Curso 2009/10
CIENCIAS Y TECNOLOGÍAS/13
I.S.B.N.: 978-84-7756-949-7

DAVID PÉREZ PADILLA

Ecología trófica del Alcaudón Real e implicaciones en la dispersión secundaria de semillas en las islas Canarias

Directores
MANUEL NOGALES HIDALGO
ANNA TRAVESET VILAGINÉS

SERVICIO DE PUBLICACIONES
UNIVERSIDAD DE LA LAGUNA

SOPORTES AUDIOVISUALES E INFORMÁTICOS
Serie Tesis Doctorales

Latitud Meridional

La l escribe una isla
de volcán y trampas de fuego.
Listas (sumas) de antifaz
juegan a ser ciencia.

Cenizas de tonos grises
visten llanos salpicados de verde.
Conciben a pinceladas y plumazos
una sutil estepa.

En las sílabas de un tarso
se dibujan las siembras del sur.
Entretanto se despunta
un sol primerizo y soñoliento.

Los latidos parpadean
y obedecen al paisaje
que te ha visto nacer.

Cada temporada vendré a buscar
tus vuelos rasos
y tus aleteos presas del baile.

Eres al malpaís que habitas
la fe de sus semillas.

A tus semillas vuelves,
y el malpaís es tu esperanza.

Cuando llega la tarde,
el alisio regresa
para abrigar su volcán,
refrescar tu energía,
regalar al espino
otro dormidero.

Virginia Díaz.

“No hay un camino hacia la felicidad, la felicidad es el camino”.

A MIS PADRES

AGRADECIMIENTOS

A mis padres, porque siempre me han apoyado sin pedirme nada a cambio, sin condiciones, me han dado la posibilidad de eligir siempre mi camino y gracias a ellos y a su esfuerzo he podido llegar hasta aquí. Gracias por haber confiado en mí. Igualmente quiero agradecer al resto de mi familia más cercana, mis hermanos Inma y Migue, por su apoyo en este largo recorrido.

Manuel Nogales (Pelucho) y Anna Traveset, mis directores de Tesis, que me dieron la oportunidad de embarcarme en esta maravillosa experiencia, los cuales me han guiado, ayudado y apoyado en todo momento, dándome las directrices oportunas para llevar este proyecto a buen puerto.

Juan Carlos Illera, aunque no firme esta tesis doctoral como otro codirector de tesis, se lo merecería ya que sus críticas constructivas y apoyo en los diferentes trabajos realizados me han hecho crecer un poquito en este largo camino de la ciencia.

A Jairo Patiño, fueron muchas emociones vividas en esa casa de Bajamar, da gusto tener a un amigo para compartir todas las vivencias que conlleva una tesis doctoral. En esta etapa de la vida hemos ido de la mano y al mismo paso. Como diría él ¡Pura vida!.

A Lola Guil, le tengo que agradecer todo el apoyo y la ayuda en esta última etapa de la tesis doctoral; ha estado siempre para la buenas y para las no tan buenas, con un ofrecimiento desinteresado y creciendo juntos en diferentes aspectos de la vida. Gracias mi niña Lola!!.

A Raquel Gutiérrez, no sólo por la ayuda en el trabajo de la tesis, tanto en el campo como en el laboratorio, sino por lo más importante, por la ayuda en la vida, fueron muchos momentos geniales los que pude compartir con ella durante el transcurso de esta tesis, y serán muchísimos más los que nos quedan por delante. Gracias por enseñarme a ver la vida con esa positividad que siempre desprendes.

A Alejandro Padrón (Faneke), largas jornadas de campo con él, ya que siempre estuvo dispuesto a disfrutar y también a sufrir un poquito en cada uno de los distintos viajes que hicimos juntos (La Palma, La Graciosa, Alegranza, etc.). Su fino humor y disfrute por los pájaros siempre hacían más amenos los días de campo. También agradecerle la elaboración de los distintos mapas de la tesis.

A Toni Pérez Delgado, fue una experiencia enriquecedora compartir, con un amigo, tanto el trabajo de campo como parte de la identificación de los insectos en el laboratorio. Aunque parecíamos más un matrimonio, por eso de las discusiones, siempre acabábamos riendo y contentos de las diferentes jornadas.

A Gustavo y Virginia, mi familia canariona, que siempre estuvieron dispuestos a dejarme un huequito en su casa durante mis estancias en Gran Canaria, ofreciéndome alojamiento, manutención y sobre todo, amistad.

A nuestra pequeña familia del Grupo de Ecología y Evolución en Islas: Beatriz Rumeu, Aarón González, Patricia Marrero, Félix Medina, Benigno Padrón, Marta López, Airam Rodríguez, Alejandro González (Jano), Juan Carlos Illera y Manuel Nogales. A cual mejor, me alegro de haber formado parte de este gran grupo de profesionales que siempre estuvieron dispuestos a ayudarme en las diferentes etapas de la tesis, y sobre todo y lo más importante, que se ha creado una amistad entre todos que espero que dure para siempre.

Fueron muchos los que compartieron más de una jornada de campo conmigo a lo largo de esta tesis, los miembros del GEEI, Diego Jordano y Mario, Anita Portero, Nicolás Martín, Rubén Barone, Keith Emmerson, Rafa Barrientos, Quirina, Gustavo Viera, Toni Pérez, Beni y Elena, y alguno más que seguro que se me olvida, pero que igualmente les estoy agradecido.

Otros, como Ruben Barone, Beneharo Rodríguez, Keith Emerson, Felipe Siverio, José Juan Hernández, Alejandro Betoret, Bernardo López o Gustavo Peña, me cedieron desinteresadamente información de campo, además de material fotográfico de alta calidad que he usado en el transcurso de este periodo.

A Jairo, Kati, y Nuria, porque juntos aprendimos que las causas justas, si se luchan, terminan por lograrse. El Gobierno de Canarias nos enseñó a conocer

algunos de nuestros límites a lo largo de nueve meses de trabajo no remunerado, y al final, hasta se recuerda como una experiencia bonita!!!

Concepción Nieves y el “Equipito” de Tagoro Medioambiente (Francisco, Manuel y Andrés), que no solo me ayudaron en la mayoría de los experimentos de germinación, sino que estuvieron ahí para multitud de cosas, desde la captura de lagartos hasta el arreglo de más de un coche, invernadero, etc.

Al Centro de Recuperación de La Tahonilla y a su Gente (Caloli, Juan, Fernando, Roberto) que me permitieron desarrollar la experimentación con lo cernícalos en cautividad y colaboraron en todo lo posible, facilitando enormemente la labor.

Diferentes organismos proporcionaron los permisos oportunos para desarrollar el trabajo de campo sin obstáculo alguno; mencionar a los cabildos de las diferentes islas, al Gobierno de Canarias así como al Parque Nacional del Teide.

Virginia Díaz además del bonito poema que me realizó para la tesis, me acompañó y ofreció su coche recién salido del concesionario para realizar parte del trabajo de campo en Lanzarote y Fuerteventura. Me alegro de haber compartido, otra vez, esas intensas jornadas de campo.

Fernando Vizcaíno, sin duda de las personas más eficientes en la administración de la Universidad de La Laguna, facilitando la dura tarea que no le gusta a nadie, la burocracia y el eterno papeleo que conlleva una tesis doctoral.

Por último, no quiero acabar si agradecer a todas las personas que me he cruzado en mi última estancia a Norwich; muchos sabrán que existe un antes y un después de esta etapa, y en Inglaterra me he sentido casi como en Canarias. Gracias a la “latin mafia”: José Alvés, Verónica Méndez, Christiana Faria, Lorenzo Zanette, Clara Moyano, Alex García y Sara López. También a los nativos, especialmente a Lewis Spurgin, Alba Warn y, como no, a David Richardson que me ha demostrado que la calidad humana está por encima de la calidad científica.

Gracias a todos!!!!

ÍNDICE

INTRODUCCIÓN

Las islas oceánicas y los procesos ecológicos y evolutivos

Las islas oceánicas han jugado un papel básico en el estudio y avance de muchos aspectos relacionados con la ecología y la evolución. Estos particulares ecosistemas emergen de los fondos marinos desprovistos de vida, y poco a poco van siendo colonizados por la biota capaz de llegar y establecerse en ellos. Estos procesos de colonización están íntimamente relacionados con características geográficas de las islas, como su tamaño y distancia al continente (MacArthur & Wilson 1967), con propiedades intrínsecas de las especies colonizadoras, como su capacidad de dispersión y establecimiento en el lugar de arribada y, por último, con las singularidades de los ecosistemas y comunidades insulares que han de ser colonizadas (Whittaker & Fernández-Palacios 2007). Todos estos condicionantes dan lugar al poblamiento de las islas oceánicas, en las cuales existe un empobrecimiento de especies en relación a ecosistemas similares en los continentes. La menor complejidad de las islas oceánicas respecto a los ecosistemas continentales facilita el estudio de numerosos procesos ecológico-evolutivos (Carlquist 1974, Grant 1998, Olesen & Jordano 2002, Emerson 2002). Una vez las especies logran colonizar las islas, éstas sufren una relajación ecológica debido a que muchos competidores y depredadores se encuentran ausentes (Lomolino 1984, Buckley & Jetz 2007), pudiendo desarrollar procesos ecológicos tales como: el establecimiento en nuevos hábitats, el aumento de la diversidad de su espectro alimentario, o el incremento de las densidades poblacionales.

Ecología trófica

La ecología trófica de las especies está íntimamente relacionada con diversos comportamientos como la competencia, la depredación, la selección de hábitat, el gregarismo, etc. Las relaciones alimentarias de competencia interespecífica suelen ocurrir entre especies que ocupan un mismo nicho trófico, mientras que existen otras relaciones que ocupan diferentes niveles como por ejemplo las relaciones herbívoro-planta, frugívoro-planta o frugívoro-depredador. Todas estas interacciones producen redes más o menos complejas en las que una especie influye de manera considerable en diferentes aspectos de un ecosistema. El estudio de estas interacciones tróficas facilita la detección de las especies “clave” en el ecosistema, es decir, aquéllas que son altamente influyentes y de cuya abundancia y relaciones depende la existencia o el mantenimiento de otras muchas especies (Hunter & Price 1992).

Los estudios de selección de dieta analizan la composición de presas o tipos de alimento que un animal incluye en su dieta. Además, explican las preferencias por un tipo u otro de sustento, el aumento de esa preferencia cuando el alimento se encuentra con rapidez, la selección de determinados nutrientes que pueden ser muy escasos, o las razones de porqué un alimento no se incluye en la dieta a pesar de ser relativamente abundante (Marti et al. 1993, Costa et al. 2008). Todos estos comportamientos de alimentación tienen como objetivo principal el maximizar la tasa de ganancia energética, permitiendo así satisfacer otros requerimientos energéticos importantes no relacionados directamente con la alimentación como la reproducción, la defensa, la migración, etc. (Blondel et al. 1991, Visser et al. 1998, McWilliams et al. 2004, Illera & Díaz 2006). Existen diversas teorías como la del “forrajeo óptimo”, que predice las reglas usadas por los predadores para optimizar la ingestión de alimento. Cuando la densidad del alimento es alta, el predador suele especializarse en presas de alta calidad e ignora las de bajo contenido alimenticio, mientras que si la densidad del alimento disminuye, el predador se vuelve menos selectivo y amplía el rango de selección de las presas (Krebs et al. 1983, Stephens & Krebs 1986).

La dispersión de semillas en ecosistemas insulares

Las interacciones entre especies constituyen la base del funcionamiento y la dinámica de los ecosistemas. En islas, las relaciones ecológicas entre plantas y animales pueden adquirir una enorme importancia en el mantenimiento de la alta biodiversidad que presentan estos lugares. Estos hábitats son especialmente sensibles a cualquier modificación de las relaciones entre especies, ya que la pérdida de una de éstas puede llevar a la drástica reducción o extinción de otras muchas que puedan estar interaccionando con ella. Estas interacciones, pese a la gran importancia que presentan en los ecosistemas, han recibido muy poca atención en el campo de la biología de la conservación, y aún conocemos muy poco acerca de la estructura de estos mutualismos en comunidades altamente diversas.

La dispersión de semillas está considerada como un proceso crucial en los ciclos de vida y en la distribución espacial de las poblaciones vegetales (Schupp 1993). Estos eventos posibilitan la colonización de nuevos lugares apropiados, en los cuales las plántulas se pueden establecer y desarrollar tras encontrar las semillas las condiciones óptimas para su germinación. La dispersión de semillas suele ser ventajosa para muchas plantas, ya que así evitan la presencia de enemigos naturales (depredadores de semillas, patógenos, herbívoros, etc.) que suelen concentrarse en las cercanías de los parentales (Hulme 1998). En el caso de que las semillas no sean dispersadas y se establezcan debajo de los parentales, la supervivencia de los nuevos individuos suele ser escasa, debido a que tienen que competir por los mismos recursos con las plantas ya establecidas. La distribución espacial de las semillas tras su dispersión es conocida con el término de “lluvia de semillas” (Janzen 1971). Dos son los factores que influyen principalmente en esta distribución: 1) la relación entre el número de semillas y la distancia al origen, y 2) la dirección respecto a la planta madre. Si la dispersión de las semillas es ventajosa para una determinada especie vegetal, normalmente las diásporas o propágulos suelen poseer mecanismos que favorecen los procesos dispersivos (Ridley 1930). Numerosas especies de plantas presentan frutos con coberturas comestibles (pulpa), que suelen tener características (color, olor, forma, aporte nutritivo, etc.) que son, muchas veces, adaptaciones de las plantas a la dispersión de sus semillas y consecuencia de la selección realizada por los diferentes dispersores (Jordano 1995).

En plantas que producen frutos carnosos, los vertebrados son los principales dispersores de semillas (Jordano 2000, Stiles 2000). El efecto del paso de las semillas a través del tracto digestivo del animal depende tanto de las características morfológicas (e.j. longitud del tracto digestivo o la presencia de molleja) como de las fisiológicas (e.j. fluidos del aparato digestivo). Por ello, dependiendo del tipo de animal que disperse las semillas, las consecuencias para éstas podrán variar considerablemente.

En general, tres clases distintas de vertebrados participan en la mayoría de los sistemas de dispersión de semillas: reptiles, aves y mamíferos (Fenner 2000, Stiles 2000). Sin embargo, la saurocoria (dispersión de semillas por reptiles) es un fenómeno que ocurre esencialmente en islas (Olesen & Valido 2003). El papel que juegan los lagartos como dispersores de semillas en islas es más importante y frecuente de lo que se pensaba (Pérez-Mellado & Corti 1993, Pérez-Mellado & Traveset 1999, Valido 1999, van Damme 1999, Cooper & Vitt 2002, Olesen & Valido 2003, Rodríguez et al. 2008). Una de las causas de este fenómeno es la ampliación de nicho trófico de los lagartos en islas (Gorman 1979, Nogales 1999), cuyas densidades suelen ser mayores que en los continentes, en parte debido a la baja competencia y depredación que sufren (Case 1975, Benett & Gorman 1979, Schoener & Schoener 1980, Rodda & Dean-Bradley 2002, Brown et al. 1992, Olesen & Valido 2003, Buckley & Jetz 2007). Uno de los ejemplos más claros de todos estos procesos se encuentra en las islas Canarias, donde los lagartos endémicos del género *Gallotia* participan activamente en la mayoría de sistemas de dispersión de semillas, pudiendo incluir en su dieta más de un 50% de frutos respecto al volumen total (Valido 1999, Valido & Nogales 1994, 2003, Valido et al. 2003, Roca et al. 2005, Rodríguez et al. 2008).

En ocasiones, los sistemas de dispersión de semillas son más complejos de lo que parecen *a priori*, ya que el transporte de las semillas puede tener lugar en varias fases (ver revisión de Vander Wall & Longland 2004). Así, la diplocoria o dispersión secundaria consiste en la dispersión de semillas tras la secuencia de dos o más eventos dispersivos. Estos procesos ofrecen diferentes beneficios a las plantas, ya que la primera fase de dispersión de la semilla facilita su salida de las inmediaciones de los parentales, evitando así la posible competencia y depredación, mientras que la segunda fase dispersiva ayuda a la expansión y colonización de nuevos hábitats, permitiendo a las plantas ser desplazadas a larga distancia (Fig. 1, Vander Wall & Longland 2004). Los estudios de dispersión de semillas a larga distancia han adquirido en los últimos años una gran importancia, demostrando la influencia de éstos en diferentes aspectos como la colonización de islas o de hábitat remotos, la conexión entre hábitats fragmentados o la facilitación de la coexistencia de especies (Higgins & Richardson 1999, Cain et al. 2000, Nathan & Muller-Landau 2000, Nathan et al. 2003, 2008, Higgins et al. 2003, Trakhtenbrot et al. 2005, Nathan 2006, Spiegel & Nathan 2007).

La dispersión secundaria de semillas puede ser producida por la combinación de varios agentes dispersivos, tanto abióticos (e.j. viento, agua) como bióticos (e.j. mamíferos, aves, insectos), que ocasionan diferentes tipos de procesos (Forget & Milleron 1991, Levey & Byrne 1993, Vander Wall 2002, Pizo et al. 2005). La mayoría de los procesos de diplocoria sólo incluyen una única digestión de las semillas producida por uno de los dispersores (Ridley 1930), mientras que el otro movimiento suele llevarse a cabo en el exterior de los animales. No obstante, la dispersión secundaria de semillas puede ser algo más compleja, viéndose las semillas afectadas por una doble ingestión (doble endozoocoria) (Fig. 1). Estos procesos suelen ser ocasionados por depredadores que se alimentan de frugívoros que previamente han ingerido frutos. La dispersión secundaria de semillas mediada por la interacción frugívoro-depredador es un fenómeno raro, que se ha descrito en escasos estudios y de forma muy superficial (Damstra 1986, Hall 1987, Dean & Milton 1988, Nogales et al. 1996, Clarke et al. 2003). Sólo algunos estudios realizados en el islote de Alegranza (Lanzarote), han investigado este fenómeno con cierta profundidad y en un contexto ecológico (Nogales et al. 1998, 2002). En ellos se describe la dispersión secundaria de las semillas de una única especie de planta, el Espino de Mar (*Lycium intricatum*; Solanaceae), en cuyo sistema interviene un dispersor primario de dimensiones reducidas, el Lagarto Atlántico (*Gallotia atlantica*), y dos dispersores secundarios que son el Alcaudón Real (*Lanius meridionalis*) y el Cernícalo Vulgar (*Falco tinnunculus*). Los resultados más importantes obtenidos mostraron que el Alcaudón Real, aunque está considerado como un dispersor indirecto no especializado, favoreció la germinación de las semillas del Espino de Mar; mientras que el Cernícalo Vulgar destruyó gran parte de las semillas durante la segunda digestión. A pesar del interés de estos trabajos, sólo algunos aspectos como la viabilidad y germinación de las semillas antes y después de los diferentes tratamientos digestivos, fueron estudiados.

Sin embargo, existen varias cuestiones y factores importantes en el sistema de dispersión secundaria de semillas que quedaron sin resolver. El grosor de la testa y la dureza de las semillas después de los diferentes tratamientos digestivos, las distancias de dispersión de las semillas o el lugar de deposición de las mismas, así como el comportamiento de los diferentes dispersores, constituyen piezas clave en el mejor entendimiento de un proceso ecológico complejo que posibilita la dispersión de semillas a larga distancia.

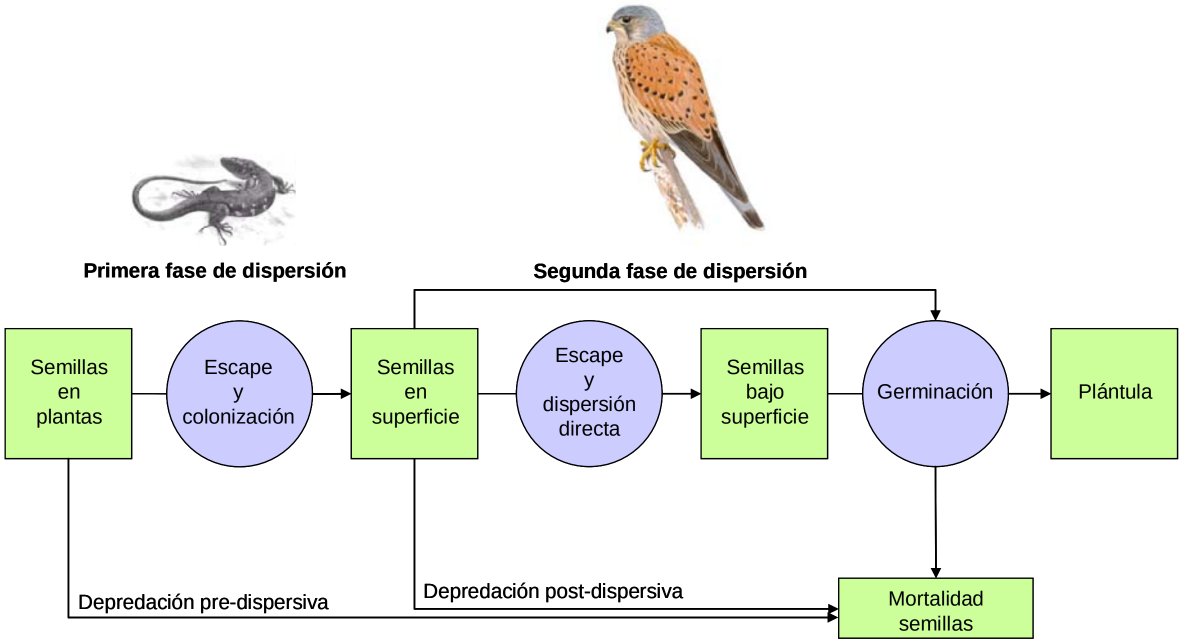


Figura 1.- Representación de los beneficios potenciales de la dispersión secundaria de semillas, desde que se desarrollan en la planta hasta que germinan y se establece una nueva plántula. Los rectángulos representan los estados físicos, las flechas representan los cambios de estados causados por la dispersión, la depredación o la germinación, y los círculos reflejan las ventajas más importantes de los procesos de dispersión. Figura obtenida y modificada a partir de Vander Wall & Longland (2004). Dibujo del lagarto de Peter J. Smit; dibujo del Cernícalo Vulgar de Juan M. Varela, tomada de la Enciclopedia Virtual de Vertebrados Españoles, Museo Nacional de Ciencias Naturales.

El Alcaudón Real (Lanius meridionalis)

El género *Lanius* (O. Passeriformes, F. Laniidae) engloba a 27 especies distribuidas por África, Asia, Europa y América del Norte (Lefranc & Worfolk 1997, del Hoyo et al. 2008). Con respecto a sus principales rasgos descriptivos, posee una máscara negra, una larga cola y un pico ganchudo adaptado a la depredación, semejante al de los falconiformes. Suele alimentarse de insectos y pequeños vertebrados, destacando su característico método de empalamiento de presas en arbustos espinosos. Con respecto al comportamiento de ensartar las presas, se han descrito muchas hipótesis. Algunos autores lo consideran como una herramienta para poder desmembrar las presas; otros, un método para emparentarse, marcar territorios, como despensa de alimento, o incluso para acceder a presas que pueden llegar a ser tóxicas (Yosef & Pinshow 2005, Antczak et al. 2005 y referencias citadas). Los alcaudones son aves territoriales en las que el macho es el principal encargado de defender el territorio, incluso fuera de la época de cría (Yosef 1992, Simek 2001, Soobramoney et al. 2004, Collister & Wilson 2007, Kriŝtín et al. 2007, Pasinelli et al. 2007). Los territorios tienen tamaños diferentes, entre 10 y 100 hectáreas, y la puesta suele estar compuesta por unos 4-6 huevos (del Hoyo et al. 2008).

El Alcaudón Real se considera actualmente una especie distinta al Alcaudón Norteño (*Lanius excubitor*) (Snow & Perrins 1998, Lefranc & Worfolk 1997, Sangster et al. 2002, del Hoyo et al. 2008), aunque en el pasado se encontraban englobadas en la misma especie. El Alcaudón Real se distribuye en zonas áridas de la región Saharo-Síndica y suroeste de Europa (sur de Francia y Península Ibérica), estando reconocidas unas diez subespecies distintas (Lefranc & Worfolk 1997). En Canarias habita la subespecie endémica *Lanius meridionalis koenigi*, una de las dos subespecies insulares que existen de Alcaudón Real y la única presente en el Atlántico. La otra subespecie insular es *L. m. uncinatus*, cuya distribución se restringe a la isla de Socotra (República de Yemen). En Canarias, *L. m. koenigi* ocupa las islas de Tenerife, Gran Canaria, Fuerteventura y Lanzarote, estando presente en zonas xéricas de matorral abierto tanto de zonas costeras como de alta montaña (Martín & Lorenzo 2001). Recientemente, estudios genéticos han demostrado cómo la subespecie canaria está más relacionada genéticamente con la subespecie del norte de África *L. m. algeriensis* que con la subespecie nominal *L. m. meridionalis,* que se encuentra en la Península Ibérica y sur de Francia (González et al. 2008, Klassert et al. 2008).

Previo a la realización de la presente Tesis Doctoral, ningún estudio específico había sido publicado en relación a la dieta o cualquier otro aspecto de la biología del Alcaudón Real en las islas Canarias. Sólo se tenía constancia de algunos datos de historia natural tomados en el islote de Alegranza (10.2 km^2), los cuales indicaban que los lagartos y los escarabajos eran la base principal de la dieta (Martín & Lorenzo 2001). Otros estudios llevados a cabo en el mismo islote, demostraron cómo el Alcaudón Real actuaba de forma efectiva como un dispersor secundario de semillas del Espino de Mar (*Lycium intricatum*), al depredar sobre el lagarto frugívoro *Gallotia atlantica* (Nogales et al. 1998, 2002). Sin embargo, en ecosistemas continentales sí que se habían realizado algunos estudios sobre la ecología trófica del Alcaudón Real. En el desierto de Néguev, situado al sur de Israel, trabajos llevados a cabo sobre la dieta de la subespecie *L. m. elegans/aucheri,* tanto de adultos como de pollos, mostraron que las principales presas consistían en lagartos y escarabajos (Yosef et al. 1991, Budden & Wright 2000). Por otro lado, investigaciones realizadas con la subespecie nominal *L. m. meridionalis* en la Península Ibérica (Hernández et al. 1993, Hernández 1995a, 1995b, 1995c, Hódar 2006) y en el sur de Francia (Lepley et al. 2004), demostraron que los artrópodos eran las presas principales en la dieta de los alcaudones durante todo el año. Asimismo, existen diferentes trabajos sobre la ecología trófica del Alcaudón Norteño (*L. excubitor*) que han posibilitado la realización de estudios comparativos sobre la influencia de la latitud en la dieta de los alcaudones. La dieta del Alcaudón Norteño se ha estudiado con mayor profundidad que la del Alcaudón

Real, destacando la presencia de mamíferos de pequeño tamaño durante todo el año (e.j. *Microtus* spp.) y observando un incremento en la proporción de aves durante el invierno, o en primavera para algunas poblaciones (Cade 1967, Huhtala et al. 1977, Bassin et al. 1981, Grünwald 1983, 1984, Olsson 1986, Atkinson & Cade 1993, Hromada & Krištín 1996, Lorek et al. 2000, Karlsson 2001, 2002). Finalmente, Schön (1998) y Lepley et al. (2004) observaron un claro gradiente latitudinal entre la dieta de los alcaudones. El Alcaudón Norteño, situado en hábitats más fríos y en latitudes más norteñas, se alimenta principalmente de presas endotérmicas, mientras que el Alcaudón Real, depreda principalmente sobre presas ectotérmicas en áreas más templadas, donde se sitúa su rango de distribución.

Respecto a la selección de presas por parte de los alcaudones, existe todavía bastante poca información. En los escasos estudios existentes, se ha considerado al Alcaudón Real como un depredador oportunista y generalista, que tiende a capturar las presas más abundantes en las diferentes épocas del año (Hernández et al. 1993). No obstante, otras investigaciones han demostrado que los alcaudones tienen preferencia por hábitats con abundancia de insectos de gran talla, reflejando así una clara selección del territorio debido a la disponibilidad de presas (Atkinson & Cade 1993, Hernández 1993, Lefranc & Worfolk 1997, Karlsson 2004). Teniendo en cuenta la teoría del forrajeo óptimo (Krebs et al. 1983), muchas veces, en condiciones extremas y normalmente con escasez de alimento, una forma de obtener el mayor aporte energético consiste en concentrarse en las presas de mayor tamaño (Craig 1978, Karlsson 2001). Diversos trabajos realizados por Karlsson (2001, 2002) con el Alcaudón Norteño en Finlandia, reflejan cómo esta especie puede cambiar su dieta en función de las condiciones climáticas, principalmente debido a la presencia o ausencia de nieve.

OBJETIVOS DE LA TESIS DOCTORAL

Los ecosistemas insulares oceánicos ofrecen un marco ideal para el estudio de procesos ecológico-evolutivos, que en los continentes resulta más complicado debido a la alta complejidad y al mayor número de especies que existe en ellos. Una de las tendencias más importantes que desarrollan los vertebrados terrestres en islas es la amplitud del hábitat y del nicho trófico, debido principalmente a la menor competencia y depredación que sufren las especies que logran colonizar las islas (Gorman 1979, Nogales 1999). La reducción de los competidores y depredadores también puede producir un aumento en la abundancia de las poblaciones insulares respecto al continente, dando origen al fenómeno denominado *compensación de densidades* (MacArthur 1972, Blondel et al. 1988). En las islas Canarias existen algunos ejemplos muy claros que cumplen la hipótesis de la compensación de densidades, como es el caso de los lagartos endémicos (Castanet & Báez 1988, Molina-Borja 1991, Rodríguez et al. 1994, Valido 1999, Olesen & Valido 2003), o algunas aves que, por lo general, suelen ser especies o subespecies endémicas del archipiélago (Carrascal & Palomino 2005).

La presente Tesis Doctoral se divide en dos grandes bloques conformados por el desarrollo de un total de cinco trabajos de investigación específicos, que se enumerarán a continuación utilizando para ello números romanos (I-V). El primero de estos bloques, que se denomina a partir de ahora “Ecología trófica del Alcaudón Real”, evalúa los patrones alimentarios de esta especie depredadora, y los posibles efectos tanto para la especie como para el ecosistema en el que habita. Asimismo, en dicho bloque también se establecen las diferencias encontradas entre los patrones observados en ecosistemas insulares y continentales. Por otro lado, el segundo de los bloques: "Dispersión secundaria de semillas en las islas Canarias", desarrolla en profundidad la interacción de los alcaudones con una de sus principales presas, los lagartos, y examina cuáles son las consecuencias que esta depredación puede tener para algunas especies vegetales que presentan frutos carnosos. Además, se compara este fenómeno con el producido por el Cernícalo Vulgar, otro depredador presente en Canarias que ocupa un nivel trófico similar y que incluye en su dieta una alta proporción de lagartos. Así, se valoran los efectos que producen ambas aves depredadoras en el sistema de dispersión secundaria de semillas en distintos hábitats del archipiélago canario. Específicamente, tres son los trabajos realizados en relación al estudio de la Ecología trófica del Alcaudón Real (I, II, III), y dos relacionados con la Dispersión secundaria de semillas en las islas Canarias (IV, V).

Ecología Trófica del Alcaudón Real

I. Dieta estacional de una población insular endémica de Alcaudón Real *Lanius meridionalis koenigi* en Tenerife, islas Canarias

En una primera aproximación al estudio de la ecología trófica del Alcaudón Real en las islas Canarias, se evaluó la composición estacional de la dieta teniendo en cuenta la disponibilidad de presas en un medio xérico situado en el sur de Tenerife. Además, se realizó un estudio de la amplitud de nicho trófico a lo largo de las diferentes estaciones y, por último, una comparación de los patrones tróficos encontrados en un ecosistema insular frente aquellos observados en diferentes ecosistemas continentales. Se compararon distintas poblaciones tanto de Alcaudón Real como de Alcaudón Norteño, comprobando cómo varía la dieta y la selección de presas en un gradiente latitudinal norte-sur.

II. Ecología trófica del Alcaudón Real (*Lanius meridionalis*) en hábitats insulares: la influencia de la altitud y la estacionalidad

En un segundo trabajo más profundo sobre la ecología trófica de los alcaudones reales en las islas Canarias, se estudió la influencia de la altitud y la estacionalidad en los distintos hábitats donde se encuentra presente la especie (zonas de matorral costero y de alta montaña). Para ello, se seleccionaron hábitats de piso basal de dos islas diferentes (Tenerife y Lanzarote), y otro situado en la alta montaña de la isla de Tenerife (Parque Nacional del Teide). Con ello se comprobó la variación de la dieta tanto a nivel interinsular como intrainsular. Además, teniendo en cuenta la mayor estacionalidad presente en la zona de alta montaña de Tenerife, con cambios muy bruscos entre los veranos calurosos e inviernos fríos y con presencia de nieve (Bustos & Delgado 2004), la hipótesis de partida era que el Alcaudón Real, en la alta montaña, presentaría una dieta más similar a las dietas continentales en comparación con las poblaciones situadas en el matorral costero, donde existe un clima claramente más homogéneo a lo largo de todo el año. También se realizó una aproximación a la teoría del forrajeo óptimo (Emlen 1966, Krebs et al. 1983), que predice cómo los depredadores obtienen el máximo de energía posible invirtiendo el menor esfuerzo. Bajo condiciones climáticas extremas, normalmente con una menor disponibilidad de alimento, una forma efectiva de obtener el aporte energético necesario consiste en seleccionar presas de mayor tamaño. Por ello, en la zona de alta montaña, la cual presenta condiciones climáticas extremas, cabía esperar que los alcaudones seleccionaran presas de mayor talla que en los hábitats costeros.

III. Selección de tallas de lagartos insulares por dos especies simpátricas de aves depredadoras

En el último de los trabajos de este primer bloque, se estudió la selección trófica de dos especies depredadoras que viven en simpatría en las diferentes estaciones del año, el Alcaudón Real y el Cernícalo Vulgar. Ambas especies tienen como base de su dieta durante todo el año a los lagartos endémicos del género *Gallotia*. Debido a que estas dos especies depredadoras poseen un nivel trófico muy similar y se alimentan de presas muy parecidas, tenemos un marco ideal para estudiar posibles fenómenos de competencia interespecífica o, por el contrario, si existe una segregación en la depredación de diferentes tallas de lagartos, evitando así la posible competencia.

Dispersión secundaria de semillas en las islas Canarias

IV. Sistemas de dispersión secundaria de semillas, lagartos frugívoros y aves depredadoras en zonas volcánicas de malpaíses insulares

En las islas Canarias, el papel que juegan los lagartos como dispersores de semillas es altamente significativo, ya que en el volumen total de sus dietas pueden llegar a incluir más de un 50% de frutos (Valido 1999, Valido & Nogales 1994, 2003, Valido et al. 2003, Roca et al. 2005, Rodríguez et al. 2008). En el archipiélago, los alcaudones y los cernícalos incluyen una alta proporción de lagartos en sus dietas. Esta depredación puede jugar un papel muy importante en los ecosistemas insulares, ya que en muchas ocasiones estas aves actúan como dispersores secundarios de semillas de distintas especies de plantas con frutos carnosos. El principal objetivo de este trabajo fue evaluar el efecto tanto de los dispersores primarios (lagartos) como de los secundarios (alcaudones y cernícalos), en el sistema de dispersión de semillas. Para ello, se compararon dichos efectos sobre tres especies distintas de plantas, que difieren en el tamaño y dureza de sus semillas. En primer lugar, se examinaron las correlaciones entre la aparición de semillas y los restos de lagartos en el interior de las egagrópilas de las dos aves depredadoras. Esto permitía cerciorarse de que estábamos frente a un fenómeno de dispersión secundaria de semillas, y éstas no procedían de una ingestión directa por parte de las aves. Por otro lado, se analizaron los efectos del paso de las semillas a través del tracto digestivo de los dispersores, observando las posibles consecuencias en el grosor de la testa, en la dureza, en la germinación o en la viabilidad, para cada una de las especies de plantas seleccionadas. Por último, se estudió la distribución espacial de semillas producida por los diferentes dispersores y se calcularon las distancias de movimiento de cada uno de ellos, para así tener una idea de la potencialidad de este sistema en la colonización de nuevos hábitats, dentro de una misma isla o incluso entre islas.

V. Comportamiento de los cernícalos en la depredación de lagartos frugívoros: implicaciones en la dispersión secundaria de semillas

Trabajos previos sobre la dispersión secundaria de semillas de diferentes especies de plantas, consideraban al Cernícalo Vulgar como un dispersor efectivo únicamente de las plantas con semillas de gran dureza y tamaño, ya que aquellas semillas de pequeño y mediano tamaño mostraban ser incapaces de resistir los jugos digestivos de esta rapaz diurna (Nogales et al. 2002, 2007). Estos estudios previos se realizaron mediante el análisis de las semillas aparecidas en el interior de las egagrópilas, estando sometidas a una doble digestión. Por otro lado, destacaba el hecho de que el número de semillas encontradas en las egagrópilas de los cernícalos, consecuencia de la interacción con los lagartos, era claramente inferior al que cabría esperar dada la alta proporción de lagartos que esta ave incluye en su dieta. Además, en los diferentes muestreos llevados a cabo durante la Tesis Doctoral para la colecta de egagrópilas de cernícalos, aparecieron también en los posaderos restos de tractos digestivos de lagartos con semillas en su interior, reflejando un comportamiento particular de la especie. Por todo lo anteriormente expuesto, el último de los objetivos planteados consistió en el estudio del comportamiento de depredación de los cernícalos sobre los lagartos, para comprobar qué influencia tenía dicho comportamiento en el sistema de dispersión de semillas. Para ello, se realizaron estudios tanto en el campo como en cautividad, pudiendo así controlar de forma exhaustiva todo el proceso de depredación y el destino final de las semillas.

MATERIALES Y MÉTODOS

Áreas de estudio

Las islas Canarias constituyeron el escenario donde se desarrolló toda la investigación de la presente tesis. Este archipiélago, de origen volcánico, se localiza en el extremo oriental del Océano Atlántico (27º37’-29º25’N, 13º20’-18º19’W), a unos 100 km de la costa africana. La mayor parte de los trabajos (I, II, III, IV) se llevaron a cabo en tres espacios naturales protegidos, dos de ellos en la isla de Tenerife (Malpaís de La Rasca y el Parque Nacional del Teide) y otro en Lanzarote (Malpaís de La Corona) (Fig. 2).

El Malpaís de La Rasca se encuentra situado en el extremo sur de Tenerife, estando declarado como Reserva Natural Especial (Martín et al. 1995). Posee una superficie de 3.15 km^2, con un clima xérico, una temperatura media anual de 22ºC y la menor precipitación media anual de la isla (98 mm; Marzol Jaén 1988). En este enclave pueden diferenciarse dos periodos estacionales: una estación seca que incluye la primavera y el verano (11,2 mm y 22,5º C de precipitación y temperatura media, respectivamente), y una estación húmeda que engloba el otoño y el invierno (86,7 mm y 22ºC de precipitación y temperatura media, respectivamente). La vegetación consiste en un matorral xerofítico abierto, con predominio de *Launaea arborescens*, *Lycium intricatum*, *Salsola divaricata*, *Schizogyne glaberrima*, *Euphorbia balsamifera, E. canariensis, Reseda scoparia, Periploca laevigata, Plocama pendula* y *Opuntia dillenii* (Arco-Aguilar et al. 1997). En esta área de estudio se desarrollaron los trabajos I, parte del II, y el III.

El Parque Nacional del Teide posee una superficie de 190 km^2 y se encuentra situado a unos 2.000 m sobre el nivel del mar. Es un área de alta montaña formada principalmente por elementos volcánicos de lapilli y rocas (Carracedo 2008). Posee un clima extremo, con inviernos fríos y presencia de nieve, y veranos secos y calurosos. La precipitación y temperatura media anual ronda los 400 mm y 11,5ºC, respectivamente (Bustos & Delgado 2004). Consiste en un matorral, donde destaca la abundancia de especies arbustivas endémicas como es el caso de la Retama del Teide y el Codeso de Cumbre (*Spartocytisus supranubius* y *Adenocarpus viscosus*, repectivamente; Fabaceae), además de otras especies como la Hierba Pajonera (*Descurainia bourgeauana*; Brassicaceae) o el Rosalito de Cumbre (*Pterocephalus lasiospermus*; Dipsacaceae) (Wildpret & Martín 2004). En este espacio natural protegido se llevó a cabo parte del trabajo II.

El Mapaís de La Corona está catalogado como Monumento Natural dentro de la Red de Espacios Protegidos de Canarias (Martín et al. 1995). Se encuentra situado en el norte de Lanzarote, presentando una superficie de 18 km^2. Este malpaís posee un origen relativamente reciente (≈ 21.000 años; Carracedo et al. 2003), y una precipitación y temperatura media anual de 157 mm y 21ºC, respectivamente. La vegetación está costituida por un matorral xerofítico abierto donde destacan especies como *Euphorbia regis-jubae*, *E. balsamifera*, *Launaea arborescens*, *Kleinia neriifolia*, además de especies con frutos carnosos como *Lycium intricatum*, *Rubia fruticosa*, *Asparagus nesiotes* y *A. arborescens*. En esta área de estudio se realizó parte del trabajo II, y el IV en su totalidad.

Por último, el estudio número V se desarrolló en nueve localidades diferentes situadas en las zonas de medianías del norte de Tenerife (Fig. 2). Estás áreas están caracterizadas por un clima xérico, con una temperatura y una precipitación media anual de 21ºC y 100-400 mm, respectivamente (Marzol Jaén 1988). La vegetación consiste en un matorral xerofítico abierto dominado por *Rubia fruticosa, Euphorbia obtusifolia, E. canariensis, Lycium intricatum, Withania aristata, Periploca laevigata* y diversas especies del género *Opuntia*.

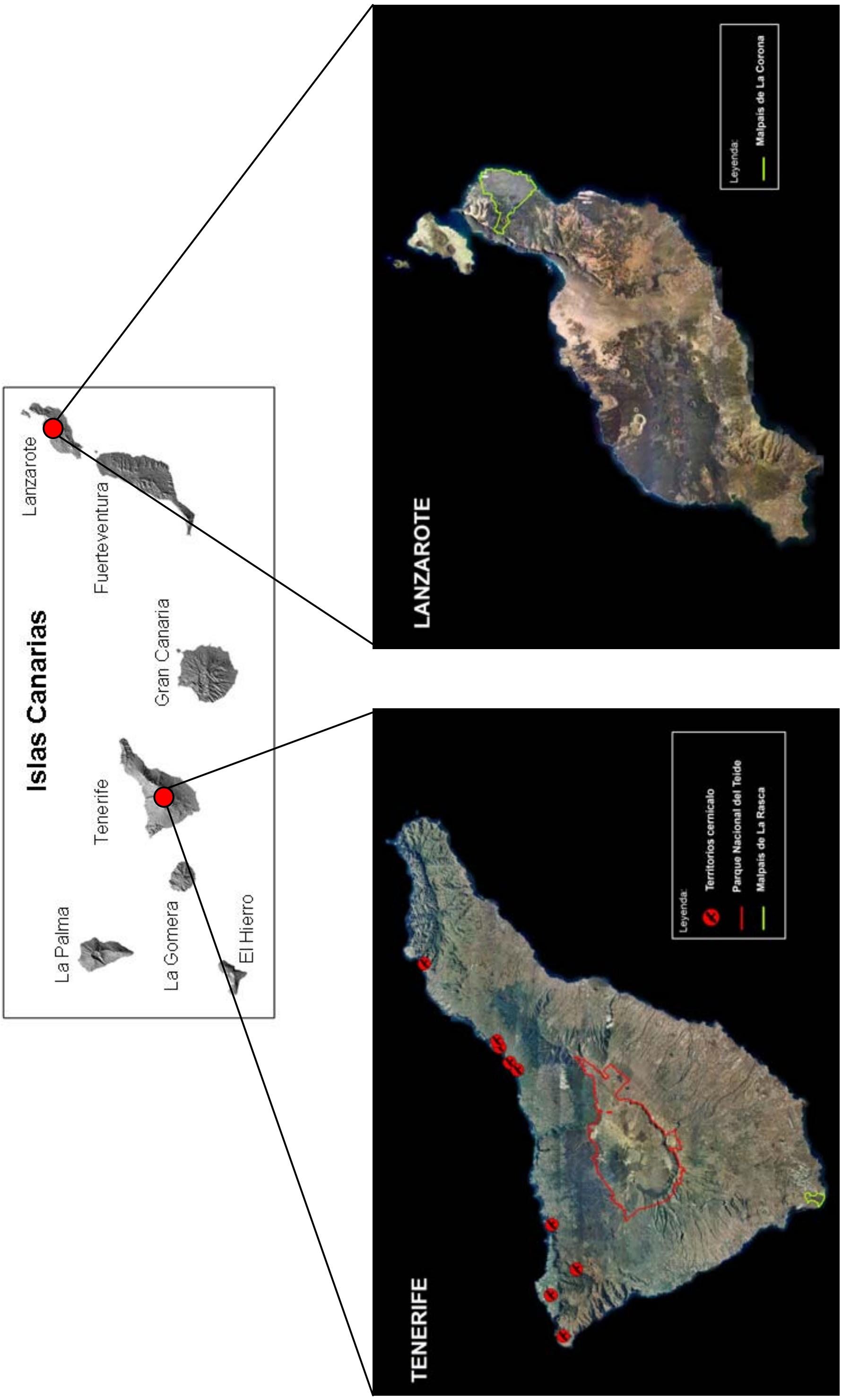


Figura 2.- Mapa de las áreas de estudio en las cuales se realizaron los distintos trabajos de la presente tesis doctoral.

METODOLOGÍA

I, II. Ecología Trófica del Alcaudón Real

El trabajo de campo relacionado con el estudio de la ecología trófica del Alcaudón Real se llevó a cabo a lo largo de un año en las diferentes áreas de estudio. En cada una de las estaciones del año se colectaron alrededor de 100 egagrópilas de alcaudones en cada localidad. Para evitar los posibles problemas de pseudoreplicación, se colectó un máximo de 10 egagrópilas por territorio, realizando una limpieza posterior de los distintos posaderos para evitar en siguientes muestreos la recogida de egagrópilas pertenecientes a la estación anterior. Un total de 1.139 egagrópilas fueron analizadas utilizando el método propuesto por Rosenberg & Cooper's (1990), mediante el cual se identificaron y contabilizaron todos los restos de artrópodos y vertebrados bajo una lupa binocular (16x).

Se obtuvo el número de individuos de cada tipo de presa en las diferentes estaciones. El peso húmedo de cada una de las presas se calculó utilizando para ello una media representativa de las distintas presas. Así, se analizó el aporte de biomasa de cada presa con respecto a la biomasa total.

Para el análisis de la selección trófica del Alcaudón Real, se calculó la disponibilidad de presas en los distintos hábitats donde la especie se encuentra presente. La cuantificación de la abundancia relativa de invertebrados se realizó mediante el conteo directo de todos los individuos (≥5 mm; Hernández et al. 1993) presentes en el interior de un área de 1 m^2 durante dos minutos. Un total de 210 recuentos se llevaron a cabo en cada una de las distintas estaciones y hábitats, distribuidos en un total de 42 transectos. La abundancia relativa de lagartos se calculó mediante 35 transectos lineales de 100 m de longitud en cada estación y hábitat, contabilizando todos los lagartos detectados en una banda de 5 m situada a ambos lados del observador (Díaz & Carrascal 1990).

El estudio de la selección de tallas por el Alcaudón Real, tanto de invertebrados como de lagartos, se desarrolló a través de la clasificación de los mismos en diferentes categorías. Los invertebrados se dividieron en cuatro categorías (pequeños: 5-10 mm; medianos: >10-15 mm; grandes: >15-20 mm; muy grandes: >20 mm). Por otro lado, los lagartos se clasificaron en tres categorías en función de la longitud hocico-cloaca (pequeños: < 5cm; medianos: 5-10 cm; grandes: >10cm).

III. Selección de tallas de lagartos por dos especies simpátricas

En las diferentes estaciones del año se colectó un total de 440 y 486 egagrópilas de alcaudones y cernícalos, respectivamente, en el Malpaís de La Rasca. Para evitar una posible seudoreplicación de datos, se analizó un máximo de 30 egagrópilas frescas de cernícalos y 10 de alcaudones, por territorio y estación. Cada egagrópila fue examinada individualmente, y en cada una de ellas se contabilizaron y midieron diferentes tipos de huesos de lagarto que proporcionaron información diagnóstica: fémures, húmeros, tibias, parietales y cinturas pelvianas, además de las mandíbulas y los maxilares. Las medidas obtenidas se emplearon en los modelos de regresión descritos por Nogales & Valido (1999), los cuales relacionan la longitud hocico-cloaca con las medidas de los huesos anteriormente mencionados.

El estudio de la selección de tallas se realizó mediante el cálculo de la abundancia relativa de los lagartos en las diferentes estaciones del año, siguiendo el método propuesto por Díaz y Carrascal (1990).

IV. Sistemas de dispersión secundaria de semillas

El trabajo de campo se desarrolló durante cuatro años consecutivos en el Malpaís de La Corona. Durante este periodo, se colectaron alrededor de 200 frutos (≈ 5 por planta) de tres especies distintas de plantas con frutos carnosos (*Lycium intricatum, Rubia fruticosa* y *Asparagus nesiotes*). Asimismo, se obtuvieron 566 excrementos de lagartos, 342 egagrópilas de alcaudones y 371 egagrópilas de cernícalos en un área de 4.000 m^2, minimizando así el posible efecto de la planta madre. Todo este material fue usado para evaluar el efecto del tratamiento digestivo de los distintos dispersores en la viabilidad y germinación de las semillas.

Las semillas detectadas en las diferentes muestras fueron clasificadas en función de su aspecto externo como semillas sanas y semillas dañadas. Aquellas en aparente buen estado fueron sometidas al test de viabilidad del tetrazolio (cloruro de trifenil tetrazolium; TTC). Se evaluó un total de 50 semillas por tratamiento. Por otro lado, se realizaron experimentos de germinación en un invernadero entre los meses de octubre a marzo, siguiendo las recomendaciones de Traveset & Verdú (2002), utilizando 200 semillas por tratamiento. El análisis de la reducción de la testa de las semillas, tras los diferentes tratamientos digestivos, se llevó a cabo en un total de 15 semillas por tratamiento, realizando diez medidas distintas en cada una de las semillas. Para ello se empleó un microscopio conectado a un ordenador con el software Image Pro-Plus vs. 4.5.1.2.2. La dureza de las semillas se calculó a través de una prensa electrónica (Zwick/Z100), y con la ayuda del programa "testxpart Machine".

Para el estudio de la distribución espacial de semillas producida por los diferentes dispersores, se contabilizaron las semillas dispersadas por cada uno de ellos en tres microhábitats previamente seleccionados (suelo, pequeños promontorios y grandes promontorios). Además, en estos mismos microhábitats se realizó un análisis de la abundancia relativa y distribución espacial de cada una de las especies de plantas estudiadas. Conjuntamente, se calcularon las distancias de movimientos de los dispersores secundarios, mediante observaciones directas y utilizando medidas de GPS asociadas con medidas en mapas de alta resolución, para evitar así posibles errores de muestreo.

V. Comportamiento de los cernícalos en la depredación sobre los lagartos

El estudio se realizó en el norte de Tenerife, en nueve localidades diferentes y en un total de 15 territorios de cernícalos. Las localidades se seleccionaron teniendo en cuenta que la especie *Rubia fruticosa* se encontrara presente. Se colectaron 200 frutos de 40 plantas distintas (control), para evaluar el efecto en la germinación de las semillas que pasan por el tracto digestivo de los distintos dispersores. Un total de 600 excrementos de lagartos, 660 egagrópilas de cernícalos y 36 tubos digestivos de lagartos desechados por los cernícalos, fueron a su vez colectados. Todas las muestras eran frescas, y las semillas encontradas en cada una de ellas se utilizaron para cuantificar la dispersión secundaria realizada por los cernícalos, así como para evaluar los efectos en la germinación.

La valoración del comportamiento de depredación de los cernícalos sobre los lagartos se realizó a través de experimentos en cautividad en el que se emplearon cinco cernícalos distintos (un adulto y un juvenil de cada sexo, y un macho subadulto). El estudio fue llevado a cabo en el centro de recuperación de La Tahonilla (Cabildo de Tenerife), en jaulas de 3,5 x 3 x 3 m. Todas las secuencias de depredación fueron grabadas a través de una cámara de vídeo conectada a un televisor externo. Los cernícalos fueron alimentados con un lagarto al día, hasta un total de 6 lagartos por cada uno de los cinco individuos. Antes de ser depredados, cada lagarto era medido, pesado, y se le introducían diversas “cuentas” de un color específico, similares en tamaño a *R. fruticosa*. De este modo, gracias a la fácil detección de las cuentas de colores, se pudo hacer un seguimiento minucioso del camino que seguirían las semillas tras la depredación. Además, se controló el tiempo de permanencia de las cuentas en el interior de los lagartos antes de la depredación, para comprobar si esto influía en el número de semillas indirectamente ingeridas por los cernícalos. En los días posteriores a la depredación, se colectaron los restos de lagarto desechados por los cernícalos (cabezas y tubos digestivos), y las egagrópilas de los cernícalos. De esta forma, se detectó el destino de todas las cuentas que fueron introducidas en el interior de los lagartos antes de la depredación.

Análisis de Datos

Se realizaron múltiples comparaciones, como la composición en las dietas, la selección de tallas, la abundancia de presas en la dieta, la comparación entre localidades, hábitats y estacionalidad, el número de semillas en las distintas muestras, el efecto de los tratamientos digestivos sobre las semillas, etc. Se emplearon diferentes tests, tanto paramétricos como no paramétricos (cuando los datos no admitían los requerimientos de un test paramétrico, incluso después de realizar las correspondientes transformaciones). Los diferentes tests utilizados fueron: Chi-cuadrado, Razón de Verosimilitud (“G”), ANOVA de uno y dos factores con pruebas a posteriori de Sheffé, ANOVA de dos factores anidado, test de Wilcoxon, Kruskal-Wallis, Mann Whitney, y Kolmogorov-Smirnov, además de otros tests multivariantes como el análisis de correspondencia corregido. Cuando fue necesario utilizar el mismo conjunto de datos, se tuvo en cuenta la corrección *a posteriori* de Bonferroni. Todos los análisis se realizaron con los paquetes estadísticos SPSS 14.0 y 15.0, y CANOCO.

Por otro lado, se emplearon diferentes índices con diferentes objetivos. El índice de Morisita se empleó para el estudio de la similaridad estacional de la dieta del alcaudón, el índice de Levin permitió analizar la amplitud de nicho trófico (Krebs 1989), mientras que el índice de forrajeo de Savage (1931) con las modificaciones propuestas por Manly et al. (1993), sirvió para el análisis de la selección trófica tanto de los alcaudones como de los cernícalos.

RESULTADOS

I. Dieta estacional de una población insular de Alcaudón Real

En este primer trabajo se analizaron 440 egagrópilas de alcaudones, identificando un total de 5.112 presas. El 85,4% de las presas correspondió a coleópteros, dominando los curculiónidos y tenebriónidos. En relación a la biomasa aportada por las diferentes presas, claramente fueron los vertebrados los que efectuaron un mayor aporte (87,6%), destacando los lagartos con un 64% de la biomasa total. La variación estacional de la dieta fue escasa, observándose una gran homogeneidad y un alto consumo de escarabajos y lagartos durante todo el año. El análisis de la selección trófica reveló una selección positiva sobre varias especies de coleópteros, himenópteros (no-Formicidae) y ortópteros, mientras que los arácnidos y los formícidos fueron seleccionados de forma negativa.

II. Ecología trófica del Alcaudón Real (*Lanius meridionalis*) en diferentes hábitats insulares

Se identificó un total de 10.179 presas en el análisis de 1.139 egagrópilas de Alcaudón Real, con un ratio 1:10 de vertebrados e invertebrados. No obstante, la biomasa estuvo claramente dominada por los vertebrados (94%) destacando, como presas principales, los lagartos (70%) y los ratones de campo (21%). La variación estacional de la dieta estuvo muy marcada en el hábitat de alta montaña, mientras que en las zonas costeras se observó una mayor homogeneidad en las distintas estaciones. El patrón de la variación estacional en la zona de alta montaña fue más similar a otras áreas continentales, como la Península Ibérica y el sur de Francia. Durante todo el año, la predominancia de los coleópteros en la dieta se vio reflejada en los distintos hábitats donde fue estudiada la dieta, excepto en la zona de alta montaña, donde únicamente se observó un aumento de la depredación de escarabajos en invierno. Así, otras presas como himenópteros y ortópteros destacaron en la dieta de los alcaudones de la alta montaña en verano y otoño, respectivamente. En relación a los vertebrados, el pico de depredación se observó en primavera y verano en la zona costera y de alta montaña de Tenerife, mientras que en Lanzarote la mayor depredación de vertebrados se produjo en otoño e invierno.

Para el estudio de la selección trófica, se calculó la abundancia relativa de presas en un matorral costero y en otro de alta montaña. A pesar de no encontrarse diferencias significativas en cuanto a la abundancia de presas entre ambas zonas, los alcaudones en la alta montaña depredaron más frecuentemente invertebrados y vertebrados de mayor talla.

III. Selección de tallas de lagartos realizada por dos especies simpátricas

En el presente estudio se comprobó la importancia de los lagartos en la dieta de dos especies de aves depredadoras que habitan, en numerosas ocasiones, en simpatría. Más del 50% de la biomasa total fue aportada por los lagartos tanto en la dieta del Alcaudón Real como en la del Cernícalo Vulgar. Los alcaudones capturaron tallas de lagartos más pequeños que los cernícalos durante todas las estaciones (media de la longitud hocico-cloaca: 7,4 ± 1,9 vs. 9,4 ± 2,1 cm, respectivamente). Los lagartos medianos fueron los más abundantes en la dieta de los alcaudones, mientras que en la de los cernícalos destacaron los medianos y grandes. Ambos depredadores presentaron el mismo patrón de depredación a lo largo del año, aumentando la ingestión de lagartos de gran talla en primavera.

Finalmente, considerando la disponibilidad de lagartos en el medio, los alcaudones presentaron una menor selección trófica que los cernícalos. Los alcaudones seleccionaron positivamente los lagartos de mediana talla (5-10 cm) en primavera, y negativamente los de pequeña talla (<5 cm) en otoño e invierno. Los cernícalos en cambio, reflejaron una mayor selección trófica, optando por los lagartos de gran talla (>10 cm) y descartando los de pequeña talla, durante todo el año.

IV. Sistemas de dispersión secundaria de semillas

Las semillas de las tres especies de plantas estudiadas aparecieron asociadas a restos de lagartos en el interior de las egagrópilas de los alcaudones y de los cernícalos. Esto indica que la procedencia de dichas semillas fue debido a la interacción frúgívoro-depredador. La mayor parte de las semillas encontradas correspondió a *Lycium* (74,7%), seguidas por las de *Rubia* (22,5%) y por último, por las de *Asparagus* (2,8%). En el análisis de las muestras, tanto del dispersor primario como de los dispersores secundarios, se observó como del total de las semillas encontradas el 68,5% fueron detectadas en el interior de las egagrópilas de los alcaudones, el 28,6% en los excrementos de los lagartos, y el 2,9% en las egagrópilas de los cernícalos. Las semillas de *Lycium* y de *Rubia* que pasaron por el tracto digestivo de los cernícalos, presentaron un menor grosor de testa si se comparan con las semillas control y aquellas dispersadas por los lagartos y por los alcaudones. En el caso de las semillas de *Asparagus*, se observó la menor reducción en la testa con respecto a las semillas control, pero debido al bajo tamaño muestral no fue posible realizar ningún tipo de análisis estadístico. En concordancia con los datos de los análisis del grosor de la testa, las semillas de *Lycium* y *Rubia* que fueron dispersadas secundariamente por los cernícalos, presentaron valores de viabilidad y germinación claramente inferiores al resto.

En relación a la distribución espacial de semillas llevada a cabo por cada uno de los dispersores, se observó un uso diferencial de los diferentes microhábitats estudiados. Así, los lagartos fueron los que transportaron un mayor número de semillas al microhábitat de suelo, mientras que los alcaudones y los cernícalos realizaron lo propio en los pequeños y grandes promontorios, respectivamente. Finalmente, se detectaron considerables diferencias en las distancias de movimientos de los dispersores primarios y secundarios. Los cernícalos fueron los que realizaron los movimientos de mayor distancia (506,4 ± 361,2 m; rango 75-1500 m), seguidos de los alcaudones (76,0 ± 49,9 m; rango: 75-250 m) y por último, los lagartos con las distancias más cortas (1,22 m; rango: 0,6-2,5 m; Gómez & Bravo, com. pers.).

V. Comportamiento de los cernícalos en la depredación de lagartos

En el análisis de las egagrópilas de cernícalos del norte de Tenerife, se comprobó cómo todas las semillas de *Rubia fruticosa* se encontraban asociadas a restos de lagartos. Por otro lado, debido al comportamiento de depredación de estas aves, se encontraron y analizaron numerosos tubos digestivos de lagartos. El mayor número de semillas por muestra fue detectado en el interior de los tubos digestivos de los lagartos, seguido por los excrementos de lagartos y por último, el menor número apareció en el interior de las egagrópilas de los cernícalos. Las semillas control y las obtenidas en los tubos digestivos de los lagartos fueron las que presentaron significativamente un mayor porcentaje de germinación, seguidas de las semillas procedentes de los excrementos de los lagartos, y finalmente de aquellas encontradas en las egagrópilas de los cernícalos.

Las pruebas en cautividad mostraron un comportamiento de depredación sobre los lagartos similar en todos los cernícalos. En todos los casos analizados (n = 30), los cernícalos, una vez capturaban un lagarto, lo decapitaba y seguidamente desechaba su tubo digestivo (desde el estómago hasta la cloaca). Tras la depredación, el número de cuentas (simulando semillas) encontradas en el interior de los tubos digestivos fue claramente superior (89%) al número de cuentas encontradas en las egagrópilas (11%). Estas cantidades no se vieron influenciadas por el tamaño de los lagartos; sin embargo, el tiempo de permanencia de las cuentas en el interior de los lagartos sí que influyó en el número de cuentas que era ingerido indirectamente por los cernícalos. El número final de cuentas encontrado en las egagrópilas, aumentaba cuando los cernícalos depredaban sobre los lagartos con tres horas o menos de retención de cuentas en su interior.

DISCUSIÓN GENERAL

Ecología trófica del Alcaudón Real

Las investigaciones relacionadas con la ecología trófica de las especies permiten el conocimiento de muchas de las interacciones que se producen en los ecosistemas, facilitando la detección de especies claves claramente influyentes en el mantenimiento y equilibrio de otras muchas especies. La relativa simplicidad de las islas oceánicas con respecto a las zonas continentales, en términos de diversidad de especies y de interacciones ecológicas (Carlquist 1974, Olesen & Jordano 2002), hacen de estos lugares escenarios idóneos para el estudio de fenómenos ecológico-evolutivos, como por ejemplo los estudios de ampliación de nicho trófico de algunos vertebrados (Grant 1965, MacArthur 1972, Nogales & Hernández 1994).

La dieta del Alcaudón Real en las islas Canarias estuvo dominada por insectos (principalmente coleópteros) en cuanto a número de presas, y por lagartos en relación a la biomasa aportada en la dieta. En general, los alcaudones presentaron una tendencia hacia la depredación sobre las presas más abundantes en el medio, reflejando un carácter generalista previamente descrito para la especie en zonas continentales (Hernández 1993, Lefranc & Worfolk 1997). En las islas, la dieta estuvo dominada por animales ectotérmicos, lo que apoya la hipótesis de la variación latitudinal en la dieta de los alcaudones propuesta por Schön (1998) y Lepley et al. (2004). Si se comparan las dietas del Alcaudón Norteño, situado en latitudes más frías del norte de Europa con la dieta del Alcaudón Real, en latitudes más cálidas del sur, se observa una clara dominancia de animales endotérmicos (mamíferos) en los primeros (Bassin et al. 1981, Grünwald 1984, Olsson 1986, Schön 1998, Karlsson 2002), y de ectotérmicos (insectos y reptiles) en los segundos (Yosef et al. 1991, Hernández et al. 1993, Budden & Wright 2000, Hódar 2006).

La proporción de lagartos en la dieta de los alcaudones del archipiélago es la mayor registrada hasta la actualidad, lo que permite considerar a los lagartos como una pieza clave en estos ecosistemas insulares. La elevada cantidad de lagartos detectada en la dieta es debida, principalmente, a la abundancia de estos reptiles en todos los hábitats de las islas. En general, algunos animales que logran colonizar las islas presentan mayores abundancias con respecto a las especies continentales, todo ello como consecuencia de la escasa depredación y competencia que sufren, además de que desarrollan una ampliación de su nicho trófico (Case 1975, Benett & Gorman 1979, Evans & Evans 1980, Brown et al. 1992, Olesen & Valido 2003). Este fenómemo (compensación de densidades) también ocurre en las islas Canarias, y los lagartos del género *Gallotia* constituyen un claro ejemplo (Castanet & Báez 1988, Molina-Borja 1991, Rodríguez et al. 1994, Valido 1999, Olesen & Valido 2003).

En el análisis de la dieta de los alcaudones en los distintos hábitats donde la especie se encuentra presente, se observó una mayor variación estacional en la zona de alta montaña respecto al matorral costero. Los cambios climáticos, bruscos y estacionales, detectados en la zona de Las Cañadas del Teide sugieren que los alcaudones se comportan como depredadores oportunistas en las diferentes estaciones, aprovechando los recursos que presentan una mayor disponibilidad en cada una de ellas. La teoría del forrajeo óptimo predice una maximización de energía por parte de los depredadores, concentrándose en las presas más abundantes del momento (MacArthur & Pianka 1966). En Las Cañadas, la dieta está caracterizada por diferentes taxones: himenópteros polinizadores en primavera y verano, coincidiendo con la época de floración de la zona; ortópteros en verano y otoño, encontrándose el pico de disponibilidad de saltamontes en estas estaciones; y coleópteros (Scarabaeidae) en invierno, tras su explosión poblacional con las primeras lluvias. Como consecuencia de un drástico cambio en el ambiente o en la disponibilidad de los recursos, los depredadores no especialistas son capaces de alterar sus dietas con gran facilidad, incluyendo nuevos taxones que les sean energéticamente rentables (Ben-David et al. 1997, Correia 2001). La mayor estacionalidad detectada en la dieta de la alta montaña refleja patrones similares a los encontrados en algunas áreas continentales, como la Península Ibérica y el sur de Francia (Hernández et al. 1993, Lepley et al. 2004, Hódar 2006). Estas áreas, al igual que Las Cañadas, presentan estaciones muy marcadas con inviernos fríos y húmedos, y veranos secos y calurosos.

En relación a los vertebrados, el mayor número de lagartos depredados por los alcaudones en los dos hábitats de Tenerife se encontró en primavera y verano, coincidiendo con las épocas de nidificación y abandono de los pollos del nido. En el sur de la Península Ibérica se ha observado el mismo patrón, aumentando la depredación de lagartos durante el periodo de cría de los alcaudones (Hódar 2006). Sin embargo, a pesar de que en el periodo de reproducción la depredación de lagartos fue elevada en Lanzarote, la mayor proporción de lagartos se detectó en otoño e invierno, posiblemente aprovechando la explosión de juveniles en estas épocas (Valido 1999).

La selección de presas por parte de los alcaudones en Canarias reveló que los individuos presentes en la zona de alta montaña capturan los invertebrados y los lagartos de mayor talla. Diferentes estudios han demostrado la preferencia de los alcaudones por hábitats de forrajeo con abundancia de grandes insectos (Atkinson & Cade 1993, Hernández 1993, Lefranc & Worfolk 1997, Karlsson 2004). Asimismo, los datos son coherentes con la teoría del forrajeo óptimo, la cual predice que los depredadores obtienen el máximo de energía con el menor esfuerzo posible (Emlen 1966, Krebs et al. 1983). Por otro lado, en condiciones climáticas adversas y normalmente con escasez de alimento, una forma efectiva de obtener la mayor cantidad de energía posible es concentrándose en las presas de mayor tamaño, siempre y cuando sean las más rentables (Craig 1978, Karlsson 2001).

Otro de los factores destacables en el estudio de la ecología trófica es la competencia entre especies que ocupan el mismo nivel trófico. Sin embargo, muchas veces la coexistencia de estas especies en una comunidad se ve facilitada por la segregación de alguno de los nichos, o del uso diferencial de un recurso clave (Schoener 1974, Chesson & Huntly 1997, Barrientos & Virgós 2006). En la presente tesis se comprobó la importancia de los lagartos en la dieta de dos especies que a menudo habitan en simpatría, el Alcaudón Real y el Cernícalo Vulgar. Dado que se trata de dos depredadores no especialistas, el elevado consumo de lagartos es atribuible a las altas densidades de esta presa en los distintos hábitats de Canarias (Olesen & Valido 2003). Teniendo en cuenta las diferentes hipótesis sobre competencia interespecífica, cuando un recurso clave en las dietas de dos especies simpátricas se hace abundante, se observa un gran solapamiento en las dietas debido a la relajación de la competencia (Lack 1946, Schoener 1982, Gerstell & Bednarz 1999). En el Malpaís de La Rasca, se comprobó cómo los alcaudones seleccionaron lagartos de menor talla que los cernícalos, realizando ambas especies un uso diferencial de los lagartos, evitando así, la posible competencia entre ellos. Además, existe una correlación positiva entre la talla de las especies y la energía requerida por cada una de ellas (Julien-Laferriere 1999, García & Arroyo 2005). Diversos estudios han señalado que los alcaudones seleccionan presas de pequeño y mediano tamaño, evitando las de gran talla (Yosef 1993, Hernández 1995a, Probst et al. 2003). Esto se puede considerar como un compromiso entre el tamaño de la presa y la energía invertida en la captura, transporte y manipulación de la misma. Por otro lado, ambos depredadores utilizan diferentes técnicas en la captura de sus presas; los alcaudones suelen esperan en los posaderos la aparición de la presa, mientras que los cernícalos suelen detectar a las presas en vuelo. Por ello, la técnica empleada por los cernícalos se puede considerar energéticamente más costosa (Masman et al. 1988), seleccionando así presas de mayor tamaño (lagartos) y evitando aquellas de pequeña talla.

Dispersión secundaria de semillas en las islas Canarias

La importancia de los lagartos como dispersores de semillas en islas se ha demostrado en diversas investigaciones (Pérez-Mellado & Corti 1993, Pérez-Mellado & Traveset 1999, van Damme 1999, Cooper & Vitt 2002, Olesen & Valido 2003, Rodríguez et al. 2008). En las islas Canarias, los lagartos frugívoros del género *Gallotia* en ocasiones pueden ser depredados por aves de presa, las cuales pueden actuar como dispersoras secundarias de semillas (Nogales et al. 1998, 2002). Esta interacción produce un proceso de doble endozoocoria, con diversas consecuencias para las semillas. En la presente tesis se estudia en profundidad el efecto tanto del dispersor primario (lagartos) como de sus dos principales depredadores en las islas (Alcaudón Real y Cernícalo Vulgar), sobre las semillas de tres especies de plantas con frutos carnosos (*Lycium intricatum*, *Rubia fruticosa* y *Asparagus nesiotes*).

El elevado número de semillas de *Lycium* detectado en las diferentes interacciones se debe principalmente a la abundancia de semillas por fruto que presenta la especie (*Lycium*: 7,43 ± 3; *Rubia*: 1,4 ± 0,3; *Asparagus*: 1 ± 0; Nogales et al. 2002, 1999), y al largo periodo de fructificación de la misma. Además, a pesar de que en la interacción *Gallotia* x *Lanius* fue donde se detectó el mayor número de semillas dispersadas (65%), los lagartos claramente dispersan un número superior de semillas, debido a la alta densidad de éstos en las islas. La diferencia en el número de semillas detectado, es consecuencia del bajo tiempo de retención de las semillas en el interior de los alcaudones frente a los lagartos (45-55 min y 2,4 ± 1,5 días, respectivamente; Olsson 1985, Valido & Nogales 2003).

El efecto del tratamiento digestivo de cada uno de los dispersores afectó de manera singular a cada especie de semilla. El tratamiento digestivo de los cernícalos disminuyó de forma considerable el grosor de la testa, la viabilidad y la germinación de las semillas de pequeño y mediano tamaño (*Lycium* y *Rubia*), mientras que los lagartos y los alcaudones no tuvieron consecuencias negativas sobre las mismas. Sin embargo, las semillas de gran dureza y tamaño (*Asparagus*), resistieron en perfecto estado el tratamiento digestivo de esta rapaz diurna. Todo parece indicar que la fuerte acción enzimática de los jugos gástricos de los cernícalos (Duke et al. 1976, Brown et al. 1993), junto al elevado tiempo de retención de las semillas en el interior de su tracto digestivo (12-23,5h; Balgooyen 1971), produce una clara disminución en la viabilidad de las semillas de pequeño y mediano tamaño.

La distribución espacial de las semillas producida por los distintos dispersores fue claramente diferencial. Teniendo en cuenta que las diferentes especies de plantas se encuentran presentes en los tres microhábitats seleccionados, existe una alta probabilidad de que el origen de esas plantas pueda deberse al particular uso del hábitat de cada uno de los distintos dispersores.

En un primer momento y con los datos que se tenían hasta la fecha, los resultados indicaban que los alcaudones podían ser considerados como vectores de dispersión de larga distancia más efectivos y frecuentes que los cernícalos. Sin embargo, el comportamiento de depredación detectado en los cernícalos sobre los lagartos modifica el concepto que se tenía de esta especie como un dispersor secundario de semillas poco eficiente. Los resultados obtenidos en el trabajo de campo, así como los derivados de las pruebas en cautividad, permitieron detectar un nuevo proceso de dispersión secundaria de semillas producido por los cernícalos, en el que sólo se incluye un único evento de endozoocoria. Una vez los cernícalos capturan a los lagartos y los trasladan a los posaderos, realizan su técnica particular de manipulación de la presa, consistente en desechar las cabezas y los tubos digestivos (con numerosas semillas en su interior), consumiendo el resto de la presa. De este modo, las semillas quedan exentas del fuerte tratamiento digestivo de los cernícalos y, por tanto, éstos actúan como dispersores legítimos de las semillas. Los datos de germinación se realizaron con semillas procedentes de distintos tratamientos: 1) control de *Rubia fruticosa*, 2) dispersadas por lagartos, 3) indirectamente ingeridas por los cernícalos y, 4) procedentes de los tubos digestivos de lagartos desechados por los cernícalos. Dichos datos revelaron cómo las semillas eran incapaces de resistir, en su gran mayoría, la fuerte acción enzimática de los tratamientos digestivos de los cernícalos, que reducían considerablemente la capacidad de germinación de las mismas. Por el contrario, las semillas procedentes de los tubos digestivos de los lagartos mantenían una alta capacidad de germinación, similar a las semillas control. Las características morfológicas y fisiológicas de los sistemas digestivos de los frugívoros, además de otros factores como el tiempo de retención o la escarificación de las semillas, influyen de manera notoria en la viabilidad y germinación de las semillas (Jordano 2000, Traveset 1998, Rodríguez-Pérez et al. 2005, Traveset et al. 2008).

Los experimentos realizados con los cernícalos en cautividad nos permitieron cuantificar de forma precisa la dispersión secundaria de semillas producida por esta rapaz. Se comprobó cómo la técnica de depredación de los cernícalos sobre los lagartos parece ser un comportamiento estereotipado, ya que en la totalidad de los casos se observó la misma secuencia: 1) captura, 2) decapitación y 3) eliminación de los tubos digestivos de los lagartos. Otros estudios realizados con cernícalos en cautividad han demostrado que el comportamiento de depredación de la especies no se ve modificado ni por la cautividad ni por la talla de las presas (Csermely et al. 1989, Csermely 1994). Al realizar la cuantificación del número de semillas dispersadas secundariamente por los cernícalos, se comprobó que la mayor parte de ellas acababan en el interior de los tubos digestivos de los lagartos desechados por los cernícalos. Por otro lado, un exiguo número de semillas aparecía posteriormente en el interior de las egagrópilas, debido a la ingesta involuntaria realizada por esta rapaz. Igualmente, se observó cómo este número de semillas disminuía a medida que éstas permanecían más tiempo en el interior del lagarto antes de ser depredado.

Por lo tanto, teniendo en cuenta los datos de germinación y la alta proporción de semillas encontradas en el interior de los tubos digestivos de los lagartos, se puede concluir que los cernícalos han de ser considerados como dispersores efectivos de semillas en las islas Canarias. Esta dispersión podría ser similar a la producida por el Alcaudón Real, el cual estaba considerado como un dispersor secundario altamente eficiente (Nogales et al. 1998, 2002, 2007).

Los sistemas de dispersión de semillas a larga distancia son eventos raros y estocásticos, cuya detección y cuantificación suele ser muy difícil (Higgins & Richardson 1999, Clark et al. 2001, Nathan 2006, Nathan et al. 2008). No obstante, la importancia de estos procesos normalmente es crucial para el mantenimiento de la estructura genética de las poblaciones, para aumentar el rango de expansión de una especie o para la colonización de nuevos hábitats (Cain et al. 2000, Nathan 2006, Nathan et al. 2008). En islas oceánicas como el archipiélago canario, es muy común la formación de zonas volcánicas recientes debido a las continuas erupciones. Así, se originan mosaicos volcánicos de sustratos jóvenes y antiguos donde los eventos singulares que se producen en estas islas, como el fenómeno de la dispersión secundaria de semillas, facilitan la dispersión y colonización de un gran número de especies vegetales. Debido a la alta proporción de lagartos frugívoros en la dieta de los alcaudones y de los cernícalos, y al efecto de éstos sobre las semillas, podríamos concluir que la dispersión secundaria de semillas en las islas Canarias puede ser considerada como un fenómeno regular que se produce año tras año, permitiendo la colonización de nuevas áreas por parte de numerosas especies de plantas, tanto dentro de una misma isla como incluso entre islas.

CONCLUSIONES

I. En Canarias, los alcaudones poseen una dieta generalista con una alta capacidad de modificación en función de la disponibilidad de presas. No obstante, la base alimentaria está dominada por insectos (principalmente coleópteros) en cuanto a número de presas, y por vertebrados respecto a la biomasa, destacando los lagartos durante todo el año.

II. Existe un gradiente latitudinal en la dieta de los alcaudones, observándose cómo el Alcaudón Real situado en latitudes más cálidas posee una clara preferencia por presas ectotérmicas, mientras que la dieta del Alcaudón Norteño, distribuido en latitudes más frías, está dominada por presas endotérmicas. En las latitudes meridionales ocupadas por los alcaudones reales, el rigor climático más templado de las estaciones frías permite que las presas ectotérmicas estén disponibles durante todo el año.

III. Se detectó una escasa variación estacional en la dieta de los alcaudones que habitan las zonas costeras de las islas. Sin embargo, debido a los drásticos cambios estacionales que se producen en la alta montaña, los alcaudones de estas zonas fueron capaces de modificar su alimentación para maximizar la energía requerida, detectándose una mayor heterogeneidad a lo largo del año. Este hecho hace que la dieta en la alta montaña sea similar a la que presenta la especie en áreas continentales como la Península Ibérica o el sur de Francia.

IV. A pesar de la escasa selección trófica que de forma general realizó el Alcaudón Real en Canarias, la especie mostró una preferencia por la captura de presas de gran talla, tanto de invertebrados como de lagartos, en el hábitat de alta montaña. Este hecho apoya la hipótesis de que en condiciones climáticas adversas, normalmente con escasez de alimento, una forma eficiente de obtener el máximo de energía consiste en concentrarse en las presas de mayor tamaño.

V. Los lagartos constituyeron una pieza clave en la dieta de los alcaudones, hecho que se repite con el Cernícalo Vulgar, siendo ésta una especie depredadora que ocupan un nivel trófico similar. El estudio de la selección de tallas de lagartos por ambas especies depredadoras reveló un uso diferencial de las distintas tallas, evitando así posibles procesos de competencia cuando tanto alcaudones como cernícalos se encuentran en simpatría.

VI. En Canarias, los alcaudones y los cernícalos actúan como dispersores secundarios de semillas al depredar sobre los lagartos frugívoros del género *Gallotia*. Las semillas de las plantas estudiadas aparecieron asociadas a restos de lagartos en el interior de las egagrópilas de ambos depredadores, indicando así que su presencia fue debida a la interacción frugívoro-depredador.

VII. El grosor de la testa de las semillas, en las tres especies de plantas estudiadas, se vio reducido al pasar por el tracto digestivo de los distintos dispersores. La mayor reducción se detectó en las semillas de pequeño y mediano tamaño (*Lycium* y *Rubia*) que sufrieron una segunda ingestión por parte de los cernícalos.

VIII. El paso por le tracto digestivo de los lagartos y los alcaudones no afectó negativamente a la viabilidad y germinación de las semillas; sin embargo, las semillas de *Lycium* y *Rubia* que pasaron por el de los cernícalos presentaron valores de viabilidad y germinación claramente inferiores al resto. No obstante, las semillas de *Asparagus*, caracterizadas por ser las de mayor tamaño y dureza, resistieron totalmente los jugos gástricos de esta rapaz diurna.

IX. Los distintos dispersores realizaron una distribución diferencial de las semillas en los microhábitats seleccionados, lo que sugiere que el establecimiento de las plantas en cada uno de ellos es debido a la dispersión producida por cada dispersor.

X. A pesar de que el Cernícalo Vulgar fue considerado en un principio como un dispersor ilegítimo de las semillas de pequeño y mediano tamaño, el estudio del comportamiento de depredación sobre los lagartos reveló que esta rapaz puede ser clasificada como un dispersor efectivo de todas las semillas que dispersan directamente los lagartos. Tras la captura y transporte de esta presa a los posaderos, los cernícalos decapitan a los lagartos y desechan los tubos digestivos, los cuales contienen numerosas semillas en su interior.

XI. Las semillas detectadas en el interior de los tubos digestivos de los lagartos desechados por los cernícalos, permanecieron con una alta viabilidad y capacidad de germinación. Esto se debió a que no se vieron sometidas a la potente acción de los jugos gástricos de los cernícalos, los cuales afectan negativamente y de forma considerable a las semillas pequeñas y medianas de las plantas estudiadas.

XII. La dispersión secundaria de semillas en Canarias es un proceso de dispersión a larga distancia común y efectivo, que puede facilitar y haber facilitado la colonización de nuevas áreas a numerosas especies de plantas.

REFERENCIAS

ARCO-AGUILAR, M. DEL, ACEBES-GINOVÉS, J. R., RODRÍGUEZ-RODRÍGUEZ, A., PADRÓN, P., RODRÍGUEZ-DELGADO, O., PÉREZ-DE-PAZ, P. L. & WILDPRET DE LA TORRE, W. 1997. Cormophytic vegetation of the Malpaís de La Rasca, Tenerife (Canary Islands). *Fitosociologia,* 34: 159-170.

ATKINSON, E. C. & CADE, T. J. 1993. Winter foraging and diet composition of Northern Shrikes in Idaho. *Condor*, 95: 528-535.

ANTCZAK, M., HROMADA, H., & TRYJANOWSKI, P. 2005. Spatio-temporal changes in Great Grey Shrike *Lanius excubitor* impaling behaviour: from food caching to communication signs. *Ardea,* 93: 101-107.

BALGOOYEN, T. G. 1971. Pellet regurgitation by captive Spar-row Hawks (*Falco sparverius*). *Condor*, 73: 382-385.

BARRIENTOS, R. & VIRGÓS, E. 2006. Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. *Acta Oecologica.* 30: 107-116.

BASSIN, P., HUBER, C. & ZUBER, M. 1981. Beitrag zur Ernahrung des Raubwürgers (*Lanius excubitor*) in der Nordwestschweiz (Ajoie, Kanton Jura). *Jahrbuch fur Naturhistorisches Museum Bern,* 8: 1-19.

BEN-DAVID, M., FLYNN, R. W. & SCHELL, D. M. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia,* 111: 280-291.

BENETT, A. F. & GORMAN, G. C. 1979. Population density and energetics of lizards on a tropical island. *Oecologia*, 42: 339-358.

BLONDEL, J., DERVIEUX, A., MAISTRE, M. & PERRET, P. 1991. Feeding ecology and life history variation of the Blue Tit in Mediterranean deciduous and sclerophyllous habitats. *Oecologia*, 88: 9-14.

BLONDEL, J., CHESSEL, D. & FROCHOT, B. 1988. Bird species impoverishment, niche expansion, and density inflation in mediterranean island habitats. *Ecology,* 69: 1899-1917.

BROWN, R. P., PÉREZ-MELLADO, V., DIEGO-RASILLA, J., GARCÍA, J. A., NARANJO, A. & SPEAKMAN, J. R. 1992. Individual and population energetics of a lizard on a Mediterranean islet. *Oecologia*, 91: 500-504.

BROWN, R. W., LAWRENCE, M. J. & POPE, J. 1993. Animal Tracks, Trails and Signs. Hamlyn Publishing Group Limited, London.

BUCKLEY, L. B. & JETZ, W. 2007. Insularity and the determinants of lizard population density. *Ecology Letters,* 10: 48-489.

BUDDEN, A. E., & WRIGHT, J. 2000. Nestling diet, chick growth and breeding success in the Southern Grey Shrike (*Lanius meridionalis*). *In*: Yosef, R., Lohrer, F. E., Van Nieuwenhuyse, D. & Busse, P. (eds.), Proceeding of the 3rd International Shrike Symposium. 15-18 September 2000, Gdansk, Poland. *Ring,* 22: 165-172.

BUSTOS J. J., & DELGADO, F. S. 2004. *Clima. In*: Canseco (ed.), Parque Nacional del Teide. Canseco Editores, Madrid. 73-96.

CADE, T. J. 1967. Ecological and behavioural aspects of predation by the Northern Shrike. *Living Bird,* 6: 43-86.

CAIN, M. L., MILLIGAN, B. G. & STRAND, A. E. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany*. 87: 1217-1227.

CARLQUIST, S. 1974. *Island Biology*. Columbia University Press, NY.

CARRACEDO, J. C. 2008. *El volcán del Teide: geología y volcanología del Teide y las dorsales.* Ediciones y Promociones Saquiro S. L., Santa Cruz de Tenerife.

CARRACEDO, J. C., SINGER, B., JICHA, B., GUILLOU, H., RODRÍGUEZ BADIOLA, E., MECO, J., PÉREZ TORRADO, F. J., GIMENO, D., SOCORRO, S. &

LÁINEZ, A. 2003. La erupción y el tubo volcánico del volcán de La Corona (Lanzarote, Islas Canarias). *Estudios Geológicos*, 59: 277-302.

CARRASCAL, L. M. & PALOMINO, D. 2005. Preferencias de hábitat, densidad y diversidad de las comunidades de aves en Tenerife (Islas Canarias). *Animal Biodiversity and Conservation*, 28: 101-119.

CASE, T. J. 1975. Species number, density compensation, and colonizing ability of lizards on islands in the Gulf on California. *Ecology*, 56: 3-18.

CASTANET, J. & BÁEZ, M. 1988. Date on age and longevity in *Galloti galloti* (Sauria, Lacertidae) assessed by skeletochronology. *Herpetological Journal,* 1: 218-22.

CHESSON, P. & HUNTLY, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, 150: 519-553.

CLARK, J. S, LEWIS, M. & HORVATH, L. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist,* 157: 537-554.

CLARKE R., COMBRIDGE P. & MIDDLETON, N. 2003. Monitoring the diets of farmland winter seed-eaters through raptor pellet analysis. *British Birds*, 96: 360-375.

COLLISTER, D. M. & WILSON, S. 2007. Territory size and foraging habitat of Loggerhead Shrikes (*Lanius ludovicianus*) in southeastern Alberta. *Journal of Raptor Research*, 41: 130-138.

COOPER, W. E. & VITT, L. V. 2002. Distribution, extent, and evolution of plant consumption by lizards. *Journal of Zoology*, 257: 487-517.

CORREIA, A. M. 2001. Seasonal and interspecific evaluation of predation by mammals and birds on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). *Journal of Zoology*, 255: 533-541.

COSTA, G. C., VITT, L. J., PIANKA, E. R., MESQUITA, D. O., & COLLI, G. R. 2008.

Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography*, 17: 670-677.

CRAIG, R. B. 1978. An analysis of the predatory behaviour of the Loggerhead Shrike. *Auk,* 95: 221-234.

CSERMELY, D. 1994. Does prey size affect predatory behaviour of Kestrel?. *Avocetta*. 18: 63-67.

CSERMELY, D., MAINARDI, D. & AGOSTINI, N. 1989. The predatory behaviour of captive wild kestrel, *Falco tinnunculus* L. *Bolletino Di Zoologia,* 56: 317-320.

DAMSTRA, K. 1986. Editorial (notes by George Hall). *Tree Life,* 71: 5

DEAN, W. R. J. & MILTON, S. J. 1988. Dispersal of seeds by raptors. *African Journal of Ecolology,* 26: 173-176.

DEL HOYO, J., ELLIOTT, A. & CHRISTIE, D. A. 2008. *Handbook of the birds of the World, Volume 13, Penduline-tits to Shrikes*. Lynx Edicions, Barcelona.

DÍAZ, J. A. & CARRASCAL, L. M. 1990. Regional distribution of the Mediterranean lizard: influence of habitat cues and prey abundance. *Journal of Biogeography,* 18: 1-7.

DUKE, G. E., EVANSON, O. A. & JEGERS, A. 1976. Meal to pellet intervals in 14 species of captive raptors. *Comparative Biochemical Physiology,* 53A: 1-6.

EMERSON, B. C. 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology,* 11: 951-966.

EMLEN, J. M. 1966. The role of time and energy in food preference. *American Naturalist,* 100: 611-617.

EVANS, P. G. H. & EVANS, J. B. 1980. The ecology of lizards on Praslin Island, Seychelles. *Journal of Zoology,* 191: 171-192.

FENNER, M. 2000. *Seeds, the ecology of regeneration in plant communities*. Commonwealth Agricultural Bureau International, Wallingford, UK.

FORGET, P. M. & MILLERON, T. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia,* 87: 596-599.

GARCÍA, J. T. & ARROYO, B. E. 2005. Food-niche differentiation in sympatric Hen *Circus cyaneus* and Montagu's Harriers *Circus pygargus*. *Ibis,* 147: 144-154.

GERSTELL, A. T. & BEDNARZ, J. 1999. Competition and patterns of resource use by two sympatric raptors. *Condor,* 101: 557-565.

GONZÁLEZ, J., WINK, M., GARCÍA-DEL-REY, E. & DELGADO, G. 2008. Evidence from DNA nucleotide sequences and ISSR profiles indicates paraphyly in subspecies of the Southern Grey Shrike (*Lanius meridionalis*). *Journal of Ornithology,* 149: 495-506.

GORMAN, M. 1979. *Island Ecology*. Chapman & Hall, London.

GRANT, P. R. 1965. The adaptive significance of some size trends in island birds. *Evolution,* 19: 355-367.

GRANT, P. R. 1998. *Evolution on islands*. Oxford University Press, Oxford, UK.

GRÜNWALD, H. 1983. Über Gewölle des Raubwürgers (*Lanius excubitor*) aus Überwinterungshabitaten in Südwestfalen. *Vogelwelt*, 104: 201-208.

GRÜNWALD, H. 1984. Weitere Mitteilungen zur Überwinterung des Raubwürgers (*Lanius excubitor*) im Sauerland (1982/83 und 1983/84). *Charadrius,* 20: 36-44.

HALL, G. 1987. Seed dispersal by birds of prey. *Zimbabwe Science News*, 21: 1-2.

HERNÁNDEZ, A. 1993. Biología de la familia Laniidae (alcaudón real *Lanius excubitor* L., alcaudón dorsirrojo *Lanius collurio* L., y alcaudón común *Lanius senator* L.) en la cuenca del rio Torío, provincia de León. Tesis Doctoral, Universidad de León.

HERNÁNDEZ, A., PURROY, F. J., & SALGADO, J. M. 1993. Variación estacional, solapamiento interespecífico y selección en la dieta de tres especies simpátricas de alcaudones (*Lanius* spp.). *Ardeola,* 40: 143-154.

HERNÁNDEZ, A. 1995A. Selective predation by Northern Shrikes on small mammals in a natural environment. *Journal of Field Ornithology,* 66: 236-246.

HERNÁNDEZ, A. 1995B. Temporal-spatial patterns of food caching in two sympatric Shrikes species. *Condor,* 97: 1002-1010.

HERNÁNDEZ, A. 1995C. Depredación de anfibios, reptiles y aves por tres especies de alcaudones *Lanius* spp. en el Noroeste de la Península Ibérica. *Ecología,* 9: 409-415.

HIGGINS, S. I. & RICHARDSON, D. M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist,* 153: 464-475.

HIGGINS, S. I., NATHAN, R. & CAIN, M. L. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal?. *Ecology,* 84: 1945-1956.

HÓDAR, J. A. 2006. Diet composition and prey choice of the southern grey shrike *Lanius meridionalis* L. in South-Eastern Spain: the importance of vertebrates in the diet. *Ardeola,* 53: 237–249.

HROMADA, M, & KRIŠTÍN, A. 1996. Changes in the food of the great grey shrike (*Lanius excubitor*) during the year. *Biologia,* 51: 227-233.

HUNTER, M. D. & PRICE, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73: 724-732.

HULME, P. E. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 32-46.

HUHTALA, K., ITÄMIES, J. & MIKKOLA, H. 1977. Beitrag zur Brutbiologie und Ernährung des Raubwurgers (*Lanius excubitor*) im Österbotten, Finnland. *Beitrage zur Vogelkunde Leipzig*, 23: 129-146.

ILLERA, J. C. & DÍAZ, M. 2006. Reproduction in an endemic bird of a semiarid island: a food-mediated process. *Journal of Avian Biology*, 37: 447-456.

JANZEN, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics,* 2: 465-492.

JORDANO, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist,* 145: 163-191.

JORDANO, P. 2000. Fruits and frugivory. *In*: Fenner, M. (ed.), Seeds: the ecology of regeneration in natural plant communities 2nd Edition. Commonwealth Agricultural Bureau International, Wallingford, UK. 125-166.

JULIEN-LAFERRIERE D. 1999. Foraging strategies and food partitioning in the neotropical frigivorous mammals *Caluromys philander* and *Potos flavus*. *Journal of Zoology,* 247: 71-80.

KARLSSON, S. 2001. Selection of habitat and perches by the Great Grey Shrike *Lanius excubitor* and the effects of snow layer and prey type. *Ornis Svecica*, 11: 7-18.

KARLSSON, S. 2002. Analyses on prey composition of overwintering Great Grey Shrikes *Lanius excubitor* in southern Finland. *Ornis Fennica*, 79: 181-189.

KARLSSON, S. 2004. Season-dependent diet composition and habitat use of Red-backed Shrikes *Lanius collurio* in SW Finland. *Ornis Fennica,* 81: 97-108.

KLASSERT, T. E., HERNÁNDEZ, M. A., CAMPOS, F., INFANTE, O., ALMEIDA, T., SUÁREZ, N. M., PESTANO, J. & HERNÁNDEZ, M. 2008. Mitochondrial DNA points to *Lanius meridionalis* as a polyphyletic species. *Molecular Phylogenetics and Evolution,* 47: 1227-1231.

KREBS, J. R., STEPHENS, D. W. & SUTHERLAND, W. J. 1983. Perspectives in optimal foraging. *In*: Brush, A. H. & Clark, G. A. (eds.), Perspectives in Ornithology. Cambridge University Press, Cambridge. 165-216.

KREBS, C. J. 1989. *Ecological methodology*. Harper Collins Publisher, NY.

KRIŜTÍN, A., HOI, H., VALERA, F. & HOI, C. 2007. Philopatry, dispersal patterns and nest-site reuse in Lesser Grey Shrikes (*Lanius minor*). *Biodiversity and Conservation*, 16: 987-995.

LACK, D. 1946. Competition for food by birds of prey. *Journal of Animal Ecology*, 15: 123-129.

LEFRANC, N. & WORFOLK, T. 1997. *Shrikes. A guide to the shrikes of the world*. Pica Press, Mountfield.

LEPLEY, M., THEVENOT, M., GUILLAUME, C. P., PONEL, P., AND BAYLE, P. 2004. Diet of the nominate Southern Grey Shrike *Lanius meridionalis meridionalis* in the north of its range (Mediterranean France). *Bird Study*, 51: 156-162.

LEVEY D. J. & BYRNE, M. M. 1993. Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology,* 74: 1802-1812.

LOMOLINO, M. V. 1984. Immigrant selection, predation, and distribution of *Microtus pennsylvanicus* and *Blarina brevicaudata* on islands. *American Naturalist*, 123: 468-483.

LOREK, G., TRYJANOWSKI, P. & LOREK, J. 2000. Birds as prey of the Great Grey Shrike (*Lanius excubitor*). *Ring*, 22: 37-44.

MACARTHUR, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, NY.

MACARTHUR R. H. & PIANKA, E. R. 1966. On optimal use of a patchy environment. *American Naturalist,* 100: 377-385.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

MANLY, B. F. J., MCDONALD, L. L., & THOMAS, D. L. 1993. Resource selection by animals. Statistical design and analysis for field studies. Chapman & Hall, London.

MARTI, C. D., STEENHOF, K., KOCHERT, M. N. & MARKS, J. S. 1993. Community trophic structure: the role of diet, body size, and activity time in vertebrate predators. *Oikos* 67: 6-18.

MARTÍN, A., & LORENZO, J. A. 2001. *Aves del Archipiélago Canario*. Lemus, La

Laguna.

MARTÍN, J. L., GARCÍA H., REDONDO, C. E., GARCÍA, I. & CARRALERO, I. 1995. *La Red Canaria de Espacios Naturales Protegidos.* Viceconsejería de Medio Ambiente del Gobierno de Canarias, Santa Cruz de Tenerife.

MARZOL JAÉN, M. V. 1988. *La lluvia: un recurso natural para Canarias.* Servicio de Publicaciones de la Caja General de Ahorros de Canarias, Santa Cruz de Tenerife.

MASMAN, D., DAAN, S. & DIJKSTRA C. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. *Journal of Animal Ecology*, 57: 411-432.

MCWILLIAMS, S. R., GUGLIELMO, C., PIERCE, B. & KLAASSEN, M. 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology,* 35: 377-393.

MOLINA-BORJA, M. 1991. Notes on alimentary habits and spatial-temporal distribution of eating behaviour patterns in a natural population of lizards (*Gallotia galloti*). *Vieraea*, 20: 1-9.

NATHAN, R. 2006. Long-distance dispersal of plants. *Science,* 313: 786-788.

NATHAN, R. & MULLER-LANDAU, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, 15: 278-285.

NATHAN, R., PERRY, G., CRONIN, J. T., STRAND, A. E. & CAIN, M. L. 2003. Methods for estimating long-distance dispersal. *Oikos,* 103: 261-273.

NATHAN, R., SCHURR, F. M., SPIEGEL, O., STEINITZ, O., TRAKHTENBROT, A. & TSOAR, A. 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution,* 23: 638-647.

NOGALES, M. 1999. Some ecological implications of the broadering habitat and trophic niche of terrestrial vertebrates in the Canary Islands. *Monografies de la Societat D'Història de les Balears,* 66: 67-82.

NOGALES, M. & HERNÁNDEZ, M. C. 1994. Interinsular variations in the spring and summer diet of the Raven *Corvus corax* in the Canary Islands. *Ibis,* 136: 441-447.

NOGALES, M. & VALIDO, A. 1999. Preliminary data on the structural relationships in two lacertid species of the genus *Gallotia* (Reptilia: Lacertidae) based on the skeleton. *Vieraea,* 27: 217-222.

NOGALES, M., MEDINA, F. M. & VALIDO, A. 1996. Indirect seed dispersal by the feral cats *Felis catus* in island ecosystems (Canary Islands). *Ecography,* 19: 3-6.

NOGALES, M., DELGADO, J. D. & MEDINA, F. M. 1998. Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). *Journal of Ecology,* 86: 866-871.

NOGALES, M, HERNÁNDEZ, E. C. & VALDÉS, F. 1999. Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). *Écoscience,* 6: 56-61.

NOGALES, M., QUILIS, V., MEDINA, F. M., MORA, J. L. & TRIGO. L. S. 2002. Are predatory birds effective secondary seed dispersers?. *Biological Journal of the Linnean Society,* 75: 345-352.

NOGALES, M., PADILLA, D. P., NIEVES, C., ILLERA, J. C. & TRAVESET, A. 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. *Journal of Ecology,* 95: 1394-1403.

OLESEN, J. M. & JORDANO, P. 2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology,* 83: 2416-2424.

OLESEN, J, M. & VALIDO, A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecololgy and Evolution*, 18: 177-181.

OLSSON, V. 1985. Varfågelns *Lanius excubitor* vintervanor Del IV. Behandling av bytet. *Vår Fågelvärld,* 44: 269-283.

OLSSON, V. 1986. Varfågelns Lanius excubitor vintervanor V. Bytesval. *Vår Fågelvärld,* 45: 19-31.

PASINELLI, G., MULLER, M., SCHAUB, M. & JENNI, L. 2007. Possible causes and consequences of philopatry and breeding dispersal in red-backed shrikes *Lanius collurio. Behavioral Ecology and Sociobiology,* 7: 1061-1074.

PÉREZ-MELLADO, V. & CORTI, C. 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonner zoologische Beiträge,* 44: 193-220.

PÉREZ-MELLADO, V. & TRAVESET, A. 1999. Relationships between plants and Mediterranean lizards. *Natura Croatica,* 8: 275-285.

PIZO, M. A., GUIMARAES, P. R. & OLIVEIRA, P. S. 2005. Seed removal by ants from faeces produced by different vertebrate species. *Écoscience,* 12: 136-140.

PROBST, R., WEGLEITNER, S., & SCHMID, R. 2003. Relationship of vertebrate prey size to transport mode and distance in the Northern Shrike. *Wilson Bulletin,* 115: 201-204.

RIDLEY, H. N. 1930. *The dispersal of plants throughout the world*. Reeve, Ashford, Kent. UK.

ROCA, V., CARRETERO, M. A., LLORENTE, G. A., MONTORI, A. & MARTIN, J. E. 2005. Helminth communities of two lizard populations (Lacertidae) from Canary Islands (Spain): host diet-parasite relationships. *Amphibia-Reptilia,* 26: 535-542.

RODDA, G. H. & DEAN-BRADLEY, K. 2002. Excess density compensation of island herpetofaunal assemblages. *Journal of Biogeography*, 29: 623-632.

RODRÍGUEZ, M. A., SANTOS, A. & CANTARELLA, F. 1994. Estimación del tamaño de la población de *Gallotia galloti galloti* Oudart, 1839 (Sauria: Lacertidae) en el Malpaís de Güimar (S.E. Tenerife). *Stvdia Oecologica,* 10-11: 401-407.

RODRÍGUEZ-PÉREZ, J., RIERA, N. & TRAVESET, A. 2005. Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and control conditions. *Functional Ecology,* 19:

699-706.

RODRÍGUEZ, A., NOGALES, M., RUMEU, B. & RODRÍGUEZ, B. 2008. Temporal and spatial variation in the diet of the endemic lizard *Gallotia galloti* in an insular Mediterranean scrubland. *Journal of Herpetology,* 42: 213-222.

ROSENBERG, K. V. & COOPER R. J. 1990. Approaches to avian diet analysis. *Studies in Avian Biology*, 13: 80-90.

SANGSTER, G., KNOX, A. G., HELBIG, A. J. & PARKIN, D. T. 2002. Taxonomic recommendations for European birds. *Ibis,* 144: 153-159.

SAVAGE, R. E. 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fisheries Investigations. *Ministry of Agriculture, Food and Fisheries Services 2,* 12: 1-88.

SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science,* 185: 27-39.

SCHOENER, T. W. 1982. The controversy over interspecific competition. *American Scientist,* 70: 586-595.

SCHOENER, T. W. & SCHOENER, A. 1980. Densities, sex ratio and population structure in four species of Bahamian *Anolis* lizards. *Journal of Animal Ecology*, 49: 19-53.

SCHÖN, M. 1998. On the evolution of the northern and southern group of subspecies in the Great Grey Shrike superspecies (*Lanius excubitor*). *In:* Yosef, R. & Lohrer, F. E. (eds.), Shrikes of the World II: Conservation Implementation. International Birdwatching Center in Eilat, Eilat. 9-13.

SCHUPP, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*. 107/108:15-29.

SIMEK, J. 2001. Patterns of breeding fidelity in the Red-backed Shrike (*Lanius collurio*). *Ornis Fennica*, 78: 61-71.

SNOW, D. W. & PERRINS, C. M. 1998. *The Birds of the Western Palearctic*. Oxford Univesity Press, Oxford.

SOOBRAMONEY, S., DOWNS, C. T. & ADAMS, N. J. 2004. Territorial behaviour and time budgets of the Fiscal Shrike *Lanius collaris* along an altitudinal gradient in South Africa. *African Zoology,* 39: 137-143.

SPIEGEL, O. & NATHAN, R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters,* 10: 718-728.

STEPHENS, D. W. & KREBS, J. R. 1986. *Foraging theory.* Princeton University Press, Princeton, NJ.

STILES, E. W. 2000. Animals as seed dispersers. *In*: Fenner, M. (ed.), Seed: the ecology of regeneration in plant communities. Wallingford, UK: CAB International. 111-124.

TRAKHTENBROT, A., NATHAN, R., PERRY, G. & RICHARDSON, D. M. 2005. The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions,* 11: 173-181.

TRAVESET, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspective in Plant Ecology,* 1/2: 151-190.

TRAVESET, A. & VERDÚ, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. *In*: Levey, D. J., Silva, W. R. & Galetti, M. (eds.), Seed dispersal and frugivory: ecology, evolution and conservation. CAB International Publishing, Wallingford, UK. 339-350.

TRAVESET, A., RODRÍGUEZ-PÉREZ, J. & PÍAS, B. 2008. Seed trait changes in dispersers' guts and consequences for germination and seedling growth. *Ecology*, 89: 95-106.

VAN DAMME, R. 1999. Evolution of herbivory in lacertid lizards: effects of insularity and body size. *Journal of Herpetology,* 33: 663-674.

VALIDO, A. 1999. Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. *Gallotia*, Lacertidae). Tesis Doctoral, Universidad de La Laguna.

VALIDO, A. & NOGALES, M. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos*. 70: 403-411.

VALIDO, A. & NOGALES, M. 2003. Digestive ecology of two omnivorous Canarian lizards species (*Gallotia*, Lacertidae). *Amphibia-Reptilia,* 24: 331-344.

VALIDO, A., NOGALES, M. & MEDINA, F. M. 2003. Fleshy fruits in the diet of Canarian lizards *Gallotia galloti* (Lacertidae) in a xeric habitat of the island of Tenerife. *Journal of Herpetology,* 37: 741-747.

VANDER WALL, S. B. 2002. Secondary dispersal of Jeffrey pine seeds by rodent scatter hoarders: the roles of pilfering, recaching, and a variable environment. *In*: Levey, D., Silva, W. R. & Galetti, M. (eds.), Seed dispersal and frugivory: ecology, evolution and conservation. Wallingford, UK: CAB International. 193-208.

VANDER WALL, S. B. & LONGLAND, W. S. 2004. Diplochory: are two seed dispersers better than one?. *Trends in Ecolology and Evolution*, 19: 155-161.

VISSER, M. E., VAN NOORDWIJK, A. J., TINBERGEN, J. M. & LESSELLS, C. M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London B*, 265: 1867-1870.

WHITTAKER R. J. & FERNÁNDEZ-PALACIOS J. M. 2007. Island Biogeography. Ecology, evolution and conservation. Oxford University Press, Oxford.

WILDPRET, W., & MARTÍN OSORIO, M. V. 2004. Flora vascular y vegetación. *In*: Canseco (ed.), Parque Nacional del Teide. Canseco Editores, Madrid. 97-142.

YOSEF, R. 1992. Male-biased breeding site fidelity in a population of Northern Shrikes. *Condor,* 94: 1025-1027.

YOSEF, R. 1993. Prey transport by the Loggerhead Shrikes. *Condor,* 95: 231-233.

YOSEF, R., & PINSHOW, B. 2005. Impaling in true shrikes (*Laniidae*): a behavioural and ontogenetic perspective. *Behavioural Processes,* 69: 363-367.

YOSEF, R., MITCHELL, W. A. & PINSHOW, B. 1991. The proximate costs and benefits of polygyny to male Northern Shrike. *Wilson Bulletin,* 103: 146-149.

ARTÍCULOS PUBLICADOS

I. **PADILLA, D. P.**, NOGALES, M. & PÉREZ, A. J. 2005. Seasonal diet of an insular endemic population of Southern Grey Shrike *Lanius meridionalis koenigi* on Tenerife, Canary Islands. ***Ornis Fennica*** **82**: 155-165.

II. **PADILLA, D. P.**, A. GONZÁLEZ-CASTRO, C. NIEVES & M. NOGALES. 2009. Trophic ecology of the Southern Grey Shrike (Lanius meridionalis) in insular environments: the influence of altitude and seasonality. ***Journal of Ornithology*** **150**: 557-568.

III. **PADILLA, D. P.**, NOGALES, M. & MARRERO, P. 2007. Prey size selection upon insular lizards by two sympatric predatory bird species. ***Acta Ornithologica*** **42**: 167-172.

IV. NOGALES, M., **PADILLA, D. P.**, NIEVES, C., ILLERA, J. C. & TRAVESET, A. 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. ***Journal of Ecology*** **95**: 1394-1403.

V. **PADILLA, D. P.** & NOGALES, M. 2009. Behaviour of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal. ***Behavioral Ecology*** **20**: 872-877.

PADILLA, D. P., NOGALES, M. & PÉREZ, A. J. 2005. Seasonal diet of an insular endemic population of Southern Grey Shrike *Lanius meridionalis koenigi* on Tenerife, Canary Islands. ***Ornis Fennica*** **82**: 155-165.

Ornis Fennica 82:155–165. 2005

Seasonal diet of an insular endemic population of Southern Grey Shrike *Lanius meridionalis koenigi* on Tenerife, Canary Islands

David P. Padilla*, Manuel Nogales & Antonio J. Pérez

*Padilla, D.P., Island Ecology and Evolution Research Group (IPNA-CSIC), La Laguna 38206, Tenerife, Canary Islands, Spain. dpadilla@ipna.csis.es (*Corresponding author)*
Nogales, M., Island Ecology and Evolution Research Group (IPNA-CSIC), La Laguna 38206, Tenerife, Canary Islands, Spain
Pérez, A.J., Department of Animal Biology (Zoology), University of La Laguna, 38206, Tenerife, Canary Islands, Spain

Received 19 July 2005, accepted 21 September 2005

The diet and prey selection of the Southern Grey Shrike (*Lanius meridionalis koenigi*) was studied in one of the scarce insular environments where it is present, the xeric coastal area of Tenerife (Canary Islands). The main aim of this study was to compare the general trophic patterns with respect to continental populations of Northern Grey Shrike (*Lanius excubitor*) and Southern Grey Shrike. The material analysed consisted in 440 pellets collected during the four seasons of the year in the period April 2003–March 2004. A total of 5,112 prey items were identified, 85.4% corresponding to beetles (mainly Curculionidae and Tenebrionidae) and the rest consisted of other arthropods and vertebrates. Biomass mainly constituted of vertebrates, especially lizards (64.0%). Slight seasonal variations in diet were recorded, beetles and lizards being highly consumed in all seasons. A positive selection of some beetles, non-Formicidae Hymenoptera and Orthoptera (*Schistocerca gregaria*) was observed. The data obtained in the present study confirms the hypothesis of how the Southern Grey Shrike relies on cold-blooded prey in hot climate (e.g. south of France), while the Great Grey Shrike mainly relies on warm-blooded prey in cold climate (e.g. Scandinavian Peninsula). The importance of lizards in the diet of this insular shrike population could be related to three different ecological factors: (1) the high abundance of these ectotherm vertebrates in island environments, (2) the higher effectiveness of predation and (3) lower investment of energy to capture them.

1. Introduction

The Southern Grey Shrike *Lanius meridionalis* only occurs in the old world, throughout the Saharo-Sindian xeric zone and in the extreme South-West of Europe, Iberian Peninsula and southern France, where ten subspecies are currently recognized (Lefranc & Worfolk 1997). The Canarian endemic subspecies *Lanius meridionalis koenigi* is the only island population in the Atlantic Ocean and one of the two existing insular subspecies throughout the species' range. The other is *L. m. uncinatus*, in Socotra Island (Yemen). In the Canaries it occupies the islands of Tenerife, Gran

Canaria, Fuerteventura and Lanzarote, in open shrub environments, inhabiting zones that extend from coastal xeric areas to high mountains (Martín & Lorenzo 2001). Contributions on the Southern Grey Shrike's diet ecology are scarce and restricted to only three continental zones: *Lanius meridionalis elegans/aucheri* in the Negev' desert in Israel (Yosef *et al.* 1991, Budden & Wright 2000) and *Lanius meridionalis meridionalis* in Spain (Hernández *et al.* 1993, Hernández 1995a, 1995b, 1995c) and southern France (Lepley *et al.* 2004). There, arthropods in Europe, and lizards and beetles in Israel were the most important kinds of prey.

The Southern Grey Shrike is currently considered to be a separate species from the Great Grey Shrike *Lanius excubitor* (Snow & Perrins 1998). The diet of the latter species has been studied relatively often (Cade 1967, Huhtala *et al.* 1977, Bassin *et al.* 1981, Grünwald 1983, 1984, Olsson 1986, Atkinson & Cade 1993, Hromada & Kristín 1996, Karlsson 2001, 2002). The Great Grey Shrike's main prey is small mammals (e.g. *Microtus* spp) all year round, with an increasing proportion of birds in winter and also in spring for some populations (Lorek *et al.* 2000). Schön (1998) and Lepley *et al*. (2004) showed that the Great Grey Shrike relies mainly on endothermic prey in cold climatic zones while the Southern Grey Shrike preys on ectothermic species in warmer areas. However, this hypothesis has not yet been confirmed in one of the southernmost populations of the species geographic range, which is essential for testing this latitudinal trend variation of the diet.

No reports on the shrike's diet in the Canary Islands have yet been published, and the only specific data available indicated that lizards and beetles also form a part of their staple diet (see Martín & Lorenzo 2001 and references therein). Other studies performed in the islet of Alegranza showed that *L. m. koenigi* is a legitimate secondary seed disperser of a Solanaceae plant (*Lycium intricatum*) when it preys intensively on the endemic frugivorous lizard *Gallotia atlantica* (Nogales *et al.* 1998, 2002).

Four main aims were pursued in the present study: First, we assess the seasonal diet composition of this insular endemic Shrike. Second, we evaluate trophic selection during each season. Third, we compare these insular trophic patterns with those of the different continental populations of Southern Grey Shrike. Lastly, we study how some prey items change in the shrike diet according to North-South latitudinal variation.

2. Material and methods

2.1. Study area

The volcanic Canarian Archipelago is situated in the Atlantic Ocean about 100 km from the African continent at its nearest point (27º37'–29º25'N and 13º20'–29º25'W). Fieldwork was carried out in "Malpaís de La Rasca" and surrounding areas, located at the southernmost point of Tenerife. This badland (hereafter "Malpaís") has been declared a "Special Nature Reserve" (Martín *et al*. 1995). The study area is a "Malpaís" of lava field (ca 3.15 km^2) which was produced by two main volcanic cones, Montaña Gorda and Montaña Guzada (Carracedo *et al*. 2003).

The climate is xeric, this area receiving the island's lowest mean annual rainfall (98 mm) and being one of the warmest (annual mean temperature: ca 22 ºC; Marzol Jaén 1988). However, two climatic periods can be identified in this semiarid habitat: drier (spring and summer; mean rainfall and temperature of 11.2 mm and 22.5 ºC respectively); and rainier (autumn and winter; 86.7 mm and 22.2 ºC). The vegetation consists of a sparse xerophytic shrub, mainly composed of *Launaea arborescens, Lycium intricatum, Salsola divaricata, Schizogyne glaberrima, Euphorbia balsamifera, E. canariensis, Reseda scoparia, Periploca laevigata, Plocama pendula* and the invasive *Opuntia dillenii* (for further information about vegetation see Arco-Aguilar *et al*. 1997).

2.2. Pellets sampling

The study was carried out from April 2003 to March 2004, and this period being divided into four seasons (spring: March, April and May; summer: June, July and August; autumn: September, October and November; and winter: December, January and February). A total of 440 adult pellets were collected (spring: 115, summer: 116, autumn: 93 and winter: 116) in 14 different territories (8 with breeding records and another 6 without any record of breeding). A mean number of ten pellets per territory and season was collected in order to have an adequate representation of the population diet. To minimize seasonal sample bias, only fresh pellets were collected after having regularly cleaned beneath the perches.

2.3. Diet analysis

We identified and counted all the remains of arthropods (heads, mandibles, legs and sclerotized parts) and vertebrates (bones, hair and teeth), estimating the minimum number of each prey item per pellet. To identify the ingested prey to family level, each pellet was analysed individually with a 16x binocular, following the methods of Calver & Wooller (1982), Ralph *et al.* (1985) and Moreby (1988). Doubtful prey remains were compared with the collection at the Department of Animal Biology (University of La Laguna). We also revised regularly the larders and determined those prey found in them.

The results are expressed in number of prey items that appeared each season and calculated the percentage of total number of prey items, frequency of occurrence and total biomass. Wet biomass was calculated using an average representative weight (M. Nogales unpubl.) of vertebrate prey species, lizards and geckos. Mean weights for mammals were obtained from the literature (Castells & Mayo 1993). As for arthropods, we collected several individuals (five at least) of each identified taxon in the diet, and took their live weight using an electronic balance (precision: 0.0001 g). It was decided to employ wet biomass because water is particularly essential in xeric habitats (Lepley *et al*. 2004).

2.4. Food availability

The Southern Grey Shrike hunts mainly on the ground (Cramp & Perrins 1993), although *L. m. koenigi* was observed capturing insects in shrubs. Thus, three different methods were employed to estimate invertebrate availability following Cooper & Whitmore (1990), Dahlsten *et al.* (1990) and Wolda (1990). To analyse ground arthropods, a square of 0.25 m^2 was sampled and all individuals larger than five millimetres were counted over two minutes. A total of 60 samples were taken per season, divided into 7 line transects (transect length: 200 m; and 20 m between sample square), in order to cover the major part of the shrike territories. Furthermore, 30 pitfall traps were placed in the same line transects and left in the field for one week. Propylene-glycol was placed inside to preserve the invertebrates. 10 Plants of the main species were also analysed per season (*Launaea arborescens, Lycium intricatum, Salsola divaricata, Schizogyne glaberrima, Euphorbia balsamifera* and *Plocama pendula*) to estimate the number of arthropods living in those shrubs. Each season, we placed a "beating tray" beneath these plants and gently struck them to remove the arthropods residing in the vegetation. Previously, flying insects on these plants were counted in order to identify and quantify all the arthropods in each one.

In regard to vertebrates, only the relative abundance of lizards (*Gallotia galloti*) was calculated because the remaining species were scarce in the Canarian shrike diet (see Martín & Lorenzo 2001 and references therein). Line transects (100 m length) were employed and lizards were counted from five metres on both sides of the observer (Díaz & Carrascal 1990). The censuses were begun at 12:00 hours (midday) on fair days and a total of 20 transects were performed in each season. Due to the fact that shrikes do not prey upon larger lizards (Hernández 1995c), these were classified in three different size categories (small: snout vent length, SVL: < 5 cm; medium: SVL: 5–10 cm; and large: SVL: > 10 cm).

2.5. Statistical and index analysis

In order to avoid sample bias among territories, the samples were standardised by analysing a mean of ten pellets per territory and season. Likelihood ratio tests were applied to study seasonal variations of the main items found in the diet. Similarity or overlap in Shrike diet among the different seasons was evaluated using the Morisita index of similarity for percentage of prey, in which values near "0" indicate low similarity and values near "1" indicate high similarity. Moreover, niche-breadth was assessed using the standardized Levin's niche-breadth index (*B*), where a value close to "0" indicates dietary specialization and a value close to "1" shows a broad diet (Krebs 1989).

To evaluate diet selection of the main groups of arthropods, the "forage index" FIS of Savage (1931) (eq. 1) was applied, being defined as

$$\mathrm{FIS} = \frac{U_i}{D_i}, \tag{1}$$

where the proportion of used units (U_i)is divided by the proportion of available units (D_i). The statistical significance of these measurements was tested by calculating the Manly statistic

$$\mathrm{MS} = \frac{(W_i - 1)^2}{\mathrm{SE}\,(W_i)^2}, \tag{2}$$

where W_i is the Savage "forage index" for the arthropod species *i*, and SE(W_i) its standard error. We compared MS with the corresponding critical value of a chi-square distribution with one degree of freedom (Manly *et al.* 1993). We estimated SE(W_i) on the *a priori* assumption that there was no prey selection, such that the standard error of W_i was approximated by

$$\mathrm{SE}(W_i) = \frac{\sqrt{1 - D_i}}{u_{tot} D_i}, \tag{3}$$

where u_{tot} is the total number of used resources in each season, and D_i is the proportion of available arthropods of the species *i*.

3. Results

3.1. General diet

A total of 5,112 prey items were identified, 96.3% corresponding to arthropods and the remainder consisted of vertebrates (mainly lizards) (Table 1). Beetles (85.4% of the prey items) represented the main invertebrate group, Curculionidae (49.5%) and Tenebrionidae (34.5%) being the most important. The other arthropods caught corresponded to Hymenoptera, Orthoptera, Hemiptera, Odonata, Dictyoptera, and Araneae in decreasing importance, no Lepidoptera larvae being found.

The main prey item with respect to vertebrates was constituted by reptiles (83.8%) and the remainder were small mammals. 93.7% of the reptiles corresponded to the endemic lizard (*Gallotia galloti*) while the other prey found consisted of Gekkonidae (*Tarentola delalandii*). With regard to small mammals, two introduced species in the Canary Islands, *Mus domesticus* and *Suncus etruscus,* were identified. Only five lizards and one Coleoptera (Tenebrionidae) were found in larders and, due to their low number, were not included in the diet analysis.

In terms of biomass, the diet mainly consisted of vertebrates (87.6%), the most important groups being lizards (64.0%) and house mice (21.3%). Arthropods accounted for the remainder, 12.4% (mainly Coleoptera: 9.2% and Orthoptera: 2.3%) (Table 1). Lastly, a total of 824 seeds were identified inside the pellets (13.6% of occurrence), *Lycium intricatum* (Solanaceae) being the principal species and constituting 95.4% of the total number.

3.2. Seasonal variation in diet

Despite the fact that beetles and lizards characterised the diet throughout the year, in regard to frequent presence and biomass respectively, the food spectrum of this shrike showed a seasonal variation when the data were analysed separately between two periods, one drier (spring and summer) and the other rainier (autumn and winter). A considerable overlap can be observed between seasons in these two periods (Morisita Index, spring–summer: $C_\lambda = 0.96$; autumn–winter: $C_\lambda = 0.99$). The minimum overlap corresponded to spring–autumn and summer–autumn with C_λ: 0.54 and C_λ: 0.73, respectively. Niche breadth was very restricted in all seasons, the minimum value being obtained in the drier period and the highest in the rainier one (Levin's niche-breadth index, spring: $B = 0.04$; summer: $B = 0.08$; autumn $B = 0.10$; winter $B = 0.14$).

Beetles appeared with the highest prevalence in all seasons but there were differences in composition at the family level. Curculionidae characterised the drier seasons ($G_1 = 853.53$, $P < 0.001$) and Tenebrionidae the rainier ones ($G_1 = 906.36$, $P < 0.001$). The highest frequencies of Hymenoptera,

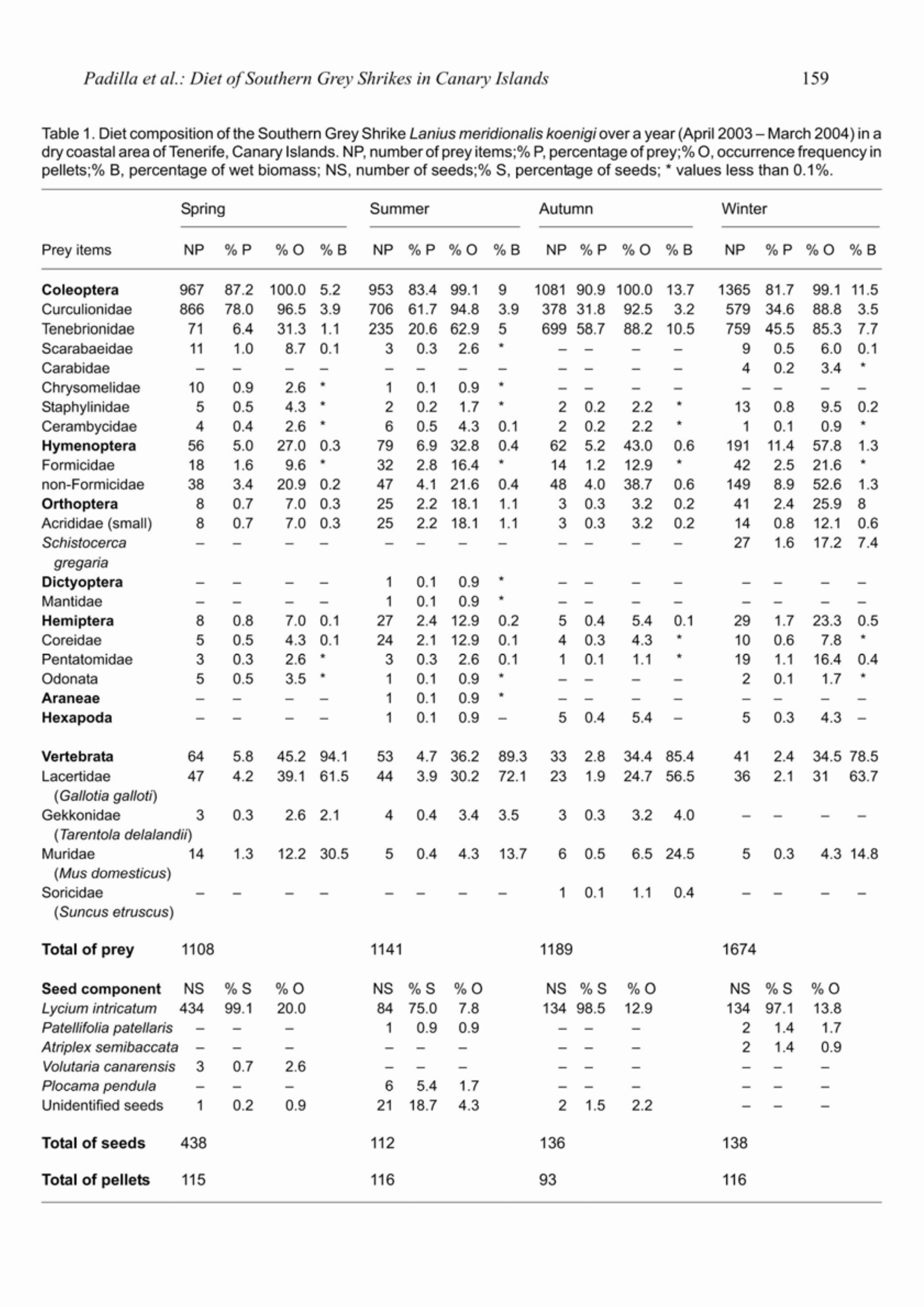


Table 1. Diet composition of the Southern Grey Shrike *Lanius meridionalis koenigi* over a year (April 2003 – March 2004) in a dry coastal area of Tenerife, Canary Islands. NP, number of prey items;% P, percentage of prey;% O, occurrence frequency in pellets;% B, percentage of wet biomass; NS, number of seeds;% S, percentage of seeds; * values less than 0.1%.

	Spring				Summer				Autumn				Winter			
Prey items	NP	% P	% O	% B	NP	% P	% O	% B	NP	% P	% O	% B	NP	% P	% O	% B
Coleoptera	967	87.2	100.0	5.2	953	83.4	99.1	9	1081	90.9	100.0	13.7	1365	81.7	99.1	11.5
Curculionidae	866	78.0	96.5	3.9	706	61.7	94.8	3.9	378	31.8	92.5	3.2	579	34.6	88.8	3.5
Tenebrionidae	71	6.4	31.3	1.1	235	20.6	62.9	5	699	58.7	88.2	10.5	759	45.5	85.3	7.7
Scarabaeidae	11	1.0	8.7	0.1	3	0.3	2.6	*	–	–	–	–	9	0.5	6.0	0.1
Carabidae	–	–	–	–	–	–	–	–	–	–	–	–	4	0.2	3.4	*
Chrysomelidae	10	0.9	2.6	*	1	0.1	0.9	*	–	–	–	–	–	–	–	–
Staphylinidae	5	0.5	4.3	*	2	0.2	1.7	*	2	0.2	2.2	*	13	0.8	9.5	0.2
Cerambycidae	4	0.4	2.6	*	6	0.5	4.3	0.1	2	0.2	2.2	*	1	0.1	0.9	*
Hymenoptera	56	5.0	27.0	0.3	79	6.9	32.8	0.4	62	5.2	43.0	0.6	191	11.4	57.8	1.3
Formicidae	18	1.6	9.6	*	32	2.8	16.4	*	14	1.2	12.9	*	42	2.5	21.6	*
non-Formicidae	38	3.4	20.9	0.2	47	4.1	21.6	0.4	48	4.0	38.7	0.6	149	8.9	52.6	1.3
Orthoptera	8	0.7	7.0	0.3	25	2.2	18.1	1.1	3	0.3	3.2	0.2	41	2.4	25.9	8
Acrididae (small)	8	0.7	7.0	0.3	25	2.2	18.1	1.1	3	0.3	3.2	0.2	14	0.8	12.1	0.6
Schistocerca gregaria	–	–	–	–	–	–	–	–	–	–	–	–	27	1.6	17.2	7.4
Dictyoptera	–	–	–	–	1	0.1	0.9	*	–	–	–	–	–	–	–	–
Mantidae	–	–	–	–	1	0.1	0.9	*	–	–	–	–	–	–	–	–
Hemiptera	8	0.8	7.0	0.1	27	2.4	12.9	0.2	5	0.4	5.4	0.1	29	1.7	23.3	0.5
Coreidae	5	0.5	4.3	0.1	24	2.1	12.9	0.1	4	0.3	4.3	*	10	0.6	7.8	*
Pentatomidae	3	0.3	2.6	*	3	0.3	2.6	0.1	1	0.1	1.1	*	19	1.1	16.4	0.4
Odonata	5	0.5	3.5	*	1	0.1	0.9	*	–	–	–	–	2	0.1	1.7	*
Araneae	–	–	–	–	1	0.1	0.9	*	–	–	–	–	–	–	–	–
Hexapoda	–	–	–	–	1	0.1	0.9	–	5	0.4	5.4	–	5	0.3	4.3	–
Vertebrata	64	5.8	45.2	94.1	53	4.7	36.2	89.3	33	2.8	34.4	85.4	41	2.4	34.5	78.5
Lacertidae (*Gallotia galloti*)	47	4.2	39.1	61.5	44	3.9	30.2	72.1	23	1.9	24.7	56.5	36	2.1	31	63.7
Gekkonidae (*Tarentola delalandii*)	3	0.3	2.6	2.1	4	0.4	3.4	3.5	3	0.3	3.2	4.0	–	–	–	–
Muridae (*Mus domesticus*)	14	1.3	12.2	30.5	5	0.4	4.3	13.7	6	0.5	6.5	24.5	5	0.3	4.3	14.8
Soricidae (*Suncus etruscus*)	–	–	–	–	–	–	–	–	1	0.1	1.1	0.4	–	–	–	–
Total of prey	1108				1141				1189				1674			
Seed component	NS	% S	% O		NS	% S	% O		NS	% S	% O		NS	% S	% O	
Lycium intricatum	434	99.1	20.0		84	75.0	7.8		134	98.5	12.9		134	97.1	13.8	
Patellifolia patellaris	–	–	–		1	0.9	0.9		–	–	–		2	1.4	1.7	
Atriplex semibaccata	–	–	–		–	–	–		–	–	–		2	1.4	0.9	
Volutaria canarensis	3	0.7	2.6		–	–	–		–	–	–		–	–	–	
Plocama pendula	–	–	–		6	5.4	1.7		–	–	–		–	–	–	
Unidentified seeds	1	0.2	0.9		21	18.7	4.3		2	1.5	2.2		–	–	–	
Total of seeds	438				112				136				138			
Total of pellets	115				116				93				116			

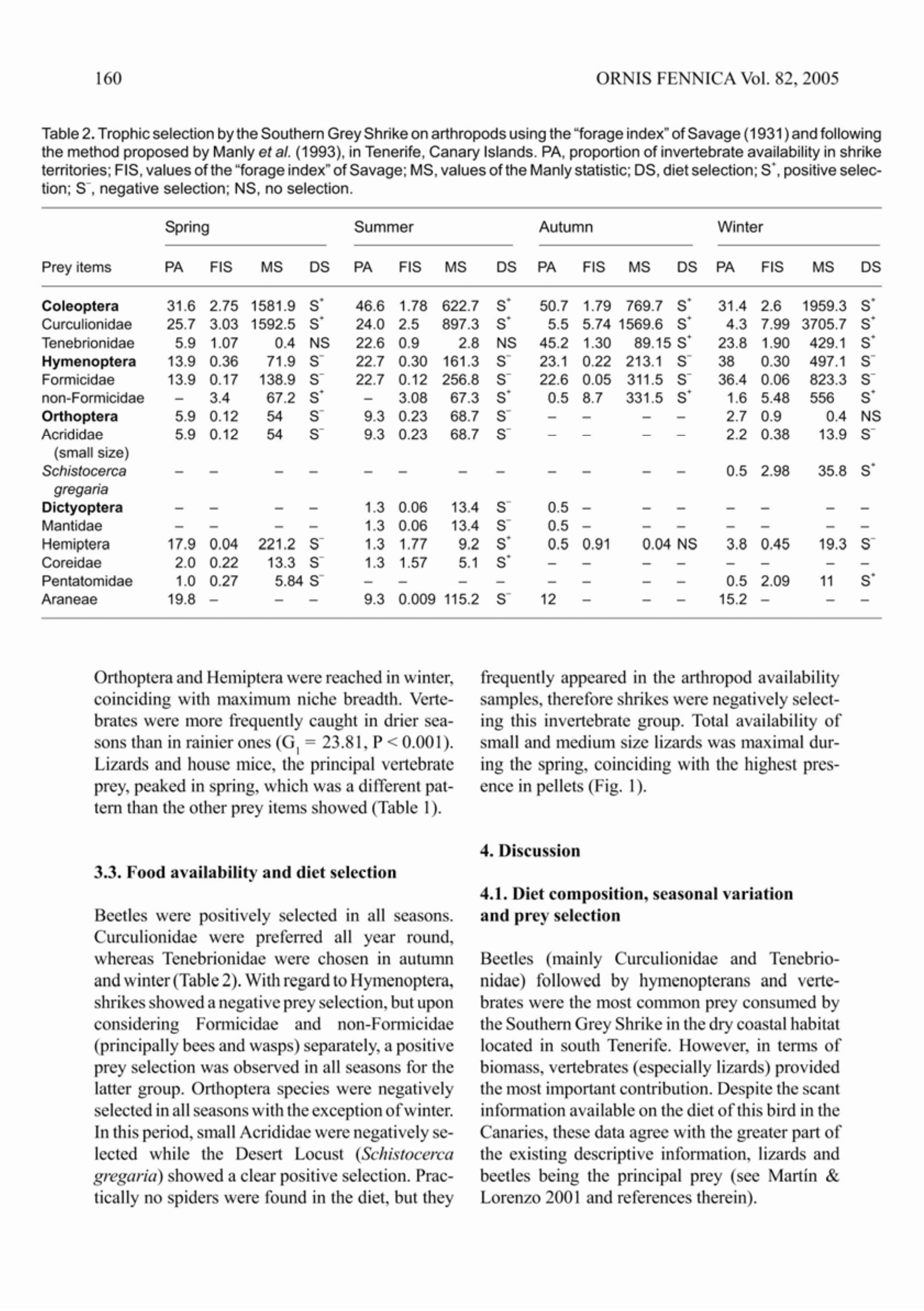


Table 2. Trophic selection by the Southern Grey Shrike on arthropods using the "forage index" of Savage (1931) and following the method proposed by Manly *et al.* (1993), in Tenerife, Canary Islands. PA, proportion of invertebrate availability in shrike territories; FIS, values of the "forage index" of Savage; MS, values of the Manly statistic; DS, diet selection; S^+, positive selection; S^-, negative selection; NS, no selection.

	Spring				Summer				Autumn				Winter			
Prey items	PA	FIS	MS	DS	PA	FIS	MS	DS	PA	FIS	MS	DS	PA	FIS	MS	DS
Coleoptera	31.6	2.75	1581.9	S^+	46.6	1.78	622.7	S^+	50.7	1.79	769.7	S^+	31.4	2.6	1959.3	S^+
Curculionidae	25.7	3.03	1592.5	S^+	24.0	2.5	897.3	S^+	5.5	5.74	1569.6	S^+	4.3	7.99	3705.7	S^+
Tenebrionidae	5.9	1.07	0.4	NS	22.6	0.9	2.8	NS	45.2	1.30	89.15	S^+	23.8	1.90	429.1	S^+
Hymenoptera	13.9	0.36	71.9	S^-	22.7	0.30	161.3	S^-	23.1	0.22	213.1	S^-	38	0.30	497.1	S^-
Formicidae	13.9	0.17	138.9	S^-	22.7	0.12	256.8	S^-	22.6	0.05	311.5	S^-	36.4	0.06	823.3	S^-
non-Formicidae	–	3.4	67.2	S^+	–	3.08	67.3	S^+	0.5	8.7	331.5	S^+	1.6	5.48	556	S^+
Orthoptera	5.9	0.12	54	S^-	9.3	0.23	68.7	S^-	–	–	–	–	2.7	0.9	0.4	NS
Acrididae (small size)	5.9	0.12	54	S^-	9.3	0.23	68.7	S^-	–	–	–	–	2.2	0.38	13.9	S^-
Schistocerca gregaria	–	–	–	–	–	–	–	–	–	–	–	–	0.5	2.98	35.8	S^+
Dictyoptera	–	–	–	–	1.3	0.06	13.4	S^-	0.5	–	–	–	–	–	–	–
Mantidae	–	–	–	–	1.3	0.06	13.4	S^-	0.5	–	–	–	–	–	–	–
Hemiptera	17.9	0.04	221.2	S^-	1.3	1.77	9.2	S^+	0.5	0.91	0.04	NS	3.8	0.45	19.3	S^-
Coreidae	2.0	0.22	13.3	S^-	1.3	1.57	5.1	S^+	–	–	–	–	–	–	–	–
Pentatomidae	1.0	0.27	5.84	S^-	–	–	–	–	–	–	–	–	0.5	2.09	11	S^+
Araneae	19.8	–	–	–	9.3	0.009	115.2	S^-	12	–	–	–	15.2	–	–	–

Orthoptera and Hemiptera were reached in winter, coinciding with maximum niche breadth. Vertebrates were more frequently caught in drier seasons than in rainier ones ($G_1 = 23.81$, $P < 0.001$). Lizards and house mice, the principal vertebrate prey, peaked in spring, which was a different pattern than the other prey items showed (Table 1).

3.3. Food availability and diet selection

Beetles were positively selected in all seasons. Curculionidae were preferred all year round, whereas Tenebrionidae were chosen in autumn and winter (Table 2). With regard to Hymenoptera, shrikes showed a negative prey selection, but upon considering Formicidae and non-Formicidae (principally bees and wasps) separately, a positive prey selection was observed in all seasons for the latter group. Orthoptera species were negatively selected in all seasons with the exception of winter. In this period, small Acrididae were negatively selected while the Desert Locust (*Schistocerca gregaria*) showed a clear positive selection. Practically no spiders were found in the diet, but they frequently appeared in the arthropod availability samples, therefore shrikes were negatively selecting this invertebrate group. Total availability of small and medium size lizards was maximal during the spring, coinciding with the highest presence in pellets (Fig. 1).

4. Discussion

4.1. Diet composition, seasonal variation and prey selection

Beetles (mainly Curculionidae and Tenebrionidae) followed by hymenopterans and vertebrates were the most common prey consumed by the Southern Grey Shrike in the dry coastal habitat located in south Tenerife. However, in terms of biomass, vertebrates (especially lizards) provided the most important contribution. Despite the scant information available on the diet of this bird in the Canaries, these data agree with the greater part of the existing descriptive information, lizards and beetles being the principal prey (see Martín & Lorenzo 2001 and references therein).

Padilla et al.: Diet of Southern Grey Shrikes in Canary Islands 161

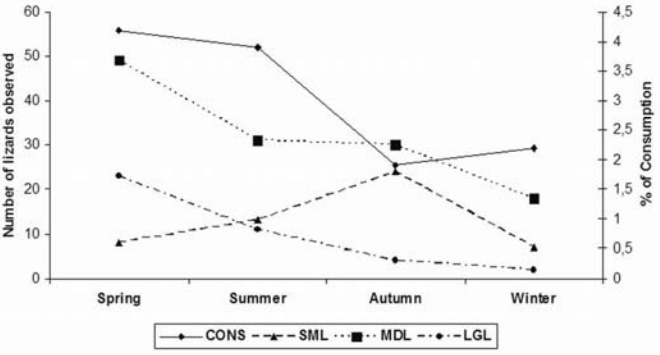


Fig. 1. Seasonal availability of lizards and their consumption by Southern Grey Shrike in a dry coastal area of Tenerife, Canary Islands. SML, small lizards; MDL, medium lizards; LGL, large lizards; CONS, consumption of small and medium size lizards.

The diet of the Canarian Southern Grey Shrike showed a slight seasonal variation, Coleoptera and vertebrates forming the most important prey throughout the year. However, some differences can be appreciated if the data are analysed as a function of the two previously defined periods (dry: spring and summer; and rainy: autumn and winter), as indicated by the results obtained in the Morisita index. These data, together with Levin's niche breadth, suggest that diet is more homogeneous during drier seasons than rainier ones, coinciding with the lowest availability of the main biomass source (the lizards). These results agree with the optimal foraging theory, in which niche breadth increases when availability of principal prey decreases (Krebs *et al.* 1983).

The relevant consumption of Curculionidae in the dry period and Tenebrionidae in the rainy one coincides with their respective population explosions in the field. The high relative importance shown by Orthoptera in winter, mainly represented by the Desert Locust (*Schistocerca gregaria*), has its origin in the arrival of the characteristically strong Saharan desert winds that carry this large insect. In general, this tendency to prey upon the most abundant available prey items coincides with the opinion of several authors, who consider the Southern Grey Shrike as a generalist predator that exhibits a great capacity to change its diet in relation to prey availability (Hernández 1993, Lefranc & Worfolk 1997).

Regarding the presence of vertebrates in this study, the highest number of captures (mainly lizards) was recorded in spring and summer (driest and hottest seasons), which coincides with shrikes nestling and fledgling periods. Furthermore, in the warmest and sunniest seasons, ectotherms such as lizards show their greatest activity. Moreover, lizards are available all year round and are thus attractive prey for Southern Grey Shrikes. In general, the abundance of some animals, such as lizards, is higher on islands than on the continent, because of lower predation and competition pressure, or larger trophic niche breadth (Case 1975, Benett & Gorman 1979, Evans & Evans 1980, Brown *et al*. 1992, Olesen & Valido 2003). The Canarian Archipelago is no exception to this phenomenon (Castanet & Báez 1988, Molina-Borja 1991, Rodríguez *et al*. 1994, Valido 1999, Olesen & Valido 2003).

Southern Grey Shrikes diet showed positive prey selection in groups such as Coleoptera and Hymenoptera (non-Formicidae) throughout the year, and Orthoptera (*Schistocerca gregaria*) in winter. This pattern coincides with those recorded in the Iberian Peninsula diet (Hernández *et al.* 1993). In addition, it is interesting to note that a total of 824 seeds were identified in pellets, the majority corresponding to *Lycium intricatum* (Solanacea). Some studies performed on Alegranza islet demonstrated that the Southern Grey Shrike is a legitimate secondary seed disperser when it catches the endemic frugivorous lizards (*Gallotia atlantica*) that have previously consumed *Lycium* fruits (Nogales *et al*. 1998, 2002). The seeds that appeared in the shrike pellets in Tenerife probably have their origin in these secondary seed dispersal processes (D.P. Padilla & M. Nogales unpubl.).

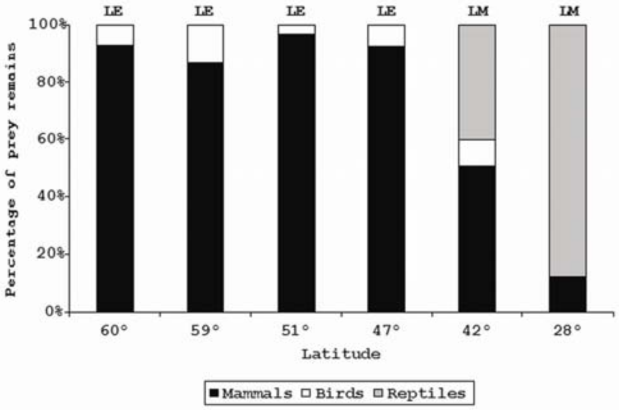


Fig. 2. Proportion of vertebrates in the diet of the Great Grey Shrike (LE) versus the Southern Grey Shrike (LM) during winter in Europe. Data taken from: 60° Finland (Karlsson 2002), 59° Sweden (Olsson 1986), 51° Germany (Grünwald 1984), 47° Switzerland (Bassin *et al.* 1981), 42° Iberian Peninsula-Spain (Hernández *et al.* 1993) and 28° Canaries (present study).

4.2. Geographical variations of species and subspecies

With regard to the latitudinal variation of the main prey consumed by the two related species of shrike, the Great Grey Shrike and the Southern Grey Shrike, important differences can be observed. One is the presence of mammals, which are the most important prey in northern geographical zones and whose frequency decreases with latitude (Bassin *et al.* 1981, Grünwald 1984, Olsson 1986, Schön 1998, Karlsson 2002). In the present study, one of the lowest latitudes examined, mammals were not frequently captured by *L. m. koenigi*, probably because the two small mammals available for the Shrike in Tenerife have nocturnal habits. We found that the highest predation on mammals occurs in spring. Nevertheless, in continental zones of Spain and France, *L. m. meridionalis* preys on mammals most frequently in autumn and winter (Hernández *et al.* 1993, Lepley *et al.* 2004). However, the presence of reptiles in the diet increases towards the southernmost latitudes (Fig. 2). It is interesting to note that the importance of reptile biomass in the Canarian shrike's diet could also be influenced by the high availability of lizards, one of the main ecological characteristics of these insular environments (Olesen & Valido 2003).

Birds could be important prey for the Great Grey Shrike in some cold habitats, especially in winter when mammals and arthropods are snowbound. Furthermore, passerine activity decreases in this season and an increased rate of successful attacks can be achieved (Grönlund *et al.* 1970, Grünwald 1983, Olsson 1986, Atkinson & Cade 1993, Hromada & Krištín 1996, Karlsson 2001, 2002).

The Southern Grey Shrike in southern France captures birds in two different seasons, summer and winter (Lepley *et al.* 2004). However, they are more successful in summer than in winter, probably because of availability of fledgling passerines. In the Iberian Peninsula the proportion of birds in Shrike diet increases in spring and summer, which coincides with the highest availability of young passerines (Hernández *et al.* 1993, Hernández 1995c). However, the absence of birds in the *L. m. koenigi* diet may be explained by greater lizard abundance, capture effectiveness, and possibly lower energy requirements for capture.

The general results obtained in this study partially agree with other continental reports on the Southern Grey Shrike diet, which suggest that the main food source is based on Coleoptera. However, the number of beetles observed in this diet study is practically twice that found in other geographical areas such as Israel, the Iberian Peninsula and France (Yosef 1991, Hernández *et al.* 1993, Lepley *et al.* 2004, respectively). Nevertheless, this high presence of beetles contrasts with the absence of other arthropod groups present in the diet in other areas, such as Arachnida or Lepidoptera. However, these last two groups could be underestimated in the pellet analysis due to their soft bodies (Tryjanowski *et al*. 2003).

In the Great Grey Shrike diet, the proportion of arthropods decreases in cold seasons (Bassin *et al.* 1981, Grünwald 1984, Olsson 1986, Karlsson 2002) due to the fact that their activity decreases along with their availability. Nevertheless, in Bulgaria, one of the lowest latitudes occupied by *L. excubitor* (c. 42º latitude), arthropods in winter are essential, forming 89.5% of the diet (Nikolov *et al.* 2004). With regards to latitudes occupied by the Southern Grey Shrike, the cold seasons are not harsh, and therefore arthropods are available throughout the year (Hernández *et al.* 1993, Budden & Wright 2000, Lepley *et al*. 2004). In the southernmost part of Tenerife, there is little seasonal climatic change, and thus arthropods are available all year round. However, we noted a drop in arthropod consumption from southern to northern latitudes in winter, probably caused by decreasing diversity and availability of insects (Munroe 1984).

Finally, the latitudinal cline described in the present contribution is in agreement with the hypothesis that the Southern Grey Shrike relies on cold-blooded prey in hot weather, while the Great Grey Shrike relies mainly on warm-blooded prey in cold weather (Schön 1998, Lepley *et al*. 2004).

Acknowledgements. We would like to express our most sincere thanks for the information provided by Rubén Barone and to Concepción Nieves for resolving our computing queries. Many friends helped us during the field work, especially Beatriz Rumeu and Aarón González. Michel Lepley, Ángel Hernández, Anna Traveset, Juan Carlos Illera, Boris Nikolov and an anonymous reviewer read the manuscript and made useful suggestions that greatly helped to improve it. A part of the bibliography was provided by the Department of Animal Biology (Zoology) of La Laguna University, and the Canarian Delegation of the Spanish Ornithological Society (SEO/BirdLife) kindly made available the distribution map of the Southern Grey Shrike in Tenerife Island. David P. Padilla is currently financed by a PhD grant awarded by the Canarian Government.

Endeemisen etelänisolepinkäispopulaation (*Lanius meridionalis koenegi*) ravinnonvalinta Teneriffalla, Kanarian saarilla

Teneriffalla tutkittiin etelänisolepinkäisen (*Lanius meridionalis koenegi*) ravintoa ja saaliinvalintaa. Tutkimuksen päätavoite oli vertailla saarella elävän populaation ravintoa mantereella elävien isolepinkäis- (*Lanius excubitor*) ja etelänisolepinkäispopulaatioihin. Huhtikuusta 2003 maaliskuulle 2004 kerättiin 440 oksennuspalloa, joista tunnistettiin 5 112 saaliseläintä. 85,4 % näistä oli kovakuoriaisia (pääosin Curculionidae ja Tenebrionidae) ja loput muita niveljälkaisia ja selkärankaisia. Pääosa ravinnon biomassasta oli selkärankaisia, erityisesti liskoja (64 %). Ravinnon koostumuksessa oli pientä vaihtelua vuoden eri aikoina, joskin kovakuoriaisia ja liskoja jäi saaliiksi paljon kaikkina vuodenaikoina. Etelänisolepinkäiset suosivat joitakin kovakuoriaisia, pistiäisiä (ei Formicidae) ja suorasiipisiä (*Schistocerca gregaria*).

Tutkimuksen aineisto tukee hypoteesia, jonka mukaan etelänisolepinkäiset panostavat vaihtolämpöisiin saaliseläimiin kuumalla säällä (Ranskan eteläosissa), kun taas isolepinkäiset suosivat tasalämpöisiä saaliseläimiä kylmässä säässä (Skandinavian niemimaalla). Liskojen suuri merkitys tämän populaation ravinnossa johtunee siitä, että niitä on saarilla paljon, niitä on tehokasta saalistaa ja täten saalistukseen kuluu vähemmän energiaa kuin muiden lajien kohdalla.

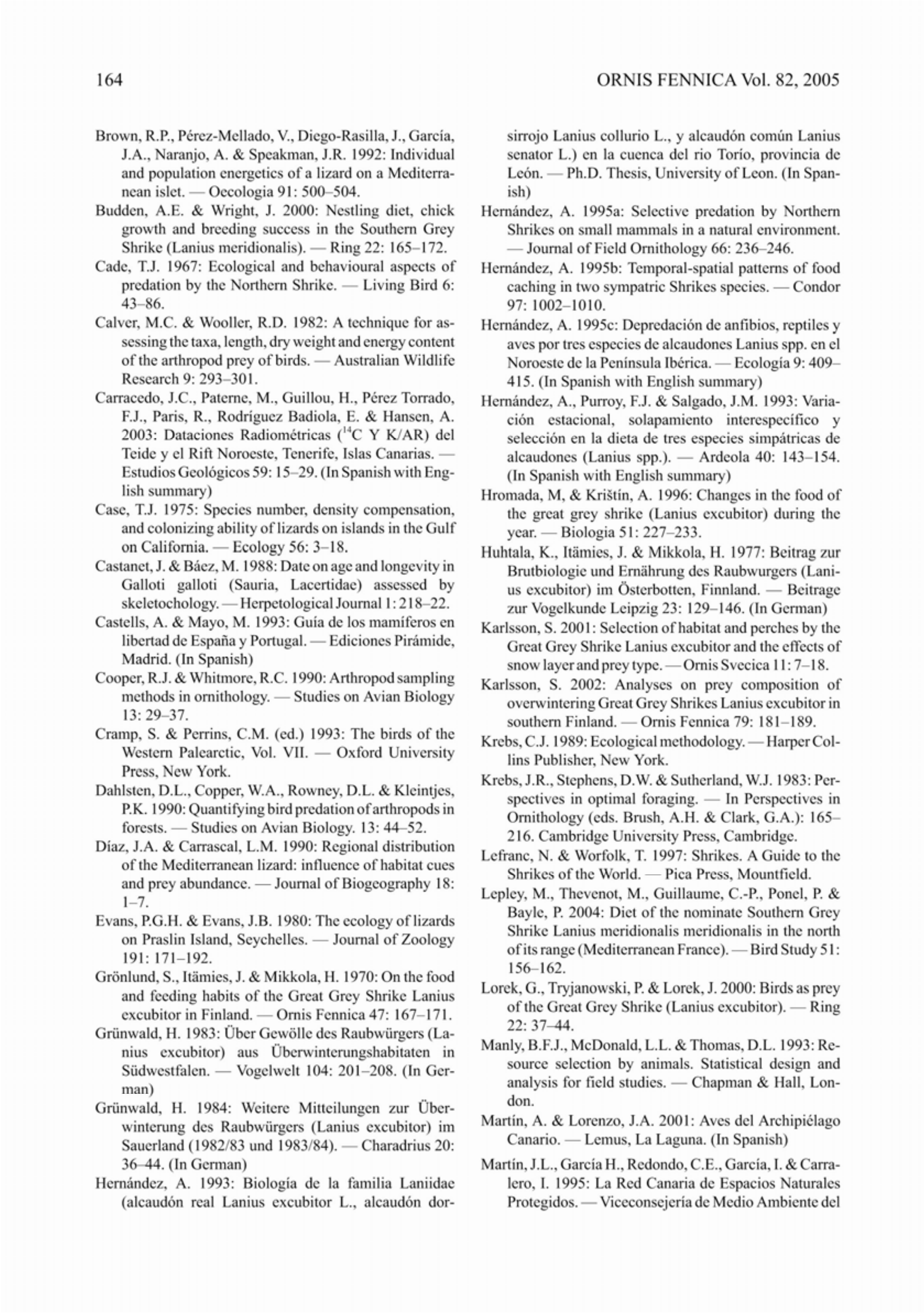
References

Arco-Aguilar, M.del, Acebes-Ginovés, J.R., Rodríguez-Rodríguez, A., Padrón, P., Rodríguez-Delgado, O., Pérez-de-Paz, P.L. & Wildpret de la Torre, W. 1997: Cormophytic vegetation of the Malpaís de La Rasca, Tenerife (Canary Islands). — Fitosociologia 34: 159–170.

Atkinson, E.C. & Cade, T.J. 1993: Winter foraging and diet composition of Northern Shrikes in Idaho. — Condor 95: 528–535.

Bassin, P., Huber, C. & Zuber, M. 1981: Beitrag zur Ernahrung des Raubwürgers (Lanius excubitor) in der Nordwestschweiz (Ajoie, Kanton Jura). — Jahrbuch fur Naturhistorisches Museum Bern 8: 1–19. (In German)

Benett, A.F. & Gorman, G.C. 1979: Population density and energetics of lizards on a tropical island. — Oecologia 42: 339–358.



Brown, R.P., Pérez-Mellado, V., Diego-Rasilla, J., García, J.A., Naranjo, A. & Speakman, J.R. 1992: Individual and population energetics of a lizard on a Mediterranean islet. — Oecologia 91: 500–504.

Budden, A.E. & Wright, J. 2000: Nestling diet, chick growth and breeding success in the Southern Grey Shrike (Lanius meridionalis). — Ring 22: 165–172.

Cade, T.J. 1967: Ecological and behavioural aspects of predation by the Northern Shrike. — Living Bird 6: 43–86.

Calver, M.C. & Wooller, R.D. 1982: A technique for assessing the taxa, length, dry weight and energy content of the arthropod prey of birds. — Australian Wildlife Research 9: 293–301.

Carracedo, J.C., Paterne, M., Guillou, H., Pérez Torrado, F.J., Paris, R., Rodríguez Badiola, E. & Hansen, A. 2003: Dataciones Radiométricas (^{14}C Y K/AR) del Teide y el Rift Noroeste, Tenerife, Islas Canarias. — Estudios Geológicos 59: 15–29. (In Spanish with English summary)

Case, T.J. 1975: Species number, density compensation, and colonizing ability of lizards on islands in the Gulf on California. — Ecology 56: 3–18.

Castanet, J. & Báez, M. 1988: Date on age and longevity in Galloti galloti (Sauria, Lacertidae) assessed by skeletochology. — Herpetological Journal 1: 218–22.

Castells, A. & Mayo, M. 1993: Guía de los mamíferos en libertad de España y Portugal. — Ediciones Pirámide, Madrid. (In Spanish)

Cooper, R.J. & Whitmore, R.C. 1990: Arthropod sampling methods in ornithology. — Studies on Avian Biology 13: 29–37.

Cramp, S. & Perrins, C.M. (ed.) 1993: The birds of the Western Palearctic, Vol. VII. — Oxford University Press, New York.

Dahlsten, D.L., Copper, W.A., Rowney, D.L. & Kleintjes, P.K. 1990: Quantifying bird predation of arthropods in forests. — Studies on Avian Biology. 13: 44–52.

Díaz, J.A. & Carrascal, L.M. 1990: Regional distribution of the Mediterranean lizard: influence of habitat cues and prey abundance. — Journal of Biogeography 18: 1–7.

Evans, P.G.H. & Evans, J.B. 1980: The ecology of lizards on Praslin Island, Seychelles. — Journal of Zoology 191: 171–192.

Grönlund, S., Itämies, J. & Mikkola, H. 1970: On the food and feeding habits of the Great Grey Shrike Lanius excubitor in Finland. — Ornis Fennica 47: 167–171.

Grünwald, H. 1983: Über Gewölle des Raubwürgers (Lanius excubitor) aus Überwinterungshabitaten in Südwestfalen. — Vogelwelt 104: 201–208. (In German)

Grünwald, H. 1984: Weitere Mitteilungen zur Überwinterung des Raubwürgers (Lanius excubitor) im Sauerland (1982/83 und 1983/84). — Charadrius 20: 36–44. (In German)

Hernández, A. 1993: Biología de la familia Laniidae (alcaudón real Lanius excubitor L., alcaudón dorsirrojo Lanius collurio L., y alcaudón común Lanius senator L.) en la cuenca del rio Torío, provincia de León. — Ph.D. Thesis, University of Leon. (In Spanish)

Hernández, A. 1995a: Selective predation by Northern Shrikes on small mammals in a natural environment. — Journal of Field Ornithology 66: 236–246.

Hernández, A. 1995b: Temporal-spatial patterns of food caching in two sympatric Shrikes species. — Condor 97: 1002–1010.

Hernández, A. 1995c: Depredación de anfibios, reptiles y aves por tres especies de alcaudones Lanius spp. en el Noroeste de la Península Ibérica. — Ecología 9: 409–415. (In Spanish with English summary)

Hernández, A., Purroy, F.J. & Salgado, J.M. 1993: Variación estacional, solapamiento interespecífico y selección en la dieta de tres especies simpátricas de alcaudones (Lanius spp.). — Ardeola 40: 143–154. (In Spanish with English summary)

Hromada, M, & Krištín, A. 1996: Changes in the food of the great grey shrike (Lanius excubitor) during the year. — Biologia 51: 227–233.

Huhtala, K., Itämies, J. & Mikkola, H. 1977: Beitrag zur Brutbiologie und Ernährung des Raubwurgers (Lanius excubitor) im Österbotten, Finnland. — Beitrage zur Vogelkunde Leipzig 23: 129–146. (In German)

Karlsson, S. 2001: Selection of habitat and perches by the Great Grey Shrike Lanius excubitor and the effects of snow layer and prey type. — Ornis Svecica 11: 7–18.

Karlsson, S. 2002: Analyses on prey composition of overwintering Great Grey Shrikes Lanius excubitor in southern Finland. — Ornis Fennica 79: 181–189.

Krebs, C.J. 1989: Ecological methodology. — Harper Collins Publisher, New York.

Krebs, J.R., Stephens, D.W. & Sutherland, W.J. 1983: Perspectives in optimal foraging. — In Perspectives in Ornithology (eds. Brush, A.H. & Clark, G.A.): 165–216. Cambridge University Press, Cambridge.

Lefranc, N. & Worfolk, T. 1997: Shrikes. A Guide to the Shrikes of the World. — Pica Press, Mountfield.

Lepley, M., Thevenot, M., Guillaume, C.-P., Ponel, P. & Bayle, P. 2004: Diet of the nominate Southern Grey Shrike Lanius meridionalis meridionalis in the north of its range (Mediterranean France). — Bird Study 51: 156–162.

Lorek, G., Tryjanowski, P. & Lorek, J. 2000: Birds as prey of the Great Grey Shrike (Lanius excubitor). — Ring 22: 37–44.

Manly, B.F.J., McDonald, L.L. & Thomas, D.L. 1993: Resource selection by animals. Statistical design and analysis for field studies. — Chapman & Hall, London.

Martín, A. & Lorenzo, J.A. 2001: Aves del Archipiélago Canario. — Lemus, La Laguna. (In Spanish)

Martín, J.L., García H., Redondo, C.E., García, I. & Carralero, I. 1995: La Red Canaria de Espacios Naturales Protegidos. — Viceconsejería de Medio Ambiente del

Gobierno de Canarias, Santa Cruz de Tenerife. (In Spanish)

Marzol Jaén, M.V. 1988: La Lluvia: un Recurso Natural para Canarias. — Servicio de Publicaciones de la Caja General de Ahorros de Canarias, Santa Cruz de Tenerife. (In Spanish)

Molina-Borja, M. 1991: Notes on alimentary habits and spatial-temporal distribution of eating behaviour patterns in a natural population of lizards (Gallotia galloti). — Vieraea 20: 1–9.

Moreby, S.J. 1988: An aid to the identification of arthropod fragments in the faeces of gamebird chicks (Galliformes). — Ibis 130: 519–526.

Munroe, E. 1984: Biogeography and evolutionary history: wide-scale and long-term patterns of insects. — In Ecological Entomology (ed. Huffaker, C.B. & Rabb, R.L.): 279–304. Wiley, New York.

Nikolov, B.P., Kodzhabashev, N.D. & Popov, V.V. 2004: Diet composition and spatial patterns of food caching in wintering Great Grey Srikes (Lanius excubitor) in Bulgaria. — Biological Letters 41: 119–133.

Nogales, M., Delgado, J.D. & Medina, F.M. 1998: Shrikes, lizards and Lycium intricatum (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canary Islands). — Journal of Ecology 86: 866–871.

Nogales, M., Quilis, V., Medina, F.M. Mora, J.L. & Trigo, L.S. 2002: Are predatory birds effective secondary seed dispersers? — Biological Journal of the Linnean Society 75: 345–352.

Olesen, J.M. & Valido, A. 2003: Lizards as pollinators and seed dispersers: an island phenomenon. — Trends in Ecology and Evolution 18: 177–181.

Olsson, V. 1986: Varfågelns Lanius excubitor vintervanor V. Bytesval. — Vår Fågelvärld 45: 19–31. (In Sweden with English summary)

Ralph, C.P., Nagata, S.E. & Ralph, C.J. 1985: Analysis of droppings to describe diets of small birds. — Journal of Field Ornithology 56: 165–174.

Rodríguez, M.A., Santos, A. & Cantarella, F. 1994: Estimación del tamaño de la población de Gallotia galloti galloti Oudart, 1839 (Sauria: Lacertidae) en el Malpaís de Güimar (S.E. Tenerife). — Studia Oecologica 10–11: 401–407.

Savage, R.E. 1931: The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. — Fisheries Investigations, Ministry of Agriculture, Food and Fisheries Series 2, 12: 1–88.

Schön, M. 1998: On the evolution of the northern and southern group of subspecies in the Great Grey Shrike superspecies (Lanius excubitor). — In Shrikes of the World II: Conservation Implementation (eds. Yosef, R. & Lohrer, F.E.): 9–13. International Birdwatching Center in Eilat, Eilat, Israel.

Snow, D.W. & Perrins, C.M. (ed.) 1998: The Birds of the Western Palearctic. — Oxford University Press, Oxford.

Tryjanowski, P., Karg, M.K. & Karg, J. 2003: Food of the Red-backed Shrike Lanius collurio: a comparison of three methods of diet analysis. — Acta Ornithologica 38: 59–64.

Valido, A. 1999: Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. Gallotia, Lacertidae). — Ph.D. Thesis, University of La Laguna. (In Spanish)

Wolda, H. 1990: Food availability for an insectivore and how to measure it. — Studies on Avian Biology 13: 38–43.

Yosef, R., Mitchell, W.A. & Pinshow, B. 1991: The proximate costs and benefits of polygyny to male Northern Shrike. — Wilson Bulletin 103: 146–149.

PADILLA, D. P., A. GONZÁLEZ-CASTRO, C. NIEVES & M. NOGALES. 2009. Trophic ecology of the Southern Grey Shrike (Lanius meridionalis) in insular environments: the influence of altitude and seasonality. ***Journal of Ornithology*** **150**: 557-568.

J Ornithol (2009) 150:557–568
DOI 10.1007/s10336-009-0381-7

ORIGINAL ARTICLE

Trophic ecology of the Southern Grey Shrike (*Lanius meridionalis*) in insular environments: the influence of altitude and seasonality

**D. P. Padilla · A. González-Castro ·
C. Nieves · M. Nogales**

Received: 1 April 2008 / Revised: 7 November 2008 / Accepted: 13 January 2009 / Published online: 24 February 2009

Abstract The seasonal diet and prey selection of the Southern Grey Shrike (*Lanius meridionalis*) was studied in two different insular habitats: shrub environments of the Canary Islands in coastal and high mountain zones. We measured, in each season, food availability and prey size in order to determine prey size selection of shrikes along an altitudinal gradient. Moreover, we compared the diet patterns observed with those documented on the continent, to determine if Southern Grey Shrikes in the islands' high mountain zone (which has a continental climate) showed seasonal diet variation similar to those in northern continental areas. We analysed a total of 1,139 shrike pellets collected in 1 year and identified 10,179 prey items. Numerically arthropods (91%), and in terms of biomass lizards (70%) were the main prey consumed by the shrikes. The proportions of the main prey items differed significantly between seasons and habitats. Diet in the coastal areas was less variable than in the high mountain zone. The greater seasonal climatic variation in the high mountain zone was associated with diet patterns similar to those found in some northern continental areas, such as the Iberian Peninsula and southern France. Finally, shrikes selected the largest prey in the high mountain habitat. This suggests that foraging behaviour in this species is related to climatic conditions, as the biggest and most profitable prey were consumed in the most harsh habitats.

Communicated by T. Friedl.

D. P. Padilla (✉) · A. González-Castro · C. Nieves ·
M. Nogales
Island Ecology and Evolution Research Group (IPNA-CSIC),
Avda. Astrofísico Francisco Sánchez 3, 38206 La Laguna,
Tenerife, Canary Islands, Spain
e-mail: dpadilla@ipna.csic.es

Keywords Canary Islands · Coastal xeric and high mountain shrubs · *Lanius meridionalis koenigi* · Prey selection · Seasonal climatic changes

Introduction

Oceanic islands are ideal places to study evolutionary ecology in terrestrial vertebrates adapted to these unique ecosystems (Gorman 1979; Nogales 1999). The relative simplicity of oceanic islands in terms of species biodiversity and ecological interactions compared to mainland ecosystems (Olesen and Jordano 2002) make them interesting systems in which to study evolutionary ecology phenomena such as the relatively broad trophic niche of some vertebrates (Grant 1965; MacArthur et al. 1972; Nogales and Hernández 1994). However, as far as we know, feeding diversity has not been evaluated in populations of the same species that live in different island environments. Insular populations of the Southern Grey Shrike (*Lanius meridionalis*) provide an opportunity to assess inter-island variation in diet ecology.

The Southern Grey Shrike occurs in the Saharo-Sindian xeric zone of south-west Europe (Lefranc and Worfolk 1997). The Southern Grey Shrike, which has distinct ecological characteristics such as habitats and diet, has been recently split from the Great Grey Shrike (*L. excubitor*) (Sangster et al. 2002). The Great Grey Shrike occupies cold habitats and preys mainly on warm-blooded animals (birds and mammals), while the Southern Grey Shrike preys mainly on cold-blooded animals (Schön 1998; Lepley et al. 2004; Padilla et al. 2005). The subspecies *L. m. koenigi*, endemic to the Canary Islands, is one of the few insular shrike populations in the world. It occupies the islands of Lanzarote, Fuerteventura, Gran Canaria and Tenerife humeral, tibia, pelvic girdle and parietal), mandibles or maxillaries of reptiles and mammals.

We recorded the percentage of each prey item with regard to the total number of prey items and the biomass as a percentage of the total biomass contents. To calculate wet biomass, we used average representative weights of known vertebrate prey species (lizards and geckos) (M. Nogales, unpublished data). In the case of mammals, we employed mean weights from the literature (Castells and Mayo 1993). For arthropods, we collected at least five individuals of each taxon and measured their mean live weight using an electronic balance (precision 0.0001 g). We employed wet biomass because water is especially important in xeric habitats since it is a limited resource (Lepley et al. 2004).

To determine if Southern Grey Shrikes preyed selectively on a particular size of invertebrate prey, we classified the invertebrates found into four categories (small 5–10 mm; medium >10–15 mm; large >15–20 mm; very large >20 mm). Since in most cases only remains of invertebrates were found in pellets, to assign each prey taxon to its size category we measured a minimum of five individuals of each taxon found in the diet analysis, obtained from the reference collection of the Department of Animal Biology-Zoology (University of La Laguna).

We examined in detail the body size of the main prey that provided the largest biomass (Lacertid lizards, *Gallotia galloti* on Tenerife and *G. atlantica* on Lanzarote) (Martín and Lorenzo 2001; Padilla et al. 2005). We measured the length of the main bones that were found complete and well-preserved in pellets (jaws, maxillaries, parietals, pelvic girdle, femora, tibiae and humeri). We used the regression models detailed by Nogales and Valido (1999), which provide data on relationships between lizard snout to vent length (SVL) and the lengths of the main bones.

To study prey selection by shrikes along an altitude gradient, we estimated the availability of the main prey (invertebrates and lizards) in Las Cañadas del Teide (high mountain zone) and compared our data with those from Padilla et al. (2005, 2007) in Malpaís de La Rasca (coastal zone). All the data were collected in the same period using the same sampling methods, to avoid possible biases due to inter-annual fluctuations in prey availability. To quantify invertebrate availability, we counted all individuals larger than 5 mm in a 1-m^2 quadrat for 2 min. A total of 210 quadrat counts were taken in each season. Quadrats were placed 20 m apart on 42 line transects in seven different shrike territories. To estimate the relative abundance of lizards, we walked a total of 35 line transects, each 100 m long, in the same seven shrike territories, and counted all lizards within 5 m of the transect (Díaz and Carrascal 1990). We classified the lizards into three size categories to determine if the shrikes were selecting specific sizes of lizard (small SVL $<$ 5 cm; medium SVL 5–10 cm; large SVL $>$ 10 cm).

Statistical and index analysis

Ordination tests are multivariate techniques used to find patterns within complex data sets. For example, they can be used to describe relationships between species and ecological factors such as prey availability through space and time (ter Braak and Šmilauer 1998). Detrended correspondence analysis (DCA) is an indirect gradient analysis method which is especially useful to evaluate the variation in species composition, unconstrained by the particular variable measured. To analyse the relationships among the abundance and biomass of the main prey groups in the diet of shrikes with respect to each study area and season, a DCA was calculated in CANOCO (ter Braak and Šmilauer 1998). The prey abundance and the biomass parameters were considered separately in the analyses. In order to compare island versus continental shrike diets, data from three localities in the Canaries and three localities on the mainland were included in the analyses. We used percentage of prey items and biomass per study site.

We also used likelihood ratio tests to identify habitat and seasonal variation in shrike diet, to compare the mean invertebrate prey size in the diet among the three different study sites and seasons, to evaluate differences in food availability between coastal and high mountain zones, to test the association between the presence of seeds with lizard remains and finally to compare the number of invertebrates that appeared in the diet of the Southern Grey Shrike and the Great Grey Shrike. For the comparison of the diet patterns of the endemic Canarian shrike subspecies *L. m. koenigi* with other shrike populations, data were obtain from documented studies: Hódar (2006), Hernández et al. (1993) and Lepley et al. (2004) in relation to the Southern Grey Shrike, and Nikolov et al. (2004) and Karlsson (2002) in relation to the Great Grey Shrike. To compare differences in the size of lizards found in pellets among seasons and localities, we used a two-way ANOVA test after arcsin data transformation to reach normality, and Scheffé post hoc tests. Furthermore, we compared differences in lizard sizes between islands using a one-way ANOVA test. Where it was necessary to use the same data set, we corrected significance a posteriori by using the sequential Bonferroni procedure. We performed all analyses using the SPSS statistical package (version 15.0).

We used the "forage index" of Savage (1931), followed by the method proposed by Manly et al. (1993), to calculate diet selection by shrikes on an altitudinal gradient. For further information about the use of this index see Padilla et al. (2005).

Results

General diet

We identified a total of 10,179 prey items in the analysis of 1,139 pellets, the ratio of vertebrates to invertebrates being 1:10 (Table 1). Insects were the staple prey in shrike diets, and beetles proved to be the insects most often consumed (mainly Curculionidae, Tenebrionidae and Scarabaeidae; 70% of the total prey items), followed by hymenopterans (principally Apidae and Vespidae; 12%) and grasshoppers (Acrididae; 6%). Among vertebrates, reptiles were the most frequently identified prey (87%), especially the endemic lizards *Gallotia* spp. (97% of reptiles found); the principal mammal species was the non-native house mouse *Mus domesticus* (12% of vertebrates). With respect to biomass, vertebrates (94%) were the most important group, and lizards (70%) and house mice (21%) were the principal prey.

Only a small number of prey were found in larders in each study area all year round (one Coleoptera and five lizards in Malpaís de La Rasca; one Coleoptera, one Orthoptera and ten lizards in Las Cañadas del Teide; and no prey in Malpaís de La Corona). Due to these scarce prey numbers, these data were not included in the diet analysis so as to make a suitable comparison among habitats.

A total of 5,891 seeds of nine different plant species were found in shrike pellets in the two coastal study areas. The most commonly found seeds were from two species with fleshy fruits: *L. intricatum* (Solanaceae) (86% of total seeds) and *R. fruticosa* (Rubiacea) (3%; Table 2). In contrast, only one seed, from *S. supranubius* (Fabaceae), was found in shrike pellets from Las Cañadas del Teide. We found a statistically significant association between seeds of all plant species and lizard remains in shrike pellets (Likelihood ratio test, $P < 0.001$ for all comparisons).

Seasonal and habitat diet variation

Results of the DCA based on percentage of prey items revealed three main groups coinciding with each study site (Fig. 1). We found a more pronounced seasonal diet variation in the high mountain zone than in the coastal ones, and similar to other diet analyses made in continental areas such as Iberian Peninsula and southern France (Fig. 1). Beetles were the most important prey item for shrikes, being consumed in a higher proportion in Malpaís de La Rasca than in the other two localities (Likelihood ratio test, $G = 1347.0$, $df = 2$, $P < 0.001$). However, hymenopterans ($G = 198.2$, $df = 2$, $P < 0.001$) and grasshoppers ($G = 789.7$, $df = 2$, $P < 0.001$) were more regularly consumed in Las Cañadas del Teide. Predation on vertebrates (especially lizards) was greatest in Malpaís de La Corona ($G = 408.4$, $df = 2$, $P < 0.001$).

Seasonal diet of the Southern Grey Shrike on the Canary Islands is characterised by large numbers of beetles in all seasons and habitats, except in Las Cañadas del Teide, where beetles were dominant only in winter ($G = 186.3$, $df = 3$, $P < 0.001$). Hymenoptera (mainly bees and wasps) and Orthoptera were most frequently identified in pellets in winter in both coastal zones (Malpaís de La Corona, $G = 14.1$, $df = 3$, $P = 0.003$ and $G = 15{,}5$, $df = 3$, $P < 0.001$; Malpaís de La Rasca, $G = 45.5$, $df = 3$, $P < 0.001$ and $G = 35.6$, $df = 3$, $P < 0.001$, respectively). In the high mountain zone, Hymenoptera, Hemiptera and Lepidoptera caterpillars were most frequently consumed in summer ($P < 0.001$, for all comparisons) and Orthoptera in autumn ($G = 78.9$, $df = 3$, $P < 0.001$). DCA based on percentage of biomass revealed how lizards and house mice provided the greatest biomass in shrike diet all year round (Fig. 2). Nevertheless, the peak in predation of these vertebrates occurred in the two habitats on Tenerife during spring and summer, whereas on Lanzarote vertebrates were consumed mostly during autumn and winter ($G = 53.5$, $df = 3$, $P < 0.001$). Only in Malpaís de La Corona in spring and summer were a few passerine remains found in pellets.

Prey selection

The total availability of the different invertebrate size categories, in the two zones where it was evaluated (coastal and the high mountain zones of Tenerife), only differed in relation to the medium size ($G = 13.1$, $df = 3$, $P = 0.004$), being greater in number in the high mountain zone, but only in summer ($G = 22.9$, $df = 3$, $P < 0.001$) due to the explosion of hymenopterans. However, along the altitudinal gradient, no differences were observed in the relative abundance of large and very large invertebrate sizes all year round ($G = 1.6$, $df = 1$, $P = 0.19$). Also, the total availability of each lizard size did not differ between the coastal and the high mountain zone ($G = 1.8$, $df = 2$, $P = 0.39$). Based on our pellet data, shrikes preyed upon invertebrates of the largest size class (>20 mm) more frequently in Las Cañadas del Teide than in the two coastal areas ($G = 1{,}016.5$, $df = 2$, $P < 0.001$; Table 3). The medium size class of invertebrates (>10–15 mm) was most frequently captured by shrikes in both habitats on Tenerife ($G = 319.6$, $df = 2$, $P < 0.001$), while in Malpaís de La Corona, the most frequently consumed invertebrates fell into the smallest category (5–10 mm; $G = 1{,}009.5$, $df = 2$, $P < 0.001$). There was no clear seasonal pattern of captured invertebrate prey sizes in the different study areas ($G = 1.1$, $df = 6$, $P = 0.979$).

Table 1 Diet composition (from pellet analysis) of the Southern Grey Shrike (*Lanius meridionalis koenigi*) in the main shrub environments of the Canary Islands

Prey items	Spring						Summer						Autumn						Winter					
	Coastal 1		Coastal 2		Mountain		Coastal 1		Coastal 2		Mountain		Coastal 1		Coastal 2		Mountain		Coastal 1		Coastal 2		Mountain	
	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B	%P	%B
Mollusca	0.2	+	–	–	–	–	0.1	+	–	–	–	–	0.2	+	–	–	–	–	–	–	–	–	–	–
Arthropoda																								
Araneae	0.4	+	–	–	0.4	+	–	–	0.1	+	–	–	0.2	+	–	–	–	–	0.3	+	–	–	1.0	+
Diplopoda	–	–	–	–	0.2	+	–	–	–	–	0.2	+	–	–	–	–	–	–	–	–	–	–	–	–
Diplura	–	–	–	–	0.4	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Odonata	–	–	0.5	+	–	–	–	–	0.1	+	0.4	+	–	–	–	–	–	–	–	–	0.1	+	–	–
Orthoptera	4.6	0.4	0.7	0.3	9.3	0.4	5.2	0.3	2.2	1.1	23.2	1.2	1.6	0.1	0.3	0.2	34.0	3.4	5.9	0.2	2.4	8	14.2	3.2
Dermaptera	0.1	+	–	–	0.2	+	0.1	+	–	–	0.2	+	–	–	–	–	–	–	–	–	–	–	–	–
Hemiptera	–	–	0.8	0.1	2.0	+	0.1	+	2.4	0.2	8.3	0.1	–	–	0.4	0.1	3.2	0.1	–	–	1.7	0.5	0.7	+
Plannipennia	0.1	+	–	–	–	–	0.1	+	–	–	0.2	+	–	–	–	–	0.3	+	–	–	–	–	0.4	0.1
Coleoptera	70.9	5.6	87.2	5.2	35.7	2.7	60.9	3.6	83.4	9.0	14.1	2.1	63.3	2.3	90.9	13.7	39.9	3.8	40.3	0.9	81.7	11.5	75.0	10.4
Lepidoptera	0.3	+	–	–	3.3	0.1	0.8	+	–	–	3.9	0.2	0.5	+	–	–	1.0	0.1	0.8	+	–	–	0.7	0.2
Hymenoptera	11.9	0.2	5.0	0.3	28.6	0.3	16.1	0.2	6.9	0.4	34.0	0.3	13.8	0.1	5.2	0.6	13.8	0.3	20.6	0.1	11.4	1.3	4.7	0.2
Formicidae	3.3	+	1.6	+	2.4	+	7.3	+	2.8	+	11.7	+	10.2	+	1.2	+	4.5	+	7.2	+	2.5	+	1.3	+
Non- Formicidae	8.6	0.2	3.4	0.2	26.2	0.3	8.8	0.2	4.1	0.4	22.3	0.3	3.6	0.1	4.0	0.6	9.3	0.3	13.4	0.1	8.9	1.3	3.4	0.2
Hexapoda indet	0.1	–	–	–	1.0	–	0.5	–	0.1	–	0.2	–	0.2	–	0.4	–	0.5	–	0.8	–	0.3	–	0.2	–
Vertebrata																								
Reptilia																								
Lacertidae *Gallotia* spp.	9.4	63.6	4.2	61.5	17.1	82.2	13.1	65.2	3.9	72.1	15.1	93.9	16.6	65.6	1.9	56.5	6.1	72.2	26.9	73.2	2.1	63.7	2.6	71.8
Gekkonidae	0.1	0.6	0.3	2.1	–	–	0.6	2.8	0.4	3.5	–	–	0.5	2.0	0.3	4.0	–	–	0.8	2.0	–	–	–	–
Mammalia																								
Muridae																								
Mus domesticus	1.5	25.2	1.3	30.5	1.8	14.2	1.9	23.5	0.4	13.7	0.2	2.2	3.1	30.0	0.5	24.5	1.0	20.0	3.3	22.9	0.3	14.8	0.3	13.3
Soricidae																								
Suncus etruscus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	0.4	–	–	–	–	–	–	0.2	0.7
Crocidura canariensis	0.1	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	0.7	–	–	–	–
Aves																								
Passeriformes	0.3	3.6	–	–	–	–	0.5	4.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total prey	1,074		1,108		451		849		1,141		470		559		1,189		594		387		1,674		683	
Total pellets	100		115		85		101		116		71		102		93		82		93		116		65	

%P Percentage of prey items, *%B* percentage of wet biomass, *Coastal 1* Malpaís de La Corona, *Coastal 2* Malpaís de La Rasca, *Mountain* Las Cañadas del Teide

+ Values less than 0.1%

Table 2 Proportion of seeds (%S) and frequency of occurrence (%O) of each plant species in the Southern Grey Shrike pellets in the main shrub environments of the Canary Islands

Seed component	Spring						Summer						Autumn						Winter					
	Coastal 1		Coastal 2		Mountain		Coastal 1		Coastal 2		Mountain		Coastal 1		Coastal 2		Mountain		Coastal 1		Coastal 2		Mountain	
	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O	%S	%O
Lycium intricatum	91.1	31	99.1	20	–	–	27.6	11.9	75.0	7.8	–	–	5.1	2	98.5	12.9	–	–	97.8	57	97.1	13.8	–	–
Atriplex semibaccata	0.2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	1.1	1.4	0.9	–	–
Volutaria canariensis	–	–	0.7	2.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plocama pendula	–	–	–	–	–	–	–	–	5.4	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Asparagus sp.	–	–	–	–	–	–	0.1	1	–	–	–	–	2.5	1	–	–	–	–	–	–	–	–	–	–
Rubia fruticosa	8.5	15	–	–	–	–	0.1	1	–	–	–	–	–	–	–	–	–	–	1.9	8.6	–	–	–	–
Chenopodium sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	2.2	–	–	–	–
Spartocytisus supranubius	–	–	–	–	100	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Patellifolia patellaris	–	–	–	–	–	–	–	–	0.9	0.9	–	–	–	–	–		–	–	–	–	1.4	1.7	–	–
Unidentified seeds	0.2	1	0.2	0.9	–	–	72.2	10.9	18.7	4.3	–	–	92.3	1	1.5	2.2	–	–	–	–	–	–	–	–
Total seeds	1,116		438		1		812		112		–		39		136		–		3,100		138		–	
Total pellets	100		115		85		101		116		71		102		93		82		93		116		65	

Coastal 1 Malpaís de La Corona, *Coastal 2* Malpaís de La Rasca, *Mountain* Las Cañadas del Teide

The size of lizards found in pellets varied among the three localities (two-way ANOVA, $F = 146.6$, $df = 2$, $P < 0.001$). Combining all seasons, shrikes captured smaller lizards on Lanzarote (*G. atlantica*) than on Tenerife (*G. galloti*) ($F = 328.7$, $df = 1$, $P < 0.001$; Fig. 3). Furthermore, lizard sizes in pellets differed between the two habitats of Tenerife, and shrikes preyed upon the largest lizards in the high mountain zone of Las Cañadas del Teide (Scheffé test, $P = 0.017$). The largest lizards were captured in winter and spring in the two coastal zones, and in summer in the high mountain zone of Tenerife (Fig. 3).

Selective predation by shrikes upon some of their main prey varied between the coastal zone and the high mountain zone on Tenerife (Table 4). Thus, Orthoptera (Acrididae) in the high mountain zone were positively selected all year round, whereas in the coastal zone a clear negative selection was detected. With regards to Hymenoptera (non-Formicidae), shrikes showed negative prey selection in the high mountain zone and positive selection in the coastal zone. However, other important prey, such as Coleoptera or Aranea (positively and negatively selected, respectively) presented the same pattern all year round in the two areas. Finally, medium and large lizards were positively selected, while small lizards were negatively selected in the high mountain zone (Table 4).

Discussion

Diet composition

The diet of the Southern Grey Shrike in the main habitats of the Canary Islands was dominated by insects (principally beetles) in terms of numbers, and by lizards in biomass. These data agree with previous preliminary results obtained from the species within the archipelago (Grimm 2005; Padilla et al. 2005). Other studies in continental habitats show that in the southern part of its range the Southern Grey Shrike also relies mainly on arthropods and lizards (Yosef et al. 1991; Budden and Wright 2000; Hódar 2006), whereas in northern areas, invertebrates are the most commonly consumed prey all year round (Hernández et al. 1993; Lepley et al. 2004).

Shrikes on the Canary Islands prey to a greater extent on cold-blooded animals than do those in northern continental areas. In latitudes occupied by the Southern Grey Shrike, the cold seasons are mild enough for arthropods and lizards to be available throughout the year (Yosef et al. 1991; Hernández et al. 1993; Budden and Wright 2000; Lepley et al. 2004; Padilla et al. 2005; Hódar 2006; Fig. 4a). Interestingly, the diet composition, in terms of prey items, of the Southern Grey Shrike is similar to that of the Great Grey Shrike in one

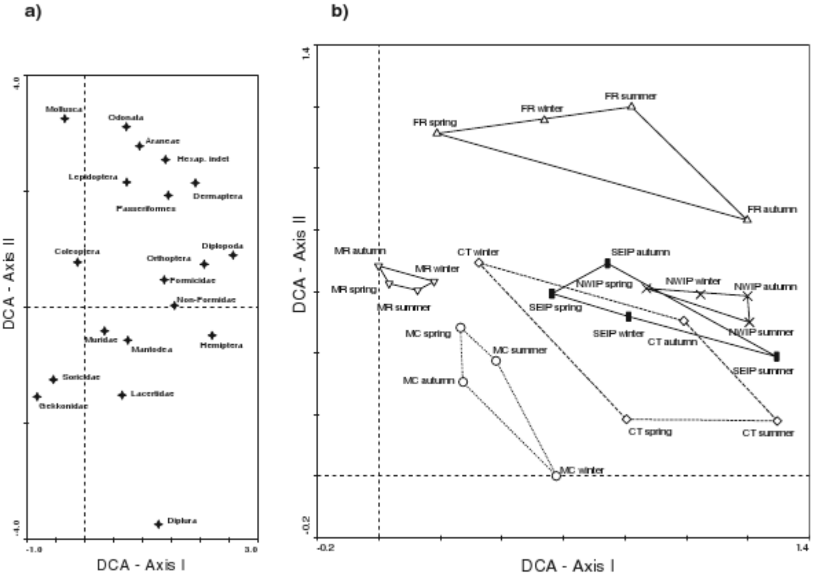


Fig. 1 Results of the detrended correspondence analysis (*DCA*) of prey abundance in the Southern Grey Shrike (*Lanius meridionalis koenigi*) seasonal diet in the Canary Islands plus three continental areas are shown. The localities studied in the Canary Islands were: Malpaís de La Corona (*MC*), Malpaís de La Rasca (*MR*) and Las Cañadas del Teide (*CT*). Mainland localities analysed were: Southeast Iberian Peninsula (*SEIP*; Hódar 2006), Northwest Iberian Peninsula (*NWIP*; Hernández et al. 1993) and Southern France (*FR*; Lepley et al. 2004). In the same analysis, species (**a**; *stars*) and plot scores (**b**; four plots each season per study area) are separate to have a clearer view of the data. The importance of each prey group is reflected by the proximity with regard to each season and study area (enclosed in the *polygons*). (Eigenvalues of *axes I and II* were 0.248 and 0.032, respectively, and the cumulative percentage of variance explained by these two axes was 66.7%)

of the lowest latitudes of its distribution (Bulgaria, $G = 0.2$, $df = 1$, $P = 0.649$), where arthropods are also the most important prey (Nikolov et al. 2004). These data clearly differ from more northern continental areas, such as Finland, where the Great Grey Shrike consumes a high proportion of vertebrates, especially mammals, in its diet (Karlsson 2002; $G = 46.6, df = 1, P < 0.001$; Fig. 4a). However, in terms of biomass, lizards were the most important group for the Southern Grey Shrike in the Canaries, whereas in Bulgaria and Finland mammals dominate the diet of the Great Grey Shrike (Fig. 4b). These data support the hypothesis proposed by Schön (1998) and confirmed by Lepley et al. (2004) and Padilla et al. (2005), that the Great Grey Shrike relies mainly on endothermal prey in cold zones while the Southern Grey Shrike preys on ectothermal species in hot climates.

The proportion in the shrike diet of lizards eaten all year round on Lanzarote and Tenerife was the greatest ever recorded for a shrike. The abundance of lizards in the diet might easily be explained by the abundance of this family of reptiles (Lacertidae) in all environments in the Canaries (Castanet and Báez 1988; Rodríguez et al. 1994; Valido 1999) and by the small size of this lizard species (Hernández et al. 2000). Such an abundance of lizards is attributed to a number of well-known evolutionary phenomena observed in oceanic islands, such as limited competitive interactions, broad niche and limited predation (Olesen and Valido 2003).

A large number of seeds—mainly *L. intricatum* (Solanaceae) and *R. fruticosa* (Rubiaceae)—appeared associated with lizard remains in shrike pellets in the coastal zones and are assumed to be secondarily dispersed by shrikes preying upon frugivorous lizards (D.P. Padilla and M. Nogales, unpublished data). Other studies in the Canary Islands have demonstrated how the Southern Grey Shrike acts as a legitimate secondary seed disperser when it preys upon the endemic frugivorous lizards (Nogales et al. 1998, 2002, 2007). The low number of seeds that appeared in the high mountain zone is related to the scarcity of fleshy fruits consumed by lizards in this habitat (Valido and Nogales 2003).

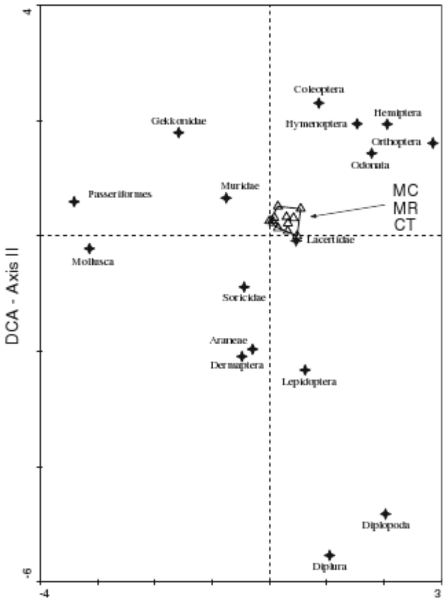


Fig. 2 Detrended correspondence analysis (*DCA*) of the importance of each prey item in the biomass of the Southern Grey Shrike diet in the Canary Islands. *MC* Malpaís de La Corona, *MR* Malpaís de La Rasca, *CT* Las Cañadas del Teide. The importance of each prey group (*stars*) is reflected by the proximity with regard to the seasonal diet of each study area (*triangles*). (Eigenvalues of *axes I and II* were 0.062 and 0.025, respectively, and the cumulative percentage of variance explained by both axes was 54.1%)

Seasonal influence on diet

There was little seasonal variation in shrike diet in the two coastal zones, where Coleoptera predominated in all seasons. Shrikes shifted their predation to different beetle families when population explosions of these groups took place (Padilla et al. 2005). Nevertheless, in the high mountain zone of Las Cañadas del Teide, seasonal variation in diet was clearly more marked. Seasonal changes in the diet of shrikes in high mountain zones suggest that the Southern Grey Shrike behaves as an opportunist predator (Hernández 1993; Lefranc and Worfolk 1997). Optimal foraging theory predicts that predators try to maximise the energy in their diet by focusing on the more abundant prey populations (MacArthur and Pianka 1966). As a consequence of a drastic environmental change or of variable resource seasonality, non-specialised predators can change their diet to include a new prey taxon when its availability renders it profitable (Ben-David et al. 1997; Correia 2001). In Las Cañadas del Teide, the main prey items available in spring and summer when the flowering period peaks were

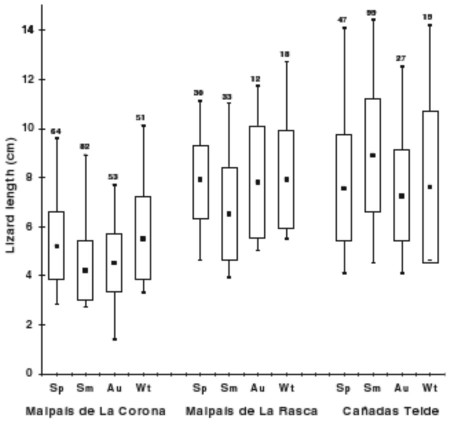


Fig. 3 Seasonal lizard lengths observed in Southern Grey Shrike pellets in the main shrub habitats of the Canaries (*Sp* spring, *Sm* summer, *Au* autumn, *Wt* winter). The *box* indicates the mean size (*filled square*) ± SD. The *bars* extending *above* and *below* each *box* show the maximum and minimum sizes. Sample sizes are indicated

Table 3 Invertebrate prey sizes captured by the Southern Grey Shrike (*P*) and prey availability (*PA*) in Southern Grey Shrike territories in three different environments of the Canarian Archipelago

	% Invertebrate prey sizes								Total of prey items
	5–10 mm		>10–15 mm		>15–20 mm		>20 mm		
	%P	% PA	%P	% PA	%P	% PA	%P	% PA	
Coastal 1	67	–	26	–	2	–	5	–	2,363
Coastal 2	38	41	59	47	1	0.6	2	11	4,900
Mountain	5	29	61	59	2	2	32	10	1,969

Data are expressed as the percentage of each size found in both diet analysis and availability analysis

Coastal 1 Malpaís de La Corona, *Coastal 2* Malpaís de La Rasca, *Mountain* Las Cañadas del Teide

Table 4 Diet selection of the main prey items of the Southern Grey Shrike on an altitudinal gradient using the "forage index" of Savage (1931) and following the method proposed by Manly et al. (1993)

Prey items	Spring						Summer						Autumn						Winter					
	Coastal			Mountain			Coastal			Mountain			Coastal			Mountain			Coastal			Mountain		
	PA	MS	DS	PA	MS	DS	PA	MS	DS	PA	MS	DS	PA	MS	DS	PA	MS	DS	PA	MS	DS	PA	MS	DS
Arthropoda																								
Aranea	19.8	–	S^-	5.7	24.4	S^-	9.3	115.2	S^-	4.6	17.1	S^-	12	–	S^-	6.2	34.5	S^-	15.2	–	S^-	6.3	31.1	S^-
Orthoptera	5.9	54	S^-	0.3	1123.2	S^+	9.3	68.7	S^-	2.7	918.9	S^+	–	–	–	28.8	15.9	S^+	2.7	13.9	S^-	11.4	6.9	S^+
Hemiptera	17.9	221.2	S^-	1.1	202.0	S^+	1.3	9.2	S^+	0.4	3169.2	S^+	0.5	0.1	NS	0.9	40.8	S^+	3.8	19.3	S^-	0.2	1.4	NS
Coleoptera	31.6	1581.9	S^+	6.6	1257.3	S^+	46.6	622.7	S^+	4.1	461.1	S^+	50.7	769.7	S^+	0.4	22909.3	S^+	31.4	1959.3	S^+	17.8	1793.9	S^+
Hymenoptera non-Formicidae	–	67.2	S^+	32.7	4.9	S^-	–	67.3	S^+	47.2	67.3	S^-	0.5	331.5	S^+	12.3	0.2	NS	1.6	556	S^+	10.1	32.2	S^-
Formicidae	13.9	138.9	S^-	12.2	44.4	S^-	22.7	256.8	S^-	1.8	332.9	S^+	22.6	311.5	S^-	10.7	19.3	S^-	36.4	823.3	S^-	2.5	3.7	NS
Vertebrata																								
Small lizard	10	1.5	NS	27.2	6.4	S^-	23.6	0.006	NS	18.7	20.4	S^-	41.4	5.4	S^-	34.9	16.8	S^-	25.9	4.2	S^-	81.3	95.3	S^-
Medium lizard	61.3	6.2	S^+	58.2	4.2	S^+	56.4	2.4	NS	62.6	0.03	NS	51.7	1.1	NS	62.8	10.1	S^+	66.7	1.3	NS	12.5	49.9	S^+
Large lizard	28.3	3.5	NS	14.6	0.1	NS	20	4.0	S^-	18.7	22.7	S^+	6.9	6.1	S^+	2.3	7.9	S^+	7.4	1.9	NS	6.2	6.3	S^+

Coastal Malpaís de La Rasca (coastal zone), *Mountain* Las Cañadas del Teide (high mountain zone), *PA* proportion of prey availability in shrike territories, *MS* values of Manly statistic, *DS* diet selection, S^- negative selection, S^+ positive selection, *NS* no selection

pollinating hymenopterans (Oromí et al. 2002). Others insects that characterised the diet in Las Cañadas del Teide were adult grasshoppers that increase in summer and autumn, and a Coleopteran species (Scarabaeidae), which becomes abundant with the first rain each winter (García Becerra et al. 1992). Many arthropods disappear during this season, especially when the ground is snow-covered, and few groups are still available. Studies carried out in Finland on Great Grey Shrikes showed that they changed their diet in response to snow (Karlsson 2001, 2002). The greater seasonal climatic change in the high mountain zone led to diet patterns similar to those found in shrikes in some northern continental areas, such as the Iberian Peninsula (Hernández et al. 1993; Hódar 2006) and southern France (Lepley et al. 2004), which have cold and warm winters and dry summers.

Regarding vertebrate prey, the highest number of lizards was found in shrike pellets in the two habitats of Tenerife in spring and summer, when shrikes have nestlings and fledglings (D.P. Padilla, unpublished data). In the south-eastern Iberian Peninsula, Hódar (2006) observed that the Southern Grey Shrike preys mainly upon lizards during its breeding season. However, although shrike predation upon lizards in their breeding season was important on Lanzarote, the highest proportion of lizards was eaten in autumn and winter, probably taking advantage of the abundant presence of juvenile lizards that have their population explosion in these seasons (Valido 1999). Only a few passerine birds were consumed in Lanzarote during spring and summer. In continental Southern Grey Shrike populations (e.g. in the Iberian Peninsula and southern France), predation upon birds also occurs during spring and summer, when the availability of fledglings of other passerines is highest (Hernández et al. 1993; Lepley et al. 2004).

Prey selection

Several researchers have demonstrated that shrikes prefer to forage in habitats with abundant large insects (Atkinson and Cade 1993; Hernández 1993; Lefranc and Worfolk 1997; Karlsson 2004). On the Canary Islands, Southern Grey Shrikes in the high mountain zone of Tenerife captured the largest invertebrate prey. This is consistent with the optimal foraging theory prediction that predators obtain the maximum possible energy from their prey by investing the minimum possible effort (Emlen 1966; Krebs et al. 1983). Under harsh conditions and usually with lower prey availability, an efficient way to obtain the greatest amount of energy could be to concentrate on large prey, but only when they are the most profitable (Craig 1978; Karlsson 2001). Shrikes in the high mountain zone are significantly bigger than those in the coastal zone of Tenerife (D.P. Padilla, unpublished data), which could also explain

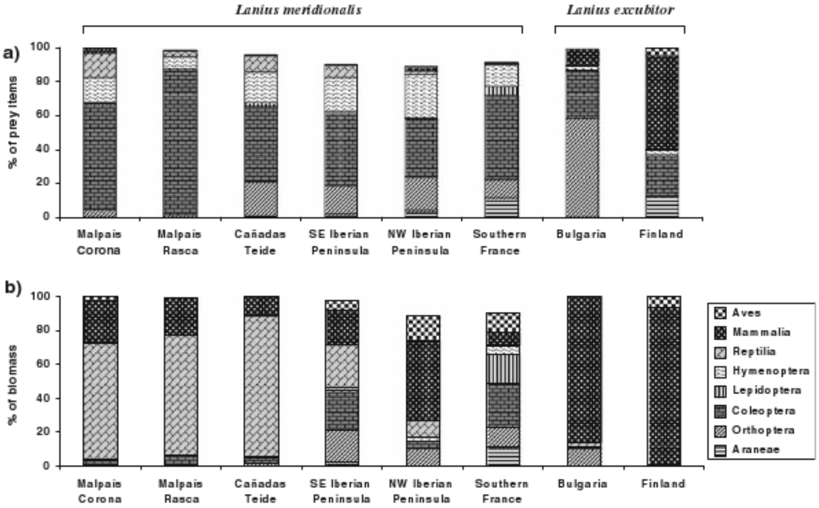


Fig. 4 **a** Proportions of the main prey items and **b** percentage of biomass in the diet of the Southern Grey Shrike and Great Grey Shrike at different latitudes in Europe. Data obtained from: Canary Islands 28–29°N (present study), Southeast Iberian Peninsula 37°N (Hódar 2006), Northwest Iberian Peninsula 42°N (Hernández et al. 1993), Southern France 43°N (Lepley et al. 2004), Bulgaria 42°N (Nikolov et al. 2004) and Finland 60°N (Karlsson 2002)

the significant differences found in prey size selection between the two zones. Thus, differences in phenotype could be related to differences in the dietary niche, and body mass is positively correlated with the amount of food required (García and Arroyo 2005; Hromada et al. 2003).

Lizards captured by shrikes in the two shrub habitats of Tenerife were significantly larger than those caught on Lanzarote. In the Canary Islands, the endemic lizard genus *Gallotia* represents an oceanic island radiation, and seven living species exist in the different islands (González et al. 1996; Nogales et al. 2001). On Tenerife, shrikes consumed *G. galloti*, which is significantly larger (snout vent length 10.7–14.5 cm) than *G. atlantica* (SVL 6.1–9.5 cm), the species consumed on Lanzarote (Hernández et al. 2000). In addition, between the two habitats of Tenerife, the largest lizards were preyed upon in the high mountain zone, where shrikes had a clear preference for large prey. Furthermore, the largest lizards were captured in winter and spring in the two coastal zones, while in the high mountain zone they were taken in summer, coinciding with the nestling and fledgling periods of the shrikes in each habitat.

Finally, although the shrikes actively selected certain invertebrates, such as Coleoptera, Hymenoptera or Orthoptera, and some differences in diet selection were detected between the coastal and the high mountain zones, in general shrikes tended to prey on the most abundant available prey, demonstrating that they acted as generalist predators. Although no differences in food availability were recorded (for instance in the case of lizards), more positive prey selection upon the largest sizes was observed in the high mountain zone than in the coastal zone. This supports the hypothesis that birds with greater body mass and living in harsh climatic conditions are able to obtain the energy they need by selectively preying on the largest available prey.

In conclusion, variation in the trophic ecology of the Southern Grey Shrike in the Canary Islands was found to be related to differences in altitude and seasonal climatic changes between the two main habitats. In the high mountain zone of Las Cañadas del Teide, seasonal variation in diet was more clearly marked than in the two coastal zones. The greater seasonal climatic change in the high mountain zone led to diet patterns similar to those found in shrikes in some northern continental areas, such as the Iberian Peninsula and southern France. Finally, the Southern Grey Shrike captured the largest prey in the high mountain zone of Tenerife, which supports the hypothesis that an efficient method to obtain the greatest possible amount of energy, under harsh conditions, is to focus on large prey.

Zusammenfassung

Nahrungsökologie des Südlichen Raubwürgers *(Lanius meridionalis)* in Insel-Habitaten: Der Einfluss von Höhe und Jahreszeit

Die jahreszeitspezifische Nahrung und die Beutewahl des Südlichen Raubwürgers auf den Kanarischen Inseln wurde in zwei verschiedenen Habitaten untersucht und zwar in Gebüschbiotopen in Küstenregionen und Höhenlagen. Zu jeder Jahreszeit nahmen wir Nahrungsverfügbarkeit und Beutetiergröße auf, um die Nahrungswahl der Würger bezüglich Beutegröße entlang eines Höhengradienten zu bestimmen. Außerdem verglichen wir die beobachteten Ernährungsmuster mit solchen, die für das Festland beschrieben sind, um herauszufinden, ob Südliche Raubwürger auf den Inseln in Höhenlagen (in denen ein Klima wie auf dem Festland herrscht) einen jahreszeitlich bedingten Nahrungswechsel zeigen, der demjenigen der nördlichen Festlandsgebiete ähnelt. Insgesamt untersuchten wir 1139 Würger-Speiballen, die innerhalb eines Jahres gesammelt wurden und bestimmten daraus 10179 Nahrungsobjekte. Als Hauptbeute wurden von den Würgern zahlenmäßig Arthropoden (91%) und hinsichtlich Biomasse Eidechsen (70%) konsumiert. Die Anteile der hauptsächlichen Beuteobjekte unterschieden sich deutlich zwischen den Jahreszeiten und zwischen den Habitaten. Die Nahrungszusammensetzung in den Küstengebieten war weniger variabel als in den Höhenlagen. Wohl aufgrund höherer jahreszeitlicher Schwankungen im Klima in den Höhenlagen ähnelten die Ernährungsmuster dort denjenigen, die in nördlichen Festlandsgebieten, wie etwa auf der Iberischen Halbinsel und in Südfrankreich vorgefunden werden. In den Habitaten der Höhenlagen schließlich wählten die Würger die größten Beuteorganismen. Das deutet darauf hin, dass das Nahrungssuchverhalten bei dieser Vogelart mit klimatischen Bedingungen zusammenhängt, wobei in den unwirtlichsten Habitaten die größten und damit ergiebigsten Beutestücke verzehrt wurden.

Acknowledgments Many colleagues helped us with fieldwork, especially Beatriz Rumeu, Juan Carlos Illera and Patricia Marrero. Heriberto López and Antonio J. Pérez helped us to identify some arthropod remains, while Pedro Oromí allowed us to use the arthropod reference collection of the Department of Animal Biology-Zoology (University of La Laguna). Raquel Gutiérrez provided technical logistic support. Anna Traveset, Juan Carlos Illera, José Antonio Hódar, Antony W. Diamond, Robert L. Curry, Will Cresswell and Stefan Karlsson made useful suggestions that greatly helped us to improve the manuscript. Jairo Patiño and Celia García helped us with some analyses using the CANOCO statistical package. The Cabildos of Lanzarote and Tenerife, and the staff of Teide National Park (Organismo Autónomo de Parques Nacionales) gave us permission to work in the three protected areas. David P. Padilla is currently financed by a PhD grant awarded by the Canarian Government. This contribution was part of two projects, one financed by the Spanish Ministry of Science and Technology (BOS2003-00044) and the other by the Canarian Government (PIO42004/037), both partially supported by the FEDER funds from the European Union. Our study complied with all the current laws of Spain.

References

Atkinson EC, Cade TJ (1993) Winter foraging and diet composition of northern shrikes in Idaho. Condor 95:528–535

Ben-David M, Flynn RW, Schell DM (1997) Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. Oecologia 111:280–291

Budden AE, Wright J (2000) Nestling diet, chick growth and breeding success in the southern grey shrike (*Lanius meridionalis*). In: Yosef R, Lohrer FE, Van Nieuwenhuyse D, Busse P (eds) Proceedings of the 3rd international shrike symposium, vol 22. Ring, Gdansk, pp 165–172

Bustos JJ, Delgado FS (2004) Clima. In: Canseco (ed) Parque Nacional del Teide. Canseco Editores, Madrid, pp 73–96

Castanet J, Báez M (1988) Data on age and longevity in *Galloti galloti* (Sauria, Lacertidae) assessed by skeletocology. Herpetol J 1:218–222

Castells A, Mayo M (1993) Guía de los mamíferos en libertad de España y Portugal. Ediciones Pirámide, Madrid

Correia AM (2001) Seasonal and interspecific evaluation of predation by mammals and birds on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). J Zool 255:533–541

Craig RB (1978) An analysis of the predatory behaviour of the Loggerhead shrike. Auk 95:221–234

Díaz JA, Carrascal LM (1990) Regional distribution of the Mediterranean lizard: influence of habitat cues and prey abundance. J Biogeogr 18:1–7

Emlen JM (1966) The role of time and energy in food preference. Am Nat 100:611–617

García JT, Arroyo BE (2005) Food-niche differentiation in sympatric Hen *Circus cyaneus* and Montagu's Harriers *Circus pygargus*. Ibis 147:144–154

García Becerra R, Ortega Muñoz G, Pérez Sánchez JM (1992) Insectos de Canarias. Cabildo Insular de Gran Canaria, Las Palmas de Gran Canaria

González P, Pinto F, Nogales M, Jiménez-Asensio JJ, Hernández, Cabrera VM (1996) Phylogenetic relationships of the Canary Islands endemic lizard genus *Gallotia* (Sauria: Lacertidae), inferred from mitochondrial DNA sequences. Mol Phyl Evol 6:63–71

Gorman ML (1979) Island ecology. Chapman & Hall, London

Grant PR (1965) The adaptive significance of some size trends in island birds. Evolution 19:355–367

Grimm H (2005) Zur Ernährung des Kanaren-Raubwürgers *Lanius meridionalis koenigi*. Orn Jah Mus Heineanum 23:11–28

Hernández A (1993) Biología de la familia Laniidae (alcaudón real Lanius excubitor L., alcaudón dorsirrojo Lanius collurio L., y alcaudón común Lanius senator L.) en la cuenca del rio Torío, provincia de León. PhD thesis, Universidad de Castilla-León, León

Hernández A, Purroy FJ, Salgado JM (1993) Variación estacional, solapamiento interespecífico y selección en la dieta de tres especies simpátricas de alcaudones (*Lanius* spp.). Ardeola 40:143–154

Hernández E, Nogales M, Martín A (2000) Discovery of a new lizard in the Canary Islands, with a multivariate analysis of *Gallotia* (Reptilia: Lacertidae). Herpetologica 56:63–76

Hódar JA (2006) Diet composition and prey choice of the southern grey shrike *Lanius meridionalis* L. in South-Eastern Spain: the importance of vertebrates in the diet. Ardeola 53:237–249

Hromada M, Kuczyński L, Krištin A, Tryjanowski P (2003) Animals of different phenotype differentially utilise dietary niche-the case of the great grey shrike *Lanius excubitor*. Ornis Fenn 80:71–78

Karlsson S (2001) Selection of habitat and perches by the great grey shrike *Lanius excubitor* and the effects of snow layer and prey type. Ornis Svec 11:7–18

Karlsson S (2002) Analyses on prey composition of overwintering great grey shrikes *Lanius excubitor* in southern Finland. Ornis Fenn 79:181–189

Karlsson S (2004) Season-dependent diet composition and habitat use of red-backed shrikes *Lanius collurio* in SW Finland. Ornis Fenn 81:97–108

Krebs JR, Stephens DW, Sutherland WJ (1983) Perspectives in optimal foraging. In: Brush AH, Clark GA (eds) Perspectives in ornithology. Cambridge University Press, Cambridge, pp 165–216

Lefranc N, Worfolk T (1997) Shrikes. A guide to the shrikes of the world, Pica Press, Mountfield

Lepley M, Thevenot M, Guillaume C-P, Ponel P, Bayle P (2004) Diet of the nominate southern grey shrike *Lanius meridionalis meridionalis* in the north of its range (Mediterranean France). Bird Stud 51:156–162

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:377–385

MacArthur RH, Diamond JM, Karr JR (1972) Density compensation in island faunas. Ecology 53:330–342

Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals. Statistical design and analysis for field studies. Chapman & Hall, London

Martín A, Lorenzo JA (2001) Aves del Archipiélago Canario. Lemus, La Laguna

Marzol Jaén MV (1988) La Lluvia: un Recurso Natural para Canarias. Servicio de Publicaciones de la Caja General de Ahorros de Canarias, Santa Cruz de Tenerife

Moreby SJ (1988) An aid to the identification of arthropod fragments in the faeces of gamebird chicks (Galliformes). Ibis 130:519–526

Nikolov BP, Kodzhabashev ND, Popov VV (2004) Diet composition and spatial patterns of food caching in wintering great grey shrikes (*Lanius excubitor*) in Bulgaria. Biol Lett 41:119–133

Nogales M (1999) Some ecological implications of the broadening habitat and trophic niche of terrestrial vertebrates in the Canary Islands. Monogr Inst Estud Balear 66:67–82

Nogales M, Hernández MC (1994) Interinsular variations in the spring and summer diet of the Raven *Corvus corax* in the Canary Islands. Ibis 136:441–447

Nogales M, Valido A (1999) Preliminary data on the structural relationships in two lacertid species of the genus *Gallotia* (Reptilia: Lacertidae) based on the skeleton. Vieraea 27:217–222

Nogales M, Delgado JD, Medina FM (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canaries). J Ecol 86:866–871

Nogales M, Rando JC, Valido A, Martín A (2001) Discovery of a living giant lizard, genus *Gallotia* (Reptilia: Lacertidae), from La Gomera, Canary Islands. Herpetologica 57:169–179

Nogales M, Quilis V, Medina FM, Mora JL, Trigo LS (2002) Are predatory birds effective secondary seed dispersers? Biol J Linn Soc 75:345–352

Nogales M, Padilla DP, Nieves C, Illera JC, Traveset A (2007) Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. J Ecol 95:1394–1403

Olesen JM, Jordano P (2002) Geographic patterns in plant-pollinator mutualistic networks. Ecology 83:2416–2424

Olesen JM, Valido A (2003) Lizards as pollinators and seed dispersers: an island phenomenon. Trends Ecol Evol 18:177–181

Oromí P, Zurita N, Arechavaleta M, Camacho A (2002) Fauna de invertebrados del Parque Nacional del Teide. Ministerio de Medio Ambiente, Parques Nacionales, Madrid

Padilla DP, Nogales M, Pérez AJ (2005) Seasonal diet of an insular endemic population of southern grey shrike *Lanius meridionalis koenigi* on Tenerife, Canary Islands. Ornis Fenn 82:155–165

Padilla DP, Nogales M, Marrero P (2007) Prey selection of insular lizards by two sympatric predatory bird species. Acta Ornithol 42:167–172

Ralph CP, Nagata SE, Ralph CJ (1985) Analysis of droppings to describe diets of small birds. J Field Ornithol 56:165–174

Rodríguez MA, Santos A, Cantarella F (1994) Estimación del tamaño de la población de *Gallotia galloti galloti* Oudart, 1839 (Sauria: Lacertidae) en el Malpaís de Güímar (S.E. Tenerife). Studia Oecol 10–11:401–407

Rosenberg KV, Cooper RJ (1990) Approaches to avian diet analysis. Stud Avian Biol 13:80–90

Sangster G, Knox AG, Helbig AJ, Parkin DT (2002) Taxonomic recommendations for European birds. Ibis 144:153–159

Savage RE (1931) The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fish Invest Minist Agric Food Fish Ser 2 12:1–88

Schön M (1998) On the evolution of the northern and southern group of subspecies in the great grey shrike superspecies (*Lanius excubitor*). In: Yosef R, Lohrer FE (eds) Shrikes of the World II: conservation implementation. International Birdwatching Center in Eilat, Eilat, pp 9–13

ter Braak CJF, Šmilauer P (1998) CANOCO Reference manual and user's guide to Canoco for Windows: software for canonical community ordination, version 4. Microcomputer Power, Ithaca

Tryjanowski P, Hromada M, Antczak M (1999) Breeding habitat selection in the great grey shrike *Lanius excubitor*- the importance of meadows and spring crops. Acta Ornithol 34:59–63

Valido A (1999) Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. Gallotia, Lacertidae). PhD thesis, University of La Laguna, Laguna

Valido A, Nogales M (2003) Digestive ecology of two omnivorous Canarian lizard species (*Gallotia*, Lacertidae). Amphib-Reptil 24:331–344

Wildpret W, Martín MV (2004) Flora vascular y vegetación. In: Canseco (ed) Parque Nacional del Teide. Canseco Editores, Madrid, pp 97–142

Yosef R, Mitchell WA, Pinshow B (1991) The proximate costs and benefits of polygyny to male northern shrike. Wilson Bull 103:146–149

PADILLA, D. P., NOGALES, M. & MARRERO, P. 2007. Prey size selection upon insular lizards by two sympatric predatory bird species. ***Acta Ornithologica* 42**: 167-172.

ACTA ORNITHOLOGICA
Vol. 42 (2007) No. 2

Prey size selection of insular lizards by two sympatric predatory bird species

David P. PADILLA, Manuel NOGALES & Patricia MARRERO

Island Ecology and Evolution Research Group (IPNA-CSIC), C/ Astrofísico Francisco Sánchez 3, 38206 La Laguna, Tenerife, Canary Islands, SPAIN, e-mail: dpadilla@ipna.csic.es

Padilla D. P., Nogales M., Marrero P. 2007. Prey size selection of insular lizards by two sympatric predatory bird species. Acta Ornithol. 42: 167–172.

Abstract. Size-related selection of insular lizards by two sympatric predatory bird species (Southern Grey Shrike and Eurasian Kestrel) was studied in an arid insular environment. The endemic lizard genus *Gallotia* was a key resource in the diet of both predators, constituting more than 50% of the total biomass. Shrikes captured smaller lizards than kestrels during all seasons (mean snout - vent length (SVL): 7.4 ± 1.9 vs. 9.4 ± 2.1 cm respectively), presenting a sequential use of lizard sizes and avoiding potential competition. On the other hand, shrikes and kestrels showed the same seasonal variation pattern, capturing the largest lizards during their breeding periods (spring). Considering lizard availability, shrikes displayed less selective predation than kestrels in all seasons. Shrikes positively selected the medium lizard size (SVL: 5-10 cm) during the nestling period, but negatively selected the small lizard size (SVL: < 5 cm) in autumn and winter, probably due to an explosion of juvenile lizards. Lastly, kestrels appeared to be more selective, negatively choosing the small lizard size but positively selecting the largest ones all the year round (SVL: > 10 cm).

Key words: Kestrel, *Falco tinnunculus*, Southern Grey Shrike, *Lanius meridionalis*, Tenerife Lizard, *Gallotia galloti*, feeding ecology, prey selection, Canary Islands

Received — July 2007, accepted — Oct. 2007

INTRODUCTION

Potential food interference of an important key resource for two sympatric species could be minimised by the sequential use of this resource, for instance differences in circadian activity (Schoener 1974, Barrientos & Virgós 2006). The coexistence of coevolved species in a community is facilitated by the segregation of one or more niches (Schoener 1974, Chesson & Huntly 1997). Niche separation is often explained by differences in diet or feeding strategies (Julien-Laferriere 1999, Telfer & Bowman 2006). The reduction of food niche overlap is often possible by the use of different prey sizes, through food division by type or by segregation in foraging areas (Schoener 1974, García & Arroyo 2005, Barrientos & Virgós 2006). Competition theory predicts a high overlap in diets with low competition between sympatric species when a key prey resource is abundant (Lack 1946, Schoener 1982).

Several ecological phenomena describe how the species that inhabit island ecosystems often expand their niches and habitats, and exploit resources that are generally used by other species in continental environments (Whittaker & Fernández-Palacios 2007). The abundance of some animals, such as lizards, is often greater on islands than on the mainland, due to lower predation and competition pressure, or their broader trophic niche (Evans & Evans 1980, Brown et al. 1992, Olesen & Valido 2003). This is the case of the Canarian endemic genus *Gallotia*, which is represented by seven living lizard species (Nogales et al. 2001). These lizards differ in body sizes, ranging approximately between 6 and 25 cm in snout vent length (hereafter, SVL). Adult Tenerife Lizard *G. galloti* oscillates between a SVL of 10.7 and 14.5 cm. On this island, two birds are the main lizard predators, the Southern Grey Shrike *Lanius meridionalis* and the Eurasian Kestrel *Falco tinnunculus* (Martín & Lorenzo 2001) which breed

sympatrically in many areas. Both predatory birds are clearly different in size (shrikes: full length: 24–25 cm, weight: 62–63 g; kestrels: 34–38 cm and 155–225 g males; 230–270 g females), and all available evidence seems to indicate that a segregation in the predation of different lizard body sizes may be occurring in these insular environments.

In the Canary Islands, the diet of the Southern Grey Shrike is mainly made up of vertebrates, the endemic lizards *Gallotia* constituting 64% of the whole biomass (Padilla et al. 2005). In the case of the Eurasian Kestrel, the lizard biomass constitutes more than 50% of the total diet in many habitats of the archipelago (Carrillo et al. 1994, Martín & Lorenzo 2001). This high proportion of lizards in both shrike and kestrel diets is clearly related to the great abundance of these Lacertidae in island environments, the high effectiveness of predation and the low investment of energy in capturing this prey (Padilla et al. 2005).

The main aims of this study were: 1) to establish the importance of lizards in the diet of two sympatric birds of prey, the Southern Grey Shrike and the Eurasian Kestrel, 2) to determine the existence of differential predation upon different lizard sizes by these two predatory birds and, 3) to assess seasonal selective predation of lizard sizes in an arid environment of the Canary Islands.

MATERIAL AND METHODS

Study area

The volcanic Canary Islands are located in the Atlantic Ocean some 100 km from the African continent (27°37′–29°25′N, 13°20′–29°25′W). Fieldwork was carried out in "Malpaís de La Rasca" nature reserve and surrounding areas, located in the southernmost part of Tenerife. The study area consists in a recent lava field (≈ 3.15 km^2) which was produced by two main volcanic cones, Montaña Gorda and Montaña Aguzada (Carracedo et al. 2003).

The climate is xeric, with a mean annual rainfall and temperature of 98 mm and ≈ 22°C, respectively (Marzol Jaén 1988). However, two climatic periods can be identified in this semiarid habitat: dry (spring and summer; mean rainfall and temperature of 11.2 mm and 22.5°C, respectively); and rainy (autumn and winter; 86.7 mm and 22.2?C). The vegetation consists of sparse xerophytic shrub, mainly composed of *Launaea arborescens*, *Lycium intricatum*, *Salsola divaricata*, *Schizogyne glaberrima*, *Euphorbia balsamifera*, *E. canariensis*, *Plocama pendula* and the invasive *Opuntia dillenii* (Arco-Aguilar et al. 1997).

Pellet sampling

The study was performed from April 2003 to March 2004, this period being divided into four seasons (spring: March, April and May; summer: June, July and August; autumn: September, October and November; and winter: December, January and February). A total of 440 Southern Grey Shrike pellets were collected in fourteen territories (spring: 115, summer: 116, autumn: 93 and winter: 116); and a total of 486 Eurasian Kestrel pellets were taken in five different territories (spring: 141, summer: 141, autumn: 125, winter: 79). All kestrel territories overlapped with at least one shrike territory. A mean number of 10 shrike pellets and 30 kestrel pellets per territory and season were collected in order to have an adequate representation of both population diets. To minimize seasonal sample bias, only fresh pellets were collected after periodic cleaning beneath perches. We decided to use pellet samples, because well-preserved long bones are often found inside them. Moreover, we revised the shrike larders regularly and only five lizards were found, which due to their low number were not included in the analysis.

Pellet analysis and prey size

Each pellet was analysed individually, counting long bones (femoral, humeral, tibia, pelvic girdle and parietal) and mandibles or maxillaries of reptiles. Percentage of occurrence was calculated to evaluate the importance of lizards in the diet of both birds.

Length of lizards (Lacertidae, *Gallotia galloti*) main bones that appeared whole and well preserved inside pellets (jaws, maxillaries, parietals, pelvic girdle, femoral, tibias and humeri), were measured with a digital caliper to calculate body sizes. To minimise measurement bias, only one person recorded data. We used the respective regression models detailed by Nogales & Valido (1999) for *G. galloti*, which consist in relationships between lizard snout vent length (hereafter SVL) and the afore-mentioned main bones.

Gallotia galloti (SVL: 10.7–14.5 cm) is present in all habitats of Tenerife and it is the only lizard that lives in the study area (Hernández et al. 2000). To study prey size selection, the relative abundance of lizards was calculated in "Malpaís de La Rasca", using line transects (100 m length) located inside those predatory bird territories studied; all lizards that appeared up to five meters on both sides of the observer were counted (Díaz & Carrascal 1990). Censuses were made between 12:00 and 14:00 hours (maximum activity period of lizards), on fair days and a total of 20 transects were performed in each season. To ascertain if the Southern Grey Shrike and the Eurasian Kestrel were selecting specific lizard sizes, these were classified in three different categories (small: SVL < 5 cm; medium: SVL 5–10 cm; and large: SVL > 10 cm).

Statistical and index analysis

To compare the sizes of lizards captured during the annual cycle, a shrike *versus* kestrel t-student test was employed. Chi-square tests were performed to evaluate the consumption of different lizard prey sizes by each species all year round. Likelihood ratio tests were used to find out if any lizard size category was consumed more frequently in a particular season. To study seasonal differences in lizard body sizes that appeared inside each predatory bird pellet, we used parametric tests (ANOVA and Sheffé post-hoc) and non-parametric tests (Kruskal-Wallis and Mann-Whitney) for those data in which distribution did not meet the requirements of a parametric test, even after transformations (Siegel 1990). In those cases where it was necessary to use the same data set, we reduced this effect by applying a more conservative sequential Bonferroni test.

To evaluate diet selection of lizard sizes, the "forage index" of Savage (1931) was applied, followed by the method proposed by Manly et al. (1993). For further details on the use of this index see Padilla et al. (2005).

RESULTS

In "Malpaís de La Rasca" the percentage of occurrence of lizards inside pellets revealed the great importance of this prey in shrike and kestrel diets (Shrike, spring: 39.1%, summer: 30.2%, autumn: 24.7%, winter: 31%; Kestrel, spring: 75.9%, summer: 69.5%, autumn: 66.4%, winter: 30.4%).

Kestrels captured significantly larger lizards than shrikes all year round (SVL; 9.4 ± 2.1 and 7.4 ± 1.9 cm, respectively; $t = 6.80$, $df = 175$, $p < 0.001$). The medium lizard size category was the most frequent prey captured all year round by shrikes ($\chi^2 = 77.5$, $df = 2$, $p < 0.001$), while in the case of kestrels the medium and large lizard sizes were the most frequent prey captured ($\chi^2 = 44.21$, $df = 2$, $p < 0.001$) with no significant difference between them ($\chi^2 = 3.4$, $df = 1$, $p = 0.062$). A seasonal variation in lizards SVL was observed in each bird of prey (Shrikes: Kruskall-Wallis, $\chi^2 = 11.4$, $df = 3$, $p = 0.01$; Kestrels: ANOVA, $F = 4.4$, $df = 3$, $p = 0.006$). The same seasonal pattern was observed in both shrikes and kestrels; the only difference recorded being between spring and summer and, the largest lizards being captured in spring (Shrike: Mann-Whitney, $U = 276.5$, $p = 0.003$; Kestrel: Scheffé test, $p = 0.014$) (Fig. 1).

Prey size selection upon different lizard sizes by two sympatric birds of prey was calculated, observing scarce selection by shrikes. This species positively selected medium sizes (SVL 5–10 cm) in spring, whereas small lizards (SVL < 5 cm) were negatively selected in autumn and winter. The largest (SVL > 10 cm) appeared as negatively selected prey in summer, but were positively selected in autumn (Table 1). Kestrels, avoided capturing small lizards all year round, and they only appeared in those pellets collected in summer, showing a clear negative selection. In contrast, the largest lizard size was positively selected by kestrels all year round with the exception of summer when no selection was recorded (Table 1).

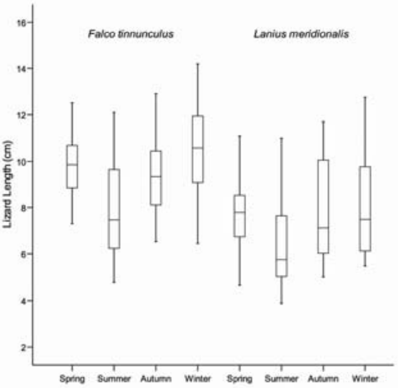


Fig. 1. Lengths (SVL) of lizards captured by the Eurasian Kestrel and the Southern Grey Shrike, in each season in Tenerife, Canary Islands. The box indicates the mean (± SD), the bars extending above and below each box illustrate maximum and minimum values.

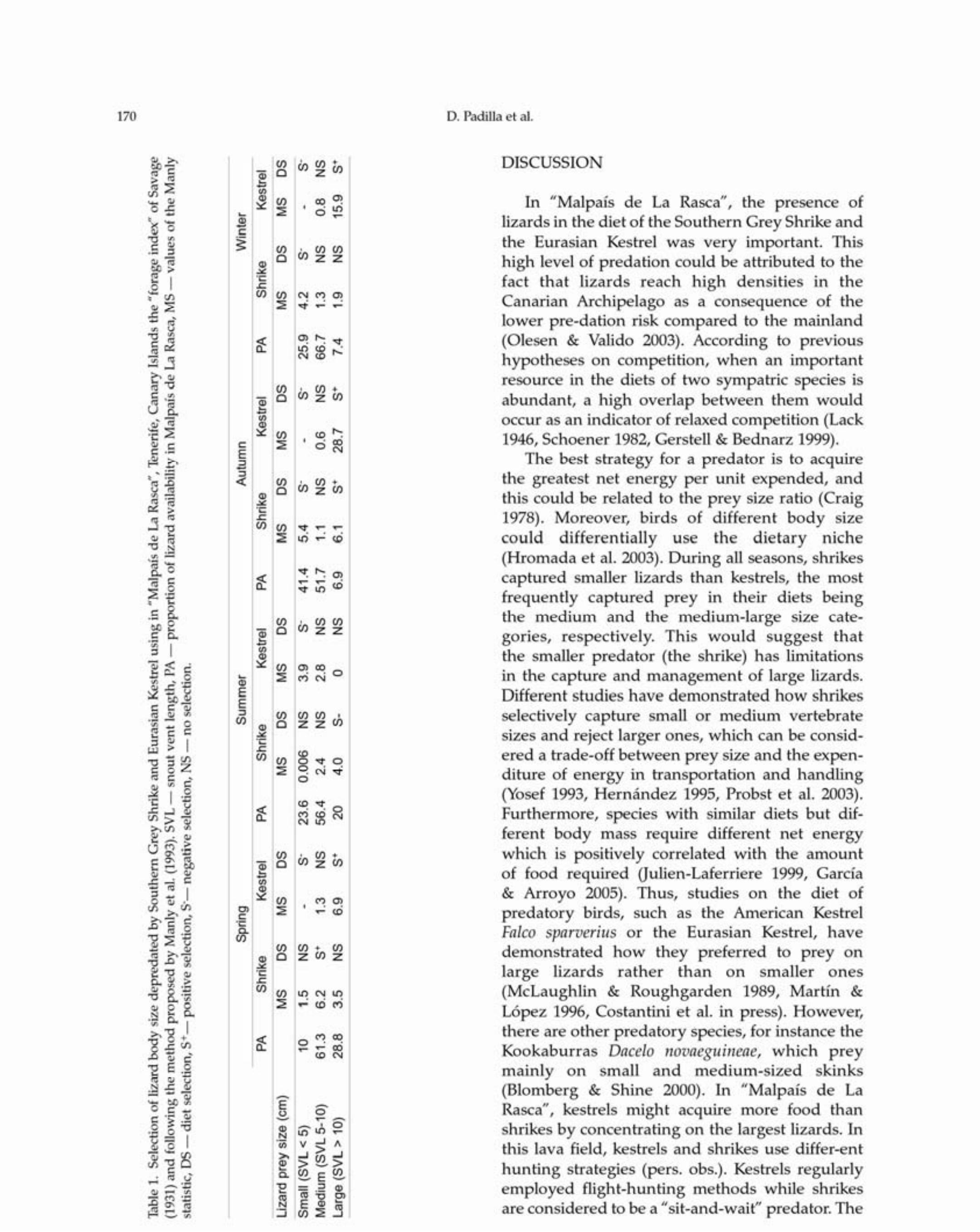


Table 1. Selection of lizard body size depredated by Southern Grey Shrike and Eurasian Kestrel using in "Malpaís de La Rasca", Tenerife, Canary Islands the "forage index" of Savage (1931) and following the method proposed by Manly et al. (1993). SVL — snout vent length, PA — proportion of lizard availability in Malpaís de La Rasca, MS — values of the Manly statistic, DS — diet selection, S^+ — positive selection, S^- — negative selection, NS — no selection.

	Spring					Summer					Autumn					Winter				
	PA	Shrike		Kestrel		PA	Shrike		Kestrel		PA	Shrike		Kestrel		PA	Shrike		Kestrel	
Lizard prey size (cm)		MS	DS	MS	DS		MS	DS	MS	DS		MS	DS	MS	DS		MS	DS	MS	DS
Small (SVL < 5)	10	1.5	NS	-	S^-	23.6	0.006	NS	3.9	S^-	41.4	5.4	S^-	-	S^-	25.9	4.2	S^-	-	S^-
Medium (SVL 5-10)	61.3	6.2	S^+	1.3	NS	56.4	2.4	NS	2.8	NS	51.7	1.1	NS	0.6	NS	66.7	1.3	NS	0.8	NS
Large (SVL > 10)	28.8	3.5	NS	6.9	S^+	20	4.0	S^-	0	NS	6.9	6.1	S^+	28.7	S^+	7.4	1.9	NS	15.9	S^+

DISCUSSION

In "Malpaís de La Rasca", the presence of lizards in the diet of the Southern Grey Shrike and the Eurasian Kestrel was very important. This high level of predation could be attributed to the fact that lizards reach high densities in the Canarian Archipelago as a consequence of the lower pre-dation risk compared to the mainland (Olesen & Valido 2003). According to previous hypotheses on competition, when an important resource in the diets of two sympatric species is abundant, a high overlap between them would occur as an indicator of relaxed competition (Lack 1946, Schoener 1982, Gerstell & Bednarz 1999).

The best strategy for a predator is to acquire the greatest net energy per unit expended, and this could be related to the prey size ratio (Craig 1978). Moreover, birds of different body size could differentially use the dietary niche (Hromada et al. 2003). During all seasons, shrikes captured smaller lizards than kestrels, the most frequently captured prey in their diets being the medium and the medium-large size categories, respectively. This would suggest that the smaller predator (the shrike) has limitations in the capture and management of large lizards. Different studies have demonstrated how shrikes selectively capture small or medium vertebrate sizes and reject larger ones, which can be considered a trade-off between prey size and the expenditure of energy in transportation and handling (Yosef 1993, Hernández 1995, Probst et al. 2003). Furthermore, species with similar diets but different body mass require different net energy which is positively correlated with the amount of food required (Julien-Laferriere 1999, García & Arroyo 2005). Thus, studies on the diet of predatory birds, such as the American Kestrel *Falco sparverius* or the Eurasian Kestrel, have demonstrated how they preferred to prey on large lizards rather than on smaller ones (McLaughlin & Roughgarden 1989, Martín & López 1996, Costantini et al. in press). However, there are other predatory species, for instance the Kookaburras *Dacelo novaeguineae*, which prey mainly on small and medium-sized skinks (Blomberg & Shine 2000). In "Malpaís de La Rasca", kestrels might acquire more food than shrikes by concentrating on the largest lizards. In this lava field, kestrels and shrikes use differ-ent hunting strategies (pers. obs.). Kestrels regularly employed flight-hunting methods while shrikes are considered to be a "sit-and-wait" predator. The

former technique is the more energetically expensive (Masman et al. 1988) and, thus, kestrels have to select the most profitable prey (largest lizards) avoiding smaller ones.

Seasonal variation patterns were similar between the two birds of prey. In both cases, significant differences were observed between spring and summer. Both predators chose the largest lizards in the former season, coinciding with their breeding periods. In this season their respective offspring increase the demand for food, making this a stringent period for the parents since they have to dedicate most of their time to parental care and they could concentrate on a specific prey size (Costantini et al. 2005).

With respect to selective predation, the Southern Grey Shrike presented a scarce selection on lizard size, showing a certain tendency towards opportunistic behaviour (Table 1). However, in spring, coinciding with the nestling period, medium lizard size (SVL 5–10 cm) was positively selected. In contrast, in autumn and winter, when an explosion of juvenile lizards occurred (small size; SVL < 5 cm) they were negatively selected. On the other hand, kestrels showed a more selective behaviour than shrikes, clearly negatively selecting the small lizard size all year round and positively selecting the larger ones. Shrikes and kestrels presented similar patterns in lizard choice only in autumn and winter. In this period, energy expenditure is minimised because they are not breeding, and can probably spend more time selecting the most profitable food by rejecting smaller lizards.

ACKNOWLEDGEMENTS

We are grateful to Concepción Nieves and Raquel Gutiérrez who made parts of the measures of the lizard bones. The manuscript was read and improved by Juan Carlos Illera, Anna Traveset, Beatriz Rumeu and Piotr Tryjanowski. This research was supported by grants to David P. Padilla and Patricia Marrero from the Canarian Government and Proyectos Intramurales Especiales (2004 3 0E 169) of the Spanish National Scientific Research Council, respectively. It was also partially financed by the project PI042004/037 (Consejería de Educación, Cultura y Deportes, Gobierno de Canarias), which are partially supported by Feder funds from the European Union.

REFERENCES

Arco-Aguilar M. del, Acebes-Ginovés J. R., Rodríguez-Rodríguez A., Padrón P., Rodríguez-Delgado O., Pérez-de-Paz P. L., Wildpret de la Torre W. 1997. Cormophytic vegetation of the Malpaís de La Rasca, Tenerife (Canary Islands). Fitosociologia 34: 159–170.

Barrientos R., Virgós E. 2006. Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. Acta Oecol. 30: 107–116.

Blomberg S. P., Shine R. 2000. Size-based predation by kookaburras (*Dacelo novaeguineae*) on lizards (*Eulamprus tympanum: Scincidae*): what determines prey vulnerability? Behav. Ecol. Sociobiol. 48: 484–489.

Brown R. P., Pérez-Mellado V., Diego-Rasilla J., García J. A., Naranjo A., Speakman J. R. 1992. Individual and population energetics of a lizard on a Mediterranean islet. Oecologia 91: 500–504.

Carracedo J. C., Paterne M., Guillou H., Pérez Torrado F. J., Paris R., Rodríguez Badiola E., Hansen A. 2003. [Radiometric records (^{14}C Y K/AR) of El Teide and the Northwest Rift, Tenerife, Canary Islands]. Estudios Geol. 59: 15–29.

Carrillo J., Hernández E. C., Nogales M., Delgado G., García R., Ramos T. 1994. Geographic variation in the spring diet of *Falco tinnunculus* L. on the islands of Fuerteventura and El Hierro (Canary Islands). Bonn. zool. Beitr. 45: 39–48.

Chesson P., Huntly N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am. Nat. 150: 519–553.

Costantini D., Bruner E., Fanfani A., Dell'Omo G. In press. Male-biased predation of western green lizards by Eurasian kestrel. Naturwissenschaften.

Costantini D., Casagrande S., Di Lieto G., Fanfani A., Dell'Omo G. 2005. Consistent differences in feeding habitats between neighbouring breeding kestrels. Behaviour 142: 1409–1421.

Craig R. B. 1978. An analysis of the predatory behaviour of the Loggerhead Shrike. Auk 95: 221–234.

Díaz J. A., Carrascal L. M. 1990. Regional distribution of the Mediterranean lizard: influence of habitat cues and prey abundance. J. Biogeogr. 18: 1–7.

Evans P. G. H., Evans J. B. 1980. The ecology of lizards on Praslin Island, Seychelles. J. Zool. 191: 171–192.

García J. T., Arroyo B. E. 2005. Food-niche differentiation in sympatric Hen *Circus cyaneus* and Montagu's Harriers *Circus pygargus*. Ibis 147: 144–154.

Gerstell A. T., Bednarz J. 1999. Competition and patterns of resource use by two sympatric raptors. Condor 101: 557–565.

Hernández A. 1995. Selective predation by Northern Shrikes on small mammals in a natural environment. J. Field Ornithol. 66: 236–246.

Hernández E., Nogales M., Martín A. 2000. Discovery of a new lizard in the Canary Islands, with a multivariate analysis of *Gallotia* (Reptilia: Lacertidae). Herpetologica 56: 63–76.

Hromada M., Kuczyński L., Krištin A., Tryjanowski P. 2003. Animals of different phenotype differentially utilise dietary niche-the case of the Great Grey Shrike *Lanius excubitor*. Ornis Fennica 80: 71–78.

Julien-Laferriere D. 1999. Foraging strategies and food partitioning in the neotropical frugivorous mammals *Caluromys philander* and *Potos flavus*. J. Zool. 247: 71–80.

Lack D. 1946. Competition for food by birds of prey. J. Anim. Ecol. 15: 123–129.

Manly B. F. J., McDonald L. L., Thomas D. L. 1993. Resource selection by animals. Statistical design and analysis for field studies. Chapman & Hall, London.

Martín J., López P. 1996. Avian predation on a large lizard (*Lacerta lepida*) found at low population densities in Mediterranean habitats: an analysis of bird diets. Copeia 1996: 722–726.

Martín A., Lorenzo J. A. 2001. [Birds from the Canarian Archipelago]. Lemus, La Laguna.

Marzol Jaén M. V. 1988. [The rain: a natural resource for the Canaries]. Servicio de Publicaciones de la Caja General de Ahorros de Canarias, Santa Cruz de Tenerife.

Masman D., Daan S., Dijkstra C. 1988. Time allocation in the Kestrel (*Falco tinnunculus*), and the principle of energy minimization. J. Anim. Ecol. 57: 411–432.

McLaughlin J. F., Roughgarden J. 1989. Avian predation on *Anolis* lizards in the northeastern Caribbean: an inter-island contrast. Ecology 70: 617–628.

Nogales M., Valido A. 1999. Preliminary data on the structural relationships in two lacertid species of the genus *Gallotia* (Reptilia: Lacertidae) based on the skeleton. Vieraea 27: 217–222.

Nogales M., Rando J. C., Valido A., Martín A. 2001. Discovery of a living giant lizard, genus *Gallotia* (Reptilia: Lacertidae), from La Gomera, Canary Islands. Herpetologica 57: 169–179.

Olesen J. M., Valido A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. TREE 18: 177–181.

Padilla D. P., Nogales M., Pérez A. J. 2005. Seasonal diet of an insular endemic population of Southern Grey Shrike *Lanius meridionalis* koenigi on Tenerife, Canary Islands. Ornis Fennica 82: 155–165.

Probst R., Wegleitner S., Schmid R. 2003. Relationship of vertebrate prey size to transport mode and distance in the Northern Shrike. Wilson Bull. 115: 201–204.

Savage R. E. 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fish. Invest. Ministry Agric. Food Fish. Ser. 2. 12: 1–88.

Schoener T. W. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

Schoener T. W. 1982. The controversy over interspecific competition. Am. Sci. 70: 586–595.

Siegel S. 1990. [Non parametric statistics for the behavioural sciences]. Trillas, Mexico.

Telfer W. R., Bowman D. M. J. 2006. Diet of four rock-dwelling macropods in the Australian monsoon tropics. Austral. Ecol. 31: 817–827.

Whittaker R. J., Fernández-Palacios J. M. 2007. Island Biogeography. Ecology, Evolution and Conservation. Oxford Univ. Press, Oxford.

Yosef R. 1993. Prey transport by the Loggerhead Shrikes. Condor 95: 231–233.

STRESZCZENIE

[Selekcja na wielkość zdobyczy sympatrycznie występujących srokosza i pustułki]

Badania prowadzono od kwietnia 2003 do marca 2004 w południowej części Teneryfy (3.15 km^2, Wyspy Kanaryjskie), gdzie współwystępują dwa gatunki drapieżników polujących głównie na drobne gady — srokosz i pustułka. Ich ofiarami na terenie objętym badaniami padają przede wszystkim endemiczne jaszczurki z gatunku *Gallotia galloti*. Zebrano 440 wypluwek srokosza (115 wiosną, 116 latem, 93 jesienią i 116 zimą) oraz 486 wypluwek pustułki (odpowiednio 141, 141, 125 i 79). Wszystkie terytoria pustułek z jakich pozyskano materiał pokrywały się z przynajmniej jednym terytorium srokosza. Oprócz tego szacowano liczebności jaszczurek na transektach i klasy wielkości widzianych osobników. Wyizolowane z wypluwek kości jaszczurek były mierzone, by oszacować wielkość ofiar.

Udział szczątków jaszczurek w wypluwkach pustułek zmieniał się w ciągu roku (od 75.9% wiosną do 30.4% zimą) i pozostawał mniej więcej stały w wypluwkach srokosza (24.7-39.1%). Pustułki chwytały większe ofiary niż srokosze przez cały rok, przy czym srokosze wybierały jaszczurki należące średniej klasy wielkości. Pustułki chwytały jaszczurki średnie i duże. U obu gatunków stwierdzono różnice między sezonami (Fig. 1). Wykazano, że w przypadku srokosza, drapieżniki dokonywały pozytywnej selekcji ofiar średniej wielkości na wiosnę, zaś negatywnej małych jaszczurek jesienią i zimą. Największe jaszczurki były unikane latem, natomiast chwytane jesienią. Pustułki unikały chwytania małych ofiar przez cały rok, ta grupa pojawiała się tylko w wypluwkach znajdowanych latem, co wskazuje na zdecydowanie negatywną selekcję (Tab. 1).

NOGALES, M., **PADILLA, D. P.**, NIEVES, C., ILLERA, J. C. & TRAVESET, A. 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. ***Journal of Ecology*** **95**: 1394-1403.

Journal of Ecology 2007
95, 1394–1403

Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands

MANUEL NOGALES*†, DAVID P. PADILLA†, CONCEPCIÓN NIEVES†, JUAN C. ILLERA‡ and ANNA TRAVESET§

†Island Ecology and Evolution Research Group (CSIC-IPNA), C/Astrofísico Francisco Sánchez 3, 38206 La Laguna, Tenerife, Canary Islands, Spain, ‡Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK, §Institut Mediterrani d'Estudis Avançats (CSIC-UIB), C/Miguel Marqués 21, 07190 Esporles, Mallorca, Balearic Islands, Spain

Summary

1. Secondary seed dispersal occurs whenever a seed is dispersed in two or more different dispersal events, so that different dispersal agents (e.g. animal frugivores or invertebrates) contribute to different events. Three secondary seed dispersal systems, in which lizards and predatory birds participate, are studied in Lanzarote (Canary Islands).

2. Seeds from all three plant species studied (*Lycium intricatum*, *Rubia fruticosa* and *Asparagus nesiotes*) were found with the remains of lizards (*Gallotia atlantica*) when they appeared inside shrike (*Lanius meridionalis*) and kestrel (*Falco tinnunculus*) pellets. This suggests that these two avian predators might secondarily disperse these plants by incidentally ingesting seeds when they prey upon the frugivorous lizards.

3. *Lycium* and *Rubia* seeds dispersed by *Falco* had significantly thinner seed coats compared to the other treatments (*Gallotia* and *Lanius*) and to uningested seeds. Correlated with this result, seed hardness increased from *Lycium* (the softest coat), to *Rubia* (intermediate values), to *Asparagus*.

4. Seed viability was high in all three species, although both viability and germination were significantly reduced in seeds of *Lycium* and *Rubia* dispersed by *Falco*.

5. The seed distribution was markedly different, *Gallotia* being an important disperser in the open ground microhabitats, *Lanius* in hillocks and *Falco* in hills. Because all three plant species were present in all these microhabitats, our observations suggest that the dispersal of these plants might be associated with the differential use of the habitat by the different dispersers.

6. Synthesis: Contrary to some long-distance seed dispersal (LDD) paradigms, the complex seed dispersal systems we describe are common and affect an important number of seeds that are moved each year to particular microhabitats. Finally, the simultaneous ecological factors analysed in this study support the hypotheses that diplochory by double endozoochory could have played a more important role in LDD events than is currently recognized, both in recent volcanic areas (lowlands) and also probably in the colonization of other subtropical islands.

Key-words: Badlands, Canary Islands, diplochory, endozoochory, frugivorous lizards, island plant colonization, long-distance seed dispersal, seed coat and hardness, seed distribution, seed viability and germination.

Journal of Ecology (2007) **95**, 1394–1403
doi: 10.1111/j.1365-2745.2007.01305.x

Introduction

The intervention of two or more different agents in the dispersal of a seed is defined as diplochory (see review of Vander Wall & Longland 2004) and this multi-step ecological process is considered to be important in the

*Author to whom correspondence should be addressed: Manuel Nogales. Tel.: +34 922260190 (ext. 281). Fax: +34 922260135. E-mail: mnogales@ipna.csic.es.

reproductive cycle of some plants (Chambers & MacMahon 1994). Such a process functions because the combination of two or more dispersers can disproportionately increase the benefits of seed dispersal, for instance by reducing seed mortality and by providing long-distance seed delivery.

Secondary seed dispersal systems are widely variable because the potential combinations of dispersal agents (both abiotic and biotic) are large. Thus, secondary seed dispersal sometimes involves abiotic factors (wind, water or ballistic systems) as primary dispersal agents, and scatter-hoarding vertebrates (Vander Wall 2002) or invertebrates (Espadaler & Gómez 1996; Pizo *et al.* 2005) as secondary dispersers. In other cases, primary seed dispersal includes a first process of endozoochory, by mammals and birds, and sometimes other vertebrates (Forget & Milleron 1991; Wenny 1999), followed by secondary dispersal by invertebrates such as ants (Kauffmann *et al.* 1991; Levey & Byrne 1993) or beetles (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 2001).

Most of the seed dispersal systems in which a vertebrate frugivore participates include only one seed digestion event (Ridley 1930). However, secondary seed dispersal can be more complex, especially if a second seed digestion process is mediated through frugivore–predator interaction. This occurs whenever predatory vertebrates prey upon frugivores that have already consumed fruits, thus ingesting the entire seed load contained within the digestive tract of the prey. Although this phenomenon has rarely been described (Damstra 1986; Hall 1987; Dean & Milton 1988; Nogales *et al.* 1996), only a few studies carried out in insular environments have partially attempted to interpret it in an ecological context (Nogales *et al.* 1998, 2002). These studies, in which an endemic lizard (*Gallotia atlantica* Peters & Doria) performed the first dispersal event, focused only on a single plant species (*Lycium intricatum* Boiss., Solanaceae) on a small island (Alegranza, Canaries), and showed that successful seed survival can be affected by the secondary dispersal by avian predators that prey upon the frugivorous lizards (shrike: *Lanius meridionalis* Temminck, or kestrel: *Falco tinunnculus* Linnaeus). To date, only some factors such as viability and germination before and after gut treatment by the different dispersers were studied. However, in this complex ecological process, where seeds undergo a double gut-processing, other important factors, such as coat thickness, seed hardness and seed rain in different microhabitats, have not been evaluated. The study of these factors within such a diverse assemblage of interactions will permit a more complete interpretation of the ecological role of this secondary seed dispersal system. An additional element for evaluating the importance of these secondary seed disperser events is whether other fleshy-fruited plant species present in more complex insular habitats are also involved.

The scarification of seeds by the long residence times in guts of more than one vertebrate disperser can affect seed viability, and thus, the probability of long-distance dispersal (hereafter LDD, *sensu* Nathan 2006). In this respect, seed-coat thicknesses can sometimes account for the diverse effects of different frugivores on seed germination (Gardener *et al.* 1993; Traveset *et al.* 2001; Nogales *et al.* 2005). Seed germination may also be influenced by other factors, such as seed hardness or robustness, which might determine to some extent the strength needed for the seedling to break the seed coat. However, the demographic effects of these traits are still poorly understood.

Traditional studies on island biogeography have mentioned the importance of LDD events in insular colonization processes (e.g. Ridley 1930; Carlquist 1967). The current LDD paradigm suggests that these kinds of ecological processes are very difficult to predict and to document in time and space (Greene & Johnson 1995; Higgins & Richardson 1999; Clark *et al.* 2001). However, some studies of LDD using mechanistic models (see Nathan *et al.* 2002; Nathan & Katul 2005 and references therein) or DNA-based genotyping (Jordano *et al.* 2007) have successfully documented both frequency and distance of these events.

The present work deals with LDD systems in oceanic island environments in which two dispersers participate (double endozoochory). Furthermore, it is an environment where volcanic eruptions take place with relative frequency, on a geological time scale, and the colonization of a new lava field by organisms such as fruiting plant species is clearly a very important, albeit poorly known process. Older volcanic zones function as genetic sources, where biological material may spread and colonize the new lava fields when they cross the older zones. However, knowledge of the functioning of the mechanisms that make these colonization events possible is still scant.

This paper attempts to evaluate the effectiveness (*sensu* Schupp 1993) of secondary seed dispersal by two predatory birds (the shrike and the kestrel) in three shrubs (*Lycium intricatum*, Solanaceae; *Rubia fruticosa* Aiton, Rubiaceae; and *Asparagus nesiotes* Svent., Convallariaceae) by examining several factors simultaneously. The specific aims of this research are: (i) to document secondary dispersal events by predatory birds by examining the correlation of prey carcasses with fruiting plant seeds; (ii) to evaluate the relative importance of primary dispersers (lizards) and secondary seed dispersers (shrikes and kestrels) in the dispersal events of the three fruiting plant species; (iii) to examine changes in seed coat thickness and hardness after two vertebrate gut-passage events; (iv) to study the gut effect of reptiles and birds on seed viability and germination, (v) to assess the differential seed distribution caused by the different seed dispersers and evaluate the presence of these fleshy-fruited plant species according to their respective habitat use; and (vi) to quantify the movement distances of the seed dispersers in order to better understand the potential magnitude of these LDD processes, and their potential incidence in the colonization of fleshy-fruited plant species in recent lava flows (badlands) of volcanic islands.

Methods

STUDY AREA

The Canarian Archipelago is made up of seven main volcanic islands located between 27 to 29° N and 13 to 18° W, and less than 100 km off the north-western coast of Africa. This study has been carried out in a xeric badland (50–100 m a.s.l.) in the north of Lanzarote, one of the driest easterly islands of the Canaries. This area is known as Malpaís de La Corona and it is one of the most extensive badland areas (*c.* 18 km^2) in the entire archipelago. The age of this island has been estimated as 15.5–5.0 million years, while a relatively recent volcanic episode originated on this badland (about 21 000 years ago; Carracedo *et al.* 2003). The maximum elevation of Lanzarote is 671 m a.s.l. and its climate is semi-arid, being strongly influenced by the proximity of the African continent. Mean rainfall in this badland is 157.8 ± 80.6 mm per year ($n = 19$ years; between 1973 and 2002) and the annual mean temperature is 21 ± 0.60 °C ($n = 9$ years; period: 1989–97). Vegetation consists of sparse xerophytic shrub composed mainly of species such as *Euphorbia regis-jubae* Webb & Berthel., *E. balsamifera* Aiton, *Launaea arborescens* (Batt.) Murb., *Kleinia neriifolia* Haw., *Lycium intricatum*, *Rubia fruticosa*, *Asparagus nesiotes* and scarcer and locally distributed *A. arborescens* Willd. This badland was chosen because most of the native fleshy-fruited plant species of the island are present in the area. Therefore, this areas provides an opportunity to understand how this complex multi-dispersal process could function. These ecological events could have been decisive in the colonization of such areas by fleshy-fruited plant species in the geological past. During these colonization episodes, although the participation of short-distance dispersers (generally lizards and passerines in oceanic islands – Valido & Nogales 1994; Olesen & Valido 2003; Nogales *et al.* 2005) is frequent, LDD events of seeds are also presumably important (Moore 1999; Nogales *et al.* 2001).

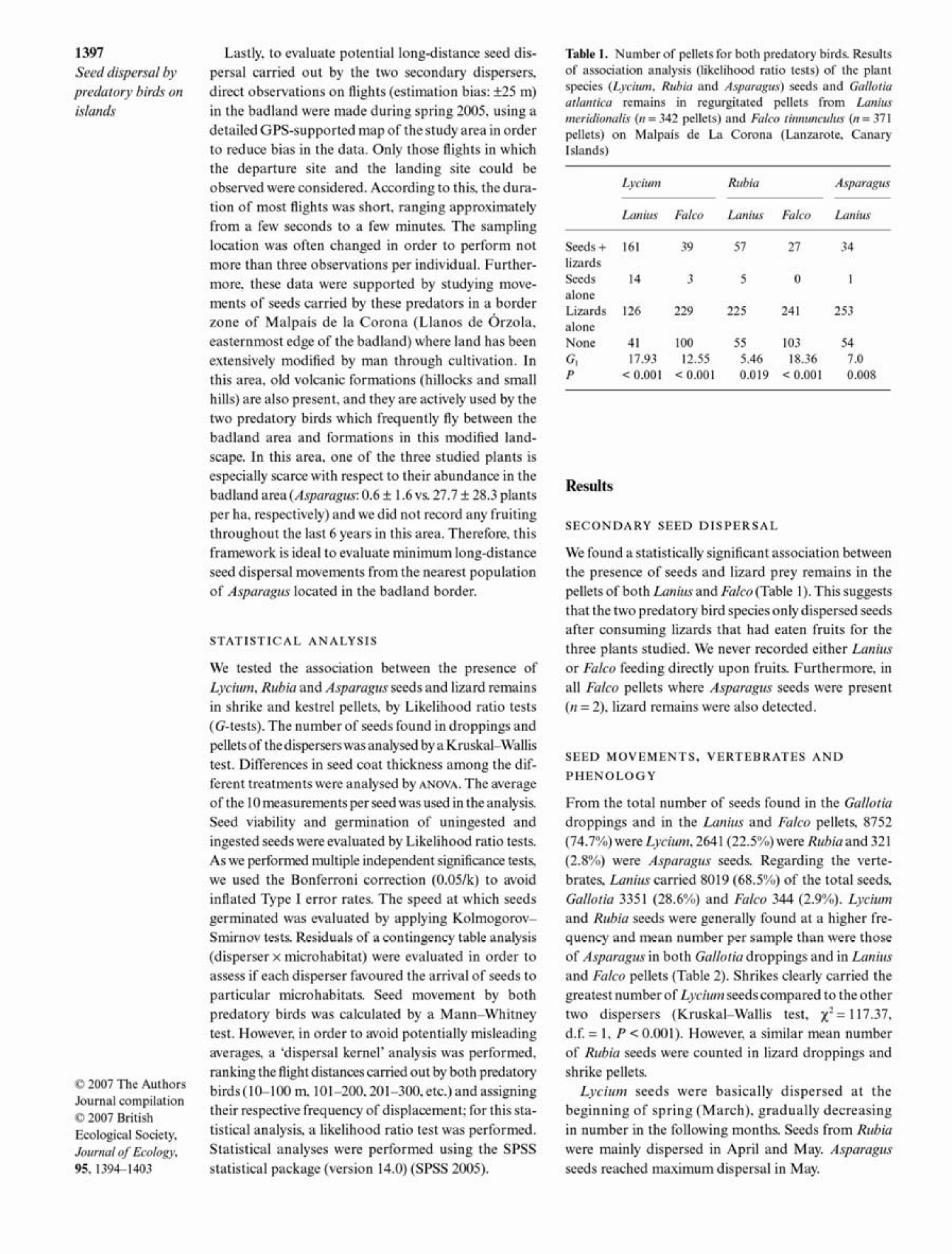
EXPERIMENTAL PROCEDURES

Fieldwork was conducted over four years (springs of 2002–05) in two sites (1.6 km apart) in Malpaís de La Corona: 'Las Tabaibitas' (100 m a.s.l.) and 'Peñas de Tao' (140 m a.s.l.). A total of 200 fruits (< 10 per plant) were directly collected from each species of plant (controls); a total of 566 lizard droppings and 713 pellets (342 from shrikes and 371 from kestrels) were also obtained during the 4-year study. These samples were collected in both study sites, over an area of 4000 m^2, to minimize the mother plant effect. They were used to evaluate the effect of gut passage by the different disperser agents on seed viability and germination. Each dropping and pellet was stored independently, and seeds were manually extracted and counted. Damaged and undamaged seeds were classified using a stereomicroscope (10× magnification) according to the visual state of seeds. Seeds were assigned to different treatments on the basis of their origin: (i) control seeds, (ii) from lizard droppings, (iii) from shrike pellets, and (iv) from kestrel pellets. Interaction effects between the apparitions of seeds linked to the presence of lizards in the pellets from each predatory bird were studied in the case of the three plants studied.

Viability was assessed for 50 seeds from each treatment, except for the *Asparagus–Gallotia–Falco* interaction due to infrequent occurrence ($n = 2$ pellets). The bioindicator 2,3,5 triphenyl-tetrazolium chloride (TTC) was used to determine viability. In addition, a germination experiment for each treatment was performed in a greenhouse over a period of 6 months (1 October 2003 to 31 March 2004). A total of 200 seeds were planted for most treatments; each seed was sown 5 mm deep independently in a 4-cm^2 pot ($n = 230$ pots per tray) containing a standard substrate (50% turf and 50% culture soil). The experiment was carried out at Tagoro (Tenerife Island; 300 m a.s.l.), with a night/day cycle similar to that found in the study area. Pots were watered every 2 days and germination date was noted when any seedling part emerged above the soil surface.

Seed coat thickness measurements were gathered from approximately 15 seeds ($n = 10$ repeated measurements per seed) from each treatment, by means of a dissecting microscope connected to a computer using Image Pro-Plus vs. 4.5.1.2.2 software (Media Cybernetics, Inc., USA). Seed hardness was measured by using an electronic press (Zwick/Roell Z100; Ulm, Germany), with the help of the 'testxpert Machine' program. Unfortunately, this machine could only be used in the case of *Asparagus* seeds, as *Lycium* and *Rubia* seeds were too flexible to obtain the breaking point. Nonetheless, from the point of view of seed consistency, we can appreciate a clear cline of decreasing hardness: *Asparagus* > *Rubia* > *Lycium*.

Seed distribution was studied by counting dispersed seeds in the three microhabitats previously classified: (i) open ground (flat rocky places with shrubby vegetation), (ii) flat-topped volcanic hillocks with shrubby vegetation (small promontories; mean size: 31.3 ± 34.6 m^2, height: 2.67 ± 1.69 m, $n = 29$), and (iii) small volcanic hills (promontories higher and larger in size than the flat-topped volcanic hillocks; mean size: 401.2 ± 383.2 m^2, height: 11.7 ± 2.75 m, $n = 10$). For this sampling, randomly placed (0.5 × 0.5 m^2) plots were used, analysing all droppings and pellets found (400 plots in the open ground, 151 in the hillocks and 37 in the hills). Furthermore, in the same plots, we counted the number of the three fleshy-fruited plant species studied in this work. Sampling of droppings, pellets and fleshy-fruited plants were carried out during two springs (2004 and 2005).



Lastly, to evaluate potential long-distance seed dispersal carried out by the two secondary dispersers, direct observations on flights (estimation bias: ±25 m) in the badland were made during spring 2005, using a detailed GPS-supported map of the study area in order to reduce bias in the data. Only those flights in which the departure site and the landing site could be observed were considered. According to this, the duration of most flights was short, ranging approximately from a few seconds to a few minutes. The sampling location was often changed in order to perform not more than three observations per individual. Furthermore, these data were supported by studying movements of seeds carried by these predators in a border zone of Malpaís de la Corona (Llanos de Órzola, easternmost edge of the badland) where land has been extensively modified by man through cultivation. In this area, old volcanic formations (hillocks and small hills) are also present, and they are actively used by the two predatory birds which frequently fly between the badland area and formations in this modified landscape. In this area, one of the three studied plants is especially scarce with respect to their abundance in the badland area (*Asparagus*: 0.6 ± 1.6 vs. 27.7 ± 28.3 plants per ha, respectively) and we did not record any fruiting throughout the last 6 years in this area. Therefore, this framework is ideal to evaluate minimum long-distance seed dispersal movements from the nearest population of *Asparagus* located in the badland border.

STATISTICAL ANALYSIS

We tested the association between the presence of *Lycium*, *Rubia* and *Asparagus* seeds and lizard remains in shrike and kestrel pellets, by Likelihood ratio tests (*G*-tests). The number of seeds found in droppings and pellets of the dispersers was analysed by a Kruskal–Wallis test. Differences in seed coat thickness among the different treatments were analysed by ANOVA. The average of the 10 measurements per seed was used in the analysis. Seed viability and germination of uningested and ingested seeds were evaluated by Likelihood ratio tests. As we performed multiple independent significance tests, we used the Bonferroni correction (0.05/k) to avoid inflated Type I error rates. The speed at which seeds germinated was evaluated by applying Kolmogorov–Smirnov tests. Residuals of a contingency table analysis (disperser × microhabitat) were evaluated in order to assess if each disperser favoured the arrival of seeds to particular microhabitats. Seed movement by both predatory birds was calculated by a Mann–Whitney test. However, in order to avoid potentially misleading averages, a 'dispersal kernel' analysis was performed, ranking the flight distances carried out by both predatory birds (10–100 m, 101–200, 201–300, etc.) and assigning their respective frequency of displacement; for this statistical analysis, a likelihood ratio test was performed. Statistical analyses were performed using the SPSS statistical package (version 14.0) (SPSS 2005).

Table 1. Number of pellets for both predatory birds. Results of association analysis (likelihood ratio tests) of the plant species (*Lycium*, *Rubia* and *Asparagus*) seeds and *Gallotia atlantica* remains in regurgitated pellets from *Lanius meridionalis* ($n = 342$ pellets) and *Falco tinnunculus* ($n = 371$ pellets) on Malpaís de La Corona (Lanzarote, Canary Islands)

	Lycium		*Rubia*		*Asparagus*
	Lanius	*Falco*	*Lanius*	*Falco*	*Lanius*
Seeds + lizards	161	39	57	27	34
Seeds alone	14	3	5	0	1
Lizards alone	126	229	225	241	253
None	41	100	55	103	54
G_1	17.93	12.55	5.46	18.36	7.0
P	< 0.001	< 0.001	0.019	< 0.001	0.008

Results

SECONDARY SEED DISPERSAL

We found a statistically significant association between the presence of seeds and lizard prey remains in the pellets of both *Lanius* and *Falco* (Table 1). This suggests that the two predatory bird species only dispersed seeds after consuming lizards that had eaten fruits for the three plants studied. We never recorded either *Lanius* or *Falco* feeding directly upon fruits. Furthermore, in all *Falco* pellets where *Asparagus* seeds were present ($n = 2$), lizard remains were also detected.

SEED MOVEMENTS, VERTEBRATES AND PHENOLOGY

From the total number of seeds found in the *Gallotia* droppings and in the *Lanius* and *Falco* pellets, 8752 (74.7%) were *Lycium*, 2641 (22.5%) were *Rubia* and 321 (2.8%) were *Asparagus* seeds. Regarding the vertebrates, *Lanius* carried 8019 (68.5%) of the total seeds, *Gallotia* 3351 (28.6%) and *Falco* 344 (2.9%). *Lycium* and *Rubia* seeds were generally found at a higher frequency and mean number per sample than were those of *Asparagus* in both *Gallotia* droppings and in *Lanius* and *Falco* pellets (Table 2). Shrikes clearly carried the greatest number of *Lycium* seeds compared to the other two dispersers (Kruskal–Wallis test, $\chi^2 = 117.37$, d.f. = 1, $P < 0.001$). However, a similar mean number of *Rubia* seeds were counted in lizard droppings and shrike pellets.

Lycium seeds were basically dispersed at the beginning of spring (March), gradually decreasing in number in the following months. Seeds from *Rubia* were mainly dispersed in April and May. *Asparagus* seeds reached maximum dispersal in May.

Table 2. Seeds from the different plant species (*Lycium*, *Rubia* and *Asparagus*) found in droppings and pellets from lizards, shrikes and kestrels in Malpaís de La Corona (Lanzarote, Canary Islands)

	Total seeds found			Seed number per dropping or pellet (mean ± SD)			Percentage of droppings or pellets where at least one seed was recorded			Percentage of undamaged seeds			Number of droppings or pellets analysed
	Lycium	*Rubia*	*Asparagus*	*Lycium*	*Rubia*	*Asparagus*	*Lycium*	*Rubia*	*Asparagus*	*Lycium*	*Rubia*	*Asparagus*	
Gallotia	1392	1717	242	2.46 ± 5.89	3.03 ± 4.37	0.43 ± 0.64	27.7	49.1	35.9	100	99.3	99.2	566
Lanius	7147	795	77	20.90 ± 38.40	2.32 ± 7.19	0.23 ± 0.82	51.2	18.1	10.2	99.7	100	100	342
Falco	213	129	2	0.57 ± 2.77	0.35 ± 1.69	0.0053 ± 0.073	11.3	7.3	0.5	99.5	99.2	100	371

Table 3. Seed coat thickness of *Lycium*, *Rubia* and *Asparagus* recorded in the different treatments (lizards, shrikes and kestrels) on Malpaís de La Corona (Lanzarote, Canary Islands); *n*: number of seeds

	Seed coat in µ (mean ± SD)						Percentage reduction (cf. control)		
	Lycium	*n*	*Rubia*	*n*	*Asparagus*	*n*	*Lycium*	*Rubia*	*Asparagus*
Control	149.03 ± 15.39	14	80.99 ± 6.25	15	56.03 ± 4.21	14	–	–	–
Gallotia	136.17 ± 16.66	14	53.09 ± 4.19	15	52.26 ± 5.75	11	8.7	34.5	6.7
Lanius	134.77 ± 14.23	14	52.63 ± 5.58	15	53.31 ± 5.32	10	9.6	34.2	4.9
Falco	125.13 ± 11.07	15	46.33 ± 4.79	15	48.37	1	16.1	57.2	13.7

SEED GUT TREATMENTS

External visual damage of seeds from the three different plant species was low; the percentage of ingested seeds that were undamaged was over 99% (Table 2). In general, decreasing differences were observed in seed coat thickness after the seeds were consumed by the different dispersers compared to control seeds (Table 3). *Lycium* seeds from *Falco* pellets had the thinnest coats of all treatments; these were significantly different from control seeds (16% of reduction; ANOVA I-test, $F = 6.67$, d.f. = 3, 53, $P = 0.001$). The greatest changes in seed coat thickness, however, were observed in *Rubia*, especially for seeds from *Falco* pellets (43% of reduction with respect to control seeds; $F = 127.29$, d.f. = 3, 56, $P < 0.001$). Unfortunately, the small sample size for *Asparagus* did not allow any statistical analysis, although the seeds of this species showed the smallest percentage of coat reduction (Table 3). Seed hardness in *Asparagus* was unaffected by ingestion by any disperser ($\chi^2 = 3.17$, d.f. = 3, $P = 0.36$). Despite the fact that it was impossible to measure the hardness of *Lycium* and *Rubia* seeds, due to flexibility restrictions (see Methods), *Lycium* seeds clearly show the softest consistency whereas *Rubia* seeds showed an apparent intermediate robustness between those of *Lycium* and *Asparagus*.

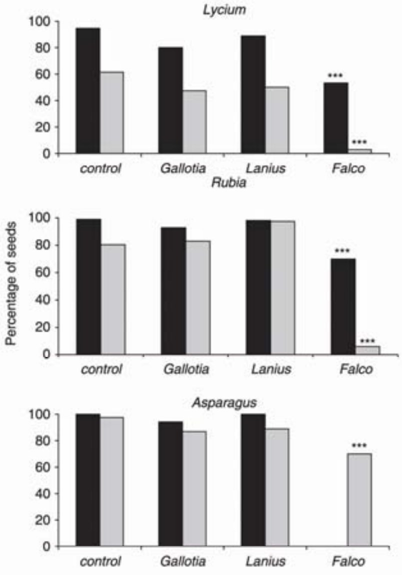


Fig. 1. Viability and germination of the different treatments of the seeds of *Lycium*, *Rubia* and *Asparagus* in Malpaís de La Corona (Lanzarote, Canaries). Black bar: viability, grey bar: germination. Viability of *Asparagus* seeds in *Falco* pellets was not analysed due to the rarity of this interaction. Significant differences, ***$P < 0.001$.

SEED VIABILITY AND GERMINATION

The viability of control seeds was high (over 90%) in all species (Fig. 1). For *Lycium* and *Rubia*, no significant differences were observed among seeds from control plants, *Gallotia* droppings and *Lanius* pellets. However, when *Falco* was involved as a secondary seed agent, viability was significantly reduced (43.6% in *Lycium* and 29.3% in *Rubia*) with respect to control seeds (Likelihood ratio test, *Lycium*: $G = 20.32$, d.f. = 1, $P < 0.001$; *Rubia*: $G = 13.82$, d.f. = 1, $P < 0.001$) and with respect to those seeds extracted from *Lanius* pellets (*Lycium*: $G = 13.38$, d.f. = 1, $P < 0.001$; *Rubia*:

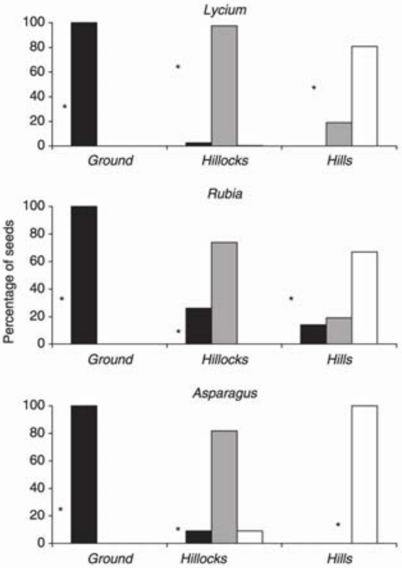


Fig. 2. Seed distribution pattern (spring 2004 and 2005 combined) of *Lycium*, *Rubia* and *Asparagus* across the three main microhabitats considered, produced by the disperser agents in Malpaís de La Corona (Lanzarote, Canaries). Black bars: *Gallotia*; grey bars: *Lanius*; white bars: *Falco*. Asterisks represent the percentage of occurrence of the different plant species in the squares (0.25 m^2) sampled in the three main microhabitats.

$G = 14.92$, d.f. = 1, $P < 0.001$). No significant effect of gut treatment on viability was observed in the case of *Asparagus* seeds.

The percentage of seeds that germinated for the three plant species was similar in control, *Gallotia* and *Lanius* treatments (Fig. 1). However, germination decreased for all species when seeds were consumed by *Falco* (Likelihood ratio tests, $P < 0.001$ for all comparisons). In the case of *Lycium* and *Rubia* seeds, the reduction was very large (95.1% and 92.5%, respectively), compared to control seeds, while it was moderate (28.2%) in *Asparagus* seeds.

The speed at which seeds germinated differed among the three plant species studied: *Lycium* seeds from three treatments (control, *Gallotia* and *Lanius*) germinated earlier than those from *Falco* pellets (Kolmogorov–Smirnov tests, $P < 0.001$). For *Rubia*, seeds from *Lanius* were the fastest to germinate compared to the remaining treatments ($P < 0.001$), while control and *Gallotia* (statistically similar) seeds germinated sooner than those from *Falco*. Lastly, in the sole case of *Asparagus* seeds where sample size was suitable for comparison purposes, no differences were observed between control seeds and those from *Gallotia* droppings ($Z = 1.06$, $P = 0.20$).

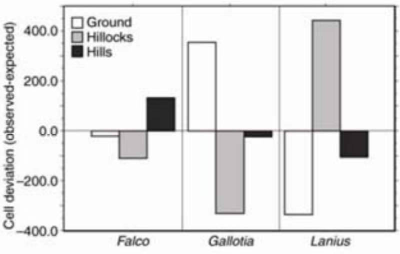


Fig. 3. Residuals of a contingency table analysis (observed cell frequency minus the expected cell frequency of dispersed seed) including disperser species and microhabitat. Bars depict the residual frequencies of dispersed seeds and their significance, indicating microhabitats favoured (positive significant residuals) or avoided (negative significant residuals) by each disperser. All values, ***$P < 0.001$.

SEED DISTRIBUTION, FLESHY FRUIT PLANT DISTRIBUTION AND VERTEBRATE MOVEMENTS

Spatial patterns of seed deposition produced by the vertebrates involved were clearly different: *Gallotia* deposited most seeds in the open ground microhabitat, *Lanius* in the hillocks and *Falco* in the hills (Fig. 2). The differences among dispersers were significant for all three species: *Lycium* ($G = 1474.4$, d.f. = 4, $P < 0.001$), *Rubia* ($G = 912.5$, d.f. = 4, $P < 0.001$) and *Asparagus* ($G = 14.6$, d.f. = 4, $P = 0.006$). Furthermore, microhabitats differed strongly in the proportions of seed contributed by the different dispersal agents ($G = 3059.5$, d.f. = 4, $P < 0.001$) (Fig. 3). All seeds arriving in the open ground habitat were dispersed by *Gallotia*, while most seeds arriving to hillocks and hills were dispersed by both predatory birds. In addition, seeds from the three plant species differed in their distribution among habitats ($G = 785.9$, d.f. = 4, $P < 0.001$). A total of 89% of *Lycium* seeds and 73% of *Asparagus* seeds were recorded in the hillocks, while 44% and 41% of *Rubia* seeds were found in the open ground and hillocks, respectively.

Movements of three dispersers were notably different. As expected, *Falco* moved the longest distances (506.4 ± 361.2 m; range: 75–1500 m; $n = 35$ movements; $n = 22$ different individuals), followed by *Lanius* (76.0 ± 49.9 m; range: 10–250 m; $n = 34$ movements; $n = 26$ different individuals) and by *Gallotia* (1.22 m; range: 0.6–2.5 m; $n = 32$ movements; $n = 6$ different individuals; A.I. Gómez & C. Hernández, pers. comm.). The 'dispersal kernel' analysis indicated that flights carried out by *Lanius* were more frequently shorter than those performed by *Falco* (Fig. 4; $G = 64.9$, d.f. = 7, $P < 0.001$). Lastly, with regards to the seed movements documented beneath the perches of both predatory birds in the hillocks and hills located in the cultivated area of Llanos de Órzola, *Lanius* moved *Asparagus* seeds a mean of 608 ± 229 m (range: 350–1150 m;

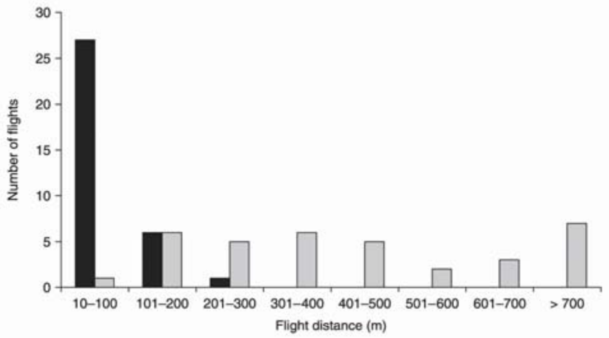


Fig. 4. 'Dispersal kernel' analysis carried out for those flights performed by both predatory bird species in Malpaís de La Corona (Lanzarote, Canary Islands). Black bars: *Lanius*; grey bars: *Falco*.

$n = 10$), while the mean movement of seeds by *Falco* was 775 ± 434 m (range: 275–1350 m; $n = 6$). These distances did not differ significantly ($U = 24.0$, $P = 0.51$).

Discussion

THE DISPERSAL SYSTEMS

Frugivorous lizards from the endemic genus *Gallotia* are frequently captured by predatory birds throughout the Canarian archipelago (Nogales *et al.* 2002). These predatory events are interesting in that whereas a double interaction of birds involved in the diplochory by endozoochory has already been described in continental environments (Ridley 1930; Damstra 1986; Hall 1987; Dean & Milton 1988), our three insular seed-dispersal systems included an endemic frugivorous lizard as the main primary disperser. The diverse physiological treatments on seeds carried out by birds and reptiles could have different effects on seed viability and germination of plants (Traveset 1998). Lizards are often abundant in insular environments, and the Canary Islands are not an exception. In addition, they are frequently involved in ecological processes such as frugivory and seed dispersal (Olesen & Valido 2003 and references therein). The diplochorous system studied here, based on predation on lizards by two predatory birds (a shrike and a kestrel), has also been observed on other islands of the Canaries. The shrike has been reported as a secondary seed dispersal agent in those islands where it is present (Lanzarote, Fuerteventura, Gran Canaria and Tenerife) and the kestrel in practically all the islands (Padilla *et al.* 2005; D.P. Padilla & M. Nogales, unpubl. data). For this reason, at least in the Canary Islands, diplochory by double endozoochory is a relatively common seed dispersal process. Further, this supports the idea of Vander Wall & Longland (2004), who argue that diplochory is a common means of seed dispersal in both temperate and tropical communities.

SEED MOVEMENTS

The greater number of *Lycium* seeds dispersed than the other two species is at least partly accounted for by the fact that their berries produce a mean of 7.43 ± 3 seeds (Nogales *et al.* 2002), many more than *Rubia* (1.4 ± 0.3; Nogales *et al.* 1999) and *Asparagus* (1.0 ± 0; $n = 40$ fruits; pers. obs.). Therefore, the ingestion of *Lycium* fruits by the primary dispersers (lizards) strongly conditions that individual lizard prey will be highly loaded with such seeds. Furthermore, the fruiting period of *Lycium* extends from January to May, compared to a shorter fruiting period for the other two plant species. Given the similar chemical composition of the pulp of the three fruits consumed by lizards (unpubl. data), consumption might be mainly determined by seasonal availability of fruits.

The number of seeds transported by each dispersal agent is one of the most important factors in seed dispersal effectiveness (Schupp 1993). In this study, the interaction *Gallotia* × *Lanius* carried more than 65% of the total seeds sampled, followed in importance by those seeds directly dispersed by *Gallotia* and the interaction *Gallotia* × *Falco*. However, although defecation and regurgitation rates range between one and two droppings/pellets per day for the three dispersers (Duke *et al.* 1976; Olsson 1985; A. Valido & M. Nogales, unpubl. data), a higher number of seeds are probably transported by lizards due to their great abundance in insular systems (Olesen & Valido 2003).

SEED TRAITS AFTER GUT TREATMENT

External damage to seeds appeared low for the different plant species and treatments. These data are consistent with earlier studies on secondary seed dispersal systems where a double digestion process occurs (Nogales *et al.* 1998, 2002).

The decreased seed coat thickness following gut passage has already been documented (Traveset *et al.*

2001; Nogales *et al.* 2005), although the effect of such changes on germination was largely unknown. Seed hardness might play a more important role in seed germination than seed coat thickness, as the hardest seeds (*Asparagus*) were the only ones that survived after the gut treatment of *Falco*. The importance of seed hardness in seed survival has been previously pointed out in legume seeds passing through the digestive tract of cattle (Gardener *et al.* 1993) and in seeds from shrubs such as *Sorbus* (Paulsen *et al.* 2006), *Phillyrea* and *Myrtus* after passing through birds' guts (Traveset *et al.*, in press). Thicker seed coats were not found to be more abraded than thinner coats and other seed coat variables need to be examined to determine which seed traits affect survival and changes in viability and germination after ingestion by dispersers.

SEED VIABILITY AND GERMINATION

Gallotia and *Lanius* did not negatively affect the viability and germination of seeds, although *Falco* clearly did. This effect is important for viability and has profound consequences for germination in the case of *Lycium* and *Rubia* seeds. Therefore, these data suggests that *Falco* is a less effective secondary seed disperser than *Lanius*. These results coincide with previous findings by Nogales *et al.* (1998, 2002) in the case of *Lycium* plants on Alegranza Island. The enzymatic action of the diurnal raptor, which is clearly stronger than in many other types of birds (Duke *et al.* 1976; Brown *et al.* 1993; Stuart & Stuart 1994), probably has a negative influence on seed survival. Furthermore, another effect that influences seed fate is gut passage time, which in the case of *Falco* (12–23.5 h; Balgooyen 1971; Duke *et al.* 1976; Yalden & Yalden 1985) is much longer than in *Lanius* (45–55 min; Olsson 1985). However, in the case of *Asparagus*, the percentage of seed germination was still high (70%), which demonstrates that this raptor can function as an appropriate secondary disperser for some plants. Seed dormancy was not observed in the case of *Asparagus*, while it was slight in *Rubia* and scarcely more important in *Lycium* seeds.

Speed of germination in the three species was clearly affected by dispersers. This differential effect on seed emergence caused by lizards and birds might be important in geographical zones where rainfall is unpredictable (e.g. the Mediterranean zone) and where the probability that seedlings can recruit successfully and for a longer period is raised (Izhaki & Safriel 1990; Traveset *et al.* 2001).

In the context of LDD events (e.g. large movements between islands), and according to the data presented in this contribution on seed coat thickness, hardness, viability and germination, *Lanius* seems to be an effective disperser for a higher number of plants than *Falco*. However, this raptor – with clearly longer gut retention times and power of flight – would be an effective disperser in the case of some plants such as *Asparagus*.

SEED SPATIAL PATTERN PRODUCED BY DISPERSERS AND PLANT DISTRIBUTION

The three plant species were present in all three main microhabitats identified (open ground, hillocks and hills) which suggests that the origin of these plants could be associated with differential habitat use by the distinct dispersers. This is supported by the fact that seed distribution produced by the primary and secondary dispersers was markedly different. *Gallotia* lizards are more frequently found in open ground (flat rocky places with shrubby vegetation), while *Lanius* use the small hillocks as perches and *Falco* the hills. The first two species function as dispersers for the different species and are probably responsible for their presence in both microhabitats. In the case of the hills, *Falco* is the sole agent responsible for the transport of all *Asparagus* seeds recorded. Taking into account the damage caused by this raptor to seeds of *Lycium* and *Rubia*, the presence of *Asparagus* could be associated with its ecological effect.

These results indicate that *Lanius* is a more frequent LDD vector than *Falco* and that this shrike transports most seeds to a particular microhabitat, the hillocks. However, *Falco* more frequently carried out longer flights than *Lanius* and this could be important for LDD events of those seeds that are able to resist the strong gut treatment. Furthermore, it is convenient to consider that *Falco* may dismember its prey before ingestion. Hence, an unknown percentage of seeds remain inside the digestive tract of the primary disperser (the lizard), having undergone only a single digestive process and remaining in a favourable state of viability (D.P. Padilla & M. Nogales, unpubl. data). Thus, *Falco* might also be involved in LDD events of *Lycium* and *Rubia* to the hills, despite the negative effect recorded on those seeds found in its pellets.

SEED DISPERSAL OF FLESHY-FRUITED PLANTS IN RECENT INSULAR VOLCANIC AREAS

In recent volcanic zones, lava flows can create a matrix of young and old substrates. However, massive eruptions can cover large areas with young volcanic materials, creating ideal frameworks to study animal and plant colonization. Furthermore, oceanic islands are simple systems compared to continental ones, and therefore their functioning can be better understood, as occurs with the seed dispersal system of the three plants studied here.

Although a large proportion of seeds from fleshy fruits are dispersed in oceanic subtropical island habitats by primary dispersers, mainly lizards and small passerines (Valido & Nogales 1994; Nogales *et al.* 2005), some seeds are transported by large long-distance dispersers (principally ravens or gulls; Nogales *et al.* 1999; Nogales *et al.* 2001). However, in addition to these primary seed dispersal systems, the ecological framework in which this study was developed permits us to assess other complex ecological phenomena, such as diplochory by double endozoochory, an ecological process which, according to all the data presented in this study, could potentially have significant consequences for long-term seed dispersal processes. Although the current paradigm on LDD suggests that these ecological processes occur rarely and are due to infrequent ecological events (Greene & Johnson 1995; Higgins & Richardson 1999; Clark *et al.* 2001), the LDD systems we are dealing with are regular and affect a great number of seeds that are being moved every year. Furthermore, these LDD systems probably accelerate plant colonization of badlands. In this regard, it is important to consider that maximum values of the minimum long-distance seed dispersal recorded for *Asparagus* in the study area was 1.15 km and 1.35 km for *Lanius* and *Falco*, respectively.

According to the gut passage time of both predatory birds, seeds remain about 45–55 min in the intestinal tract of *Lanius* (Olsson 1985) and 12–23.5 h in *Falco* (Balgooyen 1971; Duke *et al.* 1976; Yalden & Yalden 1985), and these birds reach mean cruising flight speeds of 34.0 km per h for *Lanius* (pers. obs.) and 40.9 km per h for *Falco* (Meinertzhagen 1955; Campbell & Lack 1985). Although the mean movements recorded for these birds were about 76 m and 506 m, respectively, in the hypothetical case that these birds were to fly a long distance, *Lanius* could cover about 26–31 km and *Falco* about 491–961 km before expelling the seeds, which provides insight into the potential magnitude of LDD processes in the present seed dispersal systems.

The results simultaneously obtained on the variety of ecological factors analysed in this study support the hypothesis that diplochory by double endozoochory could play a more important role in LDD events than is currently recognized, both in recent volcanic areas (lowlands) and also probably in the colonization of other islands (see Moore 1999). Furthermore, it is convenient to consider that these complex seed dispersal processes show a selective trade-off between the long gut retention time of seeds necessary to complete a LDD event, and the seed damage-cost by scarification associated with such long retention times. Our results demonstrate that while some plants may resist these ecological events, others are less likely to survive. Lastly, to have a more complete idea of the real importance of this kind of LDD system in the Canary Island flora, it will be necessary to evaluate the number of plant species that are being dispersed in the different islands by this particular multi-step process and the ecological fate of their seeds.

Acknowledgements

Francisco Valdés, Cristina Sáez, Javier Tomás and Juan Antonio Suárez helped us with different methodological tasks. Stephen Vander Wall, Pedro Jordano and Douglas Levey read the manuscript and gave all kind of suggestions. The editors Barney Davies and David Gibson, Eugene W. Schupp and one anonymous referee revised the manuscript providing several useful comments and suggestions. The Cabildo Insular de Lanzarote granted permission to work in the protected badland area. D.P.P. is financed by a PhD Thesis grant from the Canarian Government and J.C.I. by a postdoctoral fellowship from the Ministerio de Educación y Ciencia of Spain. Funds for both projects (BOS2003-00044 to M.N. and CGL2004-04884-C02-01/BOS to A.T.) were provided by the Spanish Ministry of Science and Education; we also allocated funds for the project PI042004/037 (granted to M.N.) by the Consejería de Educación, Cultura y Deportes (Canarian Government). All these projects were partially financed by FEDER funds from the European Union.

References

Andresen, E. (2001) Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in central Amazonia. *Journal of Tropical Ecology*, **17**, 61–78.

Balgooyen, T.G. (1971) Pellet regurgitation by captive Sparrow Hawks (*Falco sparverius*). *Condor*, **73**, 382–385.

Brown, R.W., Lawrence, M.J. & Pope, J. (1993) *Animal Tracks, Trails and Signs*. Hamlyn Publishing Group Limited, London.

Campbell, B. & Lack, E. (1985) *A Dictionary Of Birds*. Poyser, Calton.

Carlquist, S. (1967) The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club*, **94**, 129–162.

Carracedo, J.C., Singer, B., Jicha, B., Guillou, H., Rodríguez Badiola, E., Meco, J., Pérez Torrado, F.J., Gimeno, D., Socorro, S. & Láinez, A. (2003) La erupción y el tubo volcánico del volcán Corona (Lanzarote, Islas Canarias). *Estudios Geológicos*, **59**, 277–302.

Chambers, J.C. & MacMahon, J.A. (1994) A day in the life of a seed: movement and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*, **25**, 263–292.

Clark, J.S., Lewis, M. & Horvath, L. (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist*, **157**, 537–554.

Damstra, K. (1986) Editorial (notes by George Hall). *Tree Life*, **71**, 5.

Dean, W.R.J. & Milton, S.J. (1988) Dispersal of seeds by raptors. *African Journal of Ecology*, **26**, 173–176.

Duke, G.E., Evanson, O.A. & Jegers, A. (1976) Meal to pellet intervals in 14 species of captive raptors. *Comparative Biochemical Physiology*, **53A**, 1–6.

Espadaler, X. & Gómez, C. (1996) Seed production, predation and dispersal in the Mediterranean myrmecochore *Euphorbia characias* (Euphorbiaceae). *Ecography*, **19**, 7–15.

Estrada, A. & Coates-Estrada, R. (1991) Howler monkeys (*Allouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxlas, Mexico. *Journal of Tropical Ecology*, **7**, 456–474.

Forget, P.-M. & Milleron, T. (1991) Evidence for secondary seed dispersal by rodents in Panama. *Oecologia*, **87**, 596–599.

Gardener, C.J., McIvor, J.G. & Janzen, A. (1993) Passage of legume and grass seeds through the digestive tract of cattle and their survival in faeces. *Journal of Applied Ecology*, **30**, 63–74.

Greene, D.F. & Johnson, E.A. (1995) Long-distance wind dispersal of tree seeds. *Canadian Journal of Botany*, **73**, 1036–1045.

Hall, G. (1987) Seed dispersal by birds of prey. *Zimbabwe Science News*, **21**, 1–2.

Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, **153**, 464–475.

Izhaki, I. & Safriel, U.N. (1990) The effect of some Mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology*, **78**, 56–65.

Jordano, P., García, C., Godoy, J. & García-Castaño, J. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences USA*, **104**, 3278–3282.

Kauffmann, S., McKey, D.B., Hossaert-McKey, M. & Horvitz, C.C. (1991) Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). *American Journal of Botany*, **78**, 971–977.

Levey, D.J. & Byrne, M.M. (1993) Complex ant–plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology*, **74**, 1802–1812.

Meinertzhagen, R. (1955) The speed and altitude of bird flight. *Ibis*, **97**, 81–117.

Moore, P. (1999) A shrike for mobility. *Nature*, **379**, 22–23.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.

Nathan, R. & Katul, G.G. (2005) Foliage shedding in deciduous forest lifts up long-distance seed dispersal by wind. *Proceedings of the National Academy of Sciences USA*, **102**, 8251–8256.

Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Orem, R., Avissar, R., Pacala, S.W. & Levin, S.A. (2002) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, **418**, 409–413.

Nogales, M., Delgado, J.D. & Medina, F.M. (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canaries). *Journal of Ecology*, **86**, 866–871.

Nogales, M., Hernández, E.C. & Valdés, F. (1999) Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). *Écoscience*, **6**, 56–61.

Nogales, M., Medina, F.M., Quilis, V. & González-Rodríguez, M. (2001) Ecological and biogeographical implications of Yellow-Legged Gulls (*Larus cachinnans* Pallas) as seed dispersers of *Rubia fruticosa* Ait. (Rubiaceae) in the Canary Islands. *Journal of Biogeography*, **28**, 1137–1145.

Nogales, M., Medina, F.M. & Valido, A. (1996) Indirect seed dispersal by the feral cats *Felis catus* in island ecosystems (Canary Islands). *Ecography*, **19**, 3–6.

Nogales, M., Nieves, C., Illera, J.C., Padilla, D.P. & Traveset, A. (2005) Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. *Functional Ecology*, **19**, 429–436.

Nogales, M., Quilis, V., Medina, F.M., Mora, J.L. & Trigo, L.S. (2002) Are predatory birds effective secondary seed dispersers? *Biology Journal of the Linnean Society*, **75**, 345–352.

Olesen, J. & Valido, A. (2003) Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology and Evolution*, **18**, 177–181.

Olsson, V. (1985) The winter habits of the Great Grey Shrike, *Lanius excubitor*. 4. Handling of prey. *Var Fagelvärld*, **44**, 269–283.

Padilla, D.P., Nogales, M. & Pérez, A.J. (2005) Seasonal diet of an insular endemic population of Southern Grey Shrike *Lanius meridionalis koenigi* on Tenerife, Canary Islands. *Ornis Fennica*, **82**, 155–165.

Paulsen, T.R., Lindtjorn, O., Gjerdet, N.R. & Hogstedt, G. (2006) Avian gut passage reduces seed exit costs in *Sorbus aucuparia* (Rosaceae) as measured by a diametral compression test. *Functional Plant Biology*, **33**, 611.

Pizo, M.A., Guimaraes, P.R. & Oliveira, P.S. (2005) Seed removal by ants from faeces produced by different vertebrate species. *Écoscience*, **12**, 136–140.

Ridley, H.N. (1930) *The Dispersal of Plants Throughout the World*. L. Reeve, Ashford.

Schupp, E.W. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects* (eds T. Fleming & A. Estrada), pp. 15–29. Kluwer, Dordrecht.

Shepherd, V.E. & Chapman, C.A. (1998) Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology*, **14**, 199–221.

SPSS (2005) *SPSS for Windows Release 14.0*. SPSS, Inc., Chicago.

Stuart, C. & Stuart, T. (1994) *Tracks and Signs of Southern and East African Wildlife*. Southern Book Publishers, Cape Town, South Africa.

Traveset, A. (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics*, **1/2**, 151–190.

Traveset, A., Riera, N. & Mas, R.E. (2001) Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology*, **15**, 669–675.

Traveset, A., Rodríguez-Pérez, J. & Pías, B. (in press) Changes in seed traits in the digestive tract of dispersers and consequences for germination and seedling growth. *Ecology*.

Valido, A. & Nogales, M. (1994) Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos*, **70**, 403–411.

Vander Wall, S.B. (2002) Secondary dispersal of Jeffrey pine seeds by rodent scatter hoarders: the roles of pilfering, recaching, and a variable environment. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D. Levey, W.R. Silva & M. Galetti, M.), pp. 193–208. CAB International, Wallingford.

Vander Wall, S.B. & Longland, W.S. (2004) Diplochory: are two seed dispersers better than one? *Trends in Ecology and Evolution*, **19**, 155–161.

Wenny, D.G. (1999) Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *Journal of Tropical Ecology*, **15**, 481–496.

Yalden, D.W. & Yalden, P.E. (1985) An experimental investigation of examining Kestrel diet by pellet analysis. *Bird Study*, **32**, 50–55.

Received 12 June 07; accepted 17 August 07
Handling editor: David Gibson.

PADILLA, D. P. & NOGALES M. 2009. Behaviour of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal. ***Behavioral Ecology*** **20**: 872-877.

Behavioral Ecology
doi:10.1093/beheco/arp075
Advance Access publication 8 June 2009

Behavior of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal

David P. Padilla and Manuel Nogales
Island Ecology and Evolution Research Group (Instituto de Productos Naturales y Agrobiología-Consejo Superior de Investigaciones Científicas), C/Astrofísico Francisco Sánchez 3, 38206 La Laguna, Tenerife, Canary Islands, Spain

Secondary seed dispersal is a multistep system that includes 2 or more dispersal processes that can increase the distance from which seeds arrive. This phenomenon is relatively common in some habitats of subtropical oceanic islands due to the frequent frugivore–predator interactions found in them. In this study, we describe how the Eurasian Kestrel is an effective disperser of plants in the secondary seed dispersal process, through interaction with frugivorous lizards. Experiments using captive wild kestrels, along with field data, showed that predation of kestrels on lizards leads to a secondary seed dispersal with 2 possible outcomes: 1) most seeds (89%) are not consumed by kestrels because they reject the lizards' digestive tracts and so receive only the gut treatment of lizards and 2) a small fraction of seeds (11%) appeared inside the kestrel pellets as a result of indirect ingestion by this raptor, thus undergoing double gut treatment. So, 2 different seed dispersal distances may result from this interaction: 1) when the kestrels capture the lizard and transport it to a perch where the seed-containing guts are discarded and 2) when they indirectly ingest a few seeds from lizards, consequently increasing the dispersal distance. Seeds from the Macaronesian plant species *Rubia fruticosa* were tested, finding that those passed through kestrels had a lower germinability than those that remained inside the rejected lizards' digestive tracts, which had similar germination rates to those from control plants (uningested seeds). The kestrel can be considered an important and effective long-distance seed disperser due to the high abundance of frugivorous lizards in their diet, their stereotyped consumption behavior, and the effectiveness of their seed dispersal. *Key words:* Canary Islands, diplochory, endozoochory, frugivorous lizards, long-distance seed dispersal, predatory behavior, seed germination. *[Behav Ecol 20:872–877 (2009)]*

Secondary seed dispersal or diplochory occurs whenever a seed is dispersed in 2 or more different dispersal events by different dispersal agents (Vander Wall and Longland 2004). Both abiotic (e.g., wind and water) and biotic agents (e.g., scatter hoardings, birds, or mammals) could combine, giving rise to different kinds of secondary seed dispersal processes (Forget and Milleron 1991; Levey and Byrne 1993; Vander Wall 2002; Pizo et al. 2005). Diplochory can be adaptive, as a consequence of the increased dispersal benefits that reduce seed mortality (Vander Wall and Longland 2004). These seed dispersal processes often permit the plants to move long distances and are crucial to determining genetic structure, range expansion rates, or the colonization of new habitats (Cain et al. 2000; Nathan 2006). Most of these systems only involve a single seed digestion process, whereas the other step occurs outside the animal (exozoochory) (Ridley 1930). However, secondary seed dispersal can be more complex, especially if a second seed digestion process is mediated through frugivore–predator interaction (double endozoochory). Vertebrate frugivores are often preyed on by predatory birds, which may act as secondary seed dispersers (Ridley 1930; Van der Pijl 1982). Although a few specific descriptive contributions have been published on this matter (Damstra 1986; Hall 1987; Dean and Milton 1988; Nogales et al. 1996), many ecological aspects of this multistep process remain largely unknown.

Double endozoochory occurs in secondary seed dispersal processes of continental systems, where frugivorous birds act as primary seed dispersers and are predated on by raptors (Ridley 1930). However, in subtropical oceanic islands where frugivorous lizards are extraordinarily abundant (Olesen and Valido 2003), these reptiles are also frequently preyed on by raptors and unspecialized predatory birds (Padilla et al. 2007). This is the case of the Canary Islands, where 7 extant frugivorous lizard species of the endemic genus *Gallotia* are distributed over the islands and main islets (Nogales et al. 2001). These lizards are often preyed on by the Eurasian Kestrel (*Falco tinnunculus*) and Southern Grey Shrike (*Lanius meridionalis*) (Carrillo et al. 1994; Padilla et al. 2005, 2007). Lizards thus act as primary seed dispersers, whereas predatory birds are secondary dispersers.

Three studies have been carried out to analyze these complex seed dispersal systems involving at least 3 different plant species (*Lycium intricatum*, Solanaceae; *Rubia fruticosa*, Rubiaceae; and *Asparagus nesiotes*, Convallariaceae), which have been recorded as being dispersed secondarily by shrikes and kestrels (Nogales et al. 1998, 2002, 2007). However, in *Lycium* and *Rubia*, seed treatment in kestrel guts caused a significant reduction in seed germination with respect to control seeds, seeds ingested by lizards, and those secondarily dispersed by shrikes (Nogales et al. 2007). The simultaneous analysis of several ecological variables (number of undamaged seeds, viability, germination, or microhabitat deposition) supports the hypothesis that diplochory by double endozoochory could play a more important role in long-distance seed dispersal than currently recognized, in the colonization of both recent lava flows (Nogales et al. 2007) and other islands (see Moore 1999).

Address correspondence to D.P. Padilla. E-mail: dpadilla@ipna.csic.es.

Received 9 July 2008; revised 27 March 2009; accepted 21 April 2009.

The effect of kestrels in secondary dispersal of indirectly ingested seeds has so far been studied by focusing on some ecological and evolutionary aspects; however, the role of other factors remains largely unknown. This is the case of feeding behavior in predatory birds. It is known that shrikes very often swallow their prey entirely because their small body size means that they can capture only small and medium-sized lizards (mean snout–vent length [SVL]: 74 ± 19 mm), whereas kestrels prey on larger lizards (mean SVL: 94 ± 21 mm) (Costantini et al. 2007; Padilla et al. 2007). The Eurasian Kestrel usually dismembers its lizard prey discarding the digestive tracts (containing seeds), which are often found on their perches (Padilla DP, personal observation). Thus, as a consequence of prey handling, the true overall significance of this raptor in the secondary seed dispersal processes is unknown. Similarly, the fraction of seeds remaining inside the lizards' digestive tracts (single digestive process) compared with that indirectly ingested by kestrels (2 processes) is unclear. So, animal behavior and seed characteristics (e.g., seed coat thickness and hardness) are important factors that can be used together, to predict seed dispersal processes.

The main objective of this work was to determine the ecological role of predation by Eurasian Kestrels in seed dispersal in island ecosystems, for which we studied 1) their behavior when feeding on frugivorous lizards in the field and its effects on secondary seed dispersal processes; 2) the influence on germination of seed passage through reptile and kestrel guts; and 3) predation behavior in captivity on different sizes of lizards, quantifying the number of seeds subjected to 1 or 2 digestive processes.

METHODS

Study area

The Canary Islands (27°37′–29°25′N and 13°20′–18°19′W) are of volcanic origin and located 100 km off the Atlantic coast of northwest Africa. Fieldwork was carried out on Tenerife, the largest (2034 km^2) and highest (3718 m above sea level [a.s.l.]) island in the archipelago, with clearly defined vegetation formations according to altitude. The lowlands of this island are characterized by a xeric climate with an annual mean temperature of about 21 °C and a mean annual rainfall between 100 and 400 mm, mainly between October and February (Marzol Jaén 1988). Vegetation consists of a sparse xerophytic shrub cover, dominated by *R. fruticosa* (Rubiaceae), *Euphorbia obtusifolia* and *Euphorbia canariensis* (Euphorbiaceae), *L. intricatum* and *Withania aristata* (Solanaceae), *Periploca laevigata* (Asclepiadaceae), and the alien *Opuntia* spp. (Cactaceae).

Rubia fruticosa is a shrub endemic to the central Macaronesian archipelagos (Madeira, Salvagens, and the Canaries). It is distributed in the lowlands of all the Canary Islands and can reach a mean plant cover of about 0.5 m^2 and 0.5 m in height. It produces spherical fleshy fruits, translucent berries with an average length of 7.5 mm, a diameter of 5.6 mm, and a water content of 81.5% ($n = 40$ fruits). Each berry contains an average of 1.4 spherical seeds and the average seed weight is 8.2 mg (Nogales et al. 1999). Fruits of *R. fruticosa* are eaten by a variety of vertebrates, which include native lizards and birds (legitimate dispersers) and introduced alien mammals (illegitimate dispersers) (Nogales et al. 2005). Moreover, seeds of this species can be indirectly dispersed by kestrels and shrikes, when these prey on the frugivorous lizards (Nogales et al. 2007).

Fieldwork and experimental procedures

Fieldwork was carried out in north Tenerife (spring 2006) in 9 different localities where *R. fruticosa* was present, coinciding with 15 Eurasian Kestrel breeding territories. Control seeds were obtained from a total of 200 fruits collected directly from the mother plants ($n = 40$), to evaluate the effect on germination in comparison with those seeds that passed through the different gut treatments. Five fruits per plant were taken in order to provide a suitable representation of the different plant populations. A total of 600 lizard droppings, 660 kestrel pellets, and 36 lizard guts rejected by kestrels were collected, a similar number from each of the 15 kestrel territories. All these samples were fresh and were used to quantify the seeds indirectly dispersed by kestrels in the wild and to evaluate the effect on germination of gut passage through the different dispersers. Each dropping, pellet, and lizard gut was treated separately and seeds were manually extracted and counted.

A germination experiment was conducted in a greenhouse where the same conditions were applied to all treatments for 6 months (1 October 2006 to 31 March 2007). A total of 190 seeds from mother plants (controls), 230 from lizard droppings, 101 from kestrel pellets, and 119 from lizards' digestive tracts were randomly and independently sown 5 mm deep with each seed in a separate 4-cm^2 pot containing a standard substrate (50% peat and 50% agricultural soil). All pots were watered every 2 days, and germination was monitored every 5 days by recording newly emerged seedlings. The experiment was performed at Tagoro (north Tenerife; 300 m a.s.l.), a site with similar climatic conditions as those found in the study areas.

Captivity procedures

To evaluate the predatory behavior of the Eurasian Kestrel on frugivorous lizards, experiments were carried out in captivity (spring–summer 2007). Five wild kestrels (1 adult and 1 juvenile of each sex and 1 subadult male) were temporarily maintained in captivity at the Wildlife Rehabilitation Centre (La Tahonilla, Cabildo de Tenerife) after recovering from different types of injuries. During the experiment, all birds were in perfect physical condition and ready to be released. Captivity tests took place in a pen (3.5 × 3 × 3 m) with a perch at a height of 1.90 m across the shortest side of the pen. Each kestrel was tested individually, and all predation sequences were recorded with a video camera connected to an external TV.

Kestrels were fed once daily with a lizard (*Gallotia galloti*) that was placed in the pen. These experiments were performed in accordance with the recommendations of Huntingford (1984) and the Association for the Study of Animal Behaviour Society (2001). The number of lizards offered to kestrel during the experiments was kept to a minimum to generate adequate sample sizes. All experiments and lizard captures were carried out under the supervision and approval of the Spanish authorities (Cabildo de Tenerife, register no. 62.626). A total of 30 lizards were used in the experiment (6 per kestrel). Lizards were captured using pitfall traps, and each one was kept independently in terrariums (1 × 1 m) for not more than 2 days before offering them to the kestrels. Different lizard sizes were employed according to kestrel prey size selection in Tenerife (Padilla et al. 2007). To determine if kestrels changed their prey handling in relation to lizard sizes and if this could influence the number of seeds indirectly ingested by the kestrels, lizards were classified into 3 size categories (SVL—small, 60 to 81 mm; medium, >81 to 101 mm; and large, >101 to 131 mm). Each size category was offered in a similar proportion to each kestrel.

Before lizards were offered to the kestrels, each one was measured, weighed, and force-fed by hand with a specific color of glass beads that were similar in size to *R. fruticosa* seeds. Different colored beads were used instead of seeds, so that we could precisely identify the beads coming from each lizard. A total of 15 beads were fed to small lizards, whereas 20 beads were fed to medium- and large-sized lizards due to the gut volume of each size (Nogales M, unpublished data). The time interval between bead ingestion by lizards and their later predation by kestrels was recorded to assess its potential influence on the number of seeds that appeared inside kestrel pellets (double endozoochory) or inside the rejected lizards' digestive tracts (single endozoochory). Before different lizard sizes were offered to the kestrels, the time that glass beads remained inside the lizards, periods of 24, 12, 6, 3, and <1 h, was accurately monitored.

The following days after each lizard was consumed by a kestrel, both lizard remains (heads and guts) and kestrel pellets were collected and analyzed to determine the fate of glass beads previously introduced into the lizards.

Data analysis

Contingency analyses were used to evaluate the number of seeds found in lizard droppings, kestrel pellets, and lizards' digestive tracts from predation. We employed these analyses to gain an overall view of the data, owing to the different sizes, origin, and nature of the seed-containing samples analyzed (lizard droppings, kestrel pellets, and lizards' digestive tracts). Seed germination from the different treatments (control, lizards, kestrel pellets, and lizards' digestive tracts) was analyzed by likelihood ratio tests. When the same data set was used, a posteriori correction of significance by a sequential Bonferroni procedure was applied. To evaluate the number of beads that appeared in kestrel pellets and inside lizards' digestive tracts after predation events in captivity, a non-parametric test (Wilcoxon matched pair) was performed using the average of each kestrel in order to avoid pseudoreplication bias. This test was used because the data did not meet the requirements of a parametric test, even after transformations, and also because the number of beads appearing in pellets was clearly related to that found in the lizard guts. Influence of lizard size and the time period of beads inside lizards before predation, in relation to those beads found in the rejected lizard guts or kestrel pellets, were tested using a 2-level nested design analysis of variance, where the different kestrels were considered as a fixed factor. All data were analyzed with the SPSS (v. 15.0) software.

RESULTS

Seed movements and germination

Analysis of kestrel pellets in north Tenerife demonstrated the importance of lizards in the diet of this raptor with 63% of its pellets containing 1 or more lizards. All the *R. fruticosa* seeds that appeared inside kestrel pellets were associated with lizard remains. As a consequence of kestrel prey-handling behavior, numerous lizards' digestive tracts with a high number of *R. fruticosa* seeds inside them, usually associated with lizard heads, were found on their perches. The greatest number of seeds per sample was found in lizards' digestive tracts, followed by lizard droppings, whereas the lowest number was recorded in kestrel pellets ($G = 389.29$, degrees of freedom (df) $= 2$, $P < 0.001$) (Table 1).

A significantly greater number of control seeds germinated than seeds extracted from lizard droppings ($G = 8.80$, df $= 1$, $P = 0.003$). However, no differences were observed between control seeds and those coming from lizards' digestive tracts ($G = 0.82$, df $= 1$, $P = 0.36$). No differences in germination percentage were observed between seeds from lizards' digestive tracts and those from lizard droppings ($G = 2.68$, df $= 1$, $P = 0.101$). Finally, seeds from kestrel pellets had a clearly lower germination percentage in comparison with all treatments ($P < 0.001$, for all comparisons) (Figure 1).

The germination ratio of seeds from kestrel pellets to that of seeds from rejected lizards' digestive tracts was 1:27 (Figure 1).

Table 1

Seeds from *Rubia fruticosa* found in lizard droppings, kestrel pellets, and lizards' digestive tracts rejected by kestrels, as a consequence of their feeding behavior in Tenerife, Canary Islands

Sample type (treatment)	Seeds[a] (mean ± standard deviation)	%[b]	Total[c]	n[d]
Lizard droppings	0.97 ± 3.52	14.7	583	600
Kestrel pellets	0.15 ± 0.68	7.12	101	660
Lizards' digestive tracts	3.30 ± 8.33	25	119	36

[a] Number of seeds per sample.
[b] Frequency of occurrence.
[c] Total number of seeds found.
[d] Number of samples analyzed.

Captivity tests

All kestrels showed the same behavior when feeding on lizards. In all cases ($n = 30$ trials), kestrels decapitated the lizards and then rejected the lizards' digestive tracts (from stomach to cloaca).

After the predation experiment, the total number of glass beads (simulating seeds) introduced into the lizards were recovered. Of this total number, after the prey handling by kestrels, a significantly higher number of beads appeared inside the rejected guts (89%) with respect to that in kestrel pellets (11%) ($Z = -2.02$, $P = 0.043$). The number in guts and pellets was not significantly influenced by lizard size ($F_2 = 3.91$, $P = 0.058$ and $F_2 = 0.67$, $P = 0.52$, respectively), despite a slight increase in the number in pellets after preying on small lizards (Figure 2a). Moreover, those beads found in guts and pellets were not influenced by the particular behavior of each kestrel ($F_8 = 0.64$, $P = 0.72$ and $F_8 = 0.27$, $P = 0.96$, respectively).

Finally, the length of time between seed ingestion by lizards and their subsequent predation by kestrels had a great influence on the number of beads found in lizards' digestive

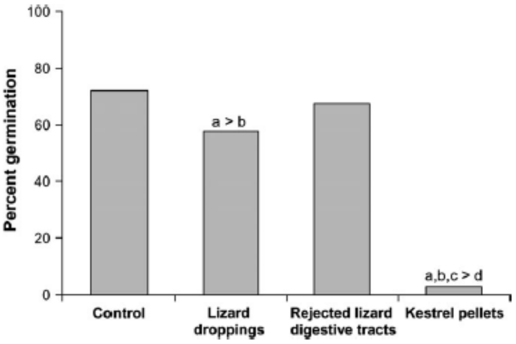


Figure 1
Seed germination of *Rubia fruticosa* of the different treatments. Significant differences in seed germination are indicated with the letters: a, control seeds; b, seeds from lizard droppings; c, seeds from rejected lizards' digestive tracts; and d, kestrel pellets.

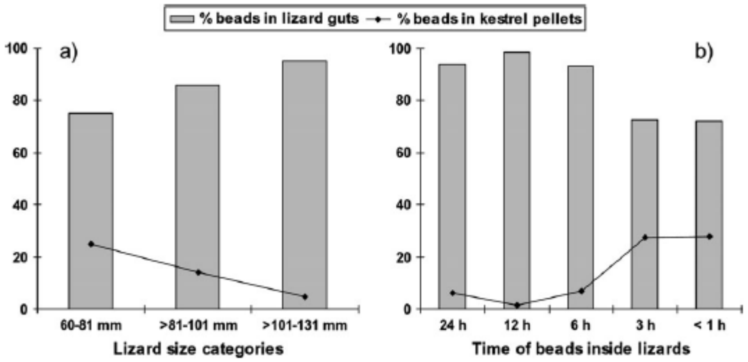


Figure 2
Influence of kestrel feeding behavior on the secondary seed dispersal processes tested in captivity, taking into account the proportion of beads that appeared in kestrel pellets (lines) and inside lizards' digestive tracts (bars): (a) after predation on different sized lizards and (b) monitoring the time elapsed between bead ingestion by lizards and their subsequent predation by kestrels.

tracts and kestrel pellets (Figure 2b). When we compared the number of beads that appeared in pellets after the different time periods, 4 times more beads were found in pellets when they had been inside the lizards for 3 h or less ($F_4 = 5.13$, $P = 0.031$).

DISCUSSION

Secondary seed dispersal

Our findings provide evidence for a newly discovered process of secondary seed dispersal by kestrels that include a single event of endozoochory. After the capture of frugivorous lizards by kestrels and the subsequent movement to their perch, this raptor acts as an effective secondary seed disperser due to its particular prey-handling technique when they reject the lizards' digestive tracts.

Seed dispersal effectiveness is of crucial importance in the survival and regeneration of plants. It is influenced by factors such as the passage of seeds through the frugivores' digestive tracts, the number of seeds transported by the dispersal agent, or the seed shadow (Schupp 1993). On islands, reptiles play an important role as seed dispersers of a wide variety of plants (Olesen and Valido 2003), and the Canary Islands harbor clear examples of this process. This archipelago supports a high abundance of frugivorous lizards (genus *Gallotia*), mostly due to their lower predation risk and competition pressures as well as their broader trophic niche (Olesen and Valido 2003). Indeed, these reptiles constitute important key resources for predators such as kestrels and shrikes (Padilla et al. 2007). Previous studies have demonstrated that these 2 birds act as secondary seed dispersers after preying on frugivorous lizards (Nogales et al. 1998, 2002, 2007). Such studies report the phenomenon of double endozoochory found in 3 plant species (*Lycium*, *Rubia*, and *Asparagus*) with different seed hardness and sizes. The different physiological treatments on seeds caused by passage through kestrels and shrikes produce diverse effects on viability and germination. Only the hard seeds of *Asparagus* survived the raptor gut passage, whereas shrikes did not negatively affect seed viability and germination of any of the 3 plant species (Nogales et al. 2007).

Our results show that *R. fruticosa* seeds were found to some extent in the kestrel pellets, although most were found in the numerous lizards' digestive tracts that kestrels left behind at the time of feeding. Thus, kestrel predation leads to secondary seed dispersal with 2 potential seed fates: 1) most of seeds are not consumed by kestrels as they are rejected along with the lizards' digestive tracts, undergoing a single (lizard) gut treatment, whereas 2) a few seeds are indirectly ingested by kestrels, undergoing a double gut treatment. Nogales et al. (2007) found that the lizard–shrike interaction transported the highest proportion (68%) of the total number of seed samples, followed by seeds directly dispersed by lizards (29%), and the lowest number of seeds was found after the lizard–kestrel interaction (3%). This study underestimated the number of seeds found in this latter interaction because only the number of seeds appearing in kestrel pellets was recorded, without taking into account the seeds remaining in the discarded lizards' digestive tracts.

Seed germination

This process can be greatly influenced by the morphological and physiological characteristics of the frugivore digestive systems and other closely related factors such as seed retention time or percentage of seed coat scarification (Jordano 1992; Traveset 1998; Rodríguez-Pérez et al. 2005). In this study, *R. fruticosa* seeds found inside kestrel pellets clearly had a lower germination percentage. These data are in agreement with those obtained by Nogales et al. (2007), so most *R. fruticosa* seeds are unable to resist the strong enzymatic action and long gut passage time (GPT) of this diurnal raptor. However, we show that most seeds remain inside the rejected lizards' digestive tracts due to the prey-handling behavior. These rejected tracts remain in the field for only a few days because ants eat practically all of them and, consequently, the seeds are released into the field (Padilla DP, personal observation). Such seeds retained a similar germination capacity to those from control plants and even greater than those dispersed directly by lizards. The higher germination percentage of seeds found in lizards' digestive tracts compared with those in lizard droppings might be because their gut transit time has been shortened by the death of the lizards. Furthermore, seeds dispersed by lizards (*G. galloti*) had a significantly reduced germination rate with respect to control seeds. This could be due to their relatively great SVL (mean: 106.4 ± 12.1 mm) and GPT (mean: 6.9 ± 3.8 days; Valido and Nogales 2003), which could reduce the seed viability of *R. fruticosa*. However, in Nogales et al. (2007), no differences in germination were observed between seeds from lizard droppings (*Gallotia atlantica*) and control seeds. *Gallotia atlantica* is a smaller lizard (SVL, mean: 60.8 ± 9.9 mm) with shorter GPT (GPT, mean: 2.4 ± 1.5 days; Valido and Nogales 2003) and with less impact on seed viability.

Taking into account the germination data and the high proportion of seeds found inside lizards' digestive tracts, it is plausible to conclude that the kestrel is in fact an effective secondary seed disperser in the Canary Islands, in a similar way to the Southern Grey Shrike, which was considered the most efficient secondary seed disperser in the Canary Islands (Nogales et al. 1998, 2002, 2007). For this reason, we suggest that this raptor may be a legitimate secondary seed disperser of the many different plant species dispersed directly by lizards in the Canaries. These lizards, of genus *Gallotia*, are considered to be one of the most important seed dispersers, often with more than 50% of their diet volume consisting of fleshy fruits (Valido and Nogales 1994; Olesen and Valido 2003; Rodríguez et al. 2008).

Predatory behavior in captivity

Our observations in captivity have demonstrated the importance of the way in which kestrels prey on frugivorous lizards and its influence on secondary seed dispersal. In all cases, the same conduct was observed, showing that lizard size did not influence the predatory behavior. This prey handling appears to be a stereotype, in which kestrels decapitate the lizards and then reject the lizards' digestive tracts. Other captivity studies also demonstrated that prey size does not modify the predation technique (Csermely et al. 1989; Csermely 1994). Our experiments indicate that the vast majority of seeds that occur inside the live lizards are later found in the rejected digestive tracts after the lizards are eaten. In contrast, only a few seeds would be subjected to a double digestion, subsequently appearing in kestrel pellets. The number of seeds dispersed secondarily by kestrels in interaction with frugivorous lizards is therefore clearly higher than those estimated by Nogales et al. (2002, 2007). Nevertheless, the number of seeds found in kestrel pellets depends on the time elapsed between seed ingestion by lizards and their later predation by kestrels. A higher number of seeds pass through a double digestion process, subsequently appearing in kestrel pellets, when the lizards eat the fruits 3 or less hours before the predation. During the predation, kestrels eat 2 muscular parts (pharynx and esophagus) of the lizards' digestive tracts. Seeds that are later found in kestrel pellets are probably those, which are still inside these tissues. Herbivorous lizards like *G. galloti* have a long transit time to increase digestive efficiency because they do not show specific anatomical traits for digestion of cellulose (Throckmorton 1973; Christian et al. 1984; Zimmerman and Tracy 1989; Valido and Nogales 2003).

Implications for long-distance seed dispersal systems

Long-distance dispersal (LDD) of plants includes rare and highly stochastic ecological events that are often difficult to detect and quantify (Higgins and Richardson 1999; Clark et al. 2001; Nathan 2006). The morphology and physiology of the dispersal units are adapted for movement by standard dispersal vectors; this is defined as a syndrome of dispersal (Van der Pijl 1982). However, a high number of plant species could move long distances due to the action of nonstandard agents (Higgins et al. 2003). In the case of fleshy fruits in subtropical oceanic islands, for instance those from *R. fruticosa*, seeds are mainly dispersed by passerines and lizards (standard dispersers) (Nogales et al. 2005). Nevertheless, nonstandard dispersers, such as kestrels and shrikes, can play an important role in LDD events when they prey on the frugivorous lizards (Nogales et al. 2007). For this reason, kestrels, with average movements of approximately 500 m (Nogales et al. 2007), can be considered an important and effective LDD vector due to the high abundance of lizards in their diet and the effectiveness of their seed dispersal, respectively. Two different seed dispersal distances may result 1) when kestrels capture the lizard and transport it to a perch where the seed-containing guts are discarded and 2) when they indirectly ingest a few seeds from lizards, subsequently increasing the dispersal distance. The second type can only be considered effective when seeds resist scarification despite the long retention time (12–23.5 h) and the strong enzymatic gut effect of this diurnal raptor. Finally, the data presented in this study demonstrate how useful animal behavior studies can be in explaining differential dispersal and potential seed distribution and how nonspecialized animals can be effective dispersers, often being responsible for LDD of plants.

CONCLUSIONS

Little attention has been given to the importance of raptors as seed dispersers in reviews of plant–animal interactions (Snow B and Snow D 1988; Fleming and Estrada 1993; Levey et al. 2001; Herrera and Pellmyr 2002; Dennis et al. 2007). However, raptors could play a valuable role as primary dispersers when they eat fruits directly (Galetii and Guimarães 2004) or as secondary seed dispersers when they prey on frugivorous animals (Galetii and Guimarães 2004; Nogales et al. 2007). The study of feeding behavior of the dispersers is also a key to understanding the true effectiveness of the seed dispersal processes. The present study changes the concept of the Eurasian Kestrel as an ineffective secondary seed disperser as previous studies tended to conclude. Now, this raptor can be considered a common and effective secondary seed disperser due to its particular prey-handling technique. They prey on frugivorous lizards, carry them to their perch, and finally reject the lizards' stomach and intestines, in which the seeds undergo only 1 digestion process. Due to this, most seeds retain high viability after the secondary dispersal process, allowing the plants to be spread long distances away from the mother plants.

FUNDING

PhD Thesis grant, Canarian Government (to D.P.P).

We would like to thank the Cabildo Insular de Tenerife for the permission and facilities provided at the La Tahonilla wildlife rehabilitation centre. This Institution also granted permission (register no. 62.626) to capture lizards and carried out experiments. Anna Traveset, Juan Antonio Fargallo, and Juan Carlos Illera critically read the manuscript and made helpful suggestions to improve it.

REFERENCES

Association for the Study of Animal Behaviour, Animal Behavior Society. 2001. Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav. 61:271–275.

Cain ML, Milligan BG, Strand AE. 2000. Long-distance seed dispersal in plant populations. Am J Bot. 87:1217–1227.

Carrillo J, Hernández EC, Nogales M, Delgado G, García R, Ramos T. 1994. Geographic variation in the spring diet of *Falco tinnunculus* L. on the islands of Fuerteventura and El Hierro (Canary Islands). Bonn Zool Beitr. 45:39–48.

Christian KA, Tracy AC, Porter WP. 1984. Diet, digestion, and food preferences of Galapagos land iguanas. Herpetologica. 40:205–212.

Clark JS, Lewis M, Horvath L. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. Am Nat. 157:537–554.

Costantini D, Bruner E, Fanfani A, Dell'Omo G. 2007. Male-biased predation of western green lizards by Eurasian kestrels. Naturwissenschaften. 94:1015–1020.

Csermely D. 1994. Does prey size affect predatory behaviour of Kestrel? Avocetta. 18:63–67.

Csermely D, Mainardi D, Agostini N. 1989. The predatory behaviour of captive wild kestrel, *Falco tinnunculus* L. Boll Zool. 56:317–320.

Damstra K. 1986. Editorial (notes by George Hall). Tree Life. 71:5.

Dean WRJ, Milton SJ. 1988. Dispersal of seeds by raptors. Afr J Ecol. 26:173–176.

Dennis AJ, Schupp EW, Green RJ, Westcott DA. 2007. Seed dispersal: theory and its application in a changing world. London: CABI publishing.

Fleming TH, Estrada A. 1993. Frugivory and seed dispersal: ecological and evolutionary aspects. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Forget P-M, Milleron T. 1991. Evidence for secondary seed dispersal by rodents in Panama. Oecologia. 87:596–599.

Galetii M, Guimarães PR. 2004. Seed dispersal of *Attalea phalerata* (Palmae) by Crested caracaras (*Caracaras plancus*) in the Pantanal and a review of frugivory by raptors. Ararajuba. 12:133–135.

Hall G. 1987. Seed dispersal by birds of prey. Zimb Sci News. 21:1–2.

Herrera CM, Pellmyr O. 2002. Plant-animal interactions: an evolutionary approach. Oxford: Blackwell Science.

Higgins SI, Nathan R, Cain ML. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology. 84:1945–1956.

Higgins SI, Richardson DM. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. Am Nat. 153:464–475.

Huntingford FA. 1984. Some ethical issues raised by studies of predation and aggression. Anim Behav. 32:210–215.

Jordano P. 1992. Fruits and frugivory. In: Fenner M, editor. Seeds: the ecology of regeneration in plant communities. Wallingford (UK): CAB International. p. 105–156.

Levey DJ, Byrne MM. 1993. Complex ant-plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. Ecology. 74:1802–1812.

Levey DJ, Silva M, Galetii M. 2001. Seed dispersal and frugivory: ecology, evolution and conservation. Wallingford (UK): CAB International.

Marzol Jaén MV. 1988. La lluvia: un recurso natural para Canarias. Santa Cruz de Tenerife (España): Servicio de Publicaciones de la Caja General de Ahorros de Canarias.

Moore P. 1999. A shrike for mobility. Nature. 379:22–23.

Nathan R. 2006. Long-distance dispersal of plants. Science. 313: 786–788.

Nogales M, Delgado JD, Medina FM. 1998. Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Alegranza, Canaries). J Ecol. 86:866–871.

Nogales M, Hernández EC, Valdés F. 1999. Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). Écoscience. 6:56–61.

Nogales M, Medina FM, Valido A. 1996. Indirect seed dispersal by the feral cats *Felis catus* in island ecosystems (Canary Islands). Ecography. 19:3–6.

Nogales M, Nieves C, Illera JC, Padilla DP, Traveset A. 2005. Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. Funct Ecol. 19:429–436.

Nogales M, Padilla DP, Nieves C, Illera JC, Traveset A. 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. J Ecol. 95:1394–1403.

Nogales M, Quilis V, Medina FM, Mora JL, Trigo LS. 2002. Are predatory birds effective secondary seed dispersers? Biol J Linn Soc. 75:345–352.

Nogales M, Rando JC, Valido A, Martín A. 2001. Discovery of a living giant lizard, genus *Gallotia* (Reptilia: Lacertidae), from La Gomera, Canary Islands. Herpetologica. 57:169–179.

Olesen J, Valido A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. Trends Ecol Evol. 18:177–181.

Padilla DP, Nogales M, Marrero P. 2007. Prey size selection of insular lizards by two sympatric predatory bird species. Acta Ornithol. 42:167–172.

Padilla DP, Nogales M, Pérez AJ. 2005. Seasonal diet of an insular endemic population of Southern Grey Shrike *Lanius meridionalis koenigi* on Tenerife, Canary Islands. Ornis Fenn. 82:155–165.

Pizo MA, Guimaraes PR, Oliveira PS. 2005. Seed removal by ants from faeces produced by different vertebrate species. Écoscience. 12:136–140.

Ridley HN. 1930. The dispersal of plants throughout the world. Ashford (UK): L. Reeve and Co. Ltd.

Rodríguez A, Nogales M, Rumeu B, Rodríguez B. 2008. Temporal and spatial variation in the diet of the endemic lizard *Gallotia galloti* in an insular Mediterranean scrubland. J Herpetol. 42:213–222.

Rodríguez-Pérez J, Riera N, Traveset A. 2005. Effect of seed passage through birds and lizards on emergence rate of Mediterranean species: differences between natural and control conditions. Funct Ecol. 19:699–706.

Schupp EW. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio. 107/108:15–29.

Snow B, Snow D. 1988. Birds and berries. Calton (UK): T & AD Poyser.

Throckmorton GS. 1973. Digestive efficiency in the herbivorous lizards *Ctenosaura pectinata*. Copeia. 1973:431–435.

Traveset A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. Perspect Plant Ecol Evol Syst. 1(2):151–190.

Valido A, Nogales M. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. Oikos. 70:403–411.

Valido A, Nogales M. 2003. Digestive ecology of two omnivorous Canarian lizards species (*Gallotia*, Lacertidae). Amphib-Reptil. 24:331–344.

Van der Pijl L. 1982. Principles of dispersal in higher plants. Berlin (Germany): Springer-Verlag.

Vander Wall SB. 2002. Secondary dispersal of Jeffrey pine seeds by rodent scatter hoarders: the roles of pilfering, recaching, and a variable environment. In: Levey D, Silva WR, Galetti M, editors. Seed dispersal and frugivory: ecology, evolution and conservation. Wallingford (UK): CAB International. p. 193–208.

Vander Wall SB, Longland WS. 2004. Diplochory: are two seed dispersers better than one? Trends Ecol Evol. 19:155–161.

Zimmerman LC, Tracy CR. 1989. Interactions between the environment and ectothermy and herbivory in reptiles. Physiol Zool. 62:374–409.