sources used to determine the trophic niche of the *Falconidae* species.

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Capítulo II

Broadening trophic niche to increase offspring condition and immunity in a raptor species

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Abstract

Strategies developed by organisms to maximize foraging efficiency have a strong influence on fitness. The way in which the range of food resources is exploited has served to classify species, populations and individuals from more specialist (narrow trophic niche) to more generalist (broad trophic niche). Recent studies have provided evidence that many of the considered generalist species/populations are actually composed of different specialist individuals (individual specialization). Even the existence of generalism as an adaptive strategy has been questioned. In this study, we investigated the relationship between trophic niche width, individual quality and offspring viability in a population of common kestrel *Falco tinnunculus* during 4 years. We showed that the diet of kestrels varied significantly among years and that individuals of better quality fed their offspring with a higher diversity of prey species and a higher amount of food. Moreover, body condition and immune response of nestlings were positively correlated with diversity of prey delivered by parents. Our study suggests that generalism has the potential to increase fitness and that broadening the trophic niche may be an adaptive strategy in unpredictable environments.

Introduction

Selective pressures derived from spatio-temporal variation in the abundance, availability and diversity of food have lead to individual foraging behaviours aimed at balancing the time and energy devoted to search, capture and handling of food items, and the amount and quality of the nutrients acquired from them (MacArthur & Pianka 1966; Begon *et al.* 2006). The efficiency of obtaining optimal food exerts strong effects on the rate of growth, development, birth and survival of individuals, promoting natural selection (Grant & Grant 2002; Bolnick 2004). The way in which feeding efficiency is maximised shapes the trophic niche of species, populations and individuals (Hutchinson 1957; Roughgarden 1972; Werner & Sherry 1987; Bolnick *et al.* 2003; Dall *et al.* 2012).

The trophic niche width, defined as the diversity of food items consumed and habitats used, is thought to play a key role in inter- and intra-specific competition and speciation (Skulason & Smith 1995; Dieckmann & Doebeli 1999). Individuals may specialize in a narrow range of resources which are different from those of their conspecific competitors to minimize resource-use overlap and competition (Bolnick *et al.* 2003; Dayan & Simberloff 2005; Santoro *et al.* 2011). Individual specialization within a population induces among-individual ecological divergence, thus competition becoming frequency dependent and favouring rare phenotypes and polymorphism (Skulason & Smith 1995; West-Eberhard 2003). Such frequency-dependent competition has the potential to drive disruptive selection (Bolnick 2004) and maintain quantitative genetic variation within populations (Bolnick & Lau 2008). Therefore, individual specialization may depend on the niche position occupied by the species and it is expected to be more frequent in predators as they show a higher degree of intraspecific competition (Estes *et al.* 2003; Svanbäck & Bolnick 2007; Quevedo *et al.* 2009).

In two recent reviews it has been reported that individual specialization is a common phenomenon and that many of the populations and/or species considered generalists (using a wide range of food resources) may actually be composed of specialist individuals (Bolnick *et al.* 2003; Araújo *et al.* 2011). Obviating the problems derived from the quantification of ecological specialization, which is highly dependent on the type of data used, the taxonomic group studied, the geographic and time scale, and the ecological mechanism of interest or the trait in question(Fox & Morrow 1981; Woo *et al.* 2008; Devictor *et al.* 2009), the existence of generalism remains contentious (Dennis *et al.* 2011; Loxdale *et al.* 2011). Ecological specialization is considered a major force by which new species emerge (Schluter 2009), reflected in an over-representation of specialist lineages in the fossil record compared to generalist ones (Eldredge & Cracraft 1980; Vrba 1987; Butlin *et al.* 2009). Some authors have even argued that ecological specialization is the main driving force leading to speciation, considering generalist strategies as only passing phases in certain evolutionary scenarios (Loxdale *et al.* 2011). However, specialists are more vulnerable to extinction as they show shorter temporal durability as a consequence of higher sensitivity to environmental changes (Clavel *et al.* 2010). Therefore, generalist strategies that might have particular disadvantages in more favourable stable environments may be advantageous in other less favourable or unpredictable situations, increasing the capacity for expansion by the colonization of new habitats, hence ensuring persistence (Thomas *et al.* 2001; Dennis *et al.* 2011). It has also been thought that generalist strategies may be selectively neutral being maintained in a population without changing the fitness of individuals (Fox *et al.* 2001).

Knowing how within-population trophic strategies are related to individual quality and fitness is a key step for our understanding of the drivers behind ecological specialisation (Mayntz & Toft 2001; Cucherousset *et al.* 2011). In systems where the quality of breeding and foraging habitats, areas or territories depend on the quality of individuals, individual diet should predict fecundity, productivity and offspring quality. Environmental conditions experienced during development determine offspring quality and have strong implications in adult phenotypes and life-history trajectories. Body mass, body condition and immunity acquired during early life have been reported to influence return rates, survival, longevity and reproduction (Metcalfe & Monaghan 2001; López-Rull *et al.* 2011; Saino *et al.* 2012). In addition, besides the obvious effects of food on body mass and condition, the amount of food consumed, but also diet composition are major factors affecting immunity of individuals at early stages of life (Chandra 1997; Mayntz & Toft 2001; Fargallo *et al.* 2002; Swamy *et al.* 2004; Triggs & Knell 2012).

The common kestrel *Falco tinnunculus*, is a raptor species showing a wide range of foraging strategies among populations from rodent specialists in Northern Europe (Hanski *et al.* 2001) to generalist in Mediterranean areas (Aparicio 2000). In this study we investigated whether the individual trophic niche width observed in a common kestrel population during 4 consecutive years was associated with individual quality and fitness components, such as offspring viability. Specifically, controlling for inter-annual variation in the diet, we studied the relationship between the diversity of prey species delivered by parents to the nest and (1) indicators of parent quality, such as clutch size (Masman *et al.* 1989; Wiehn & Korpimäki 1997;

Fargallo *et al.* 2002) and (2) indicators of offspring viability, such as body condition and immunity. We predict that if trophic generalism is a selected strategy of common kestrels in this population, wherein the availability of the resources varies widely among the years (Fargallo *et al.* 2009), the diversity of the prey consumed should be positively correlated with individual quality and offspring viability.

Materials and methods

Study species

The common kestrel (hereafter 'kestrel') is a territorial diurnal raptor species widely distributed in Eurasia and Africa being common in a broad array of habitats (Village 1990). The variety of environments occupied by kestrels predicts a great variety of foraging habits. Kestrels have been described to prey mainly on rodents (Village 1982; Korpimaeki 1986; Steen *et al.* 2011), insects (Carillo 1994; Souttou *et al.* 2007), lizards (Padilla & Nogales 2009; Carrillo & González-Dávila 2010), birds (Folgado 2010) or a variety of taxa (Aparicio 2000; this thesis). The male is the main territory and food provider from courtship to offspring independence (Village 1990; Vergara & Fargallo 2008a; Sonerud *et al.* 2014). The female, on the other hand, remains for most of the time in the surroundings of the nest to defend it from intruders and predators, and hunts only sporadically (Village 1990; Vergara *et al.* 2007; Vergara & Fargallo 2008b). Experimental studies have found that the extent of energy expenditure, hunting effort and prey delivery that males can perform during the chick-rearing period is initially set for clutch size(Masman *et al.* 1989; Korpimäki & Rita 1996; Wiehn & Korpimäki 1997; Fargallo *et al.* 2002). In addition, clutch size has been found to be positively correlated with male bright colouration (Palokangas *et al.* 1994) and male quality during courtship (Vergara *et al.* 2007; Vergara & Fargallo 2008a) and negatively with male parasite infection (Korpimäki *et al.* 1995). For these reasons clutch size is considered as a reliable indicator of male quality in this species.

Study area

The study was carried out during the kestrel breeding seasons of 2006–2009 in the region of Campo Azálvaro, located in central Spain. The study area is a treeless flat valley at 1,300 m above sea level mainly devoted to cattle raising. The climate of this region is humid Mediterranean, with dry and warm summers and cold winters. About 30–45 breeding pairs nest each year in 62 artificial nest boxes installed in the study area (Fargallo *et al.* 2009).

Prey delivered by parents

During the kestrel breeding season 81 nests (16 in 2006, 18 in 2007, 25 in 2008 and 22 in 2009) were monitored in order to record data on laying date, clutch size, hatching date and number of fledged young. At the chick age of 12–14 days a digital camera was placed at the nest in order to record prey delivered by adults when feeding the chicks. Cameras (Cylinder SONY 1/3* Super HAD connected to ARCHOS AV500 100 Gb digital recorders in 2006 and 2007 and digital camcorders SONY HandyCam 60 Gb in 2008 and 2009) were installed in the posterior wall of the nest box pointing towards the nest box entrance. Both digital recorders and camcorders were powered with 12-amp SLI batteries (24 Ah 24 V) through a voltage converter (12 V). Initially we tried to film nests continuously for 24 h or more in order to record kestrel prey deliveries from sunrise to sunset without researcher interruption, but due to technical problems some nests could not be filmed during the whole period. The daylight period at our study area during June and July is about 15 h (sunrise at 04:49 hours and sunset at 19:49 hours solar time for 1 July). Kestrels started provisioning chicks with food at 07:25 ± 1.03 hours solar time (range = 06:23–09:41 hours, $n = 58$) and stopped at 21:03 ± 0.42 hours solar time (range = 19:11–22:33 hours, $n = 71$) on average. A mean recording time of 15 h 47 s ± 3 h 52 s (range = 6 h 2 s–27 h 49 s $n = 81$) of prey delivery activity was recorded. Nests with less than 6 h of recording were excluded from the study (see below).

Recordings were displayed in the free VLC Media Player software (www.videolan.org) to identify each delivered prey item. Almost all amphibian, reptile, bird and mammal prey items were determined at species level (94 % of cases; Table 2.1). Within invertebrate prey items, field crickets *Gryllus campestris* and mole crickets *Gryllotalpa gryllotalpa* (Insecta, Orthoptera) and Mediterranean tarantula *Lycosa tarentula* (Arachnida) were easily identifiable in the recordings (Table 2.1). The rest of the arthropods were identified at the minimum possible taxonomic rank (order and family; Table 2.1).

Body measurements and nestling immunity

Nests were monitored to detect laying date (day of the first egg laid in the nest) clutch size and hatching date (day of the first egg hatched in the nest). Twenty-six days after hatching, nestlings close to fledging were weighed with a spring balance (±2 g) and wing length was measured with a metallic rule (±1 mm). The same body measurements were taken in nestlings 26 days after hatching. This same day, the common assay of intradermal injection in the wing web of the T cell mitogen phytohemagglutinin (PHA)-P (0.3 mg PHA-P dissolved in 0.1 ml of phosphate-buffered saline) was carried out. Briefly, the thickness of the wing web was measured three times with a digital calliper (±0.1 mm) at the injection site before and 24 h after the injection. The difference between mean initial web thickness and swelling is used as an estimate of immune response to the mitogen [see Fargallo *et al*. 2002 for details and repeatability]. The immunological test was always measured in the morning to avoid daytime effects (Martínez-Padilla 2006).

Table 2.1. Total numbers (N), percentage and biomass of prey items delivered by common kestrel parents to the nest over a four-year study period (2006-2009). The minimum identified taxon level is shown.

	N (%)	**% biomass**
Mammals	**624 (17.7)**	**49.7**
Crocidura russula	53 (1.5)	1.2
Microtus arvalis	571 (16.2)	48.5
Birds	**29 (0.8)**	**4.6**
Alauda arvensis	7 (0.2)	0.7
Motacilla flava	2 (0.1)	0.1
Sturnus unicolor	13 (0.4)	3.1
Passer domesticus	2 (0.1)	0.1
Petronia petronia	1 (0.1)	0.1
Passerines (unidentified)	4 (0.1)	0.5
Reptiles	**547 (15.5)**	**30.4**
Chalcides striatus	99 (2.8)	3.7
Timon lepidus	104 (2.9)	21.7
Lacerta schreiberi	11 (0.3)	1.1
Podarcis hispanica	8 (0.2)	0.0
Psammodromus hispanicus	315 (8.9)	2.5
Large Lizard	7 (0.2)	1.4
Small lizard	3 (0.1)	0.0
Amphibians	**11 (0.3)**	**0.8**
Triturus marmoratus	3 (0.1)	0.1
Pelophylax perezi	8 (0.2)	0.7
Arthropods	**2290 (65.0)**	**13.7**
Lycosa tarentula	17 (0.5)	0.1
Gryllus campestris	503 (14.3)	1.5
Acrididae	103 (2.9)	0.2
Tettigoniidae	34 (1)	0.1
Gryllotalpa gryllotalpa	1553 (44.1)	11.5
Orthoptera (unidentified)	5 (0.1)	0.0
Mantodea	1 (0.1)	0.0
Lepidoptera	1 (0.1)	0.0
Coleoptera	10 (0.1)	0.0
Insecta (unidentified)	47 (1.3)	0.3
Insecta(*larvae*)	16 (0.4)	0.0
Large prey item	2 (0.1)	0.2
Small prey item	1 (0.1)	0.0
Unidentified prey item	19 (0.5)	0.5
Total prey items	**3590**	

Prey diversity and biomass

Using PAST software (Paleontological Statistics 2001, Palaeontological Association, http://palaeo-electronica.org/2001_1/past/issue1_01.htm), the diversity of prey consumed (niche breadth) was calculated through the Shannon–Wiener index (SWI) of each nest using the lowest taxonomic rank determined in each prey item (see (Bolnick *et al.* 2002)). To calculate SWI, species level was given for amphibians, reptiles, mammals, birds, spiders, crickets and mole crickets, family for grasshoppers, bush crickets and mantises and order for beetles and butterflies or moths (larvae). Richness and diversity are expected to vary with sampling effort (Begon *et al.* 2006), In our case, neither richness ($r = 0.12$, $F_{1,79} = 1.15$, $P = 0.287$) nor SWI ($r = 0.02$, $F_{1,79} = 0.02$, $P = 0.894$) of delivered prey were associated with filming time for the range we worked with (6–28 h).

The biomass consumed by chicks in a nest during the filming period was estimated as the sum of all body masses of the delivered prey items (Fargallo *et al.* 2003). For body mass for each prey species we used the mean body mass. In some cases we had data on the body mass of the prey species captured in our study area and in other cases the data were obtained from the scientific literature (Appendix 2. 1). When a partial prey was delivered (only large lizards and voles), the animal portion was visually estimated using the following estimation: 3/4 prey, without head; 2/4 prey, without head and without superior extremities; 1/4 prey, only with tail and inferior extremities. Biomass in these prey items was calculated by multiplying the mean body mass by each fraction in each case (Fargallo *et al.* 2003). When the prey item could not be identified as belonging to a given taxon (19 out of 3,590 prey items), biomass was calculated as the weighted mean of a prey item by taking into consideration the proportion of each taxonomic group consumed in the given nest. Since not all nests could be filmed during the same period of time, the prey delivery rate (number of prey items/filming time) and the mean biomass consumed (total biomass of prey items/filming time) were estimated in order to make possible between-nest comparisons.

Statistical procedures

Statistical analyses were performed with SAS (1999) software 9.2 (SAS Institute, Cary, NC). Among-year differences in the frequency of prey consumed were analysed using logistic models (GENMOD procedure, logit link function, binomial distribution) by entering the number of items for a given prey as the dependent variable and the total number of prey items as the binomial denominator. Year was included as a factor. Post hoc contrasts were used for pair-wise annual comparisons. Variation in biomass and SWI was analysed using two different linear mixed models (LMM procedure). In the first one biomass was included as dependent variables. Clutch size (as a measure of parental quality) was included as a covariate and year as a fixed factor. The interaction between year and clutch size was also explored. In the second one SWI was the dependent variable, clutch size and biomass were included as covariates and year as a fixed factor. The interaction between year and clutch size was explored. Some nests were repeatedly occupied in different years. Since the amount of food and the diversity of prey species consumed may depend on the selected territories (nest box location), nest was included as a random factor in both models. Offspring body condition and offspring immune reaction to PHA mitogen (Figure 2.1) were also analysed using two different LMMs in which fledgling body mass and immune response were included as the dependent variables, clutch size, fledgling wing length, prey biomass and SWI were included as covariates, fledgling sex and year as fixed factors and kestrel nest as a random factor. In the model of immune response fledgling body mass was also included as a covariate. We constructed sets of models with possible combinations of independent variables. We used Akaike's information criterion corrected for small sample size (AICc) for model selection. The best model was the one with the lowest AICc value with a difference >2 from the second best model. ΔAICc and AICc weights were also calculated. Parameters were estimated using maximum likelihood in all models. Residuals obtained from all linear mixed models showed normal distributions (Shapiro–Wilk, all $P > 0.05$). Means values ± SDs are given in the text.

Results

Kestrel diet

As shown in Table 2.1, arthropods, mainly Orthoptera, were the most consumed prey by kestrels in our population, followed by micromammals, reptiles, birds and amphibians. Within species, the mole cricket *Gryllotalpa gryllotalpa*, common vole *Microtus arvalis*, field cricket *Gryllus campestris* and Spanish psammodromus *Psammodromus hispanicus* were the most preyed on species. Results indicate that five species (common vole, field cricket, mole cricket, ocellated and *Psammodromus* lizards) represent 86 % of captures and 88 % of biomass contribution to the kestrel diet in our population. Within arthropods, Arachnida (only Mediterranean tarantula) was the only group (0.1 %) not included in the Insecta taxon, for which we will refer to arthropods as 'insects' hereafter. The diet of kestrels varied among years. Inter-annual significant differences were observed in the frequency of consumption of mammals, reptiles, amphibians and insects, but not in birds (Appendix 2. 2, 2.3 and 2.4).

Biomass, prey diversity and individual quality

The mean prey biomass/h for the 4-year period was 26.4 ± 14.4 g, ranging from 3.2 to 83.9 g. The best model obtained for biomass was the one containing only clutch size as a covariate (Table 2.2; Appendix 2.5). Prey biomass was positively correlated with clutch size.

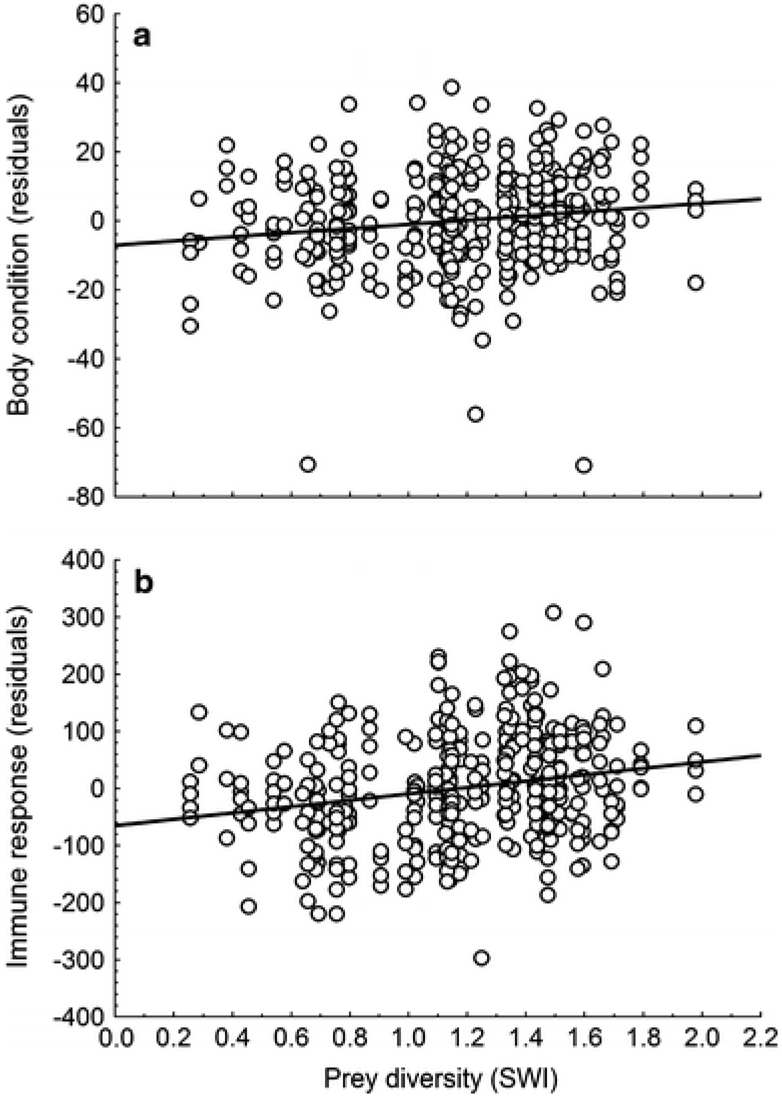

Figure 2.1 **a** Relationship between body condition (*r* = 0.13) and **b** immune response to phytohemagglutinin (*r* = 0.22) of common kestrel fledglings and diversity index (Shannon–Wiener index; *SWI*) of prey delivered by parents to the nest. Residuals extracted from the models by excluding SWI as a covariate were used to graphically represent condition and immune response

The mean prey diversity (SWI) for the 4-year period was 1.2 ± 0.4 ranging from 0.3 to 2.0. SWI was positively correlated with prey biomass (LMM, $F_{1,34} = 5.7$, $P = 0.023$); however, this variable was not retained in the best model when other variables were included (Table 2.2; Appendix 2.5). The best model obtained for SWI was the one containing clutch size, year and the interaction between both variables (Table 2.2; Appendix 2.5). SWI correlated significantly and positively with clutch size and varied significantly among years. Year 2008 showed the lowest mean SWI and differed significantly from the other 3 years (LMM, all $P < 0.01$). No significant differences were observed among the remaining years (LMM, all $P > 0.19$). Significant and positive correlations between SWI and clutch size were observed in 2006 and 2009 (LMM, both $P < 0.04$), but not in 2007 and 2008 (LMM, both $P > 0.4$).

Table 2.2. Linear mixed model (LMM) of the prey biomass and diversity (SWI) of prey delivered by common kestrels *Falco tinnunculus* to the nest. Estimates, standard errors (S.E.), 95% confidence intervals (95% CI), *F* and *P* values are shown. Prey biomass: *d.f.* = 34, *n* = 81; prey diversity (SWI): *d.f.* = 34, *n* = 81; . LD = laying date, CS = clutch size, NF = number of fledglings.

Effect	Year	Estimate	S.E.	95%CI	*F*	*P*
Prey biomass						
Intercept		-10.85	16.22	(-43.52, 21.82)	0.5	0.507
CS		8.10	3.03	(1.94, 14.26)	7.2	0.012
Prey diversity (SWI)						
Intercept		0.219	0.56	(-0.91, 1.35)	0.2	0.697
CS		0.218	0.11	(0.00, 0.44)	5.7	0.024
Year	2006	-0.827	0.79	(-2.44, 0.79)	4.3	0.013
Year	2007	1.307	0.68	(-0.01, 2.77)	-	-
Year	2008	1.030	0.72	(-0.43, 2.49)	-	-
Year	2009	-	-	-	-	-
CS*year	2006	19.68	13.86	(-0.18, 0.44)	4.9	0.007
CS*year	2007	6.30	11.78	(-0.55, -0.02)		
CS*year	2008	5.47	12.23	(-0.54, -0.01)		
CS*year	2009	-	-	-	-	-

Kestrel diet and offspring condition

The model selection procedure for fledgling body condition yielded two best models with similar AICc (Appendix 2.6). The simplest model is shown in Table 2.3. Both models showed that fledgling body condition (body mass corrected for wing length and sex as covariates) differed significantly among years. The second selected model was the same except that clutch size was included (Appendix 2.6), but had no significant effect (LMM, $F_{1,313}$ = 2.1, P = 0.151). As in the first model, the remaining variables had significant effects on body mass (LMM, all P < 0.01).

Table 2.3. Linear mixed model (LMM) of fledgling body condition (body mass corrected for wing length as a covariate) of common kestrels *Falco tinnunculus* from 2006 to 2009. Estimates, standard errors (S.E.), 95% confidence intervals (95% CI), *F* and *P* values are shown. Wald *Z* statistic is given for random factors. *d.f.* = 314, *n* = 366. LD = laying date, SWI = prey diversity, f = female and m = male.

Effect	**Year**	**Estimate**	**S.E.**	**95%CI**	***F***	***P***
Intercept		93.057	15.43	(61.97, 124.13)	50.1	<0.001
SWI		8.451	3.20	(2.15, 14.75)	7.0	0.009
Wing length		0.556	0.09	(0.37, 0.74)	36.1	<0.001
Sex (f = 0)		19.102	1.73	(15.70, 22.50)	122.2	<0.001
Sex (m = 1)		-	-	-	-	-
Year	2006	12.792	3.14	(6.61, 18.97)	20.1	<0.001
Year	2007	3.539	2.67	(-1.71, 8.78)	-	-
Year	2008	20.037	2.83	(14.47, 25.61)	-	-
Year	2009	-	-	-	-	-
		Estimate	**S.E.**	**95%CI**	**Z**	**P**
Nest		130.612	37.86	(79.49, 253.57)	3.5	<0.001

The model selection procedure for immune response to PHA in kestrel fledglings resulted in one best model (Table 2.4), although this model differed only by ΔAICc = 1.9 with respect to the second one (Appendix 2.6). Controlling for body mass, immune response of fledglings correlated positively with prey diversity (Figure 2.1), was higher in females (4.4 ± 1.4 mm) than in males (4.0 ± 1.4 mm) and varied among years (Table 2.4). The second selected model was similar except that the variable prey biomass remained in the model (Appendix 2.6), but had no significant effect (LMM, $F_{1,305} = 0.2$, $P = 0.686$). Similar to the former model, the remaining variables had significant effects on immune response (LMM, all $P < 0.01$).

Discussion

Data from recordings during the chick rearing phase showed that the common kestrel in our population preyed on a great variety of prey taxa. However over 80 % of the biomass and frequency of prey consumed were represented by only five species (common vole, ocellated lizard, psammodromus lizard, field cricket and mole cricket). In our study area inter-annual fluctuations have been reported in the abundance of some important prey species for the kestrel diet, such as the Eurasian skylark *Alauda arvensis* (Martínez-Padilla & Fargallo 2008), common vole, white-toothed shrew *Crocidura russula* and ocellated lizard (Fargallo *et al.* 2009). Our results showed that the frequency of the most consumed taxa varied significantly between years. These observations indicate environmental unpredictability of food resources in our study area and suggest a certain degree of flexibility in the foraging behaviour of kestrels, as would be expected for a generalist population.

Table 2.4. Linear mixed model (LMM) of the immune response to PHA of common kestrel *Falco tinnunculus* fledglings from 2006 to 2009. Estimates, standard errors (S.E.), 95% confidence intervals (95% CI), *F* and *P* values are shown. Wald *Z* statistic is given for random factors. *d.f.* = 306, *n* = 366. LD = laying date, SWI = prey diversity, f = female and m = male. This LMM was the one that showed the lowest *AICc* (see text).

Effect	**Year**	**Estimate**	**S.E.**	**95%CI**	***F***	***P***
Intercept		89.934	53.95	(-18.86, 198.73)	2.8	0.103
Body mass		1.247	0.26	(0.73, 1.76)	47.2	<0.001
SWI		43.575	16.03	(12.04, 75.11)	27.6	<0.001
Sex (f = 0)		39.608	10.39	(19.15, 60.07)	14.5	<0.001
Sex (m = 1)		-	-	-	-	-
Year	2006	41.895	15.41	(11.59, 72.20)	8.5	<0.001
Year	2007	-4.301	13.87	(-31.59, 22.99)	-	-
Year	2008	-39.508	15.23	(-69,49, -9.53)	-	-
Year	2009	-	-	-	-	-
		Estimate	**S.E.**	**95%CI**	**Z**	**P**
Nest		1759.8	37.33	(974.5, 4089.5)	2.8	0.002

Diet and individual quality

When controlling for inter-annual diet variation, biomass and prey diversity were both positively correlated with clutch size. In the case of prey diversity, this contribution was clearer in two of the 4 study years. Although prey biomass and prey diversity were initially correlated, this correlation was not significant anymore when year and clutch size were included in the model. Since males are the main food providers during reproduction, this indicates that prey biomass and prey diversity constitute two components of male quality for common kestrels.

These results are consistent with those found in previous studies in which clutch size was reported to be a reliable indicator of the work capacity of kestrels as they are reluctant to vary parental investment and feeding rate above or below a level set for the original clutch (Masman *et al.* 1989; Korpimäki & Rita 1996; Fargallo *et al.* 2002). The common kestrel is a territorial species in which foraging areas during reproduction are included in the breeding territories obtained by males (Village 1990). Our results indicate that individuals of better quality feed on a more diverse array of prey species within their territories. Therefore, high-quality kestrels use a broader trophic niche than low-quality kestrels in our population.

Prey diversity and offspring viability

The condition of fledglings varied among years indicating that environmental food conditions differ among years. Interestingly, prey diversity, but not biomass, correlated positively with body condition of fledglings. Therefore the diversity of prey species consumed, rather than the amount of food, is a better predictor of condition for growing kestrels. Our results suggest that by increasing the array of prey species, kestrels may be seeking nutrients that benefit the growth of chicks, instead of increasing biomass per se. The importance of nutrients in reproduction, growth and survival of organisms has largely been proved in humans and other animals. Consequently, a broader trophic niche in kestrels is associated with an increase in fitness expectancies, since body condition during growth predicts survival, lifespan, future acquisition of territories, etc. (reviewed by Metcalfe and Monaghan 2001).

Our results also showed that individuals fed with a more diverse diet showed better immunocompetence. As in the case of body condition, not only food per se, but nutritional composition plays an important role for the immune system to function efficiently. Nutritional compounds such as vitamins (A, B, C, E), minerals (Zn, Cu, Fe and Se), linoleic acid, essential amino acids, macronutrients (proteins, lipids and carbohydrates) have been shown to be required for the development, maintenance and response of the immune system affecting the susceptibility of infectious agents (Blazer 1992; Calder & Kew 2002; Klasing 2007). The diet of parents and that received during growth has been demonstrated to have effects on juvenile and adult immunity (Kidd 2004; Klasing 2007; Freitak *et al.* 2009; Hasselquist & Nilsson 2012; Triggs & Knell 2012). Particularly, the immune response to PHA is highly sensitive to environmental food conditions. In birds, this immunological measurement is generally correlated with body mass of nestlings (Tella *et al.* 2000), affected by food restrictions (Saino *et al.* 1997a; Alonso-Alvarez & Tella 2001; Fargallo *et al.* 2002; Brzek & Konarzewski 2007) and diet composition (Soler *et al.* 2003; Fitze *et al.* 2007). Our results showed that when controlling for other confounding factors, fledglings fed with a higher diversity of prey species also showed a higher immune response to PHA. Interestingly, the amount of food delivered by parents did not contribute significantly to the model. These results suggest that diets consisting of a broad trophic spectrum, rather than those based on food abundance, enhance immunity during growth. Knowing that the immune response to PHA has been considered as a good indicator of offspring recruitment rate, survival and longevity (Saino *et al.* 1997b; Christe *et al.* 1998; Hõrak *et al.* 1999; Tella *et al.* 2000; Soler *et al.* 2003; López-Rull *et al.* 2011) our study suggests that by broadening the trophic niche, kestrels have a higher chance of increasing their fitness.

A broader trophic niche observed in parents of better quality can be associated with obtaining better territories, larger areas and/or with a higher heterogeneity of microhabitats, increasing the diversity of prey species within them (Begon *et al.* 2006) or due to a greater effort in foraging behaviour devoted to increasing prey diversity, genetic quality, health status or any other characteristic indicating a better competitive capacity. In any case, our results in the common kestrel describe a close link between foraging strategy and offspring viability measured as body condition and immune response. Individuals adopting a more generalist strategy seem to be able to produce offspring with better body and immunological condition, hence with a higher fitness potential. Broadening the trophic niche may be an adaptive strategy in environments where the abundance and availability of food resources fluctuate with time. This study offers a new approach for the study of foraging strategies and highlights the need for further research on the underlying mechanisms for the relationship between diet diversity and offspring viability.

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Appendix

Appendix.2.1. Table showing prey mass (g) assigned to each prey item group. The minimum identified taxon level is shown. Bibliographic sources consulted to estimate biomass are also shown. (*) Body mass data obtained from individuals captured alive in our study area (Campo Azálvaro, Segovia, Spain).

	Prey mass
Mammals	
Crocidura russula	8.1 g , n = 310 *
Microtus arvalis	31.3 g , n = 507 *
Birds	
Alauda arvensis	35.0g , n = 8907 (1-3)
Motacilla flava	15.9 g , n = 194 (4)
Sturnus unicolor	84.5g , n = 2423 (5-7)
Passer domesticus	26.8 g , n = 341(8)
Petronia petronia	29.4 g , n = 6 (4)
Passerines (unidentified) [a]	54.0 g , n = 9 in 2006
	35.0g , n = 3 in 2008
Reptiles	
Chalcides striatus	13.3 g , n = 2 *
Timon lepidus (adult) [b]	81.6 g , n = 32 *
Timon lepidus (juvenile) [b]	43.1 g , n = 3 *
Lacerta schreiberi	29.4 g , n = 19 *
Podarcis hispanica	2.0 g , n = 22 (9)
Psammodromus hispanicus	2.7 g , n = 21 *
Large Lizard [c]	76.0g , n = 47 in 2006
	74.9 g , n = 47 in 2007
	68.6 g , n = 4 in 2008
Small lizard [c]	2.7 g , n = 323 in all years
Amphibians	
Triturus marmoratus	9.5 g , n = 18 (10-12)
Pelophylax perezi	32.7 g , n= 5 *

	Prey mass
Arthropods	
Lycosa tarentula	1.6 g , n = 234 (13)
Gryllus campestris	1.1 g , n = 26*
Acrididae	0.6 g , n = 29 (several species included)
Tettigoniidae	1.5 g , n = 14 (several species included)
Gryllotalpa gryllotalpa	2.6 g , n = 24 *
Orthoptera[d]	2.0 g , n = 526 in 2006 2.3 g , n = 609 in 2007 2.8 g , n = 406 in 2008 2.9 g , n = 652 in 2009
Mantodea	1.5 g , n = 57 (14)
Lepidoptera	0.5 g , n = 5 (14)
Coleoptera	0.6 g , n = 53 (14)
Insecta (unidentified)[e]	2.0 g , n = 537 in 2006 2.3 g , n = 616 in 2007 2.4 g , n = 413 in 2008
***Insecta* (*larvae*)**	0.14 g , n = 48 (14)
Large prey item [f]	46.0 g , n = 138in 2006
Small prey item [f]	2.0 g , n = 659in 2006
Unidentified prey item [g]	9.4 g , n = 797 in 2006 8.0 g , n = 884 in 2007

(a) For unidentified birds (all passerines) the mean bird biomass was estimated considering the mean body mass recorded for birds consumed in the same year as the bird prey item was observed.

(b) In the case of *Timon lepidus* lizards, it was possible to determine juvenile individuals, for which the age was took into account when estimating biomass.

(c) For some recordings, lizards could only be identified as large species (*Timon lepidus* or *Lacerta schreiberi*) or small species (*Podarcis hispanica* or *Psammodromus hispanicus*). Biomass was calculated as the mean body mass of both species in each group.

(d) Orthoptera species could not be determined. The mean biomass value given for this group was calculated using the weighted mean by considering the number of field crickets, mole crickets, *Tettigonidae* and *Acrididae* consumed in each year.

(e) Unidentified insects. The mean biomass value given for this group was calculated using the weighted mean by considering the numbers of each insect group consumed in each year.

(f) For three prey species (two large and 1 small), only the size of the prey item could be recorded, for which they were grouped as a large prey (mammal, bird or large lizards) or small prey (small lizards or arthropods). Amphibians were excluded due to the low frequency of consumption. The mean biomass value given for this group was calculated using the weighted mean by considering the numbers of each prey group (large and small) in each year.

(g) In 19 cases the prey species, group or size could not be recorded. The mean biomass value given for this group was calculated using the weighted mean by considering the numbers of each prey group in each year.

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Appendix 2.2. Results: Inter-annual variation in kestrel diet

The consumption of mammals varied significantly among years (GENMOD, $\chi^2_{1,3}$ = 384.2, *P* < 0.001) being significantly highest in 2008, followed by 2009 and 2006-07 having the lowest values (Appendix 2. 3 and 2.4). Contrasts showed significant differences between all pair-wise annual comparisons (all *P* < 0.001) except for 2006-07 (*P* = 0.107). Results of the model are shown in Table 2.S3. In the case of birds no significant inter-annual variation was observed (GENMOD, $\chi^2_{1,3}$ = 3.6, *P* = 0.309, (Appendix 2.3 and 2.4). Reptiles were also differently consumed among years (GENMOD, $\chi^2_{1,3}$ = 84.6, *P* < 0.001), being the highest consumption in 2006-07 and the lowest in 2008-09 (Appendix 2. 3 and 2.4). Contrasts showed significant differences between all pair-wise annual comparisons (all *P*< 0.001) except for 2006-07 and 2008-09 (both *P* > 0.11). Results of the model are shown in Appendix 2. 4. Amphibians were also differently preyed among years (GENMOD, $\chi^2_{1,3}$ = 10.5, *P* < 0.001), being more preyed in 2008 and 2009 than in 2006 and 2007 (Appendix 2.3 and 2.4). Contrasts showed significant differences in 2006-2008, 2007-2009 and 2006–2009 comparisons (all *P* < 0.040), but not for the remaining pair-wise annual comparisons (all *P* > 0.12). Finally, the consumption of arthropods was also different among years (GENMOD, $\chi^2_{1,3}$ = 92.6, *P* < 0.001) being 2008 the year in which arthropods were less frequently consumed (Appendix 2.3 and 2.4). Contrasts showed significant differences between 2008 and the other three years (all *P* < 0.001).

Appendix 2.3. Total numbers (N), percentage and biomass of prey items delivered by common kestrel parents to the nest in each study year (2006-2009). The minimum identified taxon level is shown. Similar superscript letters within the same taxonomic group indicate no significant inter-annual difference in the frequency of consumption by kestrels ($\alpha = 0.05$).

	2006		**2007**		**2008**		**2009**	
	N (%)	**% Biomass**	**N (%)**	**% Biomass**	**N (%)**	**% Biomass**	**N (%)**	**% Biomass**
Mammals	**56 (6.4)**^{a}	**22**	**81 (9)**^{a}	**38.6**	**329 (39.6)**^{b}	**83.3**	**158 (17.2)**^{c}	**44.4**
Crocidura russula	0 (0)	0	0 (0)	0	21 (2.5)	1.5	32 (3.5)	2.8
Microtus arvalis	56 (6.4)	22.0	81 (9.3)	38.6	308 (37.1)	81.8	126 (13.7)	41.6
Birds	**11 (1.2)**^{a}	**7.5**	**5 (0.56)**^{a}	**4.5**	**5 (0.6)**^{a}	**1.5**	**8 (0.9)**^{a}	**6.2**
Alauda arvensis	3 (0.3)	1.3	0 (0)	0	3 (0.4)	0.9	1 (0.1)	0.4
Motacilla flava	1 (0.1)	0.2	1 (0.1)	0.2	0 (0)	0	0 (0)	0
Sturnus unicolor	4 (0.5)	4.3	3 (0.3)	3.9	0 (0)	0	6 (0.7)	5.5
Passer domesticus	1 (0.1)	0.3	1 (0.1)	0.4	0 (0)	0	0 (0)	0
Petronia petronia	0 (0)	0	0 (0)	0	0 (0)	0	1 (0.1)	0.3
Passerines (unidentified)	2 (0.2)	1.4	0 (0)	0	2 (0.2)	0.6	0 (0)	0
Reptiles	**192 (21.9)**^{a}	**52.8**	**184 (20.5)**^{a}	**34.1**	**75 (8.9)**^{b}	**6**	**96 (10.5)**^{b}	**33.4**
Chalcides striatus	24 (2.7)	4.0	32 (3.6)	1.3	12 (1.4)	1.4	31 (3.4)	4.5
Timon Lepidus	42 (4.8)	39.2	27 (3)	24.9	3 (0.4)	1.8	32 (3.5)	27.7
Lacerta schreiberi	5 (0.6)	1.8	4 (0.4)	1.8	1 (0.1)	0.3	1 (0.1)	0.3
Podarcis hispanica	2 (0.2)	0.1	3 (0.3)	0.1	2 (0.2)	0.0	1 (0.1)	0.0
Psammodromus hispanicus	113 (12.9)	3.8	116 (12.9)	4.8	55 (6.6)	1.3	31 (3.4)	0.9
Large Lizard	4 (0.5)	3.8	1 (0.1)	0.1	2 (0.2)	1.2	0 (0)	0.0
Small lizard	2 (0.2)	0.1	1 (0.1)	1.1	0 (0)	0.0	0 (0)	0.0

	2006		**2007**		**2008**		**2009**	
	N (%)	**% Biomass**	**N (%)**	**% Biomass**	**N (%)**	**% Biomass**	**N (%)**	**% Biomass**
Amphibians	**0 (0)**[a]	**0**	**1 (0.1)**[a]	**0.5**	**4 (0.5)**[b]	**0.6**	**6 (0.7)**[b]	**2.1**
Triturus marmoratus	0 (0)	0	0 (0)	0	3 (0.4)	0.3	0 (0)	0
Pelophylax perezi	0 (0)	0	1 (0.1)	0.5	1 (0.1)	0.3	6 (0.7)	2.1
Arthropods	**595 (68.2)**[a]	**14.4**	**625 (69.5)**[a]	**22.2**	**417 (50.3)**[b]	**8.7**	**653 (70.9)**[a]	**13.7**
Lycosa tarentula	12 (1.4)	0.2	5 (0.6)	0.1	0 (0)	0.0	0 (0)	0.0
Gryllus campestris	182 (20.8)	2.5	86 (9.6)	1.4	48 (5.8)	0.5	187 (20.3)	2.2
Acrididae	15 (1.7)	0.1	15 (1.7)	0.1	4 (0.5)	0.0	69 (7.5)	0.5
Tettigoniidae	16 (1.8)	0.3	3 (0.3)	0.1	0 (0)	0.0	15 (1.6)	0.2
G. gryllotalpa	313 (35.9)	10.2	505 (56.2)	20.0	354 (42.7)	8.1	381 (41.4)	10.8
Orthoptera (unidentified)	4 (0.5)	0.1	1 (0.1)	0.1	0 (0)	0	0 (0)	0
Mantodea	0 (0)	0.0	1 (0.1)	0.1	0 (0)	0.0	0 (0)	0.0
Lepidoptera	1 (0.1)	0.0	0 (0)	0.0	0 (0)	0.0	0 (0)	0.0
Coleoptera	5 (0.6)	0.0	4 (0.4)	0.1	1 (0.1)	0.0	0 (0)	0.0
Insecta (unidentified)	41 (4.7)	1.0	2 (0.2)	0.1	4 (0.5)	0.1	0 (0)	0.0
Insecta (*larvae*)	6 (0.7)	0.0	3 (0.3)	0.1	6 (0.7)	0.0	1 (0.1)	0.0
Large prey item	2 (0.2)	1.1	0 (0)	0.0	0 (0)	0.0	0 (0)	0.0
Small prey item	1 (0.1)	0.1	0 (0)	0.0	0 (0)	0.0	0 (0)	0.0
Unidentified prey item	16 (1.8)	1.9	3 (0.3)	0.4	0 (0)	0	0 (0)	0
Total prey items	**873**		**966**		**831**		**921**	

Appendix 2.4. Logistic model (GENMOD) results on the inter-annual variation in the frequency of prey taxon consumption by common kestrels *Falco tinnunculus*. Degrees of freedom (D.F.) Estimates, standard errors (S.E.), 95% confidence intervals for the predicted value of the means (Wald 95% CI), Wald chi-squared value (Wald χ^2) and the probability of obtaining a Wald chi-squared statistic greater than that observed given that the true parameter is 0 (Pr > χ^2) are shown.

Term	**d.f.**	**Estimate**	**S.E.**	**Wald 95% CI**	**Wald χ^2**	**Pr > χ^2**
Mammals						
2006	1	-1.1056	0.1635	(-1.4260, -0.7852)	45.75	<0.001
2007	1	-0.8165	0.1453	(-1.1013, -0.5317)	31.57	<0.001
2008	1	1.1521	0.1126	(0.9315, 1.3727)	104.76	<0.001
2009	-	-	-		-	-
Birds						
2006	1	0.3759	0.4671	(-0.5395, 1.2914)	0.65	0.4209
2007	1	-0.5212	0.5720	(-1.6423, 0.5998)	0.83	0.3621
2008	1	-0.3699	0.5721	(-1.4912, 0.7514)	0.42	0.5180
2009		-	-	-	-	-
Reptiles						
2006	1	0.8850	0.1353	(0.6198, 1.1501)	42.78	<0.001
2007	1	0.7041	0.1354	(0.4387, 0.9696)	27.03	<0.001
2008	1	-0.1595	0.1621	(-0.4773, 0.1582)	0.97	0.3252
2009		-	-	-	-	-
Amphibians						
2006	1	-25.0474	114843	(-225114, 225064)	0.00	0.9998
2007	1	-1.8450	1.0811	(-3.9639, 0.2740)	2.91	0.0879
2008	1	-0.3043	0.6473	(-1.5730, 0.9643)	0.22	0.6382
2009		-	-	-	-	-
Arthropods						
2006	1	-0.1296	0.1027	(-0.3309, 0.0716)	1.59	0.2067
2007	1	-0.2847	0.0990	(-0.4787, -0.0907)	8.28	0.0040
2008	1	-0.8834	0.1004	(-1.0801, -0.6866)	77.44	<0.001
2009		-	-	-	-	-
Scale	0	1.0000	0.0000	(1.0000, 1.0000)		

Appendix 2.5. Linear mixed models (LMM) of prey biomass and prey diversity (Shannon-Wiener Index; SWI) consumed by common kestrels *Falco tinnunculus* from 2006 to 2009. Clutch size was included as a covariate and year as a fixed factor. Interaction between clutch size and year is tested. Nest location was included as a random factor. Model selection was based on the Akaike's Information Criterion corrected for small sample sizes (*AICc*). Delta (ΔAICc) and weights (wAICc) for each AICc are also shown. ld = laying date, cs = clutch size, ye = year, pb = prey biomass.

Model	***AICc***	***ΔAICc***	***wAICc***
Prey biomass			
1) cs	730.8	0	0.71
2) cs + ye	733.0	2.2	0.24
3) cs + ye + cs*ye	736.2	5.4	0.04
4) ye	740.0	9.2	0.01
Prey diversity (SWI)			
1) cs + ye + cs*ye	54.4	0	0.80
2) cs + pb + ye	57.5	3.1	0.19
3) ye	61.8	7.4	0.03
4) cs + ye	62.9	8.5	0.01
5) cs + pb	71.1	16.7	0.00

Appendix 2. 6. Five best linear mixed-models (LMM) of fledgling body mass and immune response to PHA of common kestrels *Falco tinnunculus* from 2006 to 2009. Laying date, clutch size, number of fledglings at the age of 26 days old, fledgling wing length, fledgling weight, prey diversity SWI (Shannon-Wiener Index; SWI) and biomass of prey consumed were included as covariates. Fledgling sex and year as fixed factors and kestrel nest as a random factor. Model selection was based on the Akaike's Information Criterion corrected for small sample sizes (*AICc*). Delta (ΔAICc) and weights (wAICc) for each AICc are also shown. ld = laying date, cs = clutch size, nf = number of fledglings, wl = wing length, fbm = fledgling body mass, swi = prey diversity (SWI), pb = prey biomass, sx = sex, ye = year.

Model	***AICc***	***ΔAICc***	***wAICCc***
Fledgling body mass			
1) wl + swi + sx + ye	3125.8	0	0.41
2) cs + wl + swi + sx + ye	3125.9	0.1	0.39
3) cs + wl + swi + sx + ye + cs x ye	3128.2	2.4	0.11
4) wl + sx + ye	3130.2	4.4	0.05
5) cs + wl + swi + bm + sx + ye + cs x ye	3130.4	4.6	0.04
Immune response to PHA			
1) fbm + swi + sx + ye	4198.9	0	0.70
2) fbm + swi + pb + sx + ye	4200.8	1.9	0.27
3) fbm + pb + sx + ye	4205.4	6.5	0.03
4) fbm + swi + pb + sx	4216.6	17.7	0.00
5) fbm + swi + sx	4217.0	18.1	0.00

Capítulo III:

Trophic niche in a raptor species: the relationship between diet diversity, habitat diversity and territory quality

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Abstract

Recent research reports that many populations of species showing a wide trophic niche (generalists) are made up of both generalist individuals and individuals with a narrow trophic niche (specialists), suggesting trophic specializations at an individual level. If true, foraging strategies should be associated with individual quality and fitness. Optimal foraging theory predicts that individuals will select the most favourable habitats for feeding. In addition, the "landscape heterogeneity hypothesis" predicts a higher number of species in more diverse landscapes. Thus, it can be predicted that individuals with a wider realized trophic niche should have foraging territories with greater habitat diversity, suggesting that foraging strategies, territory quality and habitat diversity are inter-correlated. This was tested for a population of common kestrels *Falco tinnunculus*. Diet diversity, territory occupancy (as a measure of territory quality) and habitat diversity of territories were measured over an 8-year period. Our results show that: 1) territory quality was quadratically correlated with habitat diversity, with the best territories being the least and most diverse; 2) diet diversity was not correlated with territory quality; and 3) diet diversity was negatively correlated with landscape heterogeneity. Our study suggests that niche generalist foraging strategies are based on an active search for different prey species within or between habitats rather than on the selection of territories with high habitat diversity.

Introduction

Optimal foraging theory predicts that individuals will select the most favourable habitats for feeding to minimize energy expenditure and maximize fitness (Pyke *et al.* 1977; Stephens & Krebs 1986). In addition, the classical niche theory predicts a positive correlation between habitat diversity/heterogeneity and diversity of species (Simpson 1949; MacArthur & Wilson 1967; Lack 1969; Tews *et al.* 2004). This is the landscape heterogeneity hypothesis (LHH)(Simpson 1949; MacArthur & Wilson 1967), and is based on the idea that more heterogeneous landscapes with higher habitat diversity may provide more diverse ways of exploiting the environmental resources (niches) than more homogenous landscapes, consequently allowing exploitation by a greater number of species (Tews *et al.* 2004; Kadmon & Allouche 2007). Although the relationship between landscape heterogeneity and species diversity has been found in general to be positive, there are cases in which the correlation is not obvious or in which a negative correlation has been observed (see Tews *et al.* 2004 for a review). This discrepancy may be due to factors such as the selected taxonomic group in each study or the size of the effective area for each species (Tews *et al.* 2004; Allouche *et al.* 2012). Taking into account both ideas it is plausible to predict that individuals, populations or species with more generalist diets (broader trophic niche) should also exploit more heterogeneous landscapes, as opposed to specialists (narrower trophic niche).

Recent research has indicated that generalist populations are uncommon and that those previously considered generalists may actually be composed of specialist individuals, suggesting the existence of individual ecological specialisation, that is, the degree to which an individual's diet is restricted relative to their population (Bolnick *et al.* 2003; Araújo *et al.* 2011). Some authors have in fact suggested that ecological specialism is the main driving force leading to speciation, considering generalist strategies as only passing phases in certain evolutionary scenarios (Loxdale *et al.* 2011). Individuals may specialize on a narrow range of resources, different from those of their conspecific competitors, and thus advantageous by reducing resource-use overlap and competition (Bolnick *et al.* 2003; Dayan & Simberloff 2005). Individual specialization is thus expected to be widespread among species occupying higher trophic levels, such as predators, due to a higher intraspecific competition for resources (Estes *et al.* 2003; Svanback & Bolnick 2007; Quevedo *et al.* 2009). However, generalism can also be adaptive in more unfavourable and/or unpredictable environments, by increasing the capabilities of foraging and the probability for expansion by the colonization of new habitats, hence ensuring persistence (Thomas *et al.* 2001; Dennis *et al.* 2011; Terraube & Arroyo 2011; Navarro-López *et al.* 2014).

In addition to increasing competition, another cost proposed for generalist strategies is the loss of foraging efficiency and, as a result, a reduction of biomass intake compared to more specialist strategies (MacArthur & Pianka 1966; Bernays & Funk 1999; Terraube & Arroyo 2011). Under this premise, individuals that are more generalist in a given population should be better able to compensate for these potential costs. A key piece to understanding the evolution of trophic strategies is determining whether the trophic niche is related to individual quality and fitness, which has been little explored in general (Mayntz & Toft 2001; Margalida *et al.* 2009; Cucherousset *et al.* 2011; Margalida *et al.* 2012; Navarro-López *et al.* 2014). It is also essential to understand the foraging strategies used by individuals to maximize fitness.

Realized trophic niche (niche that a species occupies when limiting factors, such as interspecific competition, are present) has been recently measured for common kestrels *Falco tinnunculus* in a Mediterranean mountainous area, reporting that individuals showing a broader trophic niche are those of higher quality in the population, as denoted by their higher fecundity (clutch size) and higher offspring survival prospects (better body condition and immune response of the chicks) (Navarro-López *et al.* 2014). In territorial bird species, such as most raptors, breeding performance and foraging behaviour is closely related to territory characteristics (Margalida *et al.* 2007), since a breeding territory is mainly defined as a defended area for nesting and feeding (Newton 1998). In this study, we explore the potential role of territory selection in the trophic niche width of common kestrels during an 8-year period. We analysed diet diversity, territory quality and the diversity of habitats present in territories of common kestrels. Following the LHH we predict that: 1) better territories will be those having higher landscape heterogeneity and 2) since higher quality individuals show a broader trophic niche (Navarro-López *et al.* 2014), better individuals placed in better-quality and more heterogeneous territories will consume a higher diversity of prey species.

Material and methods

Study species

The common kestrel (hereafter kestrel) is a territorial diurnal raptor species widely distributed in Eurasia and Africa and common in a broad array of habitats (Village 1990). The variety of environments occupied by kestrels predicts a great variety of foraging habits, with the kestrel considered a rodent specialist in northern populations (Village 1982; Korpimäki 1986) and preying on a great variety of taxa in more southern populations (Aparicio 2000; Navarro-López *et al.* 2014).

Ethical statement

Our study followed ethical guidelines proposed for the Spanish Royal Decree 1205/2005 on the protection of animals used in experiments and scientific research. Permission to carry out our work was given by Dirección General del Medio Natural de la Junta de Castilla y León. The Spanish Ministry of Science and Innovation (Projects: CGL2007-61395/BOS and CGL2010-15726/BOS) approved the experimental design and financed the study. Common kestrel *Falco tinnunculus* is not considered as endangered species. The research was carried out on private lands with landowner permission.

Study area and landscape heterogeneity

The study was carried out in the region of Campo Azálvaro, located in central Spain. In this region, about 30-45 breeding pairs nest each year in nest boxes over an area of 23 km^2 (Fargallo *et al.* 2009). The area is a flat treeless valley at 1300 m a.s.l., mainly devoted to cattle-raising where pasturelands represent 92% of the habitats, broom scrubland (*Cytisus scoparius*) 5%, small forest fragments (*Populus, Fraxinus, Salix, Pinus* and *Quercus*) 2% and roads, buildings and rocky lands represent around 1% (Figure 3.1). Vegetation composition of pastures is described in Torre et al. (2007). The pastureland of the study area was characterised into five different habitat types according to vegetation, humidity and ground characteristics: 1) evergreen pastures, defined as pastures with 100% vegetation coverage located around rivers, springs and other water sources that remain green (fresh) throughout the year; 2) dry pasture, defined as pastures with 100% vegetation coverage that become dry in early-middle July; 3) oat pastures, defined as pastures with 100% vegetation coverage that become dry in early-middle July with the presence of golden oat *Stipa gigantea* keeping it green throughout the year; 4) sandy pastures, defined as sparse pastures present in sandy soils where vegetation coverage is not complete; and 5) un-grazed pasture, defined as small areas of pasture with 100% vegetation coverage from which grazing is excluded by means of wire fences.

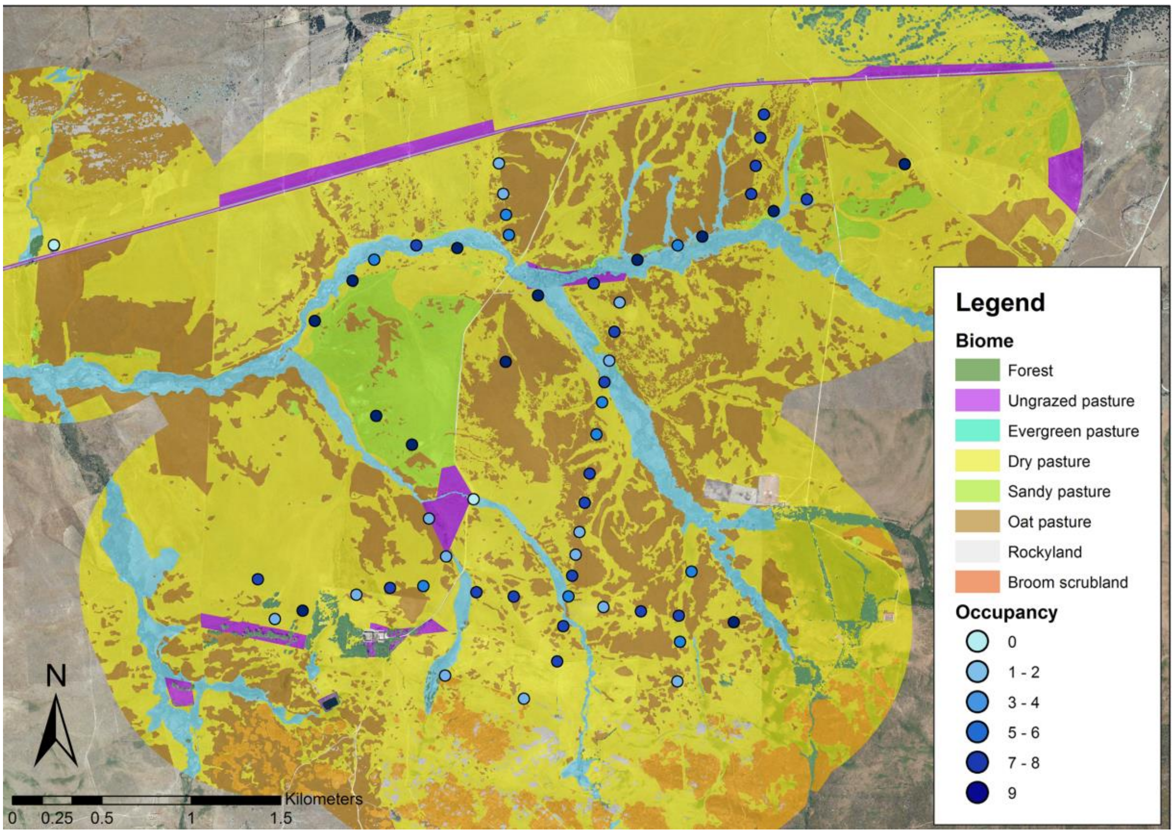

Figure 3.1. Map of habitats in the study area. Nest boxes are represented by blue dots, blue intensity represents occupancy of the nest.

To determine landscape heterogeneity in kestrel territories the extent of each habitat (pastureland type and the remaining habitats) found in the study area was estimated within an area of a radius of 1000 m around the nest box, 6.3 km^2 (Appendix 3. 1). This area was selected because breeding males hunt in 90% of cases at a distance less than 1 km from the nest in grassland habitats (Village 1990). Orthophotos with maximum resolution were obtained from the "Spanish National Institute of Geography (National Plan of Aerial Orthophotografy 2010)" and analysed in ESRI ArcGIS10Desktop software, Redlands, CA: Environmental Systems Research Institute (Tapia *et al.* 2008; Tanferna *et al.* 2013). Habitat values for each territory (arcsine transformed surface percentage) were combined in a Principal Component Analysis (Barrientos & Arroyo 2014; Ponce *et al.* 2014) that resulted in 2 main PCs (Table 3.1). PC1 explained 47% of the variance (eigenvalue = 3.78) and represents a gradient from high values of dried pastures and forest to high values of evergreen and oat pasture. PC2 explained 33% of the variance (eigenvalue = 2.62) and represents a gradient from high values of rocky lands and broom scrubland to high values of un-grazed and sandy pasture.

Table 3.1. Principal components of the composition of habitat around the kestrel nest. Axes selected were all axes with values higher than 1.0 eigenvalues.

	PC1	**PC2**
Forest	**0.797751**	0.244562
Rocky land	0.537136	**0.726177**
Broom scrubland	0.579884	**0.707719**
Evergreen pasture	**-0.903859**	-0.097197
Ungrazed pasture	0.303584	**-0.810392**
Dry pasture	**0.852612**	0.242958
Sandy pasture	-0.169799	**-0.898918**
Oat pasture	**-0.926134**	0.010760
Eigenvalues	3.783813	2.621391
Explained variance	0.472977	0.327674

Territory landscape heterogeneity (TLH) was defined as the diversity of habitats present in a kestrel territory and was calculated using the Shannon-Wiener index, in the VEGAN package of R version 2.15.2 (2012), by considering habitat richness (number of habitats present) and the expanse (surface percentage) of each habitat type. TLH correlated positively with PC1 and negatively with PC2 (PC1: $r = 0.33$, $F_{2,58} = 8.63$, $P = 0.005$; PC2: $r = -0.44$, $F_{2,58} = 15.53$, $P < 0.001$), which means that territories mainly with higher expanse of forest-dry pasture (PC1) and with sandy-ungrazed pastures (PC2) are the least heterogeneous territories.

Occupancy and territory quality

Nest boxes were monitored every year from 2005 to 2013 to record kestrel occupation, laying date (the date at which the first egg was laid) and clutch size. Occupancy was defined as the number of years a territory (nest box) was occupied over the 9-year period. Average occupancy was 4.8 ± 2.0 years, ranging from 0 to 9 years (Fig. 1). Occupancy was used to estimate territory quality, since good territories are occupied more frequently than bad territories (Sergio & Newton 2003). Controlling for year, occupancy was significantly and negatively correlated with laying date (LMM, $F_{1,222} = 13.30$, $P < 0.001$) and positively correlated with clutch size (LMM, $F_{1,222} = 6.98$, $P = 0.01$), two reliable indicators of individual quality in kestrels (Aparicio 1998; Navarro-López *et al.* 2014). Since occupancy was correlated with clutch size and laying date, we can assume that those territories with a higher occupancy are the territories preferred by individuals of better quality. This is useful to describe territory characteristics (landscape heterogeneity) in relation to territory quality. The number of occupied nest boxes around the nest can affect occupancy. Thus, breeding density was recorded and estimated as the number of breeding pairs within a 1-km radius around the nest box. One of the 62 nest boxes was moved from its place of origin during the study period, so this territory was excluded from the analyses.

Kestrel diet

From 2006 to 2013, the food provided by parents to their chicks was recorded in 170 nests (16 in 2006, 18 in 2007, 26 in 2008, 25 in 2009, 16 in 2010, 25 in 2011, 21 in 2012 and 23 in 2013). When chicks were 12-14 days old, a digital camera was placed at the nest to record prey delivered by adults when feeding the chicks. The cameras used were: a Cylinder SONY 1/3* Super HAD connected to ARCHOS AV500 100 Gb digital recorders in years 2006-2007; digital camcorders SONY HandyCam 60 Gb in years 2008-2011; and microcameras CCD 1/3 Sharp connected to AXIS Q7401 analogic video encoder in years 2012-2013. The cameras in the first two systems were installed in the posterior wall of the nest box pointing towards the nest box entrance, while in the third system the camera was installed in the lateral wall near the entrance. Both digital recorders and camcorders were powered with 12 amp SLI batteries (24 Ah 24 V) through a voltage converter (12 V). Kestrel nests were recorded continuously for 24 hours or more from sunrise to sunset without researcher interruptions, although some nests were not filmed for the entire period due to technical problems. The daylight period at our study area during June and July is about 15 hours (sunrise at 4:49 hours and sunset 19:49 hours, solar time for 24 June). On average, kestrels began provisioning chicks with food at 7:42 ± 0:58 h solar time (range = 5:30 – 9:41, n=133) and stopped at 21:04 ± 0:40 h solar time (range = 19:11 – 22:09, n=169). A mean recording time of 16.5 h ± 2.5 h of prey delivery activity was recorded (ranging from 7.7 to 22.4 h, n= 170). Recordings were displayed in the free VLC Media Player software (www.videolan.org) to identify each delivered prey item.

Diet diversity and individual quality

The diversity of prey delivered by parents was calculated through the Shannon-Wiener index of each nest using the VEGAN package of R (Oksanen *et al.* 2013). The lowest taxonomic rank was determined in each prey item (Bolnick *et al.* 2002). Almost all amphibian, reptile, bird and mammal prey items were determined at a species level (99% of cases, Table 3.2). Among invertebrate prey items, field crickets *Gryllus campestris* and mole crickets *Gryllotalpa gryllotalpa* (*Insecta, Orthoptera*) and Mediterranean tarantula *Lycosa tarentula* (*Arachnida*) were easily identifiable in the recordings (Table 3.2). The rest of the arthropods were identified at the minimum possible taxonomic rank (order and family, Table 3.2). To calculate Shannon-Wiener index, species level was used for amphibians, reptiles, mammals, birds, spiders, crickets and mole crickets, family for grasshopper, bush crickets and mantises and order for beetles, butterfly and moth larvae. Diversity is expected to vary with the sampling effort (Begon *et al.* 2006). In our case, diversity of diet was not associated with the filming time for the range we worked with (LMM, $R^2c = 0.26$, $F_{1,101} = 1.34$, $P = 0.25$). As in the previous four-year study period (Navarro-López *et al.* 2014), diet diversity was positively correlated with clutch size for the longer eight-year period in this study (LMM, $R^2c= 0.30$, $F_{1,108}= 8.58$, $P< 0.004$; see below for statistical details). Similarly indicating an association between kestrel diet diversity and individual quality.

Table 3.2. Total numbers and percentage of prey items delivered by common kestrel *Falco tinnunculus* parents to the nest over an eight-year study period (2006-2013). The minimum identified taxon level is shown.

	N (%)
Mammals	
Apodemus sylvatica	8 (0.09)
Crocidura russula	63 (0.68)
Microtus arvalis	779 (8.45)
Talpa occidentalis	1 (0.01)
Birds	
Alauda arvensis	25 (0.27)
Anthus campestris	2 (0.02)
Carduelis cannabina	2 (0.02)
Lanius senator	1 (0.01)
Motacilla flava	2 (0.02)
Passer domesticus	5 (0.05)
Petronia petronia	3 (0.03)
Sturnus unicolor	26 (0.28)
Passerines (unidentified)	24 (0.26)
Reptiles	
Chalcides striatus	248 (2.69)
Timon lepidus	311 (3.37)
Lacerta schreiberi	64 (0.69)
Podarcis hispanica	57 (0.62)
Psammodromus hispanicus	1461 (15.85)
Large Lizard	6 (0.07)
Small lizard	5 (0.05)
Amphibians	
Triturus marmoratus	3 (0.03)
Pelobates cultripes	7 (0.08)
Pelophylax perezi	27 (0.29)
Arthropods	
Lycosa tarentula	41 (0.44)
Gryllus campestris	1569 (17.02)
Acrididae	229 (2.48)
Tettigoniidae	246 (2.67)
Gryllotalpa gryllotalpa	3309 (35.9)
Orthoptera (unidentified)	5 (0.05)
Mantodea	3 (0.03)
Neuroptera	1 (0.01)
Lepidoptera	1 (0.01)
Coleoptera	482 (5.23)
Insecta (unidentified)	107 (1.16)
Insecta (*larvae*)	70 (0.76)
Unidentified prey item	24 (0.26)
Total prey items	**9217**

Statistical procedures

Statistical analyses were performed using R, version 2.15.2 (CRAN 2012). The relationship between occupancy and territory habitat characteristics (diversity and PCs) was analysed using general lineal models (LM). In a first step the relationship between occupancy (dependent variable) and territory landscape heterogeneity, TLH, (independent variable) was analysed in order to explore how territory quality varies with landscape heterogeneity (first prediction). The squared term of habitat diversity was included as an independent variable to test for a possible curvilinear relationship. In a second LM, occupancy was correlated with principal components of territory habitat (PC1 and PC2), breeding density and habitat diversity to know other environmental characteristics associated with territory quality.

Diet diversity was analysed using general linear mixed models (LMM). In a first LMM, the relationship between diet diversity and clutch size was explored. Since clutch size and laying date were closely correlated (LMM $R^2 c$= 0.17, $F_{1,101}$= 24.78, P< 0.001) the effect of laying date on clutch size was removed by including the residuals of clutch size on laying date as an independent variable. Year and nest were included as random factors. Once this association was verified, a second LMM was done to test the second prediction: a more diverse diet in good-quality individuals is obtained from a more heterogeneous territory. For this purpose diet diversity was included in the model as the dependent variable, and TLH, habitat PC1 and PC2 as covariates. Since prey abundance and availability changes as the season progresses, laying date was also included in the model as a covariate. Year and nest were included as random factors.

LMs and LMMs were performed with the *lme4* R package (CRAN 2013)(Bates *et al.* 2013) and statistics were obtained with the *lmerTest* R package (CRAN 2013) (Kuznetsova *et al.* 2013). Residuals obtained from all LM and LMMs showed normal distributions (Shapiro-Wilk, all P > 0.05). R^2 conditional (Nakagawa & Schielzeth 2013) was calculated using the *MuMln* R package (CRAN 2014) (Bartoń 2013). We constructed sets of models with possible combinations of independent variables. Akaike’s information criterion corrected for small sample size (*AICc*) was used for model selection. The best model was the one with the lowest *AICc* value with a difference > 2 from the second best model. *ΔAICc* and *AICc* weights were also calculated.

Results

Occupancy and landscape heterogeneity

Dry pasture was the most widespread habitat in the study area (58.13%,) followed by oat pasture (22.12%, Fig. 3.1 and Appendix 3.1). These two habitats were also the most commonly found in the 1km-radius areas where nest boxes were installed (53.7% and 27.4% respectively; Appendix 3.1). On average, habitat diversity in kestrel territories was 1.18 ± 0.08, ranging from 1.03 to 1.39. The LM exploring the relationship between occupancy and TLH showed a curvilinear correlation (TLH, $F_{1,58}$ = 5.44, P = 0.023, TLH^2, $F_{1,58}$ = 5.54, P = 0.02; Fig.

3.2). The highest occupancy was observed in the most and least diverse territories. When including in the model habitat PC1, habitat PC2 and breeding density as other potential explanatory variables, the best model obtained for this set of variables was the one containing the terms PC2, TLH and TLH^2 (Table 3.3). Occupancy was significantly and negatively correlated with PC2 (Table 3.3), indicating that more frequently occupied territories were those with larger expanses of ungrazed and sandy pastures and shorter expanses of rocky lands and scrubland. In the selected model the effects of TLH and TLH^2 were statistically reduced (Table 3.3). Occupancy was not significantly correlated with either breeding density or habitat PC1 (both $P > 0.11$).

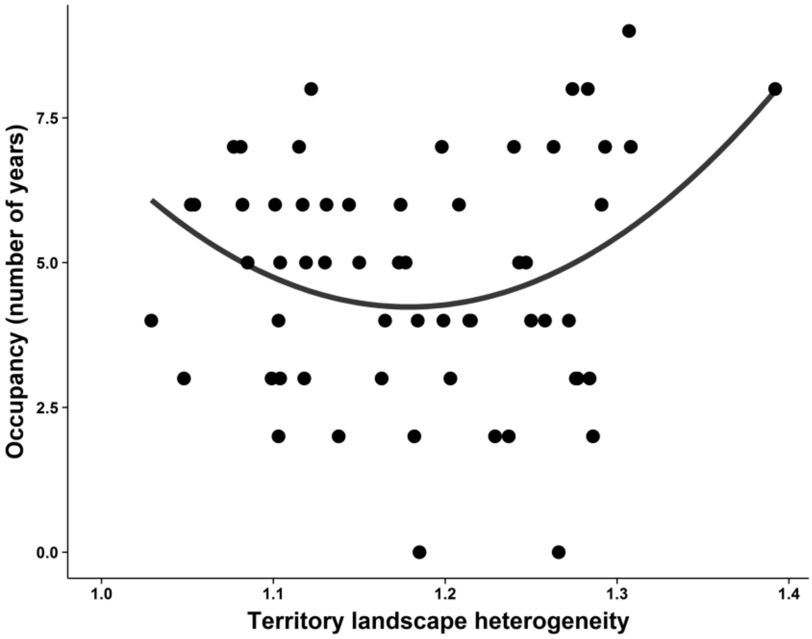

Figure 3.2. Quadratic relationship between nest box occupancy and territory landscape heterogeneity (Shannon-Wiener index of habitats) of common kestrels.

Table 3.3. Best general linear model (LM) of the occupancy of nests, as a measure of territory quality. Degrees of freedom = 56, n = 61, R^2 conditional = 0.20, estimates, standard errors (SE), *F* and *P* values are shown. (*AICc* for the initial model = 252.8, *AICc* for the second best model = 245.3, *AICc* for the best model = 242.9, *ΔAICc* =2.4).

Effect	**Estimate**	**SE**	***F***	***P***	**95 % CI**
TLH	-138.8575	80.52	2.97	0.090	(-300.096, 22.378)
TLH ^{2}	57.4116	33.97	2.86	0.097	(-10.609, 125.432)
Habitat PC 2	-0.0085	0.01	8.41	0.005	(-0.014, -0.003)

Diet, occupancy and landscape heterogeneity

As shown in Table 3.2, arthropods, mainly Orthoptera, were the most frequently consumed prey group by kestrels in the population, followed by mammals, reptiles, birds and amphibians. Within species, the mole cricket, field cricket, Spanish psammodromus *Psammodromus hispanicus*, common vole *Microtus arvalis*, ocellated lizard *Timon lepida* and Western three-toed skink *Chalcides striatus* were the six most preyed upon species (83% of prey items). Prey provisioning rate was 3.3 ± 2.1 prey items / h, ranging from 0.3 to 10.0.

The mean kestrel diet diversity for the 8-year period was 1.32 ± 0.38, ranging from 0.26 to 2.24 Shannon-Wiener index. The model selection procedure for diet diversity yielded two best models with similar *AICc* (Table 3.4). Both models showed that controlling for the effect of laying date, diet diversity was negatively correlated with TLH. The diversity of prey consumed was higher in territories with a lower diversity of habitats (Fig. 3.3). Occupancy and habitat PCs did not show statistical significant effects on diet diversity (Table 3.4).

Figure 3.3. Relationship between diet diversity (residuals) of common kestrels and territory landscape heterogeneity. Residuals were extracted by excluding territory landscape heterogeneity from the model.

Table 3.4. Best general linear mixed models (LMMs) of diet diversity in common kestrels (Shannon-Wiener index). Year and nest were included as random factors. Degrees of freedom = 108, *n* = 170, R^2 conditional = 0.31, estimates, standard errors (SE), *F* and *P* values are shown. (*AICc* for the initial model = 107.5, *AICc* for the second best model = 105.3, *AICc* for the first best model = 104.6, *ΔAICc* = 0.7).

Effect	Estimate	SE	*F*	*P*	95 % CI
1st best model					
Laying date	0.0142	0.00	35.25	< 0.001	(0.009, 0.019)
TLH	-0.7600	0.34	5.13	0.025	(-1.425, -0.095)
Habitat PC 2	-0.0402	0.03	1.79	0.183	(-0.099, 0.019)
2nd best model					
Laying date	0.0146	0.01	37.10	<0.001	(0.010, 0.019)
TLH	-0.8208	0.34	5.91	0.017	(-1.490, -0.151)
Occupancy	0.0185	0.02	1.49	0.224	(-0.012, 0.049)
Habitat PC 2	-0.0342	0.03	1.28	0.260	(-0.094, 0.026)

Discussion

Landscape heterogeneity promotes an increase in species diversity (LHH), and thus a higher diversity of habitats in kestrel territories should provide them with a greater diversity of prey in the diet. Diet diversity in this kestrel population has been observed to be positively correlated with indicators of individual quality, such as body condition and immunity of offspring and clutch size (Navarro-López *et al.* 2014, this study). Accordingly, if territory reflects individual quality, it is feasible to expect a positive correlation between habitat diversity and territory quality. Identifying territory quality of birds through occupancy has been successful for many species (Sergio & Newton 2003), although this relationship has not been as obvious for others (Germain & Arcese 2013; Zabala & Zuberogoitia 2014). In kestrels, those individuals showing earlier laying dates and larger clutch sizes are those of better quality (Aparicio 1998; Navarro-López *et al.* 2014). In addition, first occupied territories are those where individuals start breeding earlier and lay larger clutches. Furthermore, these territories were more frequently occupied than others (this study). Thus, without knowing particular territory characteristics providing quality, it is feasible to conclude that for some reason preferred territories are of better quality.

When the relationship between territory quality and territory landscape heterogeneity was analysed, the model showed that contrary to our linear prediction occupancy varied quadratically with territory landscape heterogeneity, with the most frequently occupied territories having the highest and lowest landscape heterogeneity. Since a higher heterogeneity of habitats in nest surroundings does not provide a higher diversity of food for kestrels (see below), selecting more heterogeneous territories may be advantageous for kestrels in regions with drastic spatio-temporal changes in food availability, such as the Mediterranean region (Penteriani *et al.* 2002; Tellería *et al.* 2008; Fargallo *et al.* 2009). This is due to the fact that more heterogeneous landscapes provide a wider range of alternative prey species that can benefit kestrels when changing environmental circumstances affect the abundance of the preferred prey (Penteriani *et al.* 2002). At the other extreme, high occupancy rate was also observed in the least diverse territories. This may be due to a preference of kestrels for ungrazed-sandy pastures and/or forest-dry pastures, as deduced from the correlation found between TLH and PCs. In fact, when the structure of the landscape (PCs) is included in the model, the quadratic effect of territory landscape heterogeneity is reduced and the model showed that kestrels selected territories with a higher expanse of ungrazed and sandy pastures avoiding areas with rocks and scrubs, as concluded by the correlation found between occupancy and PC2. We must also note that PCs describe the spatial structure of landscape where nest boxes were installed in our study area. Within this structure, those areas including sandy pastures are also the most distant areas from scrublands and rocky lands, which may also explain the PC2 gradient and the habitat selection of kestrels in our population.

Also contrary to our prediction, the diversity of prey consumed by kestrels was not positively, but negatively correlated with territory landscape heterogeneity. Several conclusions can be drawn from this result. Kestrels do not increase diet diversity by selecting more diverse landscape, but by actively searching for different prey species in less diverse territories. The second conclusion is that forest-dry pastures and sandy-ungrazed pastures (the main habitats represented in less diverse territories) provide the higher diversity of prey species for kestrels. Also, high landscape heterogeneity can result in patches not suitable for hunting. It should be noted that our study approach was based on a mechanistic view of individual specialisation with regard to habitat exploitation so that for each particular habitat, each particular individual is expected to search for one or several particular prey species. This approach, which allowed us to predict a more diverse diet in a more diverse landscape derived from the LHH, supposes a first step to investigate the relationship between trophic niche and habitat use. The same habitat can be occupied by different prey species and prey availability (difficulty of capture) can be different for different species occupying the same habitat type and also for the same species occupying different habitat types (Byholm *et al.* 2007; Torre *et al.* 2007; Martínez-Padilla & Fargallo 2008). In addition, the inter-annual fluctuation in the abundance of prey species also changes hunting behaviour of kestrels (Korpimäki & Norrdahl 1991; Fargallo *et al.* 2009; Navarro-López *et al.* 2014) and the interaction between habitat and prey availability. All these interactions should be investigated in future studies to account for the relationship found in this study between habitat heterogeneity of territories and kestrel diet.

In our kestrel population individuals adopting a more generalist strategy seem to be able to produce offspring with better body and immunological conditions, and hence with a higher fitness potential, as it was found for other bird species (Margalida *et al.* 2009; Margalida *et al.* 2012). Broadening the trophic niche may be an adaptive strategy in environments where the abundance and availability of food resources fluctuate with time, such as in Mediterranean regions. An interesting aspect to understanding foraging strategies is the nutritional and biomass value for the diet, as diets based on large and less mobile prey species might be more energetic in terms of biomass and hunting effort than a diverse diet based on small prey species. In a previous study carried out in our population (Navarro-López *et al.* 2014) a positive correlation between diet diversity and prey biomass was found, so that individuals consuming a greater variety of prey species also preyed on the larger and heavier prey species. Knowing the nutritional components of the different prey species will be key to understanding costs and benefits associated with foraging strategies.

Our results also showed that the diversity of the consumed prey species was not predicted by territory quality, as no correlation was found between diet diversity and occupancy. This suggests that other characteristics besides food availability are important in territory selection. Nest predation is a major selective force in the reproductive strategies of birds, since it is considered a primary source of nesting mortality (Martin 1992) and influences the choice of nest sites in small raptors including kestrels (Newton 1979). The design and location of the nest boxes in our study area were planned to minimize the risk of predation. Predation events by mammals in the first years (Fargallo *et al.* 2010) had been prevented since 1998 (some original nest box placements were avoided), and sporadic predation by eagle owls *Bubo bubo* occurred in some years during the study period. In our population, kestrels avoided nest boxes close to bush areas or forest fragments (pers. obs.) where the visibility of potential predators is low and the nest is more vulnerable to predation (Shrubb 1993). This selective pressure can also explain the correlation found between occupancy and PC2. In conclusion, our study shows that territory quality does not show a linear relationship with territory landscape heterogeneity, but a curvilinear correlation in which the most and the least diverse territories are occupied at higher rates. In addition, kestrels preferred territories with greater expanses of sandy and ungrazed pastures. Our study revealed that diet diversity in a bird species was associated with landscape characteristics. Contrary to predicted, birds may show higher diet diversity in landscapes with a lower diversity of habitats. In this mountainous Mediterranean pastureland two main habitat types, those combining sandy and ungrazed pastures and also those dry pastures close to forests islets provided the highest diversity in the kestrel diet indicating that kestrels actively search for a diversity of prey species as a foraging strategy. Furthermore, our results suggest that other territory characteristics in addition to food availability, such as possibly predation risk, play an important role in territory and nest-site selection for birds. Finally, this study provides further support to the idea that the frequency of nest occupation can be a good measurement of territory quality in birds (Sergio & Newton 2003) as concluded from its correlation with clutch size and laying date in our kestrel population.

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Appendix

Appendix 3.1. Habitats found in the study area and common kestrel territories. Percentages in the whole study area, their average around the used kestrel territories and their average around the high quality territories (occupied six or more years).

Habitat	Study area	Kestrel territories
Dry pasture	58.13	53.53
Oat pasture	22.12	27.78
Evergreen pasture	6.25	7.64
Sandy pasture	3.85	5.39
Broom scrubland	4.66	2.03
Ungrazed pasture	1.94	2.01
Forest	1.77	1.1
Rockyland	1.04	0.55

Capítulo IV

Foraging strategy in a raptor species: preference, profitability and nutritional composition of the prey

Juan Navarro-López, Rosa Nieto and Juan A. Fargallo

Abstract

Energy (expenditure and intake) and time spent on foraging activity have been the pillars for the optimal foraging theory since its inception. However, whereas the energy in prey has long been hypothesized as the main prey feature modulating foraging behaviour of predators, it has been currently shown that nutrients in the diet also influence their foraging decisions. The traditional view of carnivore predators, as compared to herbivores and omnivores, assumes that nutrient content is similar for different prey species guaranteeing nutritional balance relative to their requirements. In this chapter we investigated the optimal foraging under the central place scheme of a predator species, the common kestrel *Falco tinnunculus*, taking into account the nutritional composition and capturability of prey-species. We also assessed whether prey preference may account for prey profitability and/or nutritional composition. The result of this chapter revealed that prey load-size have a low explanatory power for large prey species and that prey capturability plays an essential role in describing foraging strategies. Regarding energetic and nutritional components of the diet, our results show that in our kestrel population prey selection was based on the energetic profitability of the prey species, but also on the protein content of the prey. Finally, we showed a high value of preference of kestrels for common voles that was not explained by any of the variables analysed.

Introduction

Optimal foraging theory focuses on determining the efficiency of individuals in obtaining food resources required for survival and reproduction (Pyke *et al.* 1977). Foraging is one of the most modelled behaviours in ecology research, current modelling including a wide array of variables ranging from predator and prey behaviour at the individual level to prey abundance or population dynamics at population level (Stephens *et al.* 2007). Still, energy (expenditure and intake) and time spent on foraging activity have been the pillars for the optimal foraging theory since its inception. Yet, many authors coincide in the need of devoting more effort to obtain empirical data in the wild, as some theoretical assumptions have been revealed to be erroneous when tested in the field, encouraging criticisms (Begon *et al.* 2006), and even harsh criticisms to the heuristic capacity of the theory (Pierce & Ollason 1987). For example, theoretical models have failed when applied to species feeding on mobile prey or when placing excessive emphasis on energy intake instead of nutritional composition (Sih & Christensen 2001; Kohl *et al.* 2015). This is particularly relevant in the case of carnivore predators, as they feed on mobile prey and it has been considered that nutritional balance is unnecessary for them (Kohl *et al.* 2015). The traditional view of carnivores, as compared to herbivores and omnivores, assumes that nutrient content is similar for different prey species guaranteeing nutritional balance relative to their requirements (Galef 1996; Kooijman *et al.* 2004) see Kohl and Christensen 2015, for a review). However, whereas the energy in prey has long been hypothesized as the main prey feature modulating foraging behaviour of predators (Whelan & Schmidt 2007) , it has been currently shown that nutrients in the diet also influence their foraging decisions (Mayntz *et al.* 2005; Mayntz *et al.* 2009; Hewson-Hughes *et al.* 2011; Schmidt *et al.* 2012; Jensen *et al.* 2014).

Within the optimal foraging theory, the central place scheme develops models for the common case of foragers that return to a fixed location between foraging trips to feed young, store food, or rest, and thus face spatial constraints on foraging (Orians & Pearson 1979). Like other behavioural models, these provisioning models emphasize how costs and benefits select for certain types of behaviour. Optimal foraging is achieved, on the one hand, by minimizing travel distance and time through selecting the foraging patches nearest to the nest and, on the other, selecting the most energy-efficient food, that is, the food with the greatest energy content per hunting time. Parent birds provisioning their offspring at the nest have been a typical study model used in the central place theory (Orians & Pearson 1979; Kacelnik & Houston 1984; Stephens *et al.* 2007). Including the classical aspects of food choice and patch exploitation, these models are focused on predicting optimal food loading in provisioning trips. The basic assumption is that foragers should choose a higher minimum prey size when prey are more abundant and when they must travel longer distances to capture it (Orians & Pearson 1979; Kacelnik & Houston 1984). Posterior refinements have been applied to better understand how theoretical prediction on food provisioning rates fit the empirical data. Time-energy is split into that expended in searching, food handling, shelf feeding, resting, etc. Thus, foraging time will depend on the individual efficiency in searching, accessing-capturing and handling food, which in turns depends on the individual inherited-learned foraging behaviour (Stephens *et al.* 2007). In the case of predators, foraging is the result of coevolutionary arms races between hunting adaptations of predators and anti-depredatory strategies of the prey-species (Woodland *et al.* 1980; Brodie III & Brodie Jr 1999). Predation risk is a major selective force, for which many ecological characteristics and morphological traits of species (including size) are derived from anti-depredatory strategies (Lima & Dill 1990; Abrams 2000; Dimitrova *et al.* 2009). However, although seemingly relevant, the potential capturability of the prey has rarely integrated in theoretical models or considered in field studies on foraging strategies (Abrams 1997).

Throughout a mechanistic view, optimal foraging theory has contributed to the understanding of how and why individuals, populations or species specialise on a given food type (trophic niche). It is thought that food specialism (low diet diversity) maximizes energy gain by feeding on the single most abundant and highest quality food item (Stephens & Krebs 1986). In the case of predators, such as raptors, it is considered that physiological, morphological and behavioural adaptations for specialism allow individuals more effective search images of the prey and higher capturing success that reduce foraging time and energy expenditure compare to generalists, high diet diversity; (Terraube *et al.* 2014). However, generalist strategies have also been observed to increase fitness components in some predator species (Margalida *et al.* 2009 ; Navarro-López *et al.* 2014). It is thought that generalist foraging is rewarded in more environmentally unstable conditions where food resources greatly fluctuate in time and space allowing to expand the niche and facilitating rapid change in the exploitation of variable and unpredictable resources (Estes *et al.* 2003; Quevedo *et al.* 2009; Navarro-López *et al.* 2014). In addition, a broad trophic niche may help to better balance nutrient requirements. This is particularly important for parents feeding their growing offspring, since the fast growth experiencing individuals during this period creates a high demand of nutrients relative to energy (Ricklefs *et al.* 1998).

A large amount of prey biomass (large size or high quantity) does not guarantee the presence of essential nutrients needed for an optimal growth or self-maintenance (Krebs & Avery 1984). Deficits in nutritional elements of the diet as such some amino acids, lipids or proteins have been observed to reduce body condition, growth rates and survival probability(Mayntz & Toft 2001; Metcalfe & Monaghan 2001; Kitaysky *et al.* 2006; Jensen *et al.* 2012). Recently it has been reported that individuals are able to regulate intake of multiple nutrients independently by choosing prey types to balance surpluses and deficits ((Raubenheimer & Simpson 2003; Mayntz *et al.* 2005; Raubenheimer *et al.* 2009; Kohl *et al.* 2015). A balanced nutrient composition may improve the expression of life-history traits, such as the immune function (Cotter *et al.* 2011), sexual display (Maklakov *et al.* 2008), body size and growth rate (Mayntz & Toft 2001; Simpson *et al.* 2004; Erlenbach *et al.* 2014), suggesting strong selection for a balanced nutrient composition of the diet. The balanced-diet hypothesis (Pulliam 1975; Lefcheck *et al.* 2013) posits that broadening trophic niche supplies a more complete range of nutrients, providing fitness benefits to the consumer (Lefcheck *et al.* 2013). Adaptive strategies for optimal or maximum growth should involve selectiveness of particular nutrients over others to provisioning nestlings, although it proximately depends on the difficulty of obtaining food of contrasting nutritional value and on the capacity of parents to procure it from their territories (Ricklefs *et al.* 1998; Dmitriew 2011; Blanco *et al.* 2014) .

In this study we examined the food provisioning to the nest of common kestrels *Falco tinnunculus* and estimated the average time that kestrels take to bring each prey species based on 12,779 provisioning recordings made during a 9-year study period. Moreover, we estimated prey abundance in the study area and in the diet and calculated indexes of prey capturability and prey preference for each species. Furthermore, we analysed energetic and nutritional composition of kestrel food by measuring calories, macronutrients (fat and proteins) and micronutrients (amino acids) in the 11 main prey species. We investigated whether the specific time a kestrel takes to provision with a given prey species was explained by its size, difficulty of capture or preference. We also assessed whether prey preference was accounted for prey profitability and/or nutritional composition. We finally tested the idea that a more selective foraging on preferred prey species promotes longer provisioning times.

Material and methods

The investigation was carried out in the region of Campo Azálvaro, located in central Spain. The study area is a treeless flat valley at 1,300 m above sea level mainly devoted to cattle raising (see Chapter III for habitat description). About 30–45 breeding pairs nest each year in 62 artificial nest boxes installed in the study area.

Prey provisioning time and prey weight

During the kestrel breeding seasons of 2006–2014 the prey items provided by parents to their chicks were recorded in 202 nests. Recording was continuous for 24 hours or more without researcher interruptions, although some nests were not filmed for the entire period due to technical problems. Recordings were made at age of 12-14 days of the chicks by placing a digital camera in the nest box (see Chapter II and III for technical details). Recordings were displayed in the free VLC Media Player software (www.videolan.org) to identify each delivered prey item. In addition, between-feeding intervals were also noted in order to estimate the "prey provisioning time" (PPT) defined as the mean time elapsed from the previous delivered prey item to the next one for the target prey species. A total 12,779 feeding intervals were recorded. Since activity of kestrels and prey species vary by time of the day, different time fractions show different prey provisioning activity (Appendix 4.1), for this reason we standardized PPT with respect the average in each hour fraction of the day. Also prey provisioning in a given nest shares environment and provisioner but environmental conditions differ among different years. To avoid pseudoreplication, PPT was obtained from a model in which standardized provisioning time was the dependent variable, prey species group was included as a fixed factor and nest and year as random factors.

Body mass of prey species was calculated as the mean body mass of the species captured in our study area or extracted from the literature when no data were available by us (Chapter II). In the case of the ocellated lizards *Timon lepidus*, prey remains found in the nests do not reach maximum sizes found in the lizard population of the study area (unpublished data), for which the weight was estimated on the basis of cranium length of the individuals found in kestrel nests as prey remains (n = 113). Cranium length explained 90% of the variance in body mass of the ocellated lizards trapped by us in the study area ($r = 0.95$, $F_{1,64} = 590.68$, $P < 0.001$, $n = 66$). Mean weight of lizards consumed by kestrels was then calculated by using the function: *weight = -79.55 + 4.81 * cranium length*, extracted from the linear regression (Table 4.1).

Nutritional composition

Protein (nitrogen), lipid content and amino acid composition were assessed in the main 11 prey species (Table 4.1) or prey groups that in total conforms 91% of kestrel diet (Chapter III, Appendix 4.2).

Table 4.1. Weight, water, protein, fat and calories for each prey species or group. Water was given as the percentage of weight lost after lyophilisation. Protein and fat contents were expressed as percentages of total nitrogen and fat in dry specimens. Calories per gram in dry specimens are also shown.

Prey species	Weight (g)	Water (%)	Protein (%)	Fat (%)	Calories/g
Microtus arvalis	31.3	72.3	21.4	2.0	1,435
Crocidura russula	8.1	65.9	26.0	4.0	1,826
Birds *(Alauda arvensis + Sturnus vulgaris)*	51.8*	64.1	25.6	4.3	1,931
Chalcides striatus	13.3	66.0	20.9	5.2	1,671
Timon lepidus	52.2**	70.0	23.6	2.6	1,519
Lacerta schreiberi	29.4	70.7	24.1	1.5	1,442
Psammodromus hispanicus	2.7	70.3	22.4	2.9	1,558
Pelophylax perezi	32.7	75.0	19.5	1.5	1,203
Gryllus campestris	1.2	73.8	19.3	1.9	1,452
Gryllotalpa grillotalpa	2.4	64.3	23.7	3.8	1,913
Acrididae-Tettigoniidae	1.2	71.1	21.5	2.3	1,611

(*) Weight of Eurasian skylarks + spotless starlings were calculated through the weighted arithmetic mean considering the occurrence of each species in kestrel diet.
(**) Ocellated lizard weight was estimated using the size of the lizards found in kestrel nests as prey remains (see text).

Nutritional values for the bird group come from spotless starlings *Sturnus unicolor* and Eurasian skylarks *Alauda arvensis* analysed together. These two species represent 77% of the bird species consumed by kestrels (Chapter III). Also, nutritional values for the *Acrididae-Tettigoniidae* group come from several different species of both Ortopthera families *Acrididae* and *Tettigoniidae*. For vertebrates we collected complete freshly hunted prey found in kestrel nests at the time we visited them. Removed prey items were replaced by commercial dead rooster chicks to compensate kestrels for food deprivation. Invertebrates (crickets, mole crickets, bush crickets and grasshoppers) are rarely found in kestrel nests, for which a permission was required to collect specimens in the field (see acknowledgements section). Collected prey items were -21 °C frozen, then stored lyophilized until they were analysed for nutritional components at the lab. Large feathers of birds (remiges and rectrices) were removed from corpses as kestrels do before eating. For nutritional analyses 9 grams of dry biomass were used in each prey species. Several specimens of the same species were homogenized together after removing water content by lyophilisation.

Total N was determined according to the Dumas' method, that is, combusting the sample at high temperature in an oxygen atmosphere. A TruSpec CN equipment (Leco Corporation, USA) was used. Gross energy (heat of combustion; calories / g) of prey species was measured in an isoperibol bomb calorimeter (Parr Instrument Co., Moline, IL). Fat content in prey items was obtained by saponification of the sample with 2N KOH in ethanolic solution.

The unsaponifiable fraction was extracted with petroleum ether (b. p. 40-60°) and evaporation of the solvent and drying were carried out at 103 ± 2 ºC to constant weight.

Amino acids were determined after protein hydrolysis in 6 M HCl plus 1% phenolin sealed, evacuated tubes at 110◦C for 24 h, by high performance liquid chromatography (Pico Tag method; Waters, Milford, MA; (Cohen *et al.* 1989)) as described by (Rivera-Ferre *et al.* 2006). Cysteine and methionine were determined as cysteic acid and methionine sulfone, respectively, obtained after oxidation with performic acid before 6 M HCl hydrolysis (Moore 1963). Tryptophan was not analysed.

Prey capturability

Potential capturability of prey species was calculated by assigning values to those different ecological features that difficult or facilitates prey capture by kestrels. Capturability indexes, like this we propose, are generally based on a human perception of the prey characteristics that difficult predation, in our case aerial predation. This makes the indexes to have an inevitable degree of subjectivity. For that reason, we used eight ecological features under the premise that the more features included the more objective will be the index. Three prey characteristics refer to the environment where the prey species live, two to prey availability and three to the behavioural anti-depredatory response. Three ecological characteristics (habitat protection, localization and abundance) were based on observations made in our particular study area. For all features they were assigned values between 1 and 3, 3 being the value expressing the highest difficulty of capture. Prey capturability was therefore defined as the sum of the eight values, higher values meaning a higher difficulty of capture (Table 4.2). The ecological characteristics were classified as follows:

A) Medium of displacement (1 = terrestrial, 2 = terrestrial-aquatic or terrestrial-aerial and 3 = mainly aerial).

B) Surface-underground way of life (1 = epigean, 2 = fossorial and 3 = subterranean).

C) Habitat protection in foraging areas (1 = exposed areas with short vegetation (mainly pastured lands), 2 = areas covered by vegetation and 3 = underground).

D) Abundance (1 = very abundant, 2 = abundant and 3 = little abundant). See Appendix 4.3.

E) Localization with respect to the kestrel breeding area (1 = present all around, 2 = local within the breeding area and 3 = local out of the breeding area). Breeding area was defined as the area where kestrel nest boxes were installed (23 km^2), considering a radius of 1000 m around the nest-box (see Navarro-López and Fargallo 2015).

F) Type of escape (1 = walking-running, 2 = jumping, 3 = flying).

G) Speed flight (1 = slow, 2 = fast and 3 = very fast).

H) Use of refuges (1 = not used, 2 = distant to the refuge and 3 = close to the refuge).

Table 4.2. Values given to each ecological prey characteristic to estimate the prey capturability index. A = medium of displacement, B = surface-subterranean way of life, C = habitat protection in foraging areas, D = abundance, E = localization, F = type of scape, G = speed flight and H = refuge using.

Prey species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**Capturability index**
Microtus arvalis	1	2	2	3	2	1	2	2	15
Crocidura russula	1	2	2	3	2	1	2	2	15
Alauda arvensis	3	1	1	3	1	3	3	1	16
Sturnus unicolor	3	1	1	3	2	3	3	1	17
Chalcides striatus	1	1	2	2	2	1	3	2	14
Timon lepidus	1	1	1	3	1	1	3	2	13
Lacerta schreiberi	1	1	2	3	3	1	3	2	16
Podarcis hispanica	1	1	1	2	2	1	2	3	13
Psammodromus hispanicus	1	1	1	2	2	1	2	2	12
Pelophylax perezi	2	1	2	3	2	2	2	3	17
Lycosa tarentula	1	3	3	1	1	1	1	3	14
Caterpillar	1	1	1	1	1	1	1	1	8
Gryllus campestris	1	2	1	1	1	1	1	3	11
Gryllotalpa gryllotalpa	1	3	3	1	1	1	1	3	14
Acrididae-Tettigoniidae	2	1	1	1	1	2	2	1	11
Coleoptera *	2	1	1	1	1	1	1	1	9

(*) Values given to the coleopteran Order are based on the main families and species observed as food in kestrel nests and recordings: *Scarabeidae* (*Scarabeinae*, *Cetoniinae* and *Melolonthinae*), *Carabidae* and *Cerambycidae*.

Prey preference and profitability

Prey preference was calculated relating the occurrence of different prey species in the diet to their abundance in the area. Since no data about the total abundance of coleopteran species was recorded, prey preference was not estimated for this species group. Thus, prey preference was calculated for a total of 15 prey species groups. Prey energetic profitability (calories / min) was calculated considering the number of calories per gram of dry weight, the proportion of dry weight with respect fresh weight and PPT in the way: energetic profitability = (dry weight * calories * proportion of dry weight)/PPT). Also, in order to know whether prey energetic profitability as a function of time depend on the difficulty to capture a prey species, we created what we called "prey foraging profitability" defined as the biomass provided by a given prey species (prey weight) in relation to the difficulty of capturing it and was calculated dividing prey weight by capturability index.

Statistical procedures

All data were analysed using linear models (LMs) in SAS 9.4 software (2002-2012 by SAS Institute Inc., Cary, NC, USA). Residuals from all LMs were checked for normality (Kolmogorov-Smirnov, $P > 0.2$ in all cases). When multiple regression models were done, Akaike's information criterion corrected for small sample size (*AICc*) was used to select the best model with possible combinations of independent variables. The best model was the one with the lowest *AICc* value with a difference >2 from the second best model. *Δ AICc* was also calculated. Contents of several amino acids were inter-correlated (see Appendix 4.4). The number of variables could not be reduced using a principal components analysis due to that the number of variables (17 amino acids) was higher than the sample size (n = 11 prey species groups) making the correlation matrix to be singular. For this reason, amino acid content in each prey species was analysed separately and Bonferroni correction for 17 tests (alpha value fixed at $P = 0.0029$) was used. Amino acid diversity was calculated through the Shannon-Wiener index.

Results

Prey provisioning time, prey size and capturability

Results of the LM showed that larger-heavier prey species and those showing higher values in the prey capturability index took significantly longer to deliver to the nest (Table 4.3). Prey size and prey capturability were intercorrelated, larger prey being more difficult to capture (LM, $r_s = 0.86$, $P < 0.001$), but the variance inflation factor for the model was adequate (Table 4.3). Analysing separately the relationship between PPT and both potential explanatory variables, it was found that the relationship between PPT and prey weight was better fitted to a decelerating exponential function (LM, $r = 0.93$, $F_{1,14} = 26.85$, $P < 0.001$, $n = 16$; Fig. 4.1 a), showing a lower *SE* (4.6) than the linear relationship (6.6). The PPT increase began to decline when prey weight exceeded around 10 g. The function curve also showed that kestrels reached a maximum threshold around 35 min to deliver a prey to the nest. Regarding PPT and prey capturability, the relationship was linear (LM, $r = 0.79$, $aR^2 = 0.59$, $F_{1,14} = 10.6$, $P < 0.001$, $n = 16$; Fig. 4.1 b).

Table 4.3. Results of the LM for prey provisioning time (PPT). Model: $r = 0.89$, $F_{2,13} = 24.23$ $P < 0.001$, $R^2 = 0.79$, tolerance 0.59 (VIF=1.7), $n = 16$.

Terms	*Estimate*	*S.E.*	*F*	*95% CI*	*P*
Prey weight	0.267	0.1	11.5	(0.09, 0.44)	0.005
Prey capturability	1.777	0.7	6.4	(0.25, 3.30)	0.025

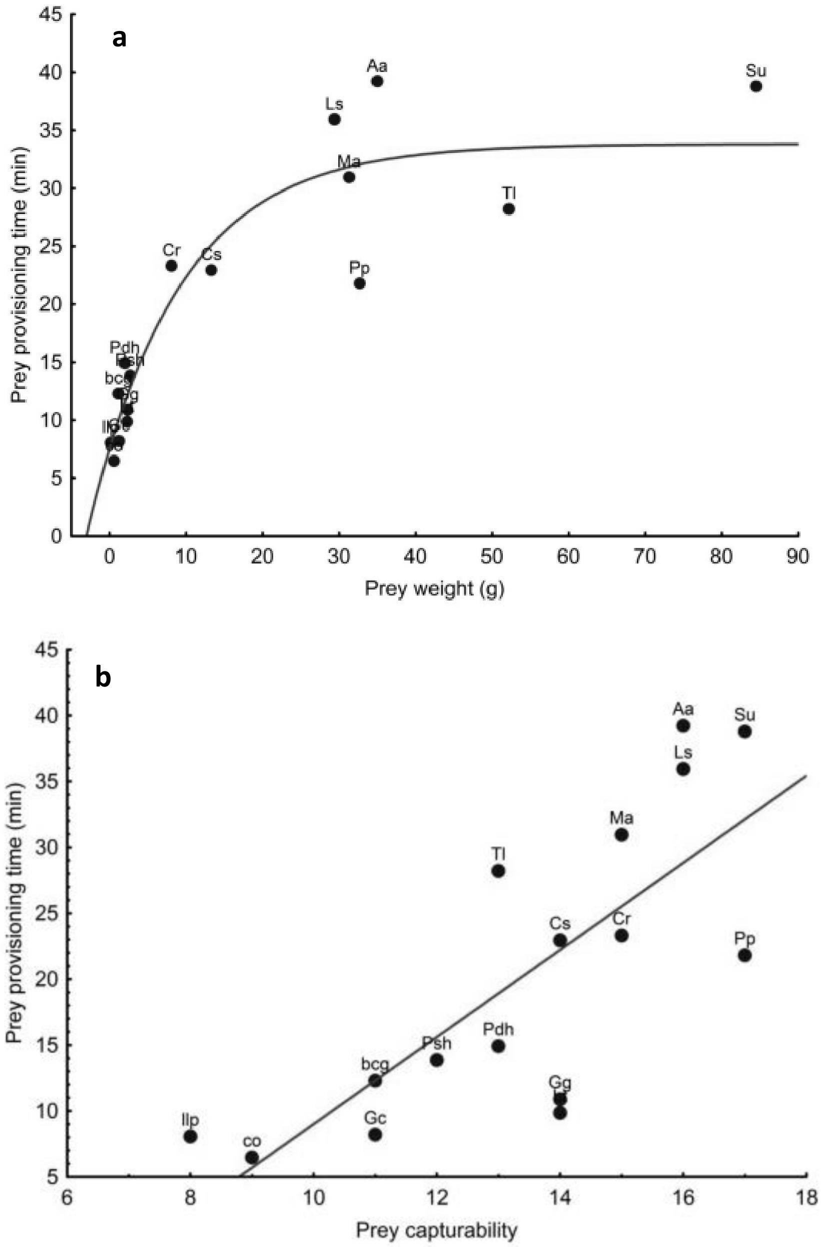

Figure 4.1 a) Decelerating exponential function describing the relationship between the mean time common kestrels take to provisioning each prey species and prey weight (PPT = 33.80 - 26.28/2^(weight/8.35)). b) Relationship between prey provisioning time and prey capturability **Aa** = *Alauda arvensis*, **bcg** = bush crickets-grasshoppers, **co** = coleopteran, **Cr** = *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc** = *Gryllus campestris*, **Gg** = *Gryllotalpa gryllotalpa*, **llp** = larvae of Lepidoptera, **Ls** = *Lacerta schreiberi*, **Lt** = *Lycosa tarentula*, **Ma** = *Microtus arvalis*, **Pdh** = *Podarcis hispanica*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon lepidus*, **Su** = *Sturnus unicolor*.

Nutritional components

The proportion of protein in prey species consumed by kestrels was on average 22.8 ± 2.3 % (range = 19.3 % – 26.0 %). The lowest values of protein content were found in field crickets *Gryllus campestris* and Perez's frogs *Pelophylax perezi* while the highest was for greater white-toothed shrews *Crocidura russula* and birds (Table 4.1). Mean fat content of kestrel prey species was 3.0 ± 1.3 % (range = 1.5 % - 5.2 %). The lowest fat content was found in Perez's frogs and Schreiber's lizards *Lacerta schreiberi* and the highest values were observed in three-toed skinks *Chalcides striatus*, birds and shrews (Table 4.1). In the case of calories, kestrel prey species have a mean value of 1,624.3 ± 234.7 cal/g (range 1,435 – 1,931 cal/g). Species providing fewest cal/g were voles, followed by Schreiber's lizards and field crickets while birds and mole crickets *G. gryllotalpa* were the most caloric (Table 4.1). Amino acid profiles for each prey species are shown in the Appendix 4.5. Aspartic and glutamic acids were the most abundant amino acids followed by arginine while cysteine and methionine were the less abundant. Alanine and tyrosine were particularly abundant in Orthopteran species. Gross energy was significantly and positively correlated with both fat and protein contents (Table 4.4). No significant correlation was found between protein and fat content ($r_s = 0.44$, $P = 0.154$, $n = 11$).

Table 4.4. Results of the LM for gross energy. Model: $r = 0.90$, $F_{2,8} = 16.5$, $P = 0.001$, $aR^2 = 0.76$, $n = 11$.

Terms	***Estimate***	***S.E.***	***F***	***95% CI***	***P***
Protein content	44.483	17.05	6.8	(0.05, 0.85)	0.035
Fat content	108.923	30.73	12.6	(0.21, 1.01)	0.008

Prey preference, nutritional composition and profitability

In decreasing order, common voles, spotless starlings, Eurasian skylarks, greater white-toothed shrews and ocellated lizards were the five most preferred prey species (Fig. 4.2). Preference for common voles was markedly higher than for the rest of prey species, in fact it became an outlier (*Grubbs test* = 2.76, $P = 0.025$). In order to better know the role of voles in the foraging strategy of kestrels, all tests were done with and without the value of preference for common voles and residuals from all models were checked for normality.

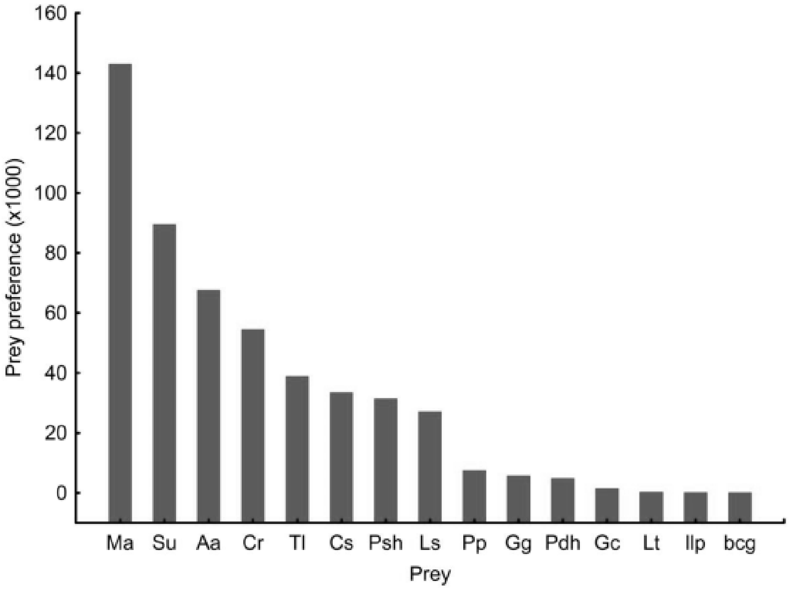

Figure 4.2. Prey preference estimated as prey occurrence in kestrel diet divided by prey abundance in the study area. **Aa** = *Alauda arvensis*, **bcg** = bush crickets-grasshoppers, **Cr** = *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc** = *Gryllus campestris*, **Gg** = *Gryllotalpa gryllotalpa*, **llp** = larvae of Lepidoptera, **Ls** = *Lacerta schreiberi*, **Lt** = *Lycosa tarentula*, **Ma** = *Microtus arvalis*, **Pdh** = *Podarcis hispanica*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon lepidus*, **Su** = *Sturnus unicolor*.

Including common voles and considering first the species for which we estimate prey preference (n = 15), results showed that prey preference was positively correlated with prey weight (LM, r = 0.60, aR^2 = 0.31, $F_{1,13}$ = 7.4, P = 0.017, n = 15; Fig. 4.3 a), but not with prey capturability (LM, P = 0.529). Also, combining both variables in the prey foraging profitability (weight / capturability), kestrel prey preference was positively correlated with prey foraging profitability (LM, r = 0.60, aR^2 = 0.31, $F_{1,13}$ = 7.2, P = 0.019, n = 15; Fig. 4.3 b), which explained a similar percentage of the variance than prey weight. Using the subsample for which nutritional components were measured (n = 11), prey preference was not correlated with any of the potential explanatory variables included in the model (prey weight, capturability, protein content, fat content; all P > 0.18). Gross energy and energetic profitability were excluded from the model, as these two variables showed high redundancy (gross energy: tolerance = 0.07, VIF = 14.3; energetic profitability: tolerance = 0.03, VIF = 33.3). To avoid multi-collinearity in the model, gross energy and energetic profitability were analysed separately. No significant correlation was found between prey preference and gross energy (LM, P = 0.831) or prey energetic profitability (LM, P = 0.201). There was also no significant correlation between prey preference and the amino acid content when fixing P value at 0.0029 after Bonferroni correction for 17 comparisons (LM, all P > 0.003) or amino acid diversity (P = 0.366).

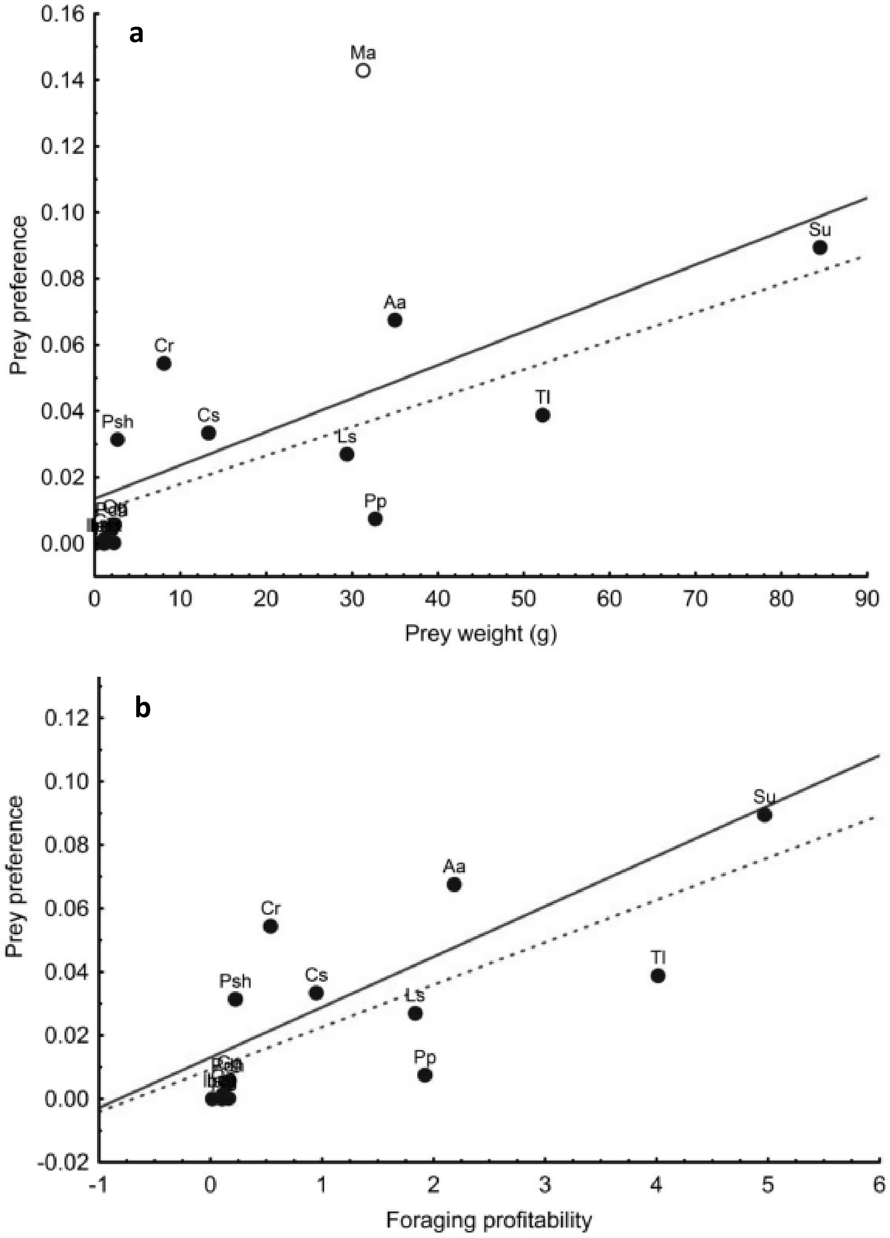

Figure 4.3. a) Relationship between prey preference and prey weight. Solid and dashed lines represent the linear function of the regression when common voles (open dot) were included and excluded, respectively**. b)** Relationship between prey preference and prey foraging profitability (prey weight / capturability index). Solid and dashed lines represent the linear function of the regression when common voles (open dot) were included and excluded, respectively. **Aa** = *Alauda arvensis*, **bcg** = bush crickets-grasshoppers, **Cr** = *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc** = *Gryllus campestris*, **Gg** = *Gryllotalpa gryllotalpa*, **llp** = larvae of Lepidoptera, **Ls** = *Lacerta schreiberi*, **Lt** = *Lycosa tarentula*, **Ma** = *Microtus arvalis*, **Pdh** = *Podarcis hispanica*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon lepidus*, **Su** = *Sturnus unicolor*.

Excluding common voles from the analyses and using the largest sample size, prey preference was similarly positively correlated with prey weight (LM, *r* = 0.76, aR^2 = 0.51, $F_{1,12}$ = 16.3, *P* = 0.002, *n* = 14; Fig. 4.2b), but not with prey capturability (LM, *P* = 0.475). Also prey preference was significantly and positively correlated with prey foraging profitability (*r* = 0.74, aR^2 = 0.51, $F_{1,13}$ = 14.3, *P* = 0.003, *n* = 15; Fig. 4.3), which also explained a similar percentage of the variance than prey weight. Using the subsample for nutrition, the best model (*AICc* = -34.0) was the one retaining only the variable protein content (LM, *r* = 0.74, aR^2 = 0.54, $F_{1,8}$ = 9.8, *P* = 0.014, *n* = 10; Fig. 4.4), the second best model included also prey weight as a not significant term (*P* = 0.155) but the fit of the model was lower (*AICc* = -21.8, $\Delta\, AICc$ = 12.2). Similarly, gross energy and energetic profitability showed low tolerance values in the model (gross energy: tolerance = 0.05, VIF = 20; energetic profitability: tolerance = 0.02, VIF = 50). To avoid potential collinearity in the model, gross energy and energetic profitability were analysed separately. No significant correlation was found between prey preference and gross energy (LM, *P* = 0.136), but in this case, prey preference was significantly and positively correlated with energetic profitability (LM, *r* = 0.69, aR^2 = 0.42, $F_{1,8}$ = 7.4, *P* = 0.026, *n* = 10; Fig. 4.5). In order to explore how protein content and energetic profitability interact to explain the variation in prey preference we included both variables in a new model as there was low redundancy between them (Tolerance = 0.78, VIF = 1.3). The model showed that prey preference was positively correlated with energetic profitability and only marginally with protein content (Table 4.5).

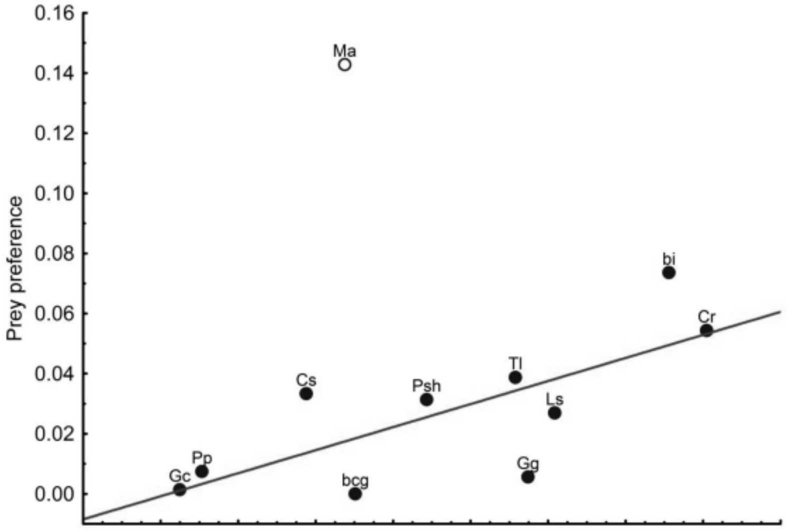

Figure 4.4. Relationship between prey preference and protein content. Line represents the linear function of the regression when common voles (open dot) were excluded from the analysis. Including common voles, the correlation was not statistically significant. **bcg** = bush cricketsgrasshoppers, **bi**=birds (skylarks + starlings), **Cr**= *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc**= *Gryllus campestris*, **Gg** = *Gryllotalpa gryllotalpa*, **Ls** = *Lacerta schreiberi*, **Ma** = *Microtus arvalis*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon Lepidus*

Table 4.5. Results of the LM for common kestrel prey preference. Model: r = 0.87, $F_{2,7}$ = 10.7, P = 0.007, aR^2 = 0.68, n = 16.

Terms	***Estimate***	***S.E.***	***F***	***95% CI***	***P***
Energetic profitability	0.0002	0.0	5.8	(-0.000, 0.010)	0.047
Protein content	1.0052	0.0	5.4	(0.000, 0.001)	0.052

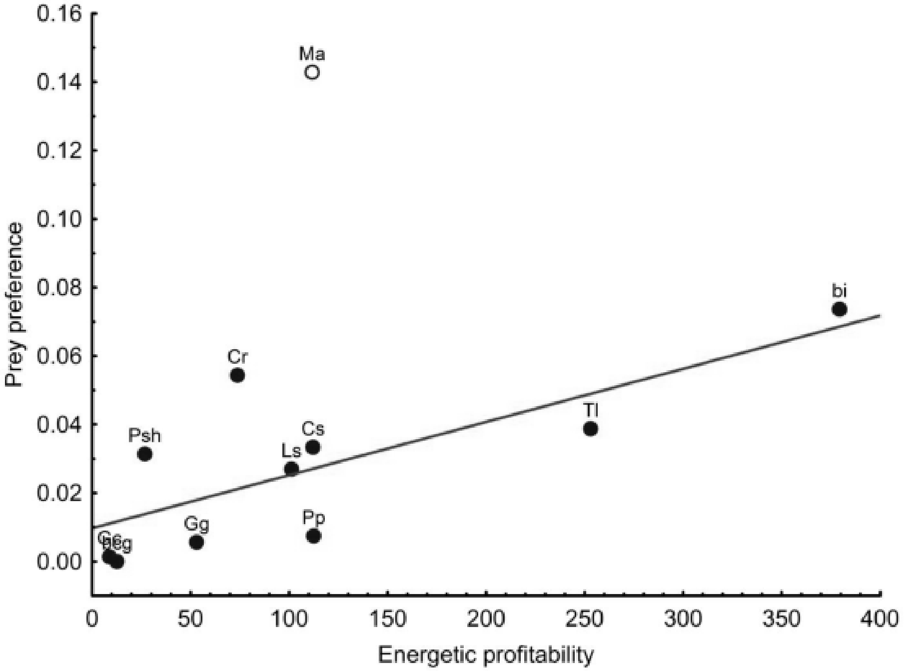

Figure 4.5. Relationship between prey preference and energetic profitability. Line represents the linear function of the regression when common voles (open dot) were excluded from the analysis. Including common voles, the correlation was not statistically significant. **bcg** = bush cricketsgrasshoppers, **bi**=birds (skylarks + starlings), **Cr**= *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc**= *Gryllus campestris*, **Gg** = *Gryllotalpa gryllotalpa*, **Ls** = *Lacerta schreiberi*, **Ma** = *Microtus arvalis*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon Lepidus*

There was also no significant correlation with amino acid content after Bonferroni correction for 17 comparisons (LM, all $P > 0.003$), or amino acid diversity (LM, $P = 0.092$).

Energetic and foraging profitability were closely correlated (LM, $r = 0.88$, $aR^2 = 0.74$, $F_{1,9} = 29.9$, $P < 0.001$, $n = 11$; Fig. 4.6).

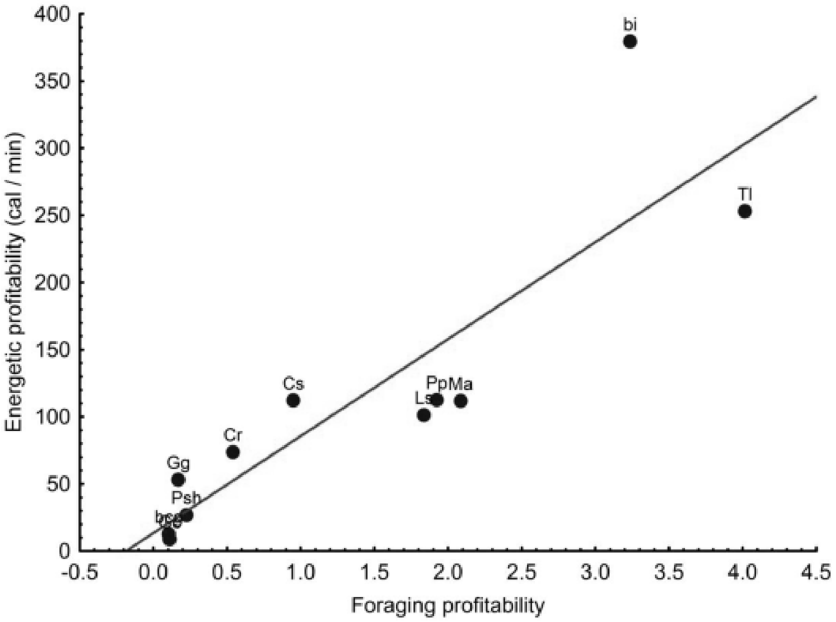

Figure 4.6. Relationship between prey energetic profitability and prey foraging profitability. **bcg** = bush crickets-grasshoppers, **bi** = birds (skylarks + starlings), **Cr** = *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc** = *Gryllus campestris*, **Gg** = *Gryllotalpa gryllotalpa*, **Ls** = *Lacerta schreiberi*, **Ma** =*Microtus arvalis*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon epidus*.

Prey provisioning time and prey preference

Finally, the relationship between PPT and prey preference was explored. Including common voles, PPT varied in an exponential decelerating way against prey preference (LM, r = 0.84, R^2 = 0.71, $F_{1,13}$ = 63.7, P < 0.001; Fig. 4.7). Data values were better fitter to the decelerating function (SE = 6.5) than to the linear function (SE = 8.0). Excluding common voles, the models also showed a significant positive correlation between PPT and prey preference (LM, r = 0.84 R^2 = 0.70 $F_{1,12}$ = 28.5, P < 0.001; Fig. 4.7). In this case, the linear function did not show a clearly better fit of the data on the base of the standard error of the regression (SE = 6.5) than an exponential decelerating function (SE = 6.4).

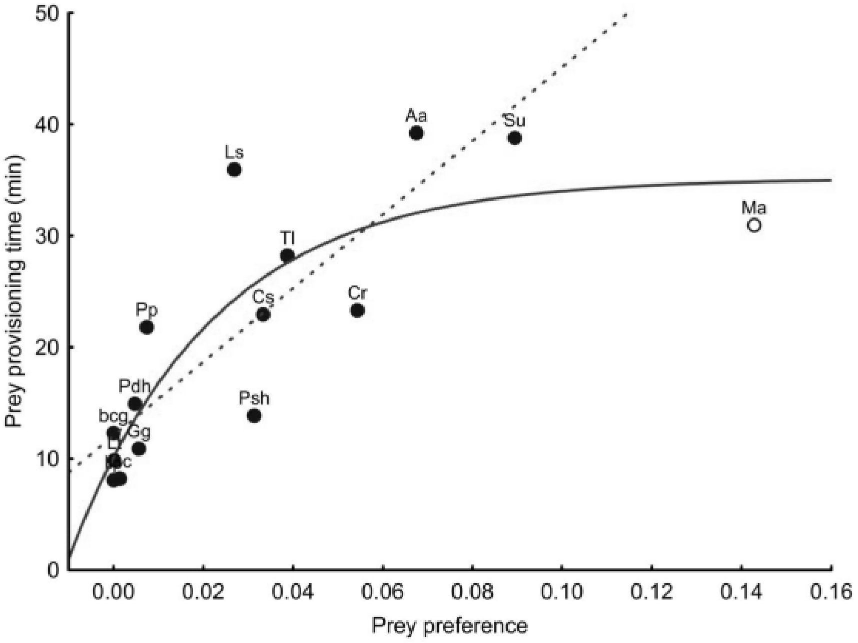

Figure 4.7. Relationship between prey provisioning time (PPT) and prey preference. Solid line represents the relationship when the value of prey preference for common voles (open dot) is included. In this case PPT was adjusted to an decelerating exponential function (PPT = 35.145 25.031/2^(prey preference/0.022)). Dashed line represents the linear relationship between PPT and prey preference when common voles were excluded. **Aa** = *Alauda arvensis*, **bcg** = bush crickets-grasshoppers, **co** = coleopteran, **Cr** = *Crocidura russula*, **Cs** = *Chalcides striatus*, **Gc** = *Gryllus campestris*, **Gg** =*Gryllotalpa gryllotalpa*, **llp** = larvae of Lepidoptera, **Ls** = *Lacerta schreiberi*, **Lt** = *Lycosa tarentula*, **Ma** = *Microtus arvalis*, **Pdh** = *Podarcis hispanica*, **Psh** = *Psammodromus hispanicus*, **Pp** = *Pelophylax perezi*, **Tl** = *Timon lepidus*, **Su** = *Sturnus unicolor*.

Discussion

Prey provisioning time

Time devoted by kestrels to provisioning the nest with a given prey depends on size (weight) and capturability of the prey species, both variables explaining a high percentage of the variance in PPT. Smaller prey took shorter times to be provisioned than larger prey. It is considered that low selectivity for prey also low feeding rate, thus shorting the between-feeding interval, while a more restrictive selection to find and capture preferred prey increases the time devoted to provisioning the nest with food (Stephens *et al.* 2007). This idea was supported by our results, as larger prey species were also the most preferred, and also, PPT was positively correlated with kestrel prey preference (discussed below). However, the relationship with prey weight was not directly proportional, but adjusted to an exponential decay (half-life increasing form) linear function. Prey weight showed a high explanatory power (steep slope) for species up to 13 g (arthropods and small lizards), while prey above 30 g had low capacity to explain the time devoted to provisioning the nest with a prey. This result might suggest in principle that among the prey sizes that kestrels can capture and bring, times longer than a certain threshold (around 35 min) make them no longer profitable. This can be expected from a central place scheme, since provisioning is predicted to be constrained by the time needed for self-feeding (Ydenberg 1994), for which it is reasonable that optimal provisioning eludes foraging events longer than the time-energy budget of individuals. Accordingly, it has been reported that common kestrels maximized daily energy gain during the chick-rearing phase within limits by adjusting hunting time below a predicted physiological maximum to guarantee the energetic balance (Masman *et al.* 1988; Masman *et al.* 1989). Our results indicate that the load-size effect for large prey does not explain itself provisioning time of a given species.

Prey size was also positively correlated with prey capturability. It is noteworthy that our prey capturability index included parameters, such as prey abundance or speed flight, that are expected to be lower and higher, respectively, for larger species. Furthermore, some large prey species in our study area, as common voles, spotless starlings, Perez's frogs and Schreiber's lizards, were highly localized. These ecological characteristics increase the difficulty for large prey to be captured. Complementary to the idea mentioned above, the positive correlation found between PPT and prey capturability allow us to suggest that the difficulty of capturing a prey is also involved in the average time that kestrel spent in provisioning the nest with a given prey species. Since prey capturability can vary among prey species of 30 g or more, our results suggest that prey capturability has a higher power to explain provisioning time in this range of prey weight as well.

The relationship between PPT and prey preference followed a decelerating exponential pattern. This was mainly due to the high preference value of kestrels for voles. When common voles were excluded from the analyses, the exponential curve did not clearly differ from a linear relationship. Our results suggest, that with the exception of voles (discussed below), prey preference help explain the differences found in PPT among different prey species and also why smaller prey species took shorter times to be provisioned.

Prey preference, prey profitability and the case of voles

The common kestrel has been traditionally considered a vole specialist species (Hanski *et al.* 2001), since voles are the main prey consumed in studied populations from northern and central latitudes of Europe (Korpimäki 1986; Masman *et al.* 1988; Village 1990). Studies in southern latitudes differ from this view and they reported a wide range of prey species present in the diet of kestrels (see (Navarro-López *et al.* 2014), Chapter II). Compared with the morphology of bird-eating falcons, the common kestrel shows a shorter wing length relative to the tail length and also shorter toes, which corresponds to phenotypes more specialized in capturing reptiles and mammals (Village 1990).

In our population, the common vole (the only vole species in the area that forages in ground surface and have also diurnal habits) is the fourth most consumed prey species representing 8% of occurrence in the diet, but the first one contributing to biomass (38%). This species also showed a markedly high prey preference value in our population, indicating that even when showing a great plasticity in prey consumption (Navarro-López *et al.* 2014), Chapter II), common kestrels selectively searches for voles when present in the area. This behaviour should be expected if predator-prey coevolution promoted morphological and physiological adaptations in kestrels to capture voles, providing this species the highest efficiency and energy reward. While our study certainly showed that kestrel prey preference was positively correlated with foraging and energetic profitability, the correlation was only true when voles were excluded from the model. The observed preference value for voles did not correspond with the expected foraging or energetic profitability.

On the contrary, bird prey species (starlings and skylarks) showed the highest energetic and foraging profitability indexes and also some of the highest prey preference values, which seems apparently contradictory. However, as in other kestrel populations (Korpimäki 1986), birds predated by kestrels during the breeding season in our study area were fledglings, being adult birds anecdotally found in kestrel nests as resulted from prey remain inspections made in our study area (pers. obs.). The naïve anti-depredatory behaviour of fledglings makes them a fruitful food resource for kestrels during its middle-end breeding season. This might explain the high values in foraging and energetic profitability and also in preference values for bird species, considering this result as derived for the opportunistic exploitation of a seasonal flourishing cheap food, the fledglings. After fledglings, reptiles and small mammals showed the highest values of profitability, as expected from kestrel phenotypes. Even so, our results do not explain so high preference of kestrels for voles. Two ideas might be behind this result. One is that the observed behaviour might be a maladaptation of kestrels in our population as a genetic burden loaded from more northern populations. A second possible explanation, is that kestrels might obtain important nutritional components from voles we did not measured in this study, since fat, protein and amino acid contents did not explain vole preference by kestrels.

Nutritional components

It is assumed that reproduction is the most energetically expensive life-history stage in terms of energy and nutrients (Martin 1987), being the chick-rearing phase the most energetically demanding period of the annual cycle (Bryant 1997; Williams 2012). Energy demands of the food provisioning during this period must be met from stored nutrient reserves or from daily food intake and, in addition, parents have to cope with the energy and nutrients demands of the chicks to grow adequately. Specifically, protein-rich food is considered a limiting factor for reaching the reproductive condition and also for somatic growth and development, for which food consumed during reproduction and that provided to developing nestlings generally has high animal protein content (Krapu 1981; Ricklefs *et al.* 1998; Blanco *et al.* 2014). Therefore, prey selection relative to protein content may determine the rate of intake and storage of parents and chicks. Accordingly, our results showed that kestrel prey preference at the chick-rearing stage was associated with the protein content of the prey species, although in the case of common voles, kestrel prey preference was higher than expected. Excluding voles, as discussed above, prey species containing more proteins were more preferred by kestrels to feed their chicks, although when the relationship was controlled for energetic profitability, the effect of protein content diminished, probably because protein content contributes in part to the gross energy

Prey capturability index

Many morphological, behavioural and ecological characteristics of species has evolved under the pressure of predation, affecting prey vulnerability and foraging strategies of predators (Endler 1991). Anti-depredatory prey traits influence both energy expenditure and time spent by predators in every step of the predation sequence (prey encounter, detection, pursuit, capture, handling and consumption), thus influencing foraging decisions at the individual level (Viitasalo *et al.* 1998; Chang & Hanazato 2003; Cresswell *et al.* 2010). Even knowing its relevance for our understanding of how animals optimize food acquisition, little effort has been made to measure the potential of capturability of the prey species in order to integrate this variable in optimal foraging models, particularly under the central place scheme. Our results evidence the explanatory capacity that an index of prey capturability has on the time devoted to provisioning the nest with a given prey species. The index we propose is an easy index to obtain by using eight scaled variables informing on ecological characteristics of each prey species-group, although three of them (habitat protection, localization and abundance) requires to have some experience in the study area. In addition, our results also show that the ratio of prey weight to the capturability index can be used as proxy of energetic profitability of prey species, facilitating the study of the individual strategies for foraging optimization.

From the perspective of the central place theory, our study explores the potential factors implied in the time required for a raptor to provision the nest with a given prey species, revealing that prey load-size (within the common range of weight-size that a raptor species can load) have a low explanatory power for large prey species and that prey capturability plays an essential role in describing foraging strategies linked to a central place system, highlighting the importance of considering capturability indexes to be included in optimal foraging models. In addition, our study gives support to the idea that selectiveness for preferred prey species increases the time devoted to provisioning them (Stephens *et al.* 2007). Regarding energetic and nutritional components of the diet, our study shows that prey selection is based on the energetic profitability of the prey species in terms of the amount of calories provided per time devoted to provisioning it, but also on the protein content of the prey. This was not the case for fat content, specific amino acid content or for amino acid diversity, concluding that prey selection for feeding offspring reflect foraging strategies aimed at achievement of certain nutrients, such as proteins, although controlling for the energetic effect of this nutrient, the explanatory power of protein content component decreases. At the same time, our study reveals the close association between energetic profitability and what we called foraging profitability considered this as the mass provided by a prey species in relation to the difficulty of obtaining it (capturability index). Finally, the high value of preference found in common kestrels for common voles was not explained by its energetic profitability, foraging profitability or its nutritional composition, which seems to be maladaptive for our kestrel population. This particular case deserves a deeper investigation for future studies in order to know the fitness components associated with vole consumption and more detailed analyses of other nutritional components not measured here.

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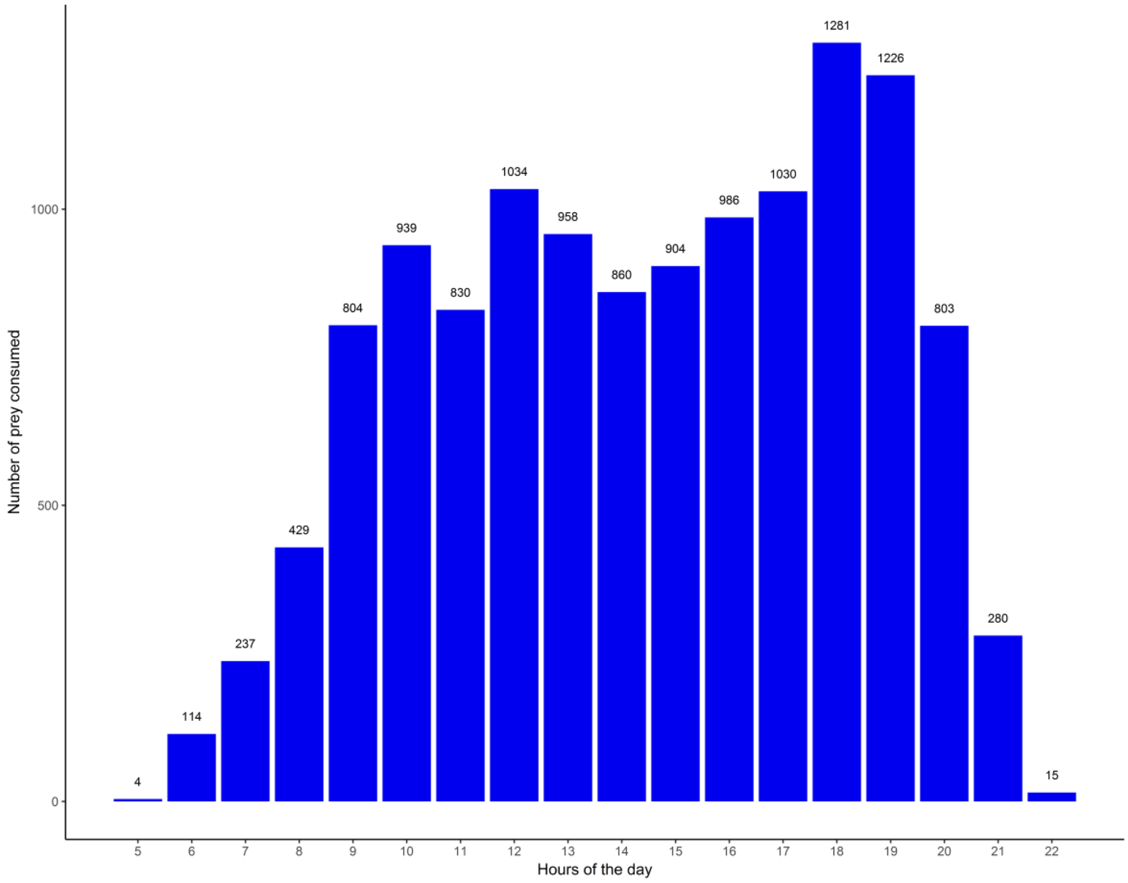
Appendix

Appendix 4.1. Prey provisioning activity in kestrel.



Appendix 4.2. Total numbers, percentage and biomass of prey items delivered by common kestrel *Falco tinnunculus* parents to the nest over an eight-year study period (2006-2014). The minimum identified taxon level is shown.

	N (%)	% biomass
Mammals	**1126 (8.8)**	**38.6**
Apodemus sylvatica	8 (0.1)	0.2
Crocidura russula	82 (0.6)	0.8
Microtus arvalis	1034 (8.1)	37.5
Talpa occidentalis	1 (0.0)	0.1
Mus musculus	1 (0.0)	0.0
Birds	**146 (1.1)**	**7.6**
Alauda arvensis	43 (0.3)	1.6
Anthus campestris	2 (0.0)	0.1
Emberiza calandra	1 (0.0)	0.1
Falco tinnunculus	1 (0.0)	0.1
Lanius senator	1 (0.0)	0.1
Linaria cannabina	4 (0.0)	0.1
Motacilla flava	5 (0.0)	0.1
Passer domesticus	5 (0.0)	0.2
Petronia petronia	5 (0.0)	0.1
Saxicola rubicola	1 (0.0)	0.0
Sturnus unicolor	22 (0.2)	2.1
Sylvia atricapilla	1 (0.0)	0.0
Passerines (unidentified)	10 (0.1)	0.6
No Passerines (unidentified)	45 (0.4)	2.5
Reptiles	**2965 (23.2)**	**34.4**
Chalcides striatus	397 (3.1)	6.3
Timon lepidus	399 (3.1)	18.3
Lacerta schreiberi	109 (0.9)	3.8
Podarcis hispanica / guadarramae	101 (0.8)	0.2
Psammodromus hispanicus	1948 (15.2)	5.5
Large Lizard [a]	6 (0.0)	0.3
Small lizard [b]	5 (0.0)	0.0
Amphibians	**44 (0.3)**	**1.6**
Triturus marmoratus	3 (0.0)	0.0
Pelophylax perezi	34 (0.3)	1.3
Pelobates cultripes	7 (0.1)	0.3
Arthropods	**8469 (66.3)**	**17.5**
Lycosa spp	47 (0.4)	0.1
Grillus campestris	2511 (19.6)	3.7
Acrididae	278 (2.2)	0.2
Tettigoniidae	450 (3.5)	0.8
G. gryllotalpa	4168 (32.6)	11.8
Orthoptera (unidentified)	5 (0.0)	0.0
Neuroptera	1 (0.0)	0.0
Mantodea	4 (0.0)	0.0
Lepidoptera	1 (0.0)	0.0
Coleoptera	760 (6.0)	0.6
Insecta (unidentified)	110 (0.9)	0.2
Insecta (*larvae*)	134 (1.0)	0.0
Unidentified prey item	29 (0.2)	0.2
Total prey items	12779	

Appendix 4.3.

Abundances were estimated as an approximate number of individuals in the whole study area (3,000 ha) using the following methodologies:

Abundances of field crickets *Gryllus campestris*, mole crickets *Gryllotalpa gryllotalpa* and wolf spiders *Lycosa tarantula* were estimated using direct counts of active borrows in 1,654 pastureland squares of 5 x 5 m between 2002 and 2015 (116 ± 20.4, range 78 – 176 squares each year). In the same squares the number of Spanish Psammodromus *Psammodromus hispanicus* individuals was also recorded. Results showed densities of 1.5 ± 2.5 individuals / 25 m^2 (range = 0 – 23) for field crickets, 0.6 ± 1.0 individuals / 25 m^2 (range = 0 – 9) for mole crickets, 0.2 ± 0.7 individuals / 25 m^2 (range = 0 – 6) for wolf spiders and 0.05 ± 0.2 individuals / 25 m^2 (range = 0 – 2). These species were present in all habitats found in the study area (Navarro-López and Fargallo 2015).

The abundance of lepidopteran larvae (caterpillars) was estimated during 2016 following the same method as above in 119 pastureland squares of 5 x 5 m randomly distributed in the study area. Larva density was 3.9 ± 11.2 individuals / 25 m^2(range = 0 – 70). Lepidopteran larvae are also present in all habitats of the study area.

The abundance of *Acrididae* and *Tettigoniidae* species was estimated by direct counts of bush crickets and grasshoppers captured using a 0.28 m diameter sweep net. Animals were captured by two parallel sweeps (one in the opposite direction of the other) describing two arcs of about 5 m each, for which the swept area was about 2.8 m^2. Each sweeping point was 10 strides apart. In total, 2309 points were swept in different pastureland habitats from 2002 to 2016 (mean = 154 ± 3.4 each year; range = 150 - 158). Results showed an average of 4.3 ± 6.8 individuals / 2.8 m^2, range = 0 – 72. *Acrididae* and *Tettigoniidae* species are present in all habitats of the study area.

For common voles *Microtus arvalis* and greater white-toothed shrews *Crocidura russula* abundance estimations were based on individual numbers recorded by trapping in the study area (see Fargallo et al. 2009) and following the capture-mark-recapture Schnabel index (Krebs 1999). Mean densities resulted in 107 voles/ha and 23 shrews/ha. Voles and shrews are rarely observed out of ungrazed pastures, this habitat representing 2% (60 ha) of all habitats present in the study area (Navarro-López and Fargallo 2015). Calculations were done considering only this habitat.

The abundance of three-toed skinks *Chalcides striatus* was calculated based on the data reported by Galán (2008), who found 188 skinks/ha on average in grasslands of NW Spain. Similar to voles and shrews, skinks are rarely observed out of ungrazed pastures, for which only this habitat was taken into account for estimations.

Wall lizards *Podarcis hispanica* were only present in rockyland, this habitat representing 1% (30 ha) of the study area (Navarro-López and Fargallo 2015). The abundance in this species was calculated by applying reported densities (102.5/0.15 ha) found in other similar areas (Diego-Rasilla and López-Mellado 2004).

The abundance of ocellated lizards *Timon lepidus* was estimated using the density of the species reported in other studies (3.2 individuals/ha; Díaz et al. 2006) and extrapolating it to the whole study area, as ocellated lizards were observed in all habitats present in the study area.

The abundance of Schreiber's green lizards *Lacerta schreiberi* was similarly estimated by using data from other studies in similar habitats (25 individuals/ha Delibes and Salvador 1986). In the case of Schreiber's green lizards, the abundance was calculated only in broom scrublands (5% of the area; Navarro-López and Fargallo 2015), as the species was only seen in this habitat.

To calculate the abundance of Perez's frogs *Pelophylax perezi*, old counts carried out in the study area in 1994 were used. The number of individuals was estimated trough indirect calculations of adult frogs observed in river ponds. These ponds are the only natural bodies of water present at the end of summer. Frogs were counted in nine randomly selected river ponds varying from 5 to 43 m long (mean = 16.7 ± 11.8 m) and estimated three times in August, September and October. Counts were done by using binoculars and from a distance that did not provoke escape responses to humans (Martín et al. 2006). A mean of 23.2 ± 16.8 (n = 9 x 3, range 0 - 70) frogs were counted in each pond (J.A. Fargallo, and E. Soto-Largo, unpublished data). Final calculation was done by multiplying mean number of frogs by 145 ponds present in 28.3 km of the Voltoya River in the study area.

Abundances of spotless starlings *Sturnus unicolor* and Eurasian skylarks *Alauda arvensis* were estimated by means of observation points along an 11-km road crossing the valley in a similar way as described by Martínez-Padilla and Fargallo (2008). Abundances found in these points were extrapolated to the rest of the study area where both species are present.

Category 1: very abundant prey species (more than 200,000 individuals in the study area)

Calculations resulted in ≈46 million individuals of **Acrididae-Tettigoniidae** (1.54 individuals / m^2 on average), ≈1.8 million **field crickets** (0.060 individuals / m^2 on average), ≈720,000 **mole crickets** (0.024 individuals / m^2 on average), ≈252,000 **wolf spiders** (0.0084 individuals / m^2 on average), ≈4.7 million **caterpillars** (0.156 individuals / m^2 on average). Abundances of **Coleoptera** species were not estimated in the field; however, they were also included within category "1" assuming that they were for sure more abundant than the less abundant species in this category (*Lycosa tarantula*).

Category 2: abundant prey species (between 200,000 and 10,000 individuals in the study area)

Calculations resulted in ≈60,000 **psammodromus lizard**, ≈20,500 **wall lizards**, ≈11,280 **three-toed skinks** in the study area.

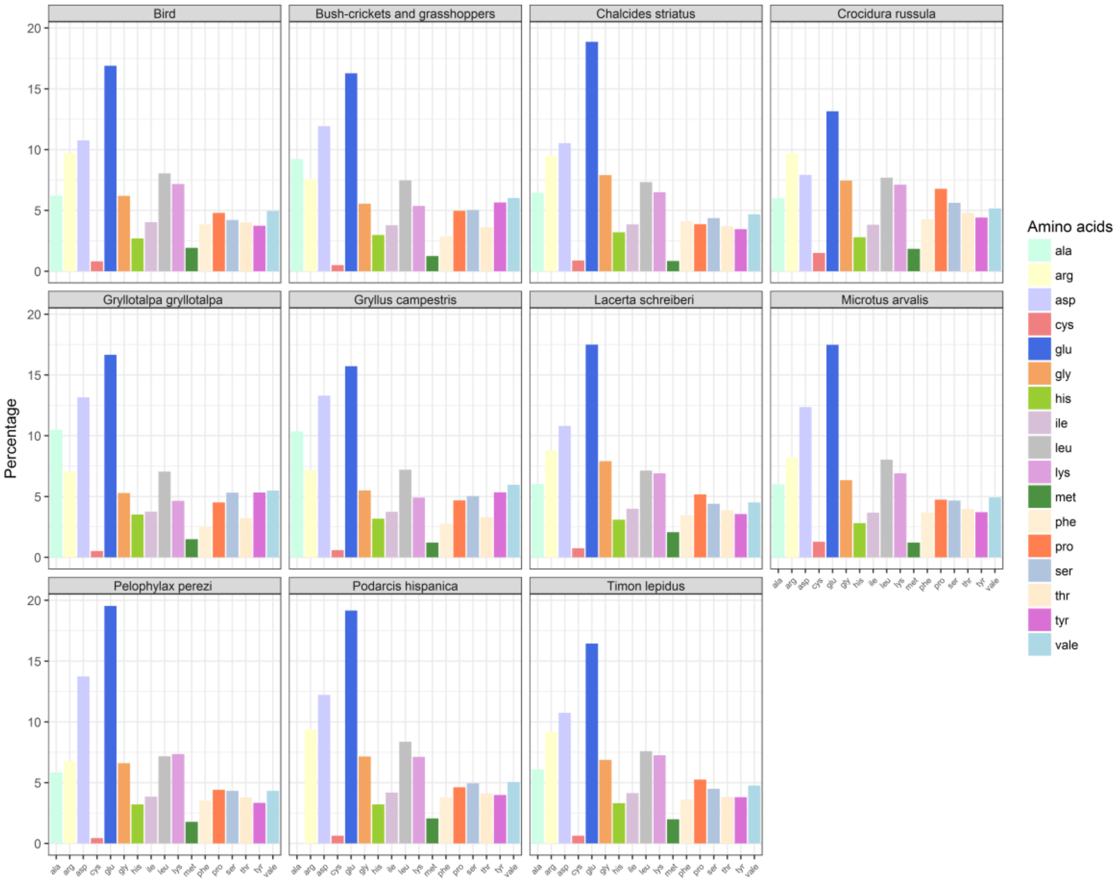
Category 3: little abundant prey species (less than 10,000 individuals in the study area)

Calculations resulted in ≈9,600 **ocellated lizards**, ≈6,420 **common voles**, ≈3,750 **Schreiber's green lizards**, ≈3,364 **Perez's frogs,** ≈1,380 **greater white-toothed shrews**, ≈637 **Eurasian skylarks** and ≈246 **spotless starlings**.

Appendix 4.4. Spearman Rank correlations among amino acid contents in 11 prey species groups. Black marked correlations reflect statistical significance at P < 0.05.

	ala	**arg**	**asp**	**cys**	**glu**	**gly**	**his**	**ile**	**leu**	**lys**	**met**	**phe**	**pro**	**ser**	**thr**	**tyr**	**val**
ala		-0.01	0.27	-0.18	-0.15	-0.32	0.34	0.26	0.02	-0.26	0.15	-0.31	0.41	**0.71**	0	**0.93**	**0.92**
arg			-0.36	**0.78**	0.38	**0.82**	0.51	**0.85**	**0.85**	**0.86**	**0.66**	**0.91**	**0.71**	0.45	**0.92**	0.082	0.16
asp				-0.39	0.33	-0.43	-0.02	-0.01	-0.1	-0.19	0.16	-0.45	0.02	0.14	-0.25	0.14	0.19
cys					0.18	**0.73**	0.2	0.48	**0.68**	**0.65**	0.28	**0.79**	0.48	0.28	**0.73**	-0.09	-0.04
glu						0.53	0.4	0.42	0.25	0.36	0.44	0.37	0.04	-0.05	0.28	-0.38	-0.29
gly							0.48	**0.61**	0.57	**0.76**	0.54	**0.89**	0.45	0.18	**0.77**	-0.29	-0.23
his								**0.79**	0.41	0.35	**0.63**	0.36	0.55	**0.61**	0.45	0.355	0.39
ile									**0.85**	**0.77**	**0.87**	**0.66**	**0.84**	**0.7**	**0.84**	0.35	0.44
leu										**0.89**	**0.76**	**0.72**	**0.78**	0.57	**0.92**	**0.75**	0.26
lys											**0.8**	**0.85**	**0.69**	0.31	**0.92**	-0.14	-0.05
met												0.49	**0.8**	0.55	**0.77**	0.19	0.27
phe													0.5	0.21	**0.82**	-0.21	-0.12
pro														**0.84**	**0.84**	0.56	**0.63**
ser															0.57	**0.82**	**0.86**
thr																0.14	0.22
tyr																	**0.99**

Appendix 4.5. Amino acid profiles for each prey species.



Capítulo V

Prey diversity and nutritional composition in the diet of a predator species: nutrient contents predict offspring body condition and immunocompetence

Juan Navarro-López, Rosa Nieto and Juan A. Fargallo.

Abstract

The optimal foraging theory predicts that individuals will select a trophic niche that maximizes energy gain in food acquisition to increase individual fitness. Specialization strategies minimize resource-use overlap among conspecifics, thus diminishing intraspecific and interspecific competition. Also thought that individual diet specialization by reducing trophic niche width maximizes energy gain by feeding on the single most abundant and highest quality food item. On the other hand, the balanced-diet hypothesis proposes that a broad trophic niche increases the likelihood of having a diet that is complementary in their nutritional composition, finding effects of nutrition on body condition, immunocompetence, growth rate and survival. In the present study we analysed nutritional composition (protein, fat and amino acid contents, amino acid diversity and calories provided) of main kestrel prey species and analysed the nutritional composition associated with diet diversity and biomass. We also explore whether there are certain nutrients associated with dietary diversity that influence offspring body condition and immunocompetence. Our results show that nutrients found in animal diets have a clear potential to explain the variation in life-history traits mediating fitness, such as body condition and immunocompetence of offspring. In addition, we found that more diverse diets also had more protein and fat contents, showed a higher diversity of amino acids and had different amino acid profiles than less diverse ones. Our results suggest that individuals feeding their offspring with a more diverse diet also benefited them by providing important nutrients for development.

Introduction

The trophic niche width, defined as the diversity of food items consumed and habitats used, is thought to play a key role in the life-history strategies of the species, determining patters of inter- and intra-specific competition and promoting speciation (Stearns 1992). The availability, abundance, quality and diversity of food, are considered major environmental pressures on which natural selection acts (Martínez-Padilla 2006). These food-related factors vary in time and space, for which foraging strategies are limited by individual energy expenditure (Stephens & Krebs 1986; Wilder *et al.* 2010; Giller & Greenberg 2015). The optimal foraging theory predicts that individuals will select a trophic niche that maximizes energy gain in food acquisition to increase individual fitness (Stephens & Krebs 1986).

Throughout a mechanistic view, optimal foraging theory has contributed to the understanding of how and why individuals, populations and species specialise on a given food type (trophic niche). One of the benefits suggested is that through specialization in a given trophic niche individuals minimize resource-use overlap among conspecifics, thus diminishing intraspecific (but also interspecific) competition. This is termed individual specialization (IS;(Bolnick 2001; Bolnick *et al.* 2003; Bolnick *et al.* 2010; Bolnick *et al.* 2011; Bolnick & Araujo 2011). IS is placed in a continuum from specialist to generalist strategies in a given population and may depend on the trophic level occupied by the species, being expected to be more frequently in predators, as they show a higher degree of intraspecific competition for resources (Estes *et al.* 2003; Svanback & Bolnick 2007; Quevedo *et al.* 2009; Araújo *et al.* 2011). It is also thought that individual diet specialization by reducing trophic niche width (specialism) maximizes energy gain by feeding on the single most abundant and highest quality food item (Stephens & Krebs 1986). In the case of predators, such as raptors, it is considered that physiological, morphological and behavioural adaptations for specialism allow individuals to reduce foraging time and energy expenditure due to their more effectively search and capture of the prey compared to individuals with a broader trophic niche (generalists; Terraube *et al*. 2011).

Fitness benefits for a generalist strategy have been documented across a wide range of taxa (Stearns 1992; Margalida *et al.* 2007; Margalida *et al.* 2009; Margalida *et al.* 2012; Navarro-López *et al.* 2014; Sonerud *et al.* 2014; Layman *et al.* 2015; Marques *et al.* 2015a; Snowberg *et al.* 2015; Svanback *et al.* 2015), including raptors species ((Margalida *et al.* 2009; Margalida *et al.* 2012), Chapter II). It is thought that generalist foraging is rewarded in more environmentally unstable conditions where food resources greatly fluctuate in time and space allowing to expand the niche and facilitating rapid change in the exploitation of variable and unpredictable resources (Estes *et al.* 2003; Quevedo *et al.* 2009). In addition, a broad trophic niche may help to better balance nutrient requirements. This is particularly important when parents are feeding their growing offspring, since the fast growth of nestlings during this period creates a high demand of nutrients relative to energy (Ricklefs *et al.* 1998).

The balanced-diet hypothesis (BDH) proposes that a broad trophic niche increases the likelihood of having a diet of food that is complementary in their nutritional composition (Mayntz & Toft 2001; Simpson *et al.* 2004; Mayntz *et al.* 2009). Thus, under the BDH it can be predicted that i) individuals should be sensitive to nutritional composition of food and ii) individuals showing a more generalist foraging strategy should have a higher fitness, if a higher complementarity of nutrients is adaptive (Lefcheck *et al.* 2013; Navarro-López *et al.* 2014). Both predictions have been evidenced (Mayntz & Toft 2001; Mayntz *et al.* 2005; Raubenheimer *et al.* 2007; Jensen *et al.* 2012; Marques *et al.* 2015b), although the effect seems to be clearer in herbivores compared to species of higher trophic levels (Lefcheck *et al.* 2013). While the consequences of the nutritional composition of food have been mainly studied in herbivores, recently authors have begun to study predatory species (Wilder *et al.* 2010), finding effects of nutrition on body condition, immunocompetence, growth rate and survival (Mayntz & Toft 2001; Metcalfe & Monaghan 2001; Kitaysky *et al.* 2006; Jensen *et al.* 2012).

In territorial species where the quality of breeding foraging areas depends on the quality of individuals, individual diet quality should predict breeding success and offspring quality. Nutritional conditions experienced during development determine body condition and health status of the offspring that in turn have strong influence on adult phenotypes, return rates, survival, longevity and reproduction (Metcalfe & Monaghan 2001; López-Rull *et al.* 2011; Saino *et al.* 2012). Furthermore, both the amount of food and the diet composition, are major factors affecting immunity of individuals at early stages of life (Chandra 1997; Fargallo *et al.* 2009; Triggs & Knell 2012; Navarro-López *et al.* 2014).

The relationship between the diversity of prey consumed and the condition-immunocompetence of offspring has been recently investigated in a generalist predator, the common kestrel *Falco tinnunculus*, reporting that high-quality parents provide their chicks with a higher diversity of prey species and that a higher diet diversity produced chicks in better body condition and with higher T-cell immune response (Navarro-López *et al.* 2014). Moreover, a broader trophic niche in this population is not associated with habitat heterogeneity around to the nest, suggesting that a generalist diet was actively searched by common kestrels (Chapter III). In the present study we analysed nutritional composition (protein, fat and amino acid contents, amino acid diversity and calories provided) of main kestrel prey species and analysed the nutritional composition associated with diet diversity and biomass. We explored whether there are certain nutrients associated with dietary diversity that influence offspring body condition and immunocompetence. If BDH is feasible for raptors, we predict that a more diverse diet should provide a better composition of nutrients that improve the body condition and immune response of the offspring.

Material and methods

The investigation was carried out in the region of Campo Azálvaro, located in central Spain. The study area is a treeless flat valley at 1,300 m above sea level mainly devoted to cattle raising (see Chapter III for habitat description). About 30–45 breeding pairs nest each year in 62 artificial nest boxes installed in the study area since 1994.

Kestrel diet

From 2006 to 2014, the prey items provided by parents to their chicks were recorded in 189 nests (13 in 2006, 17 in 2007, 26 in 2008, 25 in 2009, 14 in 2010, 25 in 2011, 20 in 2012, 22 in 2013 and 27 in 2014). When chicks were 12-14 days old, a digital camera was placed at the nest to record prey delivered by adults when feeding the chicks (for recording procedures see Chapter II). Recordings were displayed in the free VLC Media Player software (www.videolan.org) to identify each delivered prey item.

Diet diversity and biomass consumed

The diversity of prey delivered by parents was calculated through the Shannon-Wiener index (SWI) of each nest using the VEGAN package of R (Oksanen *et al.* 2013). The lowest taxonomic rank was determined in each prey item (Bolnick *et al.* 2002). Almost all amphibian, reptile, bird and mammal prey items were determined at a species level (99% of cases; see Chapter III) Among invertebrate prey items, field crickets *Gryllus campestris* and mole crickets *Gryllotalpa gryllotalpa* (*Insecta, Orthoptera*) and Mediterranean tarantula *Lycosa tarentula* (*Arachnida*) were easily identifiable in the recordings. The rest of arthropods were identified at the minimum possible taxonomic rank (order and family). To calculate SWI, species level was used for amphibians, reptiles, mammals, birds, spiders, crickets and mole crickets, family for grasshopper, bush crickets and mantises and order for beetles, butterfly and moth larvae. Diversity is expected to vary with the sampling effort (Begon *et al.* 2006). In our case, diversity of diet was not associated with the filming time (LMM, $R^2c = 0.24$, $F_{1.45} = 0.58$, $P = 0.45$) for the recording range we worked with (6-28 h).

The biomass consumed by chicks in a nest during the filming period was estimated as the sum of all body masses of the delivered prey species (Fargallo *et al.* 2003; Navarro-López *et al.* 2014). Body mass for each prey species was calculated as the mean body mass of the species (see Chapter II for more details). In some cases we had data on the body mass of the prey species captured in our study area and in other cases the data were obtained from the scientific literature (see Chapter II for more details).When a partial prey was delivered (only large lizards, birds and voles), the animal portion was visually estimated using the following estimation: 3/4 prey without head, 2/4 prey without head and without superior extremities, 1/4 prey only with tail and inferior extremities. Biomass in these prey items was calculated by multiplying the mean body mass by each fraction in each case. When the prey item could not be identified as belonging to a given taxon (5 out of 9538 prey items), biomass consumed was calculated as the weighted mean of a prey item considering the proportion of each taxonomic group consumed in the given nest. Since not all nests could be filmed during the same period of time, the mean biomass consumed (biomass hereinafter) was calculated as total biomass of prey items / filming time in order to make possible between-nest comparisons.

Parent quality

As indicators of parental quality we used body condition of both male and female parents (see below) and breeding parameters, such us clutch size and laying date. Experimental studies have found that the extent of male energy expenditure, hunting effort and prey delivery during the chick-rearing period is initially set for clutch size (Masman *et al.* 1989; Wiehn & Korpimäki 1997; Fargallo *et al.* 2002). Furthermore, clutch size has been found to be positively correlated with male bright colouration (Palokangas *et al.* 1992) and male quality during courtship (Vergara *et al.* 2007; Vergara & Fargallo 2008) and negatively with male parasite infection (Korpimäki *et al.* 1995). In addition, parents breeding early in the season also produce chicks that survive better (Cavé 1968; Village 1990). For these reasons clutch size and laying date are considered as reliable indicators of male quality in this species.

Body measurements and immunity of fledglings

Twenty-six days after hatching; nestlings were weighted with a spring balance (± 2 g) and wing length was measured with a metallic rule (± 1 mm). During 2006 to 2009 the immune response of the chicks was measured using the common assay of intradermal injection in the wing web of the T-cell mitogen phytohemagglutinin-P (PHA). 0.3 mg of phytohemagglutinin-P dissolved in 0.1 ml of phosphate-buffered saline was injected in each assay. Twenty-four hours later the inflammatory reaction to the mitogen was measured (see Fargallo *et al.* 2002 for details and repeatability). The mean differences of the measures before and 24 hours after the injection were used as an estimate of the PHA-immune response (Fargallo *et al.* 2002). The immunological test was always measured in the morning to avoid daytime effects (Martínez-Padilla 2006).

Nutritional composition

Protein (nitrogen), lipid content and amino acid composition were assessed in the main 11 prey species (Chapter III) or prey groups that in total conform the 91% of kestrel diet (Navarro-López and Fargallo 2015; Chapter III). Nutritional values for the bird group come from spotless starlings *Sturnus unicolor* and Eurasian skylarks *Alauda arvensis* analysed together. These two species represent 77% of the bird species consumed by kestrels (Navarro-López and Fargallo 2015; Chapter III). Also, nutritional values for the *Acrididae-Tettigoniidae* group come from several different species of both Ortopthera families *Acrididae* and *Tettigoniidae*. For vertebrates we collected complete freshly hunted prey found in kestrel nests at the time we visited them. Removed prey items were replaced by commercial dead rooster chicks to compensate kestrels for food deprivation. Invertebrates (crickets, mole crickets, bush crickets and grasshoppers) are rarely found in kestrel nests, for which a specific permission was required to collect specimens in the field (see acknowledgements section). Collected prey items were -21 °C frozen, then stored lyophilized until they were analysed for nutritional components at the lab. Large feathers of birds (remiges and rectrices) were removed from corpses as kestrels do before eating. For nutritional analyses 9 grams were used in each prey species. Several specimens of the same species were homogenized together after removing water content by lyophilisation. Analyses for the determination of protein, fat, water, calories and amino acid contents in each prey species are described in Chapter IV. We calculated the percentage of proteins and fat for each diet, defined as the percentage of grams of proteins and fat consumed with respect to the total grams consumed by each nest.

Statistical procedures

All data were standardized for each year (mean of 0 and standard deviation of 1) to aid direct comparisons in diet and nutritional variables. Biomass and diet diversity were analysed using general linear mixed models (LMMs) in which body condition of parents, laying date and clutch size were used as explanatory independent variables and nest was included in the model as a random factor. In the case of diet diversity, biomass was also included as an independent variable. Sample size for these analyses was n = 157, which matches with the number of males captured over the 9-year study period. Body condition of parents was calculated as the scaled mass index (SMI) following Peig and Green (2009). SMI adjusts the mass of all individuals to the mass they would have if they had the same body size, using the equation of the linear regression of log10 body mass on log10 wing length, estimated by type-2 (standardized major axis; SMA) regression (Peig & Green 2009). SMI was calculated for males and females separately.

In order to reduce nutritional variables, calories *per* gram, protein and fat contents in the diet were combined in a principal component analysis (PCA) to reduce the number of variables. PCA of nutritional components resulted in only one component (nutritional PC1) grouping the three variables and explaining 80 % of the variance (Appendix 5.1). Nutritional PC1 combined direct increasing gradients of calories *per* gram, protein and fat contents. Same as nutritional variables, data on the content of the 17 different amino acids measured were also combined in a PCA. Amino acid PCA resulted in three axes (Appendix 5.2). PC1 explained 38% of the variance and combined direct increasing gradients of arginine, glutamic acid, glycine, leucine, lysine, phenylalanine, proline and threonine. PC2 explained 30 % of the variance and combined direct increasing gradients of alanine, aspartic acid, serine, tyrosine and valine. PC3 explained 23 % of the variance and combined direct increasing gradients of histidine, isoleucine and methionine and an inverse increasing gradient of cysteine (Appendix 5.2).

Nutritional PC1 as dependent variable was analysed using a LMM, in which diet diversity and biomass, laying date and clutch size were included as explanatory independent variables and nest as a random factor. Amino acid diversity, amino acid PC1, PC2 and PC3 as dependent variables were analysed using LMMs in which diet diversity and biomass were included as explanatory independent variables. Since amino acids are provided by proteins, the proportion of protein content in the diet was included in these analyses as a covariate. Nest was included as a random factor in all models. Since the number nutritional dependent variables was high (five) Bonferroni correction for multiple tests was applied.

Fledgling body condition (body mass controlled by wing length) and PHA-immune response as dependent variables were analysed in two separated LMMs in which diet diversity, amino acid diversity, amino acid PC1, PC2, PC3, biomass, calories, protein content, fat content, laying date and clutch size were included as explanatory independent variables, sex as a fixed factor and nest and female (mother) identity as random factors.

In all statistical models, we followed a backwards-stepwise selection procedure, in which all terms were initially included. Terms showing $P > 0.10$ were removed sequentially. Variance inflation factors (VIFs) of each variable were checked in initial models. Residuals from all models were checked for normality. Parameters were estimated using maximum likelihood in all models. Means values ± SDs are given in the text. Statistical analyses were performed with SAS (1999) software 9.4 TS (2002-2012, SAS Institute, Cary, NC).

Results

Biomass, diet diversity and parent quality

Biomass was positively correlated with clutch size (Table 5.1). No significant correlations were found between biomass and either male condition, female condition or laying date (LMM, all $P > 0.16$). Parents having larger clutch sizes also contributed higher biomass. Diet diversity was significantly and positively correlated with clutch size, laying date and biomass (Table 5.1). No significant correlations were found for either male or female condition (both $P > 0.14$). Diets showed higher prey diversity at the end of the breeding season, in nests with larger clutch sizes and when the biomass provided was higher.

Table 5.1. Results of LMMs for biomass and diet diversity.

Dep. variables	Terms	*Estimate*	*S.E.*	*F*	*D.f.*	*95% CI*	*P*
Biomass							
	Clutch size	0.269	0.08	12.7	106	(0.12, 0.42)	<0.001
Diet diversity							
	Clutch size	0.203	0.08	6.6	104	(0.05, 0.36)	0.012
	Laying date	0.401	0.08	25.9	104	(0.25, 0.56)	<0.001
	Biomass	0.199	0.08	6.8	104	(0.05, 0.35)	0.011

Nutritional components and diet diversity

Results of the LMM showed that nutritional PC1 was negatively correlated with diet diversity (Table 5.2), but not with biomass (LMM, $P = 0.191$), that is, diets showed more protein and fat contents and were more caloric in broods fed with lower prey diversity (Fig. 5.1). Controlling for protein content, LMM for amino acid diversity of the diet was significantly and positively correlated with diet diversity (Table 5.2) and marginally, but not significantly so with biomass (Table 5.2). More diverse diets also had a higher diversity of amino acids (Fig 5.2). Controlling for protein content, amino acid PC1 was significantly and positively correlated with both diet diversity and biomass (Table 5.2). More diverse diets and with higher biomass also have higher amounts of the amino acids arg, glu, gly, leu, lys, phe, pro and thr. Controlling for protein content, amino acid PC2 was significantly and negatively correlated diet diversity (Table 5.2). No significant correlation was found for biomass (LMM, $P = 0.151$). More diverse diets had lower contents of ala, asp, ser, tyr and val. Controlling for protein content, amino acid PC3 was significantly and positively correlated with diet diversity and negatively with biomass (Table 5.2), although the effect of biomass was not considered significant after Bonferroni correction. Diets more diverse also had higher amino acid contents of his, ile, met and lower of cys.

Table 5.2. Results of the LMM for nutritional PC1 (principal component combining calories, protein and fat contents), amino acid (AA) diversity, amino acid PC1 (principal component combining arg, glu, gly, leu, lys, phe, pro and thr), PC2 (principal component combining ala, asp, ser, tyr and val) and PC3 (principal component combining his, ile, met and cys). Variance inflation factors for variables in the models were adequate (highest VIF = 1.1), *n* = 189. Asterisks represent statistically significant *P* values after Bonferroni correction for 12 tests (alpha value fixed at *P* = 0.0042).

Dep. Variable	**Terms**	***Estimate***	***S.E.***	***F***	***D.f.***	***95% CI***	***P***
Nutritional PC1							
	Diet diversity	-0.343	0.07	24.1	133	(-0.48, -0.21)	<0.001*
AA diversity							
	Diet diversity	0.367	0.06	37.5	131	(0.25, 0.49)	<0.001*
	Biomass	0.098	0.06	2.8	131	(-0.02, 0.21)	0.096
	Protein	0.571	0.06	93.1	131	(0.45, 0.69)	<0.001*
AA PC1							
	Diet diversity	0.211	0.06	15.6	131	(0.10, 0.32)	<0.001*
	Biomass	0.165	0.05	9.6	131	(0.06, 0.27)	0.002*
	Protein	0.676	0.05	154.9	131	(0.57, 0.78)	<0.001*
AA PC2							
	Diet diversity	-0.402	0.05	58.9	132	(-0.50, -0.30)	<0.001*
	Protein	0.501	0.05	91.5	132	(0.40, 0.61)	<0.001*
AA PC3							
	Diet diversity	0.281	0.06	21.7	131	(0.16, 0.40)	<0.001*
	Biomass	-0.146	0.06	6.2	131	(-0.26, -0.03)	0.014
	Protein	0.618	0.06	107.3	131	(0.50, 0.74)	<0.001*

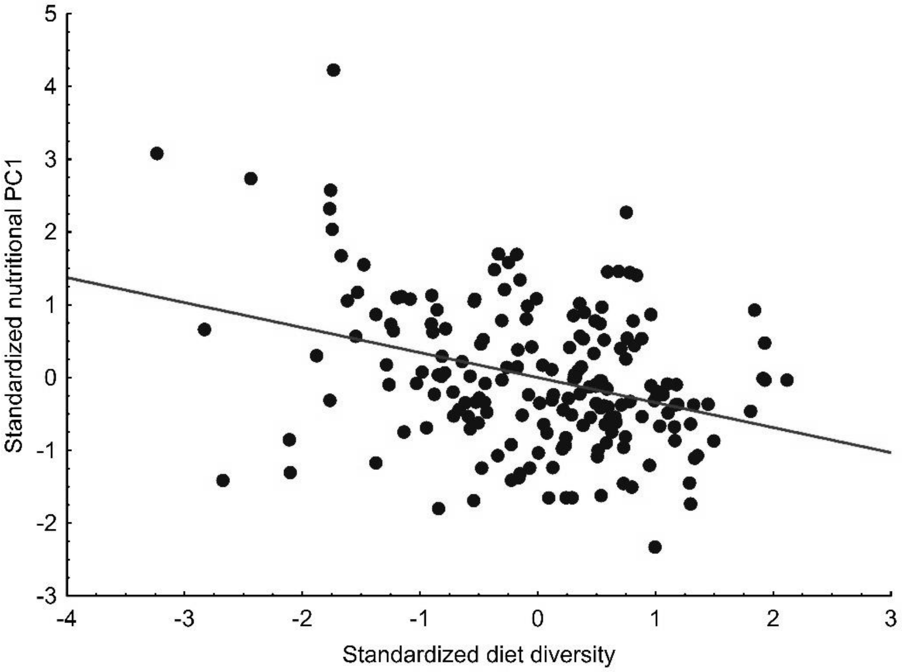


Figure 5.1. Relationship between nutritional components (calories, proteins and fat) combined in a principal component and diet diversity. Standardized data are shown.

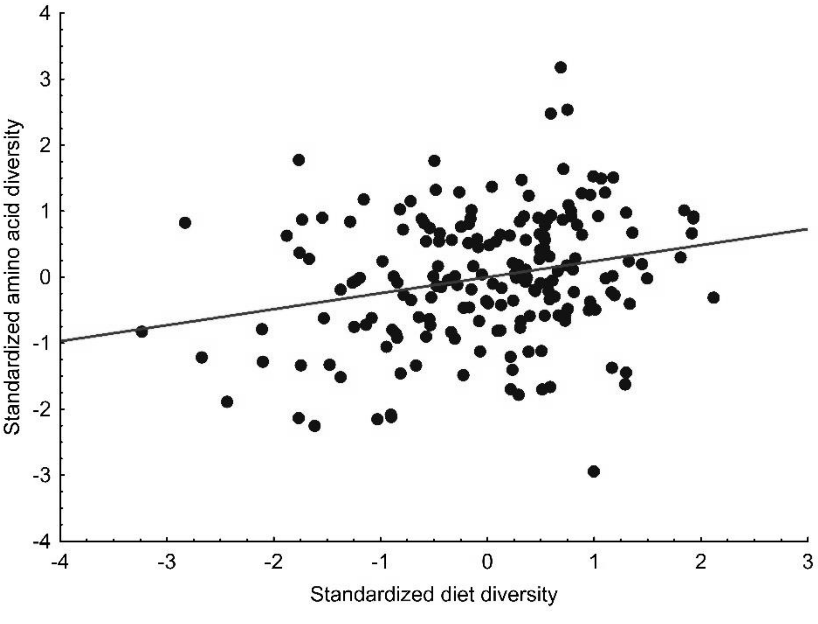


Figure 5.2. Relationship between amino acid diversity of the diet and diet diversity. Standardized data are shown.

Nutritional components, diet and offspring condition

Since calories were closely correlated with protein and fat content (see above), calories and protein content showed high VIFs (50.0 and 16.7, respectively) when included in the model with the remaining diet variables, for which they were removed from the model and analysed separately to avoid the potential effect of collinearity in the model. Controlling by the effect of sex and wing length, LMM showed that fledgling body condition was significantly and positively correlated with amino acid diversity (Fig. 5.3), marginally, but not significantly so, with amino acid PC2 significantly and negatively with diet diversity and laying date (Table 5.3). Fledgling body condition was not significantly correlated with either diet diversity, amino acid PC1, amino acid PC3, protein content, fat content or clutch size (LMM, all *P* > 0.24). Fledglings in better body condition had diets with higher amino acid diversity early in the breeding season and with lower biomass provided by parents. When calories were included in the resulted model (VIF = 3.8), showed no significant effect of this variable on fledgling body condition (LMM, *P* = 0.253). The same occurred for protein content by doing the same procedure (VIF = 2.8, *P* = 0.540).

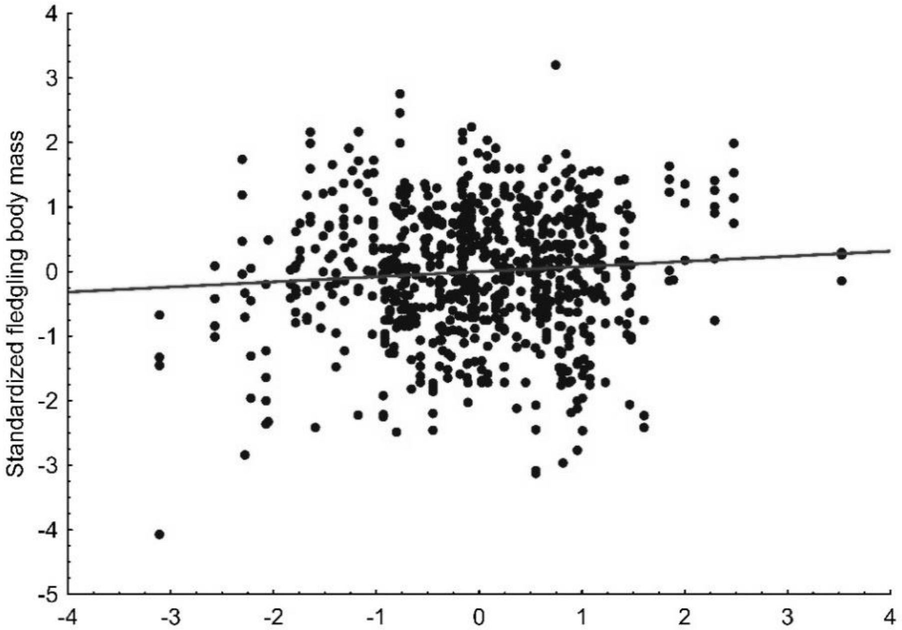


Figure 5.3. Relationship between fledgling body mass and amino acid diversity of the diet. Standardized data are shown.

Table 5.3. Results of LMM for fledgling body condition. D.f. = 618, *n* = 782.

Terms		***Estimate***	***S.E.***	***F***	***95% CI***	***P***
AA diversity		0.126	0.04	11.8	(0.05, 0.20)	<0.001
AA PC2		0.064	0.04	3.0	(-0.01, 0.14)	0.084
Biomass		-0.080	0.04	5.0	(-0.15, -0.01)	0.026
Laying date		-0.185	0.04	23.5	(-0.26, -0.11)	<0.001
Sex	Female	0.801	0.04	372.9	(0.72, 0.88)	<0.001
	Male	-	-	-	-	-
Wing length		0.286	0.02	142.1	(0.24, 0.33)	<0.001

Nutritional components, diet and offspring immunity

As in the previous model, calories and protein content showed high VIFs (66.7 and 20.2 respectively), for which the same procedure was done to avoid collinearity in the model. Controlling by the effect of sex and body mass, LMM showed that PHA-immune response was significantly and positively correlated with amino acid PC1 (Fig. 5.4), marginally, but not significantly so, with diet diversity and significantly and negatively with amino acid PC3 (Table 5.4, Fig. 5.4). PHA-immune response was not significantly correlated with either amino acid diversity, amino acid PC2, fat content, biomass, laying date or clutch size (LMM, all *P* > 0.23). Fledglings showing higher PHA-immune response had diets with higher content in the amino acids arginine, glutamic acid, glycine, leucine, lysine, phenylalanine, proline, threonine (PC1) and also in cysteine (PC3) and lower content in the amino acids histidine, isoleucine and methionine (PC3). Including calories in the resulted model (VIF = 1.8), no significant effect of this variable was observed on PHA-immune response (LMM, *P* = 0.400). The same occurred for protein content (VIF = 3.5, LMM, *P* = 0.527).

Table 5.4. Results of LMM for PHA immune response of fledglings. D.f. = 274, *n* = 349.

Terms		***Estimate***	***S.E.***	***F***	***95% CI***	***P***
Diet diversity		0.104	0.06	3.3	(-0.01, 0.22)	<0.069
AA PC1		0.192	0.06	11.2	(0.08, 0.31)	0.001
AA PC3		-0.149	0.06	7.0	(-0.26, -0.04)	0.009
Sex	Female	0.345	0.10	12.1	(0.15, 0.54)	<0.001
	Male	-	-	-	-	-
Body mass		0.340	0.06	34.0	(0.23, 0.46)	<0.001

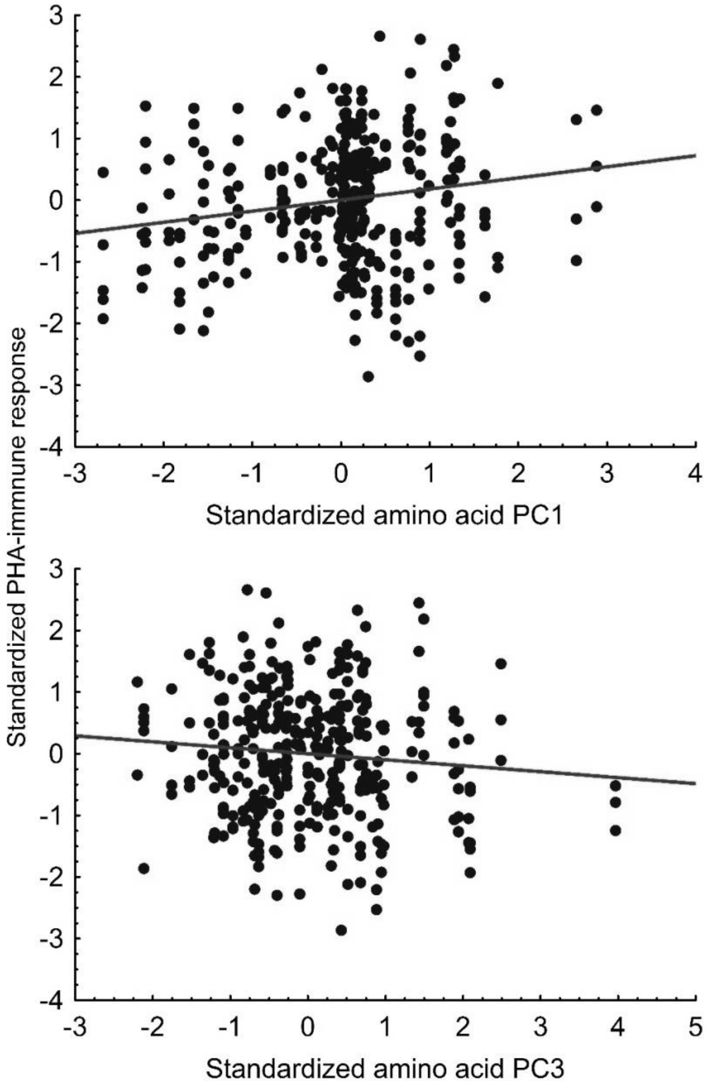


Figure 5.4. Relationship between PHA-immune response and amino acid PC1 (upper panel) and amino acid PC3 (bottom panel). Standardized data are shown.

Discussion

Using a larger sample size than in previous studies (Chapter II and Chapter III), our results showed again that kestrels of better quality, as denoted by clutch size (Chapter II), feed their chicks with a higher biomass and a more diverse diet. Controlling for the effect of clutch size, our study also evidenced that diet diversity increases as the breeding season progresses, probably because at the end of the kestrel breeding season the diversity of prey species in the study area is higher. A more stable climatology at the middle-end of the breeding season allows a more stable presence of reptile and arthropod species and also at that time the fledglings of passerine species (a kestrel's preferred prey; Chapter IV) begins to appear (unpublished data). In addition, the parents with more diverse diets were also the ones that contributed the most biomass, indicating the close connection between diet diversity a parental (mainly fathers) quality.

¿Why do better individuals provide their chicks with a more diverse diet? A first step in answering this question is to analyse the composition of nutrients associated with the diversity of prey consumed, since nutrients are the basis of the variation in diet (Westoby 1978). Our study shows that most diverse diets were less caloric and had lesser contents of protein and fat than less diverse diets. However, our study also showed that the amount of these nutrients in the range we founded them in the diet were not particularly important for fledgling condition (see below). This result , suggesting suggests that better individuals look for other nutrients or for a more balanced nutrient composition rather of than continuing increasing their to increase protein or fat intake. For example, a more diverse diet had also a more diverse amino acid content, a higher content of the amino acids arginine, glutamic acid, glycine, leucine, lysine, phenylalanine, proline, threonine (PC1) histidine, isoleucine and methionine (PC3) and have lesser content of cysteine (PC3) and also of alanine, aspartic acid, serine, tyrosine and valine (PC2). The contribution of biomass was also apparently important for amino acid diversity and the content of amino acids incorporated in PC1. Therefore, the next step in understanding the relevance of diet diversity would be in our case to find out their potential role in offspring development.

No significant correlations were found between calories, protein and fat of the diet and body condition or cell-mediated immune response of the chicks. Assuming the importance of proteins and fat for animal development, the absence of significant positive correlation indicates that the range of proteins, fat and calories found in kestrel diets in our population is above the required threshold for an optimal chick growth. It has been reported that many types of food, such as insects or fish supply so much protein that chicks must excrete excess nitrogen (Stark & Ricklefs 1998). Fledgling body condition was found to be positively correlated with diet diversity in our kestrel population (Chapter II). However, when amino acid diversity and amino acid content were included in the model, the effect of prey diversity was not significant anymore. Instead, and controlling for other explanatory variables, such as laying date and sex, fledglings showed higher body condition in nests provided with more diverse diets of amino acids, indicating a higher contribution of nutrient composition rather than prey diversity per se in offspring growth. In addition to building proteins, amino acids are important regulators of essential metabolic pathways involved in maintenance, growth reproduction and immunity, thus maximizing the efficiency of food utilization (Wu 2009). The supplement of a mixture of amino acids in the diet has been found to be beneficial for optimizing metabolic transformations to enhance muscle growth among other functions and amino acid deficiencies may impair body homeostasis, growth and development (Wu 2009). Research on the optimal amino acid dietary composition in birds has only been developed for poultry species, with almost no knowledge in wild species. Our results suggest that an amino acid balanced diet seems to be more important for an optimal growth than the merely presence of any particular amino acid, although a weak trend was found between body condition and the amino acid PC2, for which some of the amino acids conforming this component (alanine, aspartic acid, serine, tyrosine or valine) might play a relevant role in kestrel growth.

In previous studies (Chapter II), the statistical effect of biomass on fledgling body condition was not significant when prey diversity was included in the model. Increasing the sample size and combined with the effect of new variables (amino acid diversity and amino acid PC2), biomass showed a negative correlation with body mass. A possible explanation for this counterintuitive result is that diets contributing more biomass are also diets providing large prey species, such as common voles (biomass was positively correlated with the frequency of common voles: LMM, estimate = 0.303, $F_{1,133}$ = 19.1, P < 0.001), a prey preferred by the kestrels even though they are little profitable energetically (Chapter IV) and perhaps also with low content in other important nutrients not measured in this study. This should be investigated in future studies.

PHA-immune response in kestrels is considered to be a good indicator of offspring recruitment rate, survival and longevity in birds (Saino *et al.* 1997a; Saino *et al.* 1997b; Hõrak *et al.* 1999; Soler *et al.* 2003; López-Rull *et al.* 2011) and it is affected by food restrictions and body condition (Fargallo *et al.* 2002). Controlling for the effect of nutrients associated with diet diversity, our study shows that PHA-immune response of fledglings was still correlated with the diversity of prey in the diet, suggesting an important role of broadening trophic niche for this T-cell mediated immune component. Increasing the diversity of consumed prey species kestrels may have more opportunities to incorporate macro- and micronutrients required to improve functioning of the immune system. Diet diversity seemed not to affect immune response through amino acid diversity. However, kestrel fledglings showed higher immune response when fed with a diet rich in acids arginine, glutamic acid, glycine, leucine, lysine, phenylalanine, proline, threonine (PC1) and also cysteine (PC3). This result suggests that the presence of certain amino acids, rather than amino acid diversity, may be more important for adequate immunocompetence. Some of these amino acids have been found to play a role in the immune responses (reviewed by (Li *et al.* 2007). For example, arginine has been found to be implied in the regulation of cytokine production and killing of pathogens; glutamic acid in the process of T-cell response and inflammation; leucine is involved in the proliferation of lymphocytes in response to mitogens; lysine in antiviral responses; threonine in maintaining intestinal immune function and stimulation of lymphocyte proliferation (see Li *et al*. 2007). Cysteine is a scarce amino acid (the scarcest one in the kestrel diet) involved in the development of lymphoid cells as a precursor, together with glycine and glutamic acid, of glutathione, considered as the major scavenger of reactive oxygen species, being lymphocytes particularly sensitive to them (Dröge & Breitkreutz 2000).

In conclusion, our study shows that nutrients found in animal diets have a clear potential to explain the variation in life-history traits mediating fitness, such as body condition and immunocompetence in a predator species. Nutrient contents may be the key to understanding the role of food composition or biomass in offspring growth. More diverse diets contained higher diversity of amino acids and had different amino acid profiles, but contained least protein and fat percentage, also were lower caloric than less diverse ones. Some of these nutritional components, such as amino acid diversity or given amino acid profiles were associated with body condition and immunity of chicks, so it seems plausible to think that predators can develop foraging behaviours aimed at obtaining nutritionally balanced diets, as this strategy would yield fitness benefits. Causal links between condition-immunocompetence of chicks and particular nutritional components must be investigated. Our study highlights the importance of exploring nutritional components of animal diets in the wild, which is a subject scarcely investigated in spite of its potential explanatory capacity to better understand trophic ecology theory.

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Appendix

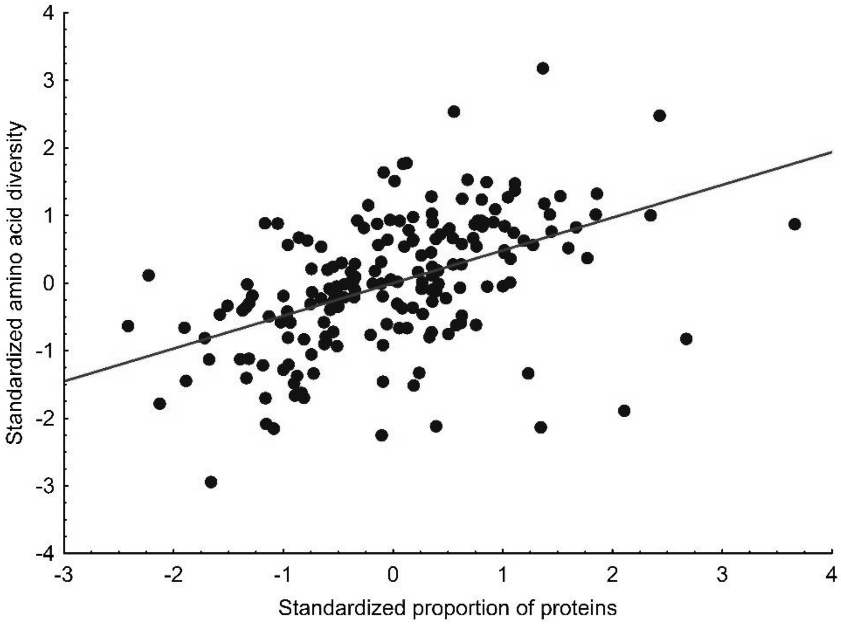
Appendix 5.1. Principal components combining calories per gram, protein content and fat content in the common kestrel diet.

Variable	**Factor**
Calories	0.965
Proteins	0.821
Fat	0.897006
Eigenvalue	2.409815
Variance explained	0.803272

Appendix 5.2. Principal components combining amino acid content in the common kestrel diet. Black marked loading are > 0.6.

	AA PC1	**AA PC2**	**AA PC3**
Alanine	-0.156082	**0.855419**	0.229032
Arginine	**0.838471**	0.007697	0.489919
Aspartic acid	-0.114038	**0.920972**	-0.11539
Cysteine	0.358585	-0.172615	**-0.893668**
Glutamic acid	**0.627198**	0.444154	0.281095
Glycine	**0.736193**	-0.277752	0.486179
Histidine	0.044672	0.523321	**0.820843**
Isoleucine	0.529424	0.329151	**0.777589**
Leucine	**0.903927**	0.363642	-0.070301
Lysine	**0.901599**	-0.379296	0.08106
Methionine	0.333959	0.163742	**0.882233**
Phenilalanine	**0.919148**	-0.351285	-0.09396
Proline	**0.713015**	0.281052	0.488609
Serine	0.052583	**0.927234**	0.258752
Threonine	**0.988258**	0.000528	-0.068113
Tyrosine	-0.211591	**0.855474**	0.444927
Valine	0.152444	**0.897587**	0.335053
Eigenvalue	6.228771	5.168976	4.117475
Explained variance	0.366398	0.304057	0.242204

Appendix 5.3. Relationship between amino acid diversity and the proportion of proteins in the diet.



Discusión integradora

Los resultados de la presente tesis responden a distintas preguntas en el marco de la ecología trófica. Esta tesis está formada por cinco capítulos centrándose en el estudio del nicho trófico de los falcónidos, con especial énfasis en el cernícalo vulgar *Falco tinnunculus.* En el capítulo I se investiga la relación entre el nicho trófico y los patrones globales de ocupación del hábitat en las especies de falcónidos. En los capítulos II y III se analiza la relación entre la amplitud del nicho trófico del cernícalo vulgar y distintas medidas de calidad del individuo así como con la heterogeneidad del hábitat en los territorios en una población situada en el centro de España. Finalmente, los capítulos IV y V se centran en la relación depredador-presa, analizando los factores que explican la elección del consumo de determinadas presas por parte del cernícalo vulgar, así como el aporte de nutrientes que conlleva el consumo de distintos conjuntos de presas.

La medida de amplitud del nicho trófico se considera que desempeña un papel clave en la comprensión de las interacciones ecológicas, relaciones tróficas, competencia inter e intra-específica y en la especiación (Skulason & Smith 1995; Dieckmann & Doebeli 1999). El capítulo I demuestra que la asignación del nicho trófico a una determinada especie puede estar sesgada por el nivel taxonómico analizado por el investigador, existiendo la posibilidad de que se produzca la sobre-representación de especies especialistas cuando los niveles taxonómicos elegidos para determinar las especies que conforman la dieta son más altos. Además, el método para cuantificar el nicho trófico puede hacer variar la catalogación de una determinada especie o población en el gradiente que va desde especies-poblaciones especialistas de reducido nicho trófico, a especies-poblaciones generalistas o de amplio nicho trófico, lo que tiene una gran relevancia en la teoría actual sobre selección de nicho y especiación. La cuantificación realizada utilizando la riqueza de especies está sujeta a una mayor dependencia tanto del esfuerzo muestral como a una magnificación del generalismo, debido a que no se puede distinguir entre consumo anecdótico y consumo frecuente. Sin embargo los índices de diversidad, como el Índice de Shannon-Wiener, minimiza este riesgo, siendo esta metodología propicia para una cuantificación más correcta de la amplitud del nicho trófico (Bolnick *et al.* 2002) .

La competencia por los recursos ha sido postulada como una de las presiones selectivas que modulan el nicho trófico y promueven la especialización ecológica (Bolnick & Fitzpatrick 2007; Poisot *et al.* 2011), considerándose ventajosa una estrategia especialista que reduzca la competencia. La elección de una estrategia de ocupación de nicho trófico puede también variar dependiendo de otras presiones selectivas, como es la predictibilidad de los recursos alimenticios en el tiempo y en el espacio (Estes *et al.* 2003; Svanbäck & Bolnick 2007; Woo *et al.* 2008; Quevedo *et al.* 2009). Una estrategia especialista produce una alta dependencia de recursos concretos que pueden estar sujetos a fluctuaciones temporales y espaciales, disminuyendo llamativamente la eficacia biológica en época de escasez. En estas circunstancias, sin embargo, una estrategia generalista puede verse favorecida al presentar una mayor capacidad para obtener recursos más diversos, y por ello además incrementar la capacidad para colonizar nuevos ambientes y regiones incrementando el éxito de permanencia en el tiempo (Thomas *et al.* 2001). Por tanto sería esperable que las especies con una estrategia más generalista habiten en una mayor área y ocupe una mayor número de biomas (Hernández Fernández & Vrba 2005; Cantalapiedra *et al.* 2011). El estudio desarrollado en el Capítulo I, es uno de los escasos estudios existentes que analiza la dieta real en distintas poblaciones de diferentes especies para determinar la certeza de la anterior premisa usando al grupo de los falcónidos como modelo de estudio. Los resultados no evidencian que las especies más generalistas ocupen áreas de mayor tamaño. Por lo tanto, la variación del tamaño del área de distribución en falcónidos debe de ser explicado por otros factores ambientales o características ecológicas del grupo más que por la amplitud del nicho trófico. Sin embargo, el estudio sí demuestra que existe una relación positiva entre la diversidad de dieta y el número de biomas habitados por cada especie, apoyando la hipótesis de que una estrategia trófica generalista permite a las especies una mayor plasticidad ambiental que se traduce en una mayor capacidad para habitar más hábitats o biomas.

El cernícalo vulgar es una de la rapaces más abundantes de Europa (Forsman 2007) presentando una amplia distribución y diversidad de hábitats ocupados en las regiones paleártica, afrotropical e indomalaya (Village 1990; Ferguson-Lees & Christie 2001). Acorde con la premisa arriba expuesta, los Capítulos II, III, IV y V reflejan una alta diversidad trófica y variación inter anual en la composición de la dieta en la población de cernícalo estudiada. En nuestra zona de estudio se han reportado fluctuaciones interanuales en la abundancia de algunas especies de presas más importantes para la dieta del cernícalo, como la alondra eurasiática *Alauda arvensis (Martínez-Padilla & Fargallo 2008)*, el topillo común *Microtus arvalis*, la musaraña común *Crocidura russula* y el lagarto ocelado *Timon lepida* (Fargallo *et al.* 2009). Estas observaciones indican una baja predictibilidad de los recursos alimenticios en nuestra zona de estudio y sugiere un alto grado de flexibilidad en el comportamiento de forrajeo de los cernícalos, como predice la idea.

El cernícalo vulgar es una especie territorial en la que las áreas de forrajeo durante la reproducción están incluidas en los territorios de cría (Village 1990). Los capítulos II y V muestran una relación positiva entre el tamaño de la puesta con la diversidad de dieta, al igual que con la biomasa aportada al nido. Ya que durante la reproducción es el macho el encargado de la captura de las presas (Village 1990), los resultados sugieren que los machos de mejor calidad, aquellos que son capaces de hacer una inversión reproductora mayor, alimentan a sus pollos con una mayor diversidad de presas. También se observa que la diversidad de la dieta, se correlaciona positivamente con la condición corporal de los pollos, es decir, los pollos alimentados con una mayor diversidad de presas poseen una mejor condición corporal. Interesantemente, la condición corporal no se explicó por un mayor aporte de biomasa, sugiriendo que una mayor diversidad de presas aporta otros elementos, probablemente nutrientes, que benefician el crecimiento de los polluelos más que el aporte de una mayor cantidad de alimento *per se*.

La importancia de los nutrientes en la reproducción, el crecimiento y la supervivencia de los individuos se ha demostrado en gran medida en los seres humanos y otros animales (Mayntz & Toft 2001; Jensen *et al.* 2012). En consecuencia, un nicho trófico más amplio podría incrementar la obtención de un mayor número de nutrientes que podría a su vez asociarse con un aumento en la eficacia biológica, a través de un incremento en la viabilidad de la descendencia Esta idea se ve reforzada cuando se analiza otro importante componente de la eficacia biológica, como es el sistema inmunitario. Se ha demostrado que la respuesta inmunitaria es un buen predictor de la tasa de reclutamiento, supervivencia y longevidad en aves (Tella *et al.* 2000; Soler *et al.* 2003; López-Rull *et al.* 2011). Además, en estudios previos se ha observado que el alimento aportado por los progenitores tiene efectos sobre el sistema inmune de los pollos y de los adultos (Kidd 2004; Freitak *et al.* 2009; Triggs & Knell 2012) . En el Capítulo II se muestra, que más que la cantidad de alimento aportada (biomasa), es la diversidad de la dieta la que explica la respuesta inmunitaria celular, siendo los pollos alimentados con una mayor diversidad de presas los que muestran una mayor respuesta inmunitaria. No existe ningún estudio que haya explorado este aspecto, sin embargo sí se sabe que ciertos compuestos nutricionales como las vitaminas, algunos minerales, ácidos esenciales, así como los macronutrientes (proteínas, lípidos, hidratos de carbono, aminoácidos) se han demostrado necesarios para el desarrollo, mantenimiento y respuesta del sistema inmune (Blazer 1992; Calder & Kew 2002). Al igual que con la condición física, los resultados presentes en esta tesis sugieren que una dieta más variada podría incrementar el aporte de nutrientes esenciales para el desarrollo del sistema inmunitario

Para poder responder a la pregunta planteada en el Capítulo II se analizó nutricionalmente lo composición de la dieta. Los resultados obtenidos muestran que las dietas más generalistas presentan un menor valor calórico, así como en contenido de proteínas y grasas. Sin embargo, los niveles de estos nutrientes no son lo suficientemente bajos como para poder influir negativamente en la condición física de los pollos. Este hecho sugiere que los mejores individuos buscan otros nutrientes o una composición nutritiva más equilibrada en lugar de aumentar el consumo de proteínas o grasa. La relación positiva entre la diversidad de dieta y la diversidad de aminoácidos consumidos, así como el mayor consumo de ciertos aminoácidos observado en las dietas más generalistas apoyarían la búsqueda de estas dietas con una composición nutricional más equilibrada. Se ha observado que el suplemento de una mezcla de aminoácidos en la dieta es beneficioso para optimizar las transformaciones metabólicas así como para aumentar el crecimiento muscular entre otras funciones, por el contrario las deficiencias de aminoácidos pueden afectar la homeostasis corporal, el crecimiento y el desarrollo (Wu 2009). Los resultados sugieren que una dieta balanceada de aminoácidos parece ser más importante para un crecimiento óptimo que la presencia de cualquier aminoácido particular, aunque se encontró una débil tendencia entre la condición corporal y un eje PC2 de aminoácidos, para el cual algunos de los aminoácidos que lo conforman podrían desempeñar un papel relevante en el crecimiento del cernícalo. Estos resultados son apoyados por la relación positiva encontrada entre la diversidad de dieta y la respuesta inmune (Capítulo V), sugiriendo que aumentando la diversidad de las especies de presas consumidas, los cernícalos pueden tener más oportunidades de incorporar nutrientes necesarios para mejorar el funcionamiento del sistema inmunológico. No obstante, los resultados obtenidos sugieren que la respuesta inmunitaria está en mayor medida influida por la presencia de ciertos aminoácidos que por la propia diversidad de los mismos.

La teoría clásica del nicho postula que una mayor heterogeneidad del hábitat proporcionaría una mayor diversidad de especies (Simpson 1949; MacArthur & Wilson 1967; Lack 1969; Tews *et al.* 2004), es lo que se conoce como la hipótesis de heterogeneidad del hábitat (LHH) y predice que los paisajes más heterogéneos con una mayor diversidad de hábitats pueden proporcionar formas más diversas de explotar los recursos ambientales (nichos) que los paisajes más homogéneos, permitiendo así la explotación de un mayor número de especies (Tews *et al.* 2004; Kadmon & Allouche 2007). En este contexto en el Capítulo III explora el rol que desempeña la heterogeneidad de hábitat en la amplitud del nicho trófico en el cernícalo. La frecuencia de ocupación de un nido se ha relacionado de forma positiva con la calidad del territorio en muchas especies de aves (Sergio & Newton 2003), siendo el número de años que se ocupa el nido un buen indicador de la calidad del territorio asociado a él. Los resultados del Capítulo III así lo evidencian, observándose que los nidos más frecuentemente ocupados fueron usados por individuos de mejor calidad que pusieron más huevos antes en la estación reproductora. Además, nuestros resultados indican la existencia de una relación cuadrática entre la calidad del territorio y la heterogeneidad de hábitat, siendo los territorios con mayor ocupación los que poseían una mayor y menor heterogeneidad. La selección de los hábitats más heterogéneos puede ser ventajoso para los cernícalos cuando las condiciones ambientales son drásticamente fluctuantes y varían la disponibilidad de alimento, como se observa en las regiones mediterráneas (Penteriani *et al.* 2002; Tellería *et al.* 2008; Fargallo *et al.* 2009). Esta ventaja radica en que los territorios más heterogéneos proveerán un mayor rango de presas alternativas de las que alimentarse cuando las condiciones ambientales fluctuantes afecten a la disponibilidad de las presas preferidas (Penteriani *et al.* 2002). Por otro lado, la alta ocupación de territorios más homogéneos puede ser explicada por una mayor presencia en estos territorios de los hábitats más favorables para el cernícalo. Finalmente, se muestra que los territorios de mejor calidad, ocupados por los individuos de mejor calidad no poseen una mayor heterogeneidad de paisaje, lo que indica que la mayor diversidad de la dieta no es un resultado coyuntural debido a la conformación del paisaje presente en el territorio o a la elección de territorios más heterogéneos paisajísticamente, sino que refleja una búsqueda activa de diferentes especies-presa por parte de los individuos reproductores de diferentes especies-presa que ofrecen a los pollos.

Cabe señalar que nuestro enfoque de estudio se basó en una visión mecanicista de la especialización individual con respecto a la explotación del hábitat de manera que para cada hábitat particular se espera que cada individuo busque una o varias especies de presas en particular. Este enfoque, que nos permitió predecir una correlación positiva entre la diversidad de dieta y un hábitat más diverso derivado de la LHH, supone un primer paso para investigar la relación entre el nicho trófico y el uso del hábitat. El mismo hábitat puede ser ocupado por diferentes especies de presas y la disponibilidad de presas (dificultad de captura) puede ser diferente para diferentes especies que ocupan el mismo tipo de hábitat y también para las mismas especies que ocupan diferentes tipos de hábitat (Byholm *et al.* 2007; Torre *et al.* 2007; Martínez-Padilla & Fargallo 2008). Además, los resultados del Capítulo III también mostraron que la calidad del territorio, medida como frecuencia de ocupación, no predice la diversidad de las especies de presas consumidas. Esto sugiere que otras características además de la disponibilidad de alimentos son importantes en la selección del territorio. La depredación es uno de los factores más importantes para la selección del territorio en rapaces de pequeño tamaño como el cernícalo vulgar (Newton 1979), por lo que la disminución del riesgo de depredación evitando determinados hábitats que por sus características serían propicios para la depredación podría explicar la frecuencia de ocupación.

De acuerdo con la teoría del forrajeo óptimo y el lugar central de forrajeo, los resultados obtenidos en el capítulo IV demuestran que el tiempo dedicado por los cernícalos para aprovisionar el nido con presas se incrementa a medida que aumenta el tamaño de la misma, y además, las presas de mayor tamaño tienden a ser también las más preferidas, apoyando la idea de que las presas preferidas son más costosas en términos de tiempo dedicado al aprovisionamiento de alimento. No obstante, los resultados indican que la relación entre la biomasa de la presa y el tiempo de aprovisionamiento se ajusta a una función de decaimiento exponencial, existiendo una mayor poder explicativo del peso para las presas menores de 13 gramos mientras que para las presas con un pesos mayores de 30 gramos el poder explicativo del peso en el modelo era bajo para explicar el tiempo dedicado al aprovisionamiento del nido con estas presas. Este resultado podría sugerir en principio que entre los tamaños de presa que los cernícalos pueden capturar y transportar, los tiempos más largos de un cierto umbral (alrededor de 35 minutos) ya no sean rentables. Este resultado es esperable dentro del modelo del lugar central en la OFT ya que el aprovisionamiento estará limitado por el tiempo necesario para la retroalimentación del modelo, por lo tanto un aprovisionamiento óptimo evitará tiempos de aprovisionamiento mayores que el presupuestado por los individuos (Stephens *et al.* 2007).

El cernícalo es considerado como un depredador especializado en el consumo de topillos (Hanski *et al.* 2001), siendo ésta la principal presa consumida en en las poblaciones del norte y centro de Europa (Korpimäki 1986; Masman *et al.* 1988; Village 1990). El alto valor de preferencia obtenido para esta especie (Capítulo IV) refleja lo esperado si la coevolución depredador-presa promueve adaptaciones morfológicas y fisiológicas en los cernícalos para capturar topillos, proporcionando esta especie la mayor eficiencia y recompensa energética dentro del set de presas del cernícalo. Los resultados obtenidos en el Capítulo IV muestran una relación positiva entre la preferencia de la presas de cernícalo y su rentabilidad energética, aunque esta relación se producía cuando el topillo era eliminado del modelo. Por lo tanto, la elevada preferencia de consumo de topillo en nuestra población no se corresponde a su rentabilidad energética, pudiendo deberse a una maladaptación de los individuos de nuestra población o bien podría existir un componente nutricional, no medido en la presente tesis, que podría explicar esta elevada preferencia. No obstante, excluyendo a los topillos, se ha comprobado que existe una sólida preferencia por los cernícalos por alimentar a los pollos con presas con un mayor contenido de proteína (Capítulo IV). La reproducción y engorde de los pollos son las fases más costosas a nivel nutricional de las historias vitales de los individuos (Martin 1987). Específicamente, los alimentos ricos en proteínas se consideran un factor limitante, estudios previos han observado que el consumo de alimentos ricos en proteínas es mayor en los épocas reproductoras así como en el alimento aportado a los pollos durante su desarrollo (Ricklefs *et al.* 1998; Blanco *et al.* 2014). Sin embargo, en nuestra población el consumo neto de proteína (biomasa de proteínas) parece no estar comprometido, nunca llegando a consumos bajos de proteínas como para influir negativamente en el peso de los pollos primando el consumo de otros nutrientes (Capítulo V). La baja rentabilidad energética de los topillos podría ser la causa de la relación negativa encontrada en el capítulo V entre la biomasa aportada y el peso de los pollos. Una posible explicación de este resultado contraintuitivo es que las dietas que aportan más biomasa son también dietas que proporcionan estadísticamente presas más grandes, como los.

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Conclusiones generales

1. La dieta de las especies de falcónidos puede predecir el grado de la heterogeneidad de hábitat que ocupan, apoyando la idea de que el aumento de la amplitud de nicho trófico incrementa la capacidad de las especies para explotar distintos hábitats.

2. La amplitud del nicho trófico asignada a una especie, población o individuo va a depender del nivel taxonómico utilizado para cuantificar tanto la riqueza como la diversidad de la dieta, por lo que se hace necesario incluir el nivel taxonómico usado en los estudios de ecología trófica. De igual forma se recomienda el uso del índice de diversidad sobre el de riqueza para una correcta determinación de la amplitud de nicho, ya que evita la sobre-representación de especies consumidas de forma casual.

3. Existe una relación estrecha en Cernicalo vulgar entre la diversidad de la dieta de los individuos y componentes de la eficacia biológica: estado físico e inmunológico de la descendencia. Esto sugiere que la amplitud de nicho trófico puede ser una estrategia bajo presión de selección a nivel intrapoblacional.

4. Los mejores territorios de cría elegidos por los individuos de mejor calidad no se asocian de forma lineal a la heterogeneidad de paisaje. Además, y contrariamente a lo esperado bajo la Hipotésis de Heterogeneidad del Paisaje, los individuos que ocuparon territorios menos heterogéneos alimentaron a su descendencia con una mayor diversidad de especies-presa, lo que sugiere una búsqueda activa de diferentes presas para incrementar la diversidad de la dieta como estrategia trófica.

5. De acuerdo con la teoría del forrajeo óptimo y el lugar central de forrajeo, se observa que para una especie depredadora el tiempo dedicado para aprovisionar el nido con presas se incrementa a medida que aumenta el tamaño de la misma y su preferencia, apoyando la idea de que las presas preferidas son más costosas en términos de tiempo dedicado al aprovisionamiento de alimento.

6. Las características ecológicas de las especies-presa que definen su potencial de captura por los depredadores juegan un papel importante en el tiempo y energía dedicado al aprovisionamiento de alimento en el nido, por lo que los índices de capturabilidad deberían ser implementados en los modelos teóricos de forrajeo óptimo y forrajeo del lugar central.

7. La preferencia de una especie depredadora por el consumo de una presa se explica por su rentabilidad energética y contenido proteico, aunque existen especies-presa con un consumo por encima de lo esperado con respecto a su valor energético y proteico. Esto podría deberse a una maladaptación de la especie depredadora en la población de estudio o a los beneficios que las especie-presa aporta, como nutrientes esenciales, que no han sido medidos en el estudio.

8. Las dietas más diversas también contienen menor porcentaje de proteína y grasa, son menos calóricas pero muestran una mayor diversidad de aminoácidos. Algunos de estos componentes nutricionales, como la diversidad de aminoácidos o los perfiles amimo-acídicos, se asocian con la condición corporal y la respuesta inmunitaria de la descendencia, por lo que parece plausible pensar que los depredadores pueden desarrollar comportamientos de forrajeo orientados a obtener dietas nutricionalmente balanceadas.