Estación Biológica Doñana CSIC

UNIVERSIDAD DE GRANADA

TESIS DOCTORAL

MAMÍFEROS CARNÍVOROS EN UN PAISAJE AGRÍCOLA: DISTRIBUCIÓN, SELECCIÓN DE HÁBITAT Y PATRONES DE MOVIMIENTO

Memoria presentada por
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para optar al grado de Doctor en Ecología
por la Universidad de Granada

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Granada, 18 de Marzo de 2011

Editor: Editorial de la Universidad de Granada
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D.L.: GR 3139-2011
ISBN: 978-84-694-3599-1

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INTRODUCCIÓN

1. El Contexto: Paisaje y Ecología del Paisaje

Aunque hay muchas formas de definir el término *Paisaje* dependiendo del aspecto a considerar, de forma general podría definirse como un mosaico de elementos relevantes desde un determinado punto de vista de interés. Por lo tanto es simplemente una porción del territorio que contiene un patrón interesante que afecta y es afectado por un determinado proceso ecológico.

El paisaje puede ser caracterizado mediante tres componentes principales:

- Estructura: organización espacial de los elementos o usos del territorio (matriz-parche-corredor).
- Función: movimiento o flujo de elementos (agua, fauna, personas, etc) a través de la estructura.
- Cambio: dinámica o transformación del modelo a lo largo del tiempo.

A su vez, la estructura del paisaje se debe a la composición, configuración y conectividad de sus elementos (Taylor et al., 1993; Hansson et al., 1995). La composición describe la proporción de cada elemento del paisaje cualitativamente diferente, sin ninguna referencia a su localización. Comparativamente, la configuración localiza de forma explícita cada elemento del paisaje en el contexto espacial, fijando la dimensión y localización de unos elementos con otros (Dunning et al., 1992). Por último, la conectividad caracteriza procesos que contribuyen a hacer del paisaje una unidad funcional y, por tanto, hace de nexo de unión entre estructura y función (Taylor et al., 1993; Taylor et al., 2006). La conectividad es específica de especie, y depende tanto de la composición y estructura del paisaje, como de la capacidad de cada organismo de moverse por él (Henein and Merriam, 1990; Taylor et al., 1993). Es importante no confundir la conectividad con una simple conexión estructural de los elementos.

Cuando se habla de la composición del paisaje, se suelen distinguir como principales componentes entre parches, matriz y corredor (Figura 1).

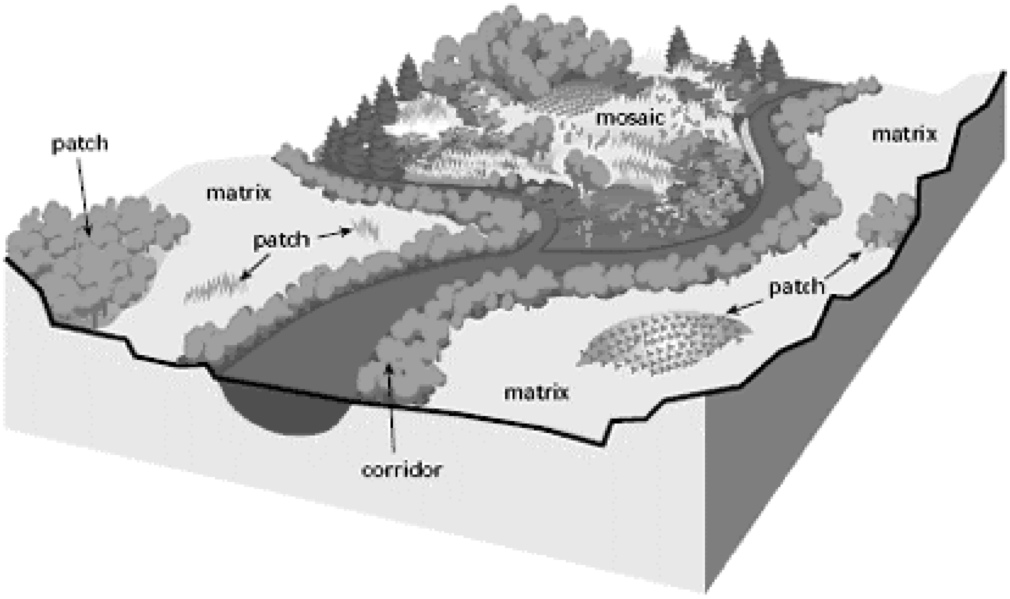


Figura 1. Principales componentes del paisaje: parche (patch), matriz (matrix) y corredores (corridors) (Jerry and Ronald, 1998).

El ***parche*** o fragmento puede definirse como una superficie homogenea no-linear que comparte similares propiedades ecológicas y difiere en apariencia de lo que le rodea (Forman and Godron, 1981). Los parches varían en tamaño, forma, tipo, heterogeneidad y características de sus bordes (Forman and Godron, 1986). De forma natural podemos encontrar constantemente parches de distinta naturaleza de las áreas circundantes debido a cambios en las características climáticas o geomorfológicas del terreno (valles glaciares, depresiones húmedas, zonas más expuestas al sol, oasis, etc), o a perturbaciones naturales, como avalanchas, tormentas, incendios, plagas de herbívoros u otros cambios. Pero estos cambios también pueden ser originados por causas antrópicas. Se le llama parche remanente al que se produce como resultado de una amplia perturbación de las zonas adyacentes a una determinada área, quedando como resto de la anterior presencia natural.

Normalmente los parches están embebidos en una ***matriz***: una superficie envolvente con diferente estructura de especies o composición. Este término es utilizado en diferentes áreas del conocimiento humano y de forma general hace referencia a una masa homogénea en la que aparecen inmersos pequeños elementos diferenciados. Por lo tanto, en el caso del paisaje, llamamos matriz al tipo de elemento de un paisaje que predomina sobre los otros (Forman and Godron, 1986).

La definición de ***corredor*** y su uso es controvertida. De forma general se puede considerar un corredor como una porción del mosaico que es usado por un organismo para moverse, explorar, dispersar o migrar (Farina, 1998). Aunque a menudo simplemente se asocia con estructuras lineales, independientemente de su funcionalidad. Es decir, la primera acepción hace referencia a su conectividad, mientras que la segunda sólo se refiere a la conexión estructural. Como ocurre con el término *conectividad*, es importante diferenciar que en el primer caso estamos tratando sobre los procesos ecológicos que tienen lugar en el paisaje, mientras que en el segundo sólo se describe un elemento estructural del mismo.

Ecología del paisaje

La ecología del paisaje es la parte de la Ciencia que se ocupa del estudio de los paisajes, atendiendo por tanto a los elementos previamente descritos: composición, estructura y función de los mismos. Incluye el estudio de los patrones que definen un determinado paisaje, las interacciones entre los elementos de esos patrones espaciales y los procesos ecológicos, y cómo esos patrones e interacciones cambian en el tiempo, así como la aplicación de esos principios en la formulación y resolución de problemas (Forman and Godron, 1986).

La cuestión general que esta disciplina intenta responder es en qué grado la estructura física del paisaje, *patrón*, afecta a las interacciones ecológicas, *procesos*, (Turner, 1989;Hansson et al., 1995). La estructura del mosaico de hábitats constriñe a los organismos que viven en él. Por ejemplo, la disponibilidad de hábitat adecuado para la reproducción y cría estará espacialmente limitada por las características estructurales del paisaje, así como las interacciones entre poblaciones de áreas adyacentes o la colonización de nuevas áreas.

2. La heterogeneidad espacial y las interacciones ecológicas

Teorías poblacionales en el marco de la Ecología del Paisaje

Hasta un pasado reciente, los modelos poblacionales suponían que el espacio y el tiempo eran homogéneos, sin tener en cuenta las dimensiones espaciales de los hábitats. Según esto, cada individuo experimentaba las mismas condiciones ambientales. Pero en la realidad, muchos hábitats ocupados por especies no son homogéneos en términos de disponibilidad de recursos, y por esta razón son percibidos como heterogéneos por individuos y subpoblaciones (Danielson, 1991;Gustafson and Gardner, 1996;Tews et al., 2004). El principal problema de este enfoque es que no consideraba que los parámetros demográficos como la natalidad, la mortalidad y la supervivencia podían depender de la heterogeneidad espacial y, por tanto, fallaban al explicar los patrones de la distribución y dinámica de las especies en amplias escalas geográficas (Levin, 1992;Fahrig and Merriam, 1994).

Con el tiempo se fueron añadiendo elementos que aumentaron la complejidad de los escenarios de las teorías poblacionales, siendo la heterogeneidad del paisaje uno de los más relevantes. Brevemente resumimos las teorías más influyentes en la actual concepción de la dinámica poblacional, como ilustración de la evolución del papel del paisaje en la interpretación de los procesos poblacionales:

Según la **teoría de Biogeografía de Islas** (MacArthur and Wilson, 1967), el número de especies presentes en una porción aislada de terreno está directamente relacionado con tres factores (Figura 2): la superficie de la isla, su aislamiento y su edad, ya que considera la colonización y extinción como los procesos fundamentales para describir la dinámica de las poblaciones. Esta teoría, si bien puede ser válida en el caso de islas oceánicas, no considera la diferente naturaleza de la matriz entre parches de hábitat en un contexto terrestre.

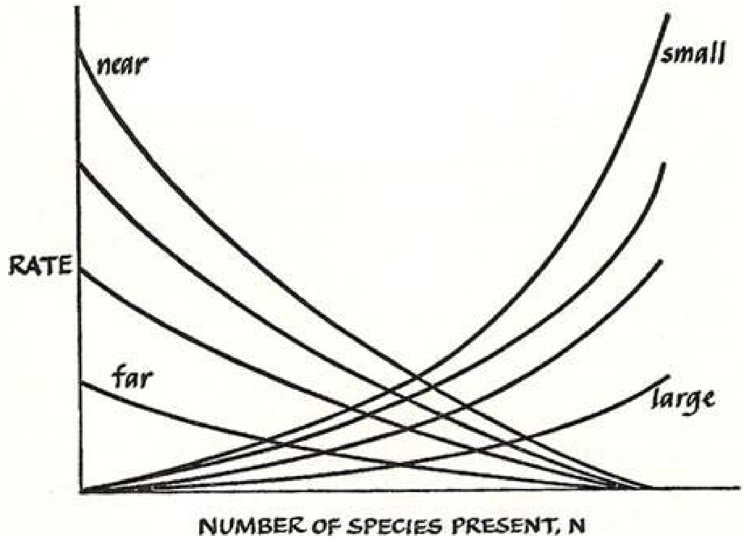


Figura 2. Relación entre la riqueza de especies, y el aislamiento y tamaño de las islas.

El término *metapoblación* fue descrito como una población de poblaciones, que se extingue y recoloniza localmente (Levins, 1970). Posteriormente, Hanski y Gilpin incorporaron el componente espacial en su **modelo de metapoblaciones** (Hanski and Gilpin, 1991), donde se sostiene que cuando las poblaciones viven en medios heterogéneos pueden estar aisladas unas de otras por hábitats hostiles o menos favorables, en cuyo caso el contacto entre ellas se mantiene mediante inmigración y emigración. El riesgo de extinción local y la probabilidad de recolonización dependerán principalmente de la capacidad de mantener el intercambio de individuos y, por tanto, de la capacidad dispersiva de los individuos, entre otros factores. Las poblaciones se consideran generalmente como componentes de una metapoblación cuando son parte de un sistema en el que la tasa de extinción y recolonización crea un flujo de individuos que aseguran la conectividad genética. Esta es una condición muy común en hábitats fragmentados y disturbados.

En el *sistema de fuente-sumidero* (Pulliam, 1988), una población fuente es aquella en la que los nacimientos exceden las muertes, y la emigración a la inmigración; mientras que una población sumidero tiene un balance negativo entre nacimientos y muertes, y la producción de juveniles no es capaz de compensar la mortalidad adulta por lo que, en ausencia de inmigración, una población sumidero tiende a la extinción. El paradigma de fuente-sumidero encontró reconocimiento pleno tras la aceptación del concepto de heterogeneidad y complejidad del paisaje. Este paradigma es muy útil en ecología del paisaje para explicar las diferentes distribuciones individuales a lo largo del paisaje. Está muy ligado al concepto de metapoblación, ya que comparten la base de las diferentes condiciones de los parches ocupados, y el intercambio de individuos para el mantenimiento del sistema.

Conceptos provenientes de otras áreas de la Ciencia sirvieron para orientar los procesos ecológicos en los paisajes. Así, la *teoría de percolación***,** que se formuló para estudiar el comportamiento de dispersión aleatoria de fluidos a través de un medio (Stauffer, 1985), según la cual en el proceso de percolación existe un límite entre regiones finitas que los fluidos no pueden traspasar cuando se alcanza un determinado umbral de percolación, ha sido empleada en el estudio del movimiento de animales y el uso de recursos (O'Neill et al., 1988;Casagrandi and Gatto, 2006;Oborny et al., 2007). Cuando un animal se mueve en un hábitat con valor igual o mayor al umbral de percolación, el organismo puede atravesar el paisaje.

Marco actual

En general, los primeros modelos propuestos para poblaciones subdivididas fallaban en que asumían que todas las poblaciones eran igualmente accesibles por los dispersores, no eran espacialmente explícitos (Fahrig and Merriam, 1994). Sin embargo, la matriz en los paisajes a menudo es altamente heterogénea, lo que implica la existencia de diferencias en distintas zonas de esta y, por tanto, un amplio número de potenciales colonizadores. La matriz puede proporcionar zonas de refugio (a modo de “stepping stones”), o zonas de alta impermeabilidad para determinadas especies como masas de agua o carreteras. La importancia del aislamiento para las islas oceánicas es matizada en las islas terrestres en función de los elementos que componen la matriz entre los parches (Norton et al., 2000). La diversidad de especies en los parches en un mosaico de hábitats estará íntimamente relacionada con las características y los procesos en el mosaico (Forman and Godron, 1986).

Importancia de la escala

El concepto de escala puede definirse como la dimensión espacial y temporal que se requiere para un cambio en la tasa a la cual ocurren los procesos y en la importancia relativa de los factores que explican dichos procesos. La definición de escala implica heterogeneidad: conforme la ventana de observación de espacio o tiempo aumenta, cambia la importancia de los organismos, sus características y los parámetros ambientales. Por tanto, la incorporación de la escala al análisis de la Ecología espacial puede ayudar a identificar los procesos que explican los patrones en amplias áreas geográficas (Doak et al., 1992;Levin, 1992).

En la misma línea, la *teoría de jerarquías* (O'Neil et al., 1986) explica como los diferentes componentes localizados a una determinada escala están en contacto con los componentes de otra escala de resolución. Considera a un sistema como componente de un sistema mayor, compuesto a su vez por otros subsistemas. Se argumenta que procesos ecológicos locales, como la competencia, depredación, procesos estocásticos y la influencia del medio ambiente físico, son los que finalmente determinan la diversidad de especies en una comunidad particular (Levin, 1992;Levin, 2000). Por tanto, quienes estén interesados en entender los patrones de distribución geográfica y de diversidad de especies, así como de la estructura y organización de comunidades, deberán abordar un enfoque que involucre diversas escalas espaciales y temporales, y donde tanto los procesos locales y como los regionales sean tomados en cuenta.

3. Los paisajes agropecuarios y la fragmentación del hábitat

Fragmentación y sus efectos sobre las poblaciones

La fragmentación es el proceso por el que un hábitat continuo se divide en trozos más pequeños (Figura 3). Como consecuencia no sólo se reduce la superficie total de un determinado hábitat, sino que aumenta el aislamiento de estos nuevos parches.

Existen crecientes evidencias de que la fragmentación disminuye la presencia de muchas especies y contribuye sustancialmente a la pérdida de biodiversidad regional y global (Saunders et al., 1991). Por un lado, favorece la aparición de especies generalistas y tolerantes de disturbios, los invasores oportunistas y las especies con menores requerimientos del hábitat que se ha visto afectado o aquellas que pueden encontrar recursos en la matriz circundante (Bowen et al., 2009). En cambio, la abundancia de las especies especialistas suele declinar, no sólo por la disminución de su hábitat preferente, sino al encontrar más resistencia en la matriz que envuelve los parches (Fahrig and Merriam, 1994). Los cambios en la abundancia relativa suele afectar a su vez la riqueza de especies total, ya sea de manera positiva o negativa.

Los principales efectos de la fragmentación del hábitat se pueden resumir en los siguientes:

- **Aumenta el aislamiento**, actuando como barrera para la dispersión de ciertas especies.
- **Disminuye el tamaño del área**; lo cual afectará a las especies dependiendo de sus requerimientos de área específicos.
- Se potencian cambios físicos y biológicos relacionados al **efecto de borde**.
- Favorece la dispersión y colonización de las nuevas "islas" creadas por **especies invasoras**.

- Las nuevas poblaciones serán **más vulnerables** ante eventos aleatorios ambientales, demográficos o genéticos.

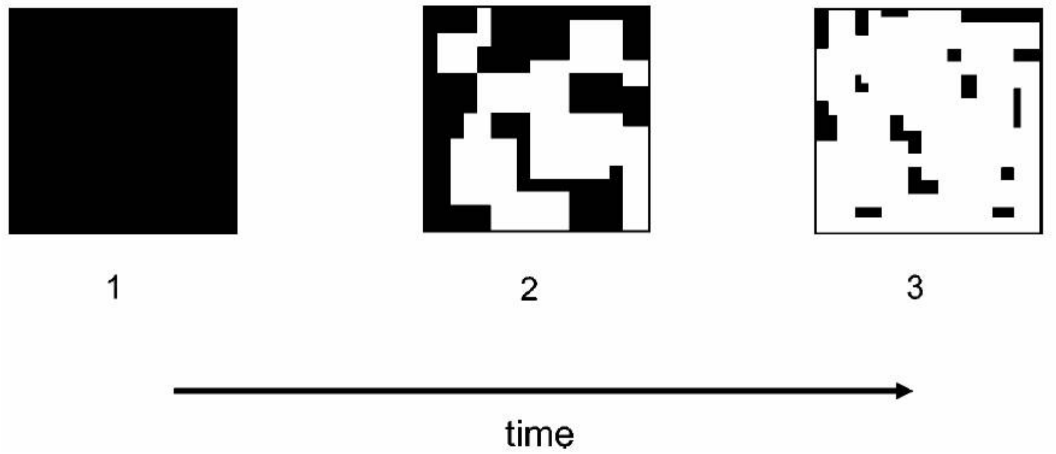


Figura 3. Proceso de fragmentación de hábitat (Fahrig, 2003)

Características de los paisajes cultivados

Una de las causas más extendidas de la modificación del medio ha sido la aplicación e intensificación de la agricultura. La característica más general de los paisajes cultivados es la remoción de la vegetación natural para la sustitución por especies cultivables, con la consiguiente pérdida y fragmentación de los hábitats originales. De forma general, la densidad de parches aumenta, mientras que decrece la variabilidad de los mismos (Forman and Godron, 1986;Bélanger and Grenier, 2002). Aparecen nuevos parches de origen antrópico, que a menudo constituyen una matriz agrícola (por ser el tipo de hábitat predominante en el paisaje), y quedan parches remanentes como el resultado de la transformación de la vegetación original en tierras de cultivo. El número de especies presentes decrece considerablemente respecto a la situación inicial, debido al dominio de las especies cultivadas. La vegetación natural remante se empobrece en especies como resultado de las repetidas perturbaciones y por el aislamiento, que dificulta la recolonización de especies tras las extinciones locales.

Adicionalmente, este cambio en la composición suele ir acompañado de cambios estructurales. De esta forma se potencia la geometrización del terreno, con la división de los campos y creación de nuevos elementos lineares o poligonales, como lindes, carreteras y diques de irrigación, entre otros (Merriam, 1988).

Para determinadas poblaciones, estos paisajes agrícolas, en los que se entremezclan parches de buena calidad en matrices relativamente inhóspitas, donde encontramos elementos conectores que, unas veces podrán tener función de corredor, y otras de barrera, pueden estar sirviendo de escenario para una metapoblación de poblaciones residentes en los parches dispersos de hábitat (Merriam, 1988). La probabilidad de recolonización dependerá de (1) las relaciones espaciales entre los elementos del paisaje usados por las poblaciones, incluyendo parches de hábitats y elementos de la matriz inter-parches a través de los cuales los individuos se dispersan, (2) las características de dispersión del organismo en cuestión y (3) de los cambios temporales en la estructura del paisaje (Fahrig and Merriam, 1994).

4. Comportamiento individual

Como hemos dicho, el mantenimiento de las poblaciones se basa en la relación de los individuos con el paisaje en el que viven. Los animales interaccionan con el paisaje por medio de su comportamiento (Forman and Godron, 1986) y, en última instancia, éste se refleja en su patrón de movimiento. El movimiento de los animales tiene importantes implicaciones para la optimización de los patrones comportamentales, como la de búsqueda de alimento, ahorro de energía, selección de hábitat y comportamiento territorial y social, entre otros (Bascompte and Vilá, 1997). A nivel poblacional, la persistencia de especies que viven en medios fragmentados a menudo dependerá de que los hábitats que componen la matriz permitan el movimiento entre parches (Fahrig and Merriam, 1985;Hanski and Gilpin, 1997). Asimismo, esta resistencia que la matriz agrícola opone al movimiento de los individuos puede ser evaluada mediante la decisión del animal de cruzarla, y la frecuencia con la que lo hace.

De forma básica podemos distinguir entre tres grandes tipos de movimiento en función de la escala de desplazamiento: en las áreas de campeo, dispersión y migración (Greenwood and Swingland, 1983;Swingland, 1983). El área de campeo de un animal es el área que usan para alimentarse y otras actividades diarias. La dispersión hace referencia al movimiento de un individuo desde el área de campeo donde había nacido hacia un nuevo área de campeo. La migración es el movimiento cíclico de individuos entre áreas separadas que son utilizadas en diferentes estaciones del año.

Hay varios factores que afectan el movimiento de una determinada especie como la densidad poblacional, barreras físicas y disponibilidad de hábitat durante la dispersión (Mauritzen et al., 1999). Pero los factores que afectan a los movimientos dentro de las áreas de campeo pueden no ser relevantes durante la dispersión, ya que varían la motivación del individuo y el conocimiento del paisaje. A nosotros nos interesan especialmente aquellos movimientos que resultan de la decisión individual sobre el conocimiento de los elementos del medio, por lo que estudiaremos los patrones de movimiento de individuos adultos y territoriales dentro de sus áreas de campeo.

Patrones de movimiento

El análisis de los patrones de movimiento de las especies debe ser esencial para la interpretación de su respuesta a fenómenos espaciales, como la fragmentación de hábitat. A un determinado nivel de fragmentación, la respuesta de las especies estará determinada por la escala a la que perciben el paisaje (Diffendorfer et al., 1995).

Una determinada trayectoria de un individuo puede ser caracterizada de forma básica mediante parámetros como la longitud total, longitud neta (distancia rectilínea entre el punto inicial y final de la trayectoria), y sinuosidad o tortuosidad (que define el grado en que una determinada trayectoria se aleja de la más recta posible).

A su vez, la trayectoria puede ser descompuesta en unidades básicas del movimiento denominadas “pasos” (steps). Esta división suele ser arbitraria, basadas en unidades temporales utilizadas para el análisis, aunque también podría usarse criterios funcionales de clasificación si se pudiera distinguir entre cambios drásticos del comportamiento (descanso, búsqueda de alimento, desplazamientos, etc). Los parámetros básicos para caracterizar estas unidades del movimiento son la velocidad (o longitud, para pasos estandarizados por unidad de tiempo), y el ángulo de giro entre dos pasos consecutivos (Figura 4).

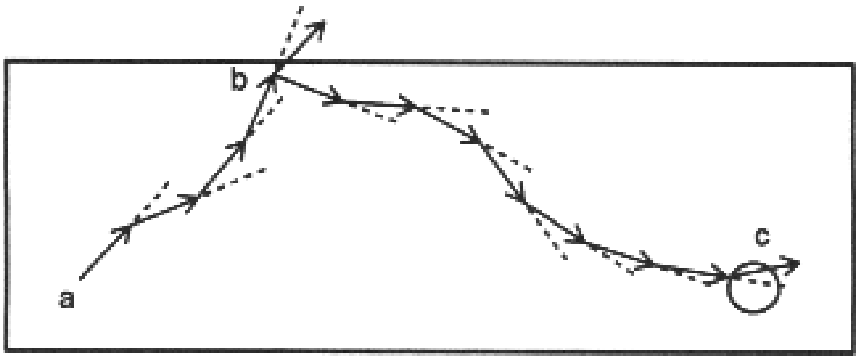


Figura 4. Descomposición de la trayectoria de movimiento en pasos (flechas). Cada paso puede ser caracterizado por su longitud y ángulo de giro respecto al siguiente paso.

La composición y estructura del paisaje puede afectar a estos parámetros de los movimientos individuales (Morales and Ellner, 2002). Normalmente se espera que los individuos se muevan de forma más tortuosa y a menor velocidad en parches de hábitat preferente, y que se desplacen de forma más recta y a mayor velocidad en hábitats inhóspitos (Benhamou and Bovet, 1989;Zollner and Lima, 2005).

5. Nuestro caso concreto: Carnívoros en paisajes Mediterráneos

Es importante identificar las especies claves en una comunidad, de cara a emprender acciones de gestión y conservación del paisaje (Lindenmayer et al., 2008). Las especies que ocupan posiciones en altos niveles tróficos, como es el caso de los predadores, suelen ser más susceptibles a los efectos de la pérdida de hábitat (Dobson et al., 2006), por lo que pueden ser buenas especies paraguas para la conservación de otras especies con menores requerimientos. Adicionalmente, los predadores presentan un papel claro en el mantenimiento directo o indirecto de la biodiversidad, mediante el control de meso-predadores y diversificación de las presas (Terborgh et al., 1999;Miller et al., 2001).

De forma general, los predadores se han visto muy perjudicados en los paisajes agrícolas, especialmente en aquellos con baja heterogeneidad de tipos de cultivo (Kruess and Tscharntke, 1994;With et al., 2002), y algunos no pueden vivir en dichos paisajes bajo ciertos umbrales mínimos de cobertura forestal (Redpath, 1995;Tewksbury et al., 1998;Beasley et al., 2007). En el caso de los mamíferos carnívoros este efecto de la fragmentación suele ser muy marcado, debido a sus altos requerimientos de hábitat forestal. Estas consideraciones, así la falta de información sobre comunidades de mamíferos carnívoros en medio transformados, son las que nos han decidido a tomar este grupo como objetivo de nuestro estudio.

Nuestra área de estudio

El área de estudio se sitúa en la llanura agrícola del río Guadiamar (Figura 4). Esta zona, eminentemente agrícola, se encuentra localizada entre las grandes masas forestales de Sierra Morena y el Entorno Natural de Doñana, así como por las masas de pinares de Aznalcázar y Puebla del Río, y por la falla del Aljarafe al este, caracterizada por un uso urbano creciente debido a la expansión del área metropolitana de Sevilla. Hacia el Oeste la llanura agrícola se extiende hasta Portugal. La cuenca se encuentra salpicada por pequeños pueblos y urbanizaciones, aunque la densidad de población humana es escasa, exceptuando el borde oriental donde comienza el área metropolitana de Sevilla. La autovía Sevilla-Huelva y otras vías de menor entidad cruzan el área de este a oeste. Entre los cultivos predominantes en la región destacan los herbáceos de secano (principalmente trigo y girasol), y el olivar. Se conservan algunas dehesas con ganado y algunos bosquetes relictos, principalmente asociados a cursos de agua de cierta envergadura. De norte a sur discurre el río Guadiamar y su vegetación de ribera, como potencial conector regional entre Sierra Morena y Doñana.

Figura 4. Situación del área de estudio en el valle del río Guadiamar.

Las especies

En base a prospecciones preliminares que se hicieron en la misma zona en busca de rastros de mesomamíferos, se detectó la presencia de tejón (*Meles meles*), gineta (*Genetta genetta*), meloncillo (*Herpestes ichneumon*) y zorro (*Vulpes vulpes*) en los fragmentos forestados del agrosistema (Rodriguez and Delibes, 2003;Rodríguez and Pereira, 2008). Tras descartar al zorro por su carácter ubiquista y oportunista (Pita et al., 2009), elegimos a las tres primeras especies como objeto principal de nuestro estudio.

El tejón es un carnívoro territorial con una amplia distribución en el Paleártico (Revilla and Palomares, 2002b). Nocturno y de mediano tamaño, es considerado un generalista trófico por la gran variedad de recursos disponibles de que hace uso (lombrices, insectos, frutos, gazapos) (Revilla and Palomares, 2002a). Pese a que en Centro Europa muestra preferencias por los bosques templados y pastos asociados, se ha demostrado que también elige las masas arbustivas como hábitat principal en climas más secos, como es el caso del Suroeste de la Península Ibérica (Revilla et al., 2000). Puede vivir en paisajes transformados por el hombre, al menos en el centro y norte de Europa. El área de campeo puede variar mucho entre individuos y en función de la productividad de los hábitats ocupados, siendo el tamaño medio de 525 hectáreas en el Suroeste de la Península Ibérica (Rodríguez, 1996).

La gineta es un carnívoro nocturno de mediano tamaño. Puede alimentarse de pequeños mamíferos, aves, reptiles o artrópodos, aunque la presa principal varía en diferentes zonas de su distribución (Virgós et al., 1999). En el Parque Nacional de Doñana, próximo a nuestra zona de estudio, análisis de dieta han mostrado una preferencia por micromamíferos, seguidos de aves, insectos, anfibios, conejos, reptiles y huevos (Palomares and Delibes, 1991a). Se ha descrito su uso de formaciones arboladas con baja cobertura arbustiva (Palomares and Delibes, 1994;Virgos and Casanovas, 1997). El área de campeo, en estudios realizados en Doñana, se sitúa en 541 hectáreas, usando un 95% de polígono convexo mínimo (Palomares and Delibes, 1994).

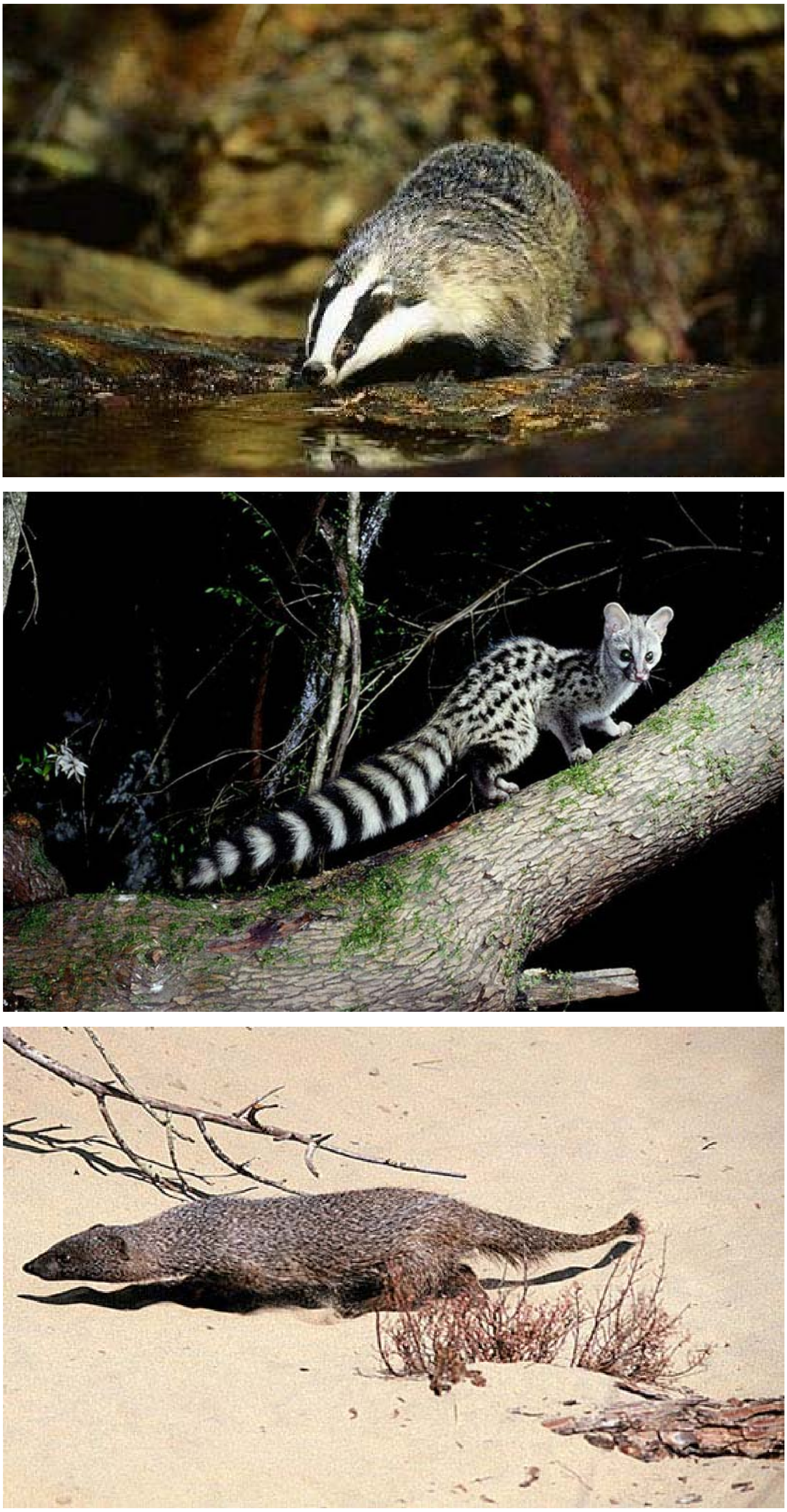


Figura 5. Tejón (foto de Antonio Vázquez), gineta (foto de Albert Miquel i Loewe) y meloncillo.

El meloncillo es un carnívoro diurno procedente de África cuya distribución en Europa se restringe al Suroeste de la Península Ibérica. Se alimenta de vertebrados de pequeño y mediano tamaño, principalmente conejos (Palomares and Delibes, 1991a). Muestran preferencias por matorrales densos como lugares para el descanso, tanto diurno como nocturno (Palomares and Delibes, 1990), y su área de campeo media ronda las 300 hectáreas (Palomares, 1994b).

6. Objetivos y estructura de la tesis

El objetivo principal de esta tesis es estudiar la interacción con el paisaje de las poblaciones de tres carnívoros de mediano tamaño viviendo en un entorno antropizado, a partir de distintas escalas tanto espaciales como de objeto de estudio: analizamos la importancia de elementos estructurales del paisaje a nivel (meta)poblacional en un sistema de fragmentos comprendidos entre Sierra Morena y el Espacio Natural de Doñana; la selección de hábitat de una población de meloncillos y otra de ginetas, viviendo en el agrosistema, y el patrón de movimiento de ambas especies como consecuencia de la interacción de los individuos con el paisaje específico en el que se relaciona.

En el **capítulo 1** (*Ocupación de parches por tres carnívoros de mediano tamaño en un paisaje agrícola*) se caracteriza el agrosistema de la Cuenca del río Guadiamar; se determinan los parches forestales, hábitat que a priori se considera preferente para las tres especies; y se determinan los principales elementos del paisaje que afectan a la presencia o ausencia de cada especie en dichos fragmentos forestales.

En el **capítulo 2** (*Ecología espacial y comportamiento de la gineta y el meloncillo en un paisaje agrícola mediterráneo*) se describen las características físicas, la ecología espacial y comportamiento de individuos de gineta y meloncillo residentes en una región seleccionada dentro del agrosistema.

El **capítulo 3** (*Importancia de conservación de estrechas líneas forerstales remanentes para el meloncillo y la gineta en un paisaje agrícola mediterráneo*) estudia de forma específica la selección de hábitat y de determinados elementos del paisaje por parte de las dos poblaciones de gineta y meloncillo, respectivamente, estudiadas en el agrosistema.

Los capítulos 4 y 5 analizan los patrones de movimiento de los individuos de gineta y meloncillo. En el **capítulo 4** (*De-construyendo áreas de campeo: Patrón de movimiento de la gineta en un paisaje agrícola*) se descompone el movimiento de un subconjunto de ginetas en sus unidades elementales y se estudian sus parámetros básicos en función de las características del entorno por el que se desplazan. Por último, en el **capítulo 5** (*Patrones de movimiento del meloncillo en dos paisajes mediterráneos diferenciados*) se estudian las diferencias en el patrón de movimiento del meloncillo en dos paisajes marcadamente diferenciados por su composición y estructura: el agrosistema del Guadiamar, y el Parque Nacional de Doñana.

CAPÍTULO 1

Patrones de ocupación de tres carnívoros en un paisaje agrícola

Patterns of patch occupancy by three carnivores in an agricultural landscape

RESUMEN

Los paisajes agrícolas se componen de un mosaico de diferentes tipos de hábitats en donde los parches relictos de vegetación natural son minoritarios. Esta fragmentación de los hábitats representa una importante amenaza para la conservación de la biodiversidad, especialmente para aquellas especies con una fuerte dependencia de coberturas forestales. El paisaje puede ser percibido y usado de forma diferente por los animales, dependiendo en sus requisitos de hábitat y su tolerancia a áreas de menor calidad.

En un paisaje agrícola del suroeste de España, hemos estudiado la influencia de la calidad y contexto de fragmentos forestados (parches) sobre la presencia de tres mamíferos carnívoros de mediano tamaño, el tejón, la gineta y el meloncillo, y hemos probado la hipótesis de que los generalistas de hábitat estarán menos constreñidos por el tamaño y calidad de los parches que las especies especialistas.

La ocupación de los parches por las tres especies estuvo influenciada tanto por la calidad como por el contexto del parche. La presencia de tejón se vio favorecida por la cobertura arbórea y arbustiva en el fragmento, la presencia de corredores estructurales y los cultivos herbáceos por debajo de un umbral del 50% del área circundante. La probabilidad de ocupación por ginetas estuvo favorecida por la presencia de arroyos en el parche y por la proporción de olivares en los alrededores del mismo, y disminuyó con la presencia de disturbios por actividades antrópicas. La probabilidad de ocupación de un parche por meloncillo aumentó con el tamaño del mismo, la proporción de coberturas arbóreas y arbustivas en su interior, la presencia de arroyos, y por la densidad de elementos lineares alrededor del fragmento. Los disturbios provocados por actividades antrópicas y la distancia a la fuente más cercana tuvieron un efecto negativo sobre la presencia de esta especie.

La cantidad de varianza independiente explicada por el contexto del parche en relación con la calidad del mismo fue mayor en el caso de la ocupación por tejón (68%) que en el caso de la gineta (26%) o meloncillo (23%), apoyando la hipótesis inicial de que las especies menos tolerantes a los cultivos y con una menor capacidad de colonización (meloncillo) será más dependiente de la calidad y tamaño de los parches forestados.

ABSTRACT

Agricultural landscapes are composed by a mosaic of different habitats where remnants patches of natural vegetation are minority. This fragmentation of habitats involves a thread to biodiversity conservation, especially for those species with strong dependence to forested covers. Landscape can be perceived and used by animals differently, depending on its habitat requirements and tolerance to less suitable areas.

In an agricultural landscape of south-western Spain we studied the influence forested fragments (patches) quality and context (agricultural matrix) in the presence of three medium-sized carnivores, the Eurasian badger, the common genet and the Egyptian mongoose, and tested the hypothesis that habitat generalist will be less constrained by patch area and quality than habitat specialist species.

Patches occupancy by all three species was influenced by both patch quality and patch context variables. Presence of badger was favoured by the tree and shrub cover within the patch, the density of shrubby linear elements around the patch, the presence of structural corridors and herbaceous crops under a threshold of 50% of the surrounding area. The probability of occupancy by genets was favoured by the presence of streams within the patch, and by the proportion of olive groves around it, but decresed with the presence of human disturbances. The probability of patch occupancy by mongooses increased with patch area, tree and shrub cover, presence of stream, and the density of shrubby linear elements around the patch. Human disturbance and the distance to the nearest source had a negative effect on the presence of this species.

The amount of independent variance explained by patch context compared with patch quality for badger occupancy (68%) was higher than for the incidence of genets (26%) and mongooses (23%), supporting our initial hypothesis that the less tolerant species to fields and with lower colonization ability (the Egyptian mongoose) would be more dependent on patch area and patch quality.

INTRODUCTION

Habitat fragmentation is a process during which a large expanse of habitat is transformed into a number of patches of smaller total area, isolated from each other by a matrix of habitats unlike the original (Wilcove et al., 1986). As a result of the native vegetation clearing to favour other landscape uses, mainly agriculture, these landscapes are composed by a mosaic of different habitats where remnants patches of natural vegetation are minority and surrounded by anthropogenic habitats, many of which can be relatively hostile to wildlife (Saunders et al., 1991;Macdonald and Rushton, 2003).

For strictly dependent species on remnant patches, population survival in these fragmented landscapes would depend on both the local extinction rate in habitat patches and on the rate of patch colonization (Turner, 1989). Metapopulation theory has been proposed to give an explanation to these processes (Hanski, 1994). Local extinctions are highly related to the amount (area) and quality of resources in the habitat patch, while local immigrations should rely on the spatial relationship between the landscape elements used by populations, including habitat patches, matrix elements inter-patches and the displacement ability of organisms (Henein and Merriam, 1990;Fahrig and Merriam, 1994). Long life species with stables home ranges, like carnivores, must be more vulnerable to habitat fragmentation effects (Wiegand et al., 2005), if they strongly select forested patches against matrix habitats.

But, in terrestrial landscapes the matrix is unusually entirely inhospitalable and, even if it is not a preferred habitat, it can be used to a greater or lesser extent by individuals (Wiens, 1996;Ricketts, 2001). Habitat quality, rather than a binary concept, can be conceived as a continuous attribute which value can rank from a minimum for the most hostile matrix, to a maximum that define the better conditions for reproduction. This gradient of values depends on the perception of each individual, and determines the usage of each habitat as a probability function. Therefore, colonization probability is not only a matter of distance but it would depend too on the permeability of the different matrix types to the animal movement

As the same landscape can present different degree of connectivity for different organisms depending on their perception, the species that find less resistance to the movement in the mosaic of less preferred patches should be less affected by habitat

fragmentation than those with higher difficulties for displacement (Taylor et al., 1993;Fahrig and Merriam, 1994;Lindenmayer et al., 2000;Ricketts, 2001;Wagner and Fortin, 2005). Then, the persistence of species living in fragmented landscapes should rely on the probability of movement among patches through the matrix habitats (Fahrig and Merriam, 1985;Hanski and Gilpin, 1997), if the species are truly constrained to these patches, or even in the possibility of using actively these less preferred habitats as a supplement (Dunning et al., 1992) or substitute of natural habitats (Norton et al., 2000). Habitat generalists, refered in this case to the preference for natural woody vegetation, can make a higher use of secondary habitats than specialist species due its behavioural or ecological plasticity, through the exploitation of the resources available in those habitat of less quality; While specialist species (Hansson, 1994;Bender et al., 1998), would restrict its usage of those secondary habitats to displacements among suitable habitat patches, and so would be especially affected by habitat fragmentation (Thomas et al., 1992;Warren et al., 2001).

We have identified all forested patches in a highly modified and fragmented agricultural landscape in South-western Spain, and studied patch occupancy by three medium-sized carnivores: Eurasian badger (*Meles meles*), common genet (*Genetta genetta*) and Egyptian mongoose (*Herpestes ichneumon*). All three species have been described as dependent on woody vegetation cover, especially scrubland, in the Mediterranean region (Palomares and Delibes, 1990;Palomares and Delibes, 1994;Virgós and Casanovas, 1997;Revilla et al., 2000), but their tolerance to non-forested habitats is still insufficiently known. Diet analysis has shown that badgers can obtain food in different crop types as olive groves and cereal crops in the Iberian Peninsula (Rosalino et al., 2005) and other European regions (Kruuk and Parish, 1985;Wilson, 1993;Roper and Lups, 1995;Balestrieri et al., 2004). Genets have scansioral habits (Heinrich, 2006), and tree holes and dense scrubland have been described as suitable refuges for this species (Palomares and Delibes, 1994;Virgos and Casanovas, 1997). Genets have also been detected in Mediterranean pinewoods (Mangas et al., 2007) and cork oak woodlands (Virgos and Casanovas, 1997;Espirito-Santo et al., 2007) of the Iberian Peninsula. Mongooses seem to avoid open areas and prefer dense vegetation in Doñana National Park (Palomares and Delibes, 1993a).

Our aims are 1) to identify characteristics of patches determining their occupancy by each species; 2) to determine which patch context attributes, if any, influence patch occupancy; and 3) to compare the relative importance of patch quality versus patch context between the species.

We expect patch quality in general, and patch area in particular, to have more relevance for species strictly dependent on woody vegetation than for those species than can also use transformed agricultural land. If all matrix habitats are in the same degree hostile for a species, we expect the distance to nearest neighbour to be the only patch context attribute determining the patch occupancy; whereas if only some species use the matrix more than expected from their availability, we would expect matrix quality, in addition to distance, to contribute to these species presence. We predict that: (a) the proportion of scrubland within patches will have a positive effect on the presence of the three species, and tree cover will favour patch occupancy by genets and badgers, but not mongooses; (b) the density of shrubby linear structures around forest patches will increase the incidence of the three species, either if linear structures are used only as occasional corridors or if they are used regularly as a source of resources; (c) since the Egyptian mongoose, has diurnal habits (Palomares and Delibes, 1992a), its incidence in fragments altered by human disturbance (usually diurnal too) will be lower than that of nocturnal species (badger and genet); Given the hypothesized tolerance of each species to the composition of the agricultural matrix, we predict that (d) the incidence of badgers will be higher than that of the other species if the matrix is dominated by cereal crops; (e) the differences in incidence between badgers and genets will decrease with increasing proportions of olive groves in the matrix, but the incidence of mongooses under these circumstances will remain very low once the effect of physical distances will be accounted for.

METHODS

Study area

We conducted our study in a 800 km^2 agroecosystem of the Guadiamar river basin, SW Spain (37º23’ N, 6º13’ W; Figure1). This landscape limits to the North and South by two large forest blocks: Sierra Morena and Doñana, respectively.

Information on landscape composition was obtained from a land cover layer (Junta de Andalucía 1999). Farmland, basically herbaceous crops (mainly cereals) and olive groves,

covers 91.6% of the landscape, whereas natural or seminatural woody cover sum up to a mere 5.4%. Dehesa, an agroforestry system that combines pastures or cereals with scattered oak trees and little or no understorey (Joffre et al., 1988), represents more than a half (56%) of natural or seminatural woody cover, followed by planted (eucaliptus or pines) or native (remnants of *Quercus* woodland) forest (29%), and scrubland, with or without scattered trees (15%). Farmland types are not homogeneously distributed across the landscape. Cereal crops abound in the northern half, where very little forest remains, while in the south olive groves dominate the mosaic and the proportion of forest is above the average (Figure 1). Most fields, groves and dehesas are bounded by thin woody hedgerows. The landscape contains six towns and seven smaller housing aggregations with a total of 31000 people. Urban uses cover 4% of the total area.

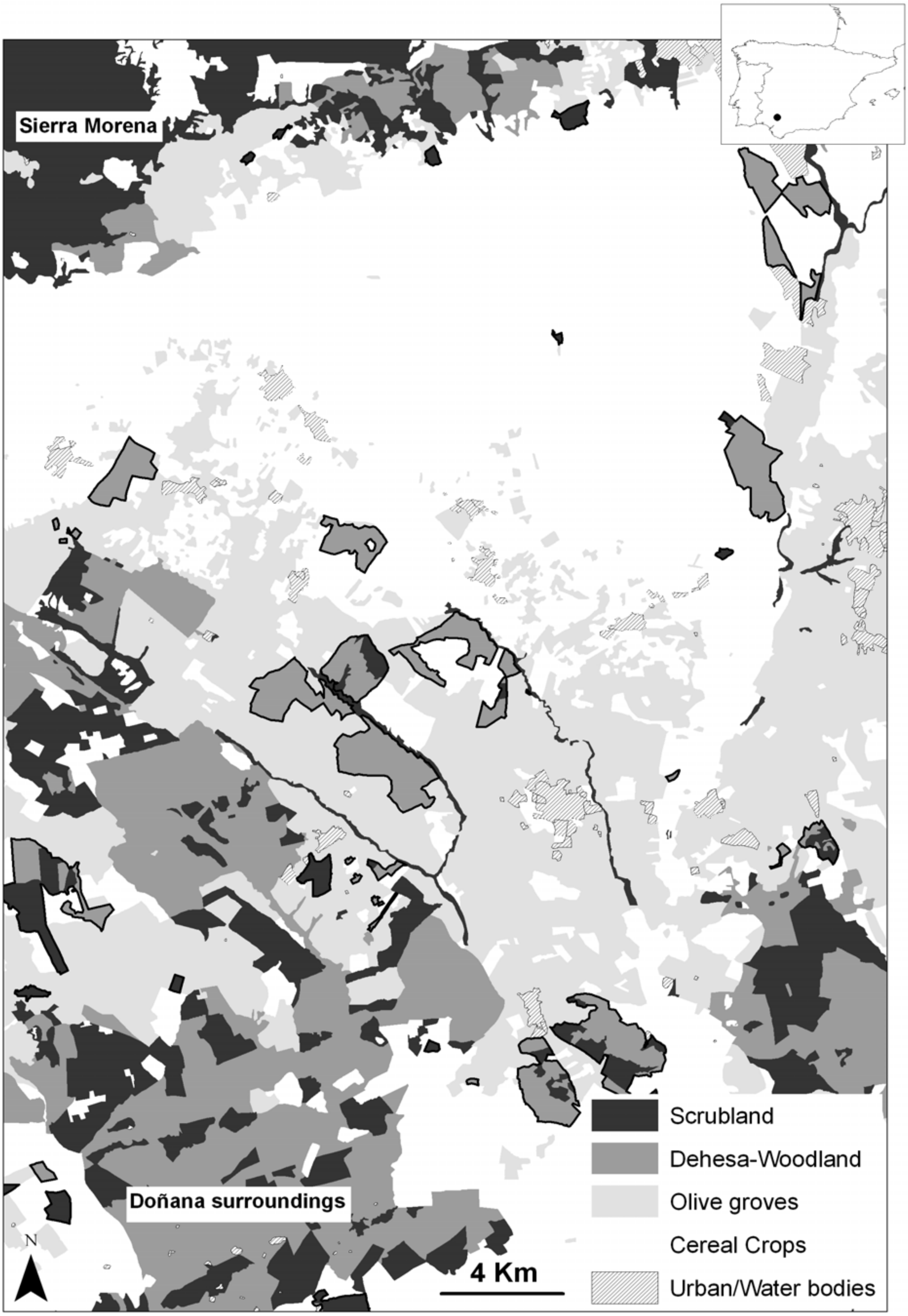


Figure 1. Location of the Guadiamar basin in south western Spain. The distribution of major habitat types is shown. Sselected patches are outlined with a thick line.

Selection and sampling of patches

We defined patches, matrix and corridors from structural attributes rather than from their function which will depend on how each species perceives habitat fragmentation. We called patches to fragments with neat discrete limits composed by woody cover, and we called matrix to everything else regardless its degree of usage by each of the studied species. We called sources to the two large forest blocks that bounded our study area to the north (Sierra Morena) and to the south (Doñana), as they contain stable populations of all three species (Rodriguez and Delibes, 2003).

We identified, checked the position, size, shape, and habitat content of 83 patches in the land cover layer through comparison with orthophotos of approximately the same date (Junta de Andalucía 2001) and field surveys. From those, we selected 55 patches after discarding a set of small patches overrepresented in the sample. Patch area ranged between 1.9 and 489.7 ha, and distance to the nearest source ranged between 40 and 9550 m.

We looked for badger, genet and mongoose signs (tracks, faeces, and burrows) and recorded any sighting while searching on foot the 55 selected patches. We assigned maximum searching times of 1, 2 and 3 hours for patches <20 ha, 20-50 ha, and >50 ha, respectively. When the patch contained more than one habitat type the searching time was distributed proportionally to the area of each habitat type. We walked randomly across the patch but tried to visit the most favourable places and substrates spotted along our trajectory. We surveyed patches twice between April and June, once during 2001 and again during 2002. We considered a species was absent from a patch when no sign was found in any of the surveys.

Landscape variables

Patch quality

Resource availability was described by patch area and the proportion of each habitat type. During the signs surveys, GPS locations were taken every 10 minutes and in a circle with a radius of 5 m we recorded a) tree, shrub, grass, and bare ground cover, b) presence of streams with dense riparian vegetation as a high quality source of food and shelter, c) presence of anthropogenic disturbances, accounting for hunting activity signs, presence of livestock, roads, and buildings inside or close to patches.

Patch context

Two indices of distance to the nearest neighbour have been calculated, namely distance to the nearest patch, independently of its size (and including sources), and distance to the nearest source. We recorded the presence of structural corridors, defined as linear structures that conforms a physical (not necessarily functional) connection between patches or between a patch and the nearest source. The proportion of cereal crops and olive groves, and the density of shrubby linear elements ($m*ha^{-1}$) were measured in a 1 km circular buffer around the patch boundaries.

Statistical Analysis

Variables selection

As patch quality variables, we selected patch area, tree and shrub cover, presence of a stream, and occurrence of disturbance (Table 1). We found a significant negative correlation between shrub and grass cover ($r=-0.49$, $p<0.001$), as well as between grass cover and bare ground ($r= -0.74$, $p<0.001$). As badgers, genets and mongooses are considered forest species, we selected shrub and tree cover as the attributes describing patch quality.

As patch context variables, we selected one of the variables expressing distance to forest, the proportion of cereal crops or olive groves around the patch, the density of shrubby linear elements (m/ha) around the patch, and the presence of structural corridors to other patch or source (Table 1). The distance to the nearest source and the distance to the nearest patch were positively correlated ($r = 0.51$, $p<0.001$). We chose distance to the nearest source for the genet as mongoose, as they may or may not be present in the nearest patch but we were sure that they occurred in the nearest source. We selected distance to the nearest patch or source for the badger as we expect this specie to make a more frequent use of matrix and its presence in patches should be more extended. The proportion of cereal crops and olive groves within 1 km of the patch were negative and significantly correlated ($r = -0.80$, $p<0.001$) as they are the dominant types of matrix in our study area. We chose one

of the two variables according to the habitat preferences for each species and to the results of the univarite analyses: olive groves for genets due to their scansorial habits, and cereal crops for badger and mongoose, as they can provide food for badgers and more shelter at the ground level than olive groves for mongooses.

Table 1. Predictors used in models of patch occupancy for Eurasian badger, common genet and Egyptian mongoose.

Patch quality	
Area	Ln(patch area)
Tree	Tree cover (%)
Shrub	Shrub cover (%)
Stream	1 = Presence of stream in the patch; 0 = absence
Disturbance	1 = Disturbance within or close to the patch; 0 = no signs of disturbance
Patch context	
Corridor	1 = Presence of woody linear elements between the focal patch and surrounding patches, or between the focal patch and the nearest source; 0 = absence
Hedge	Density of shrubby linear elements within 1 km of the patch ($m*ha^{-1}$)
Crops	Cereal crops within 1 km of the patch (%)
Olive	Olive groves within 1 km of the patch (%)
Dforest	Distance to the nearest patch or source (m)
Dsource	Distance to the nearest source (m)

Model selection

To avoid linearity assumptions, we have explored the relationship between presence/absence of carnivores and all landscape variables through the fitting of Generalized Additive Models (GAMs) with logistic link function and binomial error. When all variables showed a linear response, we used Generalized Linear Models (GLMs) with logistic link function and binomial error to describe the probability of patch occupancy for each species. In order to test our predictions we built alternative models with the presence/absence of each species as the dependent variable and the following sets of explanatory variables (Table 1): (1) patch quality, (2) patch quality and distance to the nearest forest, and (3) patch quality and patch context. To reduce the effects of colinearity, the statistical independence of predictors was tested through correlation tests. We avoided including highly correlated variables ($r > 0.5$) in the same model and, among them, we retained the more ecologically meaningful one.

Alternative models were compared by means of the second order Akaike Information Criterion (AICc), a statistical method that penalizes maximum likelihood with by the number of model parameters (Akaike, 1973). We used an additional correction term recommended when the relationship between sample size and the number of variables is smaller than 40 (Sugiura, 1978). Models with $\Delta_i<2$, where $\Delta_i=AIC_{ci}-AIC_{c\ min}$, can be considered good alternative models (Sugiura, 1978). Model selection was evaluated by calculating *Akaike weights*, ω_i, defined as:

$\omega_i= \exp(-1/2\Delta_i)/\Sigma^R_{r=1} \exp(-1/2\Delta_r)$,

where ω_i provided evidence that the model i was the best among those examined simultaneously.

Variance partitioning

For each species we analysed the hierarchical partitioning of the variance explained by each variable retained in the final model. This process involved calculation of the increase in the fit of all possible models with a particular variable compared to the corresponding increment without that variable (Mac Nally, 2002), which allowed us to identify those variables with an important independent correlation with the dependent variable, and to compare them with those that have little independent effect on that dependent variable (Carrete et al., 2007).

All statistical analyses have been performed with the software R (R Development Core Team 2008), using the packet *mgcv* for the GAMs and *hier.part* for the hierarchical partitioning (Mac Nally and Walsh, 2004).

RESULTS

Model selection

For all three species the inspection of GAMs showed a linear relationship between patch occupancy and all predictors, excepting the proportion of cereal crops around the patch and badger presence, which presented a quadratic relationship. Therefore we fitted GLMs and, in the case of badgers, the proportion of cereal crops was fitted as a polynomial with a quadratic term.

For all species the more parsimonious model was the one including simultaneously patch quality and patch context variables (Table 2).

Table 2. Alternative patch occupancy models for Eurasian badger, common genet and Egyptian mongoose. All explanatory variables were modelled as linear terms with the only exception of Crops which was fitted as a quadratic term for badgers. For each model the values of AIC_c, $\Delta_i = AIC_{ci} - AIC_{c\,min}$, and Akaike weights ($\omega_i$) are shown.

Badger	AICc	Δi	ωi
Null model			
0a. Intercept	76.7	33.5	0.000
Patch quality			
1a. Tree, Shrub	64.8	21.6	0.000
1b. Tree , Shrub, Disturbance	64.2	21.0	0.000
Patch quality and distance to forest			
2a. Tree, Shrub, Dforest	59.0	15.8	0.000
2b. Tree, Shrub, Disturbance, Dforest	58.2	15.0	0.000
Patch quality and patch context			
3a. Tree, Shrub, Hedge, Corridor, Crops	43.2	0.0	0.650
3b. Tree, Shrub, Hedge, Corridor, Crops, Dforest	44.4	1.2	0.350

Common genet	AICc	Δi	ωi
Null model			
0a. Intercept	72.2	25.5	0.000
Patch quality			
1a. Stream, Disturbance	56.4	10.1	0.004
1b. Area, Stream, Tree, Shrub	51.4	5.4	0.049
Patch quality and distance to forest			
2a. Stream, Disturbance, Dsource	55.0	26.4	0.008
2b. Area, Stream, Tree, Shrub, Dsource	54.1	24.0	0.013
Patch quality and patch context			
3a. Stream, Disturbance, Dsource, Olive	45.5	0.0	0.925

Egyptian mongoose	AICc	Δi	ωi
Null model			
0a. Intercept	79.0	34.5	0.000
Patch quality			
1a. Tree, Shrub	69.2	25.1	0.000
1b. Area, Tree, Shrub, Stream, Disturbance	52.6	9.7	0.002
Patch quality and distance to forest			
2a. Tree, Shrub, Dsource	69.8	29.3	0.000
2b. Area, Tree, Shrub, Stream, Disturbance, Dsource	44.3	34.2	0.153
Quality and parch context			
3a. Tree, Shrub, Stream, Disturbance, Area, Dsource, Hedge	41.4	0.0	0.639
3b. Tree, Shrub, Stream, Disturbance, Area, Dsource, Hedge, Corridor	43.7	3.2	0.206

In the final model for the badger, tree and shrub cover, the density of shrubby linear elements around the patch, and the presence of structural corridors had a positive effect on patch occupancy (Table 3a). The probability of badger presence in a patch increases with the proportion of cereal crops around the patch until reach a maximum value of 50% (Figure 2a), and decreases with further increase of the proportion of crops.

The probability of occupancy by genets was favoured by the presence of streams within the patch, and by the proportion of olive groves around it. Further, human disturbance had a negative effect on genet occurrence. Unexpectedly, the distance to the nearest source had a positive though relatively weak effect on genet presence (Table 3b, Figure 2b).

Table 3. Selected patch occupancy GLM models for badger, Common genets and Egyptian mongoose. *Crops* variable in the badger model is divided in its simple and quadratic terms. The independent variance explained by each variable was calculated by means of hierarchical partitioning.

Variables	Estimator	Standard error	p	Independent variance (%)
(a) Eurasian badger				
Intercept	-14.429	4.939	0.003	
Tree	0.166	0.064	0.009	21.2
Shrub	0.143	0.059	0.015	11.0
Hedge	0.524	0.213	0.014	11.3
Corridor	2.400	1.138	0.035	17.3
Crops (linear term)	-0.607	5.267	0.908	
Crops (quadratic term)	-24.666	9.219	0.007	39.2
(b) Common genet				
Intercept	-6.244	1.837	0.001	
Stream	4.215	1.451	0.004	54.9
Disturbance	-2.934	1.264	0.020	19.4
Dsource	0.001	0.000	0.036	9.7
Olive	4.215	1.451	0.004	19.9
(c) Egyptian mongoose				
Intercept	-13.090	4.835	0.007	
Area	2.973	1.383	0.031	5.4
Tree	0.099	0.045	0.027	11.7
Shrub	0.138	0.057	0.015	19.1
Stream	3.806	1.531	0.013	23.0
Disturbance	-3.365	1.743	0.053	17.5
Dsource	-0.001	0.000	0.009	9.4
Hedge	0.332	0.181	0.066	13.9

The probability of patch occupancy by mongooses increased with patch area, tree and shrub cover, presence of stream, and the density of shrubby linear elements around the patch. Moreover, human disturbance and the distance to the nearest source had a negative effect on the presence of this species (Table 3c, Figure 2c).

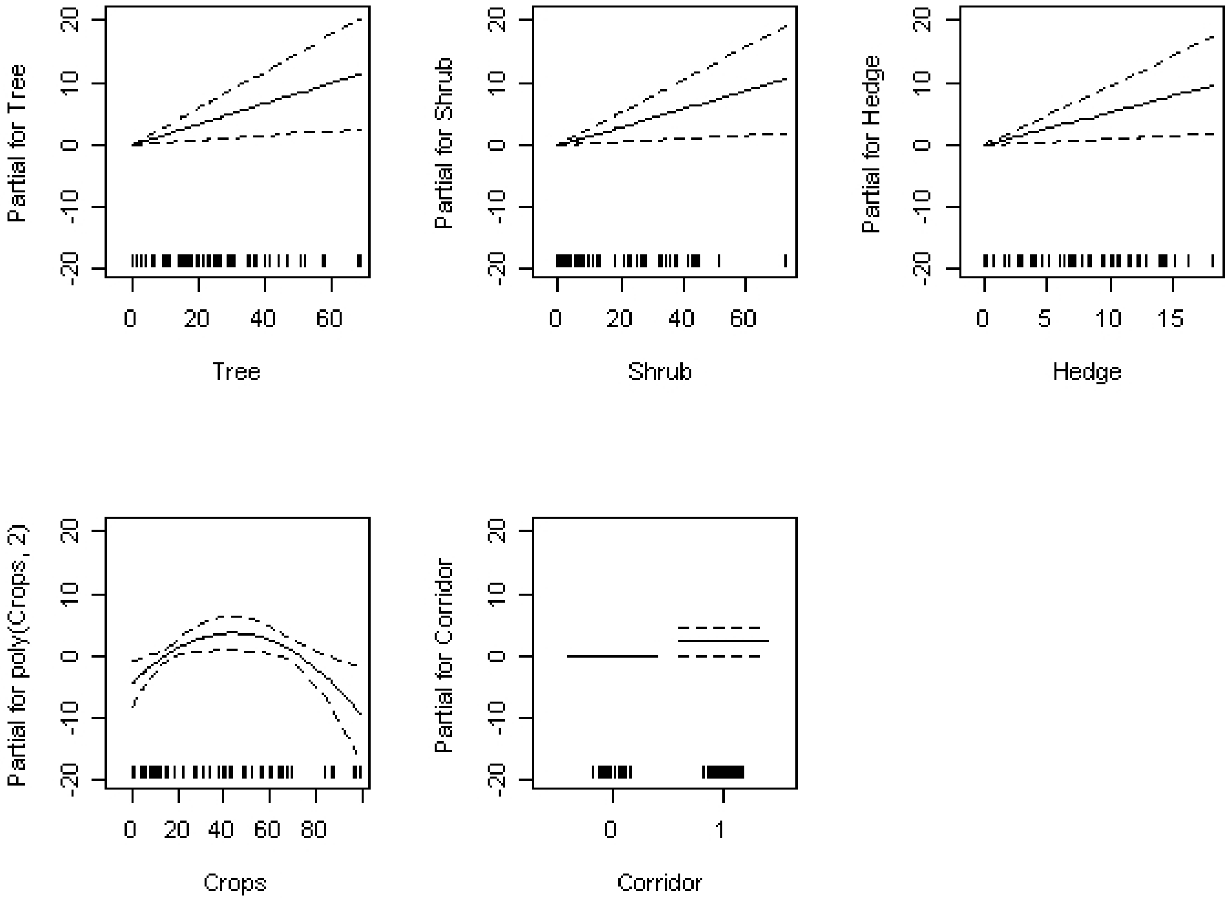
Variance partitioning

The patch occupancy model for badgers explained 61 % of the total variance in the data. The proportion of cereal crops around the patch contributed most to the explainatory power of the model (39% of the independent variance, Table 3). Summing up the independent contributions of each group of variables, patch quality explained the 32.2% of the variance, while patch context explained the remaining 67.8%.

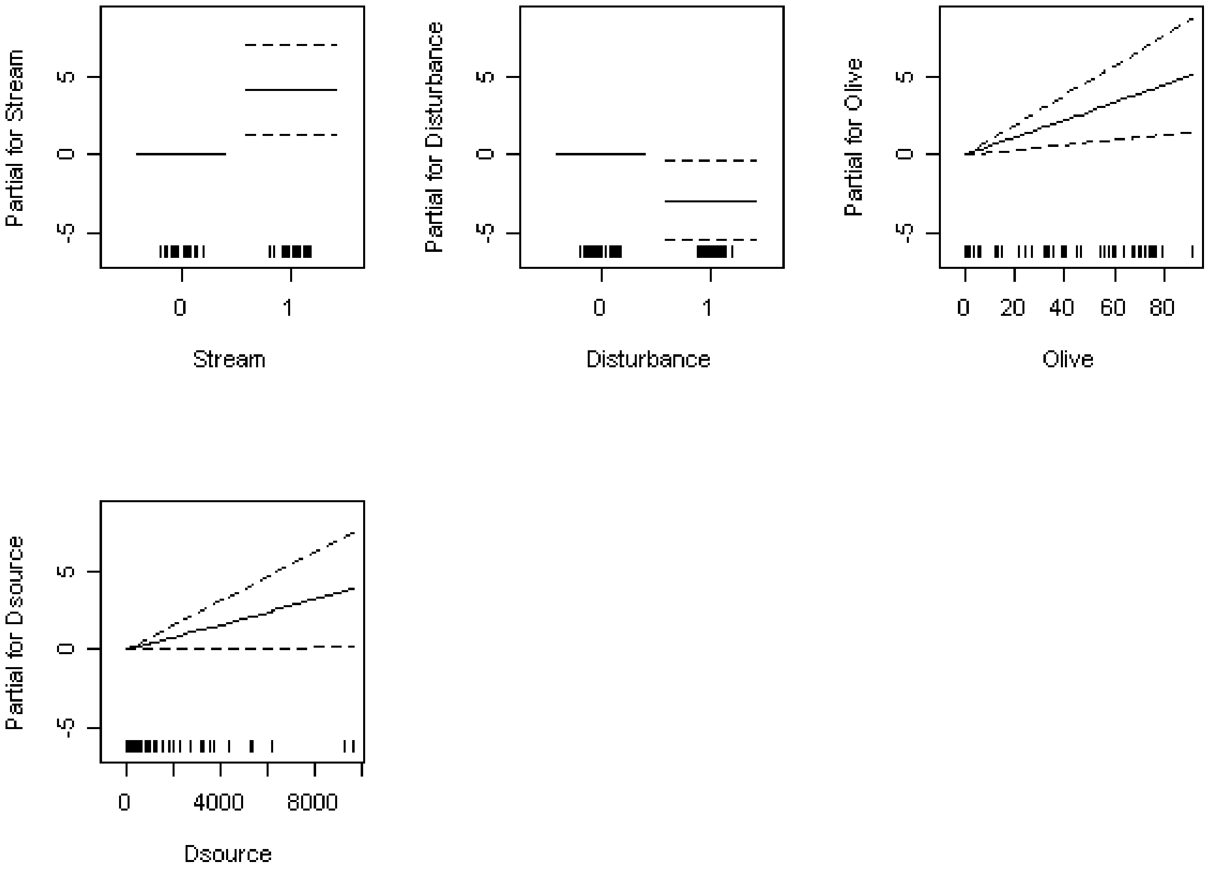
In the case of genets, the occupancy model explained 49% of the total variance. Presence of a stream within the patch explained more than a half of the independent variance (55%, Table 3b). Patch quality variables contributed 74.3% of the explained variance, while patch context variables contributed the remaining 25.7%.

Finally, the patch occupancy model for the mongoose explained 68% of the total variance. The variables with the highest explanatory power were presence of stream and proportion of scrubland within the patch, which explained 23% and 19% of the independent variance, respectively (Table 3c). The sum of independent contributions of patch quality variables amounted 76.7% of the explained variance, while patch context variables contributed the remaining 23.3%.

(a) Eurasian badger



(b) **Common genet**



(c) **Egyptian mongoose**

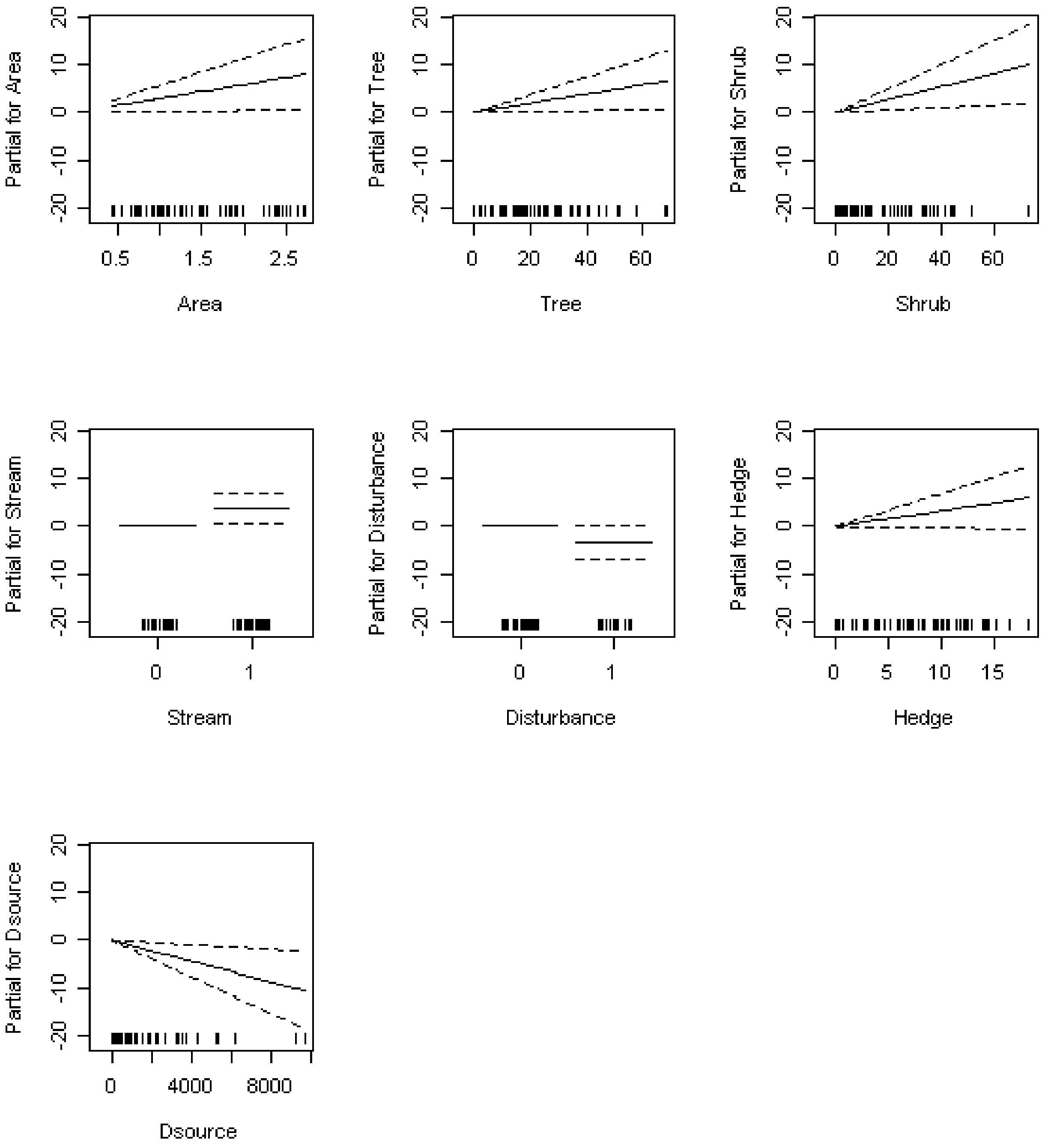


Figure 2. Partial effects of the predictors included in final patch occupancy models for (a) Eurasian badger, (b) common genet, and (c) Egyptian mongoose.

DISCUSSION

Size and quality of patches

As expected, shrub and tree cover within the patch increased the probability of badger presence. Shrubs should be especially important for this species, as the proportion of linear elements around the patch, or the presence of structural corridors connecting it to other forested habitats, seemed to benefit the presence of badgers.

In the case of genet presence, the most important variable expressing habitat quality within the patch, among those retained in the final occupancy model, was the presence of a stream. This variable accounted for more than a half of the explained variance, and might indicate the need of genets for a specific type of dense woody vegetation, rich in trees, dense shrub cover, and trophic resources. In fact, riparian forests and edge habitats often provide a higher diversity and abundance of small prey species compared with forest interior (Fuller et al., 2001;Haddad et al., 2003;Gelling et al., 2007). Anthropogenic disturbance negatively affected patch occupancy by genets. It is somewhat surprising the importance of this effect (19% of the independent explained variance) due to the strictly nocturnal activity of the genet (Palomares and Delibes, 1994), and that this species has been sometimes reported in gardens and fields close to houses (Zuberogoitia et al., 2002). Intense human activities can affect genets during their resting periods, and may also help to explain their selection of fragments containing shelter associated with dense riparian vegetation.

Mongoose is the only species in our system which significantly responded to patch area, according to the final occupancy model. This effect supports the hypothesis that mongooses are more dependent on forest cover than badgers or genets. The predicted upon woody vegetation was further supported by the positive effect of the proportion of shrubs and trees, and the presence of riparian forest and brambles associated to streams. Moreover, the amount of shrubby linear structures around the patch seemed to favour mongoose occurrence in patches, which suggests that well preserved hedgerows with dense vegetation may be important for patch colonization in this species.Human disturbance negatively affects patch occupancy by mongooses, as expected from their diurnal habits and the temporal coincidence with major human activities in agricultural lands. Sensibility to human disturbance might help explain the rather strict mongoose dependence upon dense vegetation as a source of refuge.

Context of patches

We found that herbaceous crops may favour patch occupancy by badgers under a threshold of 50% of the surrounding area, above which the effect reverts. In northern and central Europe, badgers have been reported to benefit from forest clearing by agriculture, showing affinity for heterogeneous habitats with some degree of fragmentation (Kruuk, 1978;Seiler et al., 1995). Fifty percent or less of cereal crops around the patches suggest a mosaic structure similar to that produced by the early stages of forest fragmentation by agricultural expansion. Larger proportions of crops involve a severe depletion of natural woody cover that seems to be detrimental for badger persistence. Badgers apparently do not find too much resistance in their displacements through cereal crops when these make part of heterogeneous mosaics, as crops are frequently used if adjacent to more favourable habitat (Delahay et al., 2007). However, broad areas covered with cereal crops could represent a barrier to badger movements. Although some studies have concluded that the probability of badger presence decreases with increasing distance to suitable habitat patches (Virgós and Casanovas, 1999;Virgós, 2001;Virgós, 2002), no variable representing the distance to the nearest patch or source was retained in our model. The relevance of this result increases taking into account that the proportion of forest in our study area is only 5%.

The proportion of olive groves around a patch benefited the presence of genets in patches, which is consistent with the prediction about the suitability of olive trees as a source of prey that can be exploited by genets thanks to their scansorial habits, and as a source of cavities that can be used as a refuge. Nevertheless, incidence data cannot tell whether genets are able to use this habitat type for foraging and resting, or only as a suitable connection between patches. The distance to the nearest source had a significant but weaker positive effect on patch occupancy by genet. This counterintuitive positive effect of distance to the nearest source could indirectly reflect the spatial configuration of landscape elements in the study area: streams and olive groves, which have a positive influence on genet presence, concentrate in the middle of the agro-ecosystem and relatively far away from Sierra Morena or Doñana Natural Park (Figure 1). Anyway, our results suggest that genets do not seem to find serious problems to colonise suitable patches in current mosaic configuration of this agricultural landscape.

The probability of patch occupancy by mongooses decreased with increasing distance to the nearest source, indicating a low permeability of the agricultural matrix for this

species. Density of hedges had been retained in the final model, although with a not-significant positive trend. No other patch context variable was retained by the model, suggesting that habitat quality, rather than the surrounding matrix, may be the deciding factor for the presence of mongooses. This also agrees with our initial expectations that habitat specialist would be more affected by habitat fragmentation, as they only use matrix habitats for the displacement among different forested patches, but not for the exploitation of resources. Therefore, patches occupancy by mongooses should be determined by its internal quality and the possibility of colonization from the nearest sources.

Relative importance of Quality vs. Context

Our results support the view that the way animals use landscapes is the product of the interaction between landscape structure and the requirements and perception of each species (Tischendorf and Fahrig, 2000;D'eon et al., 2002;Taylor et al., 2006;Watling and Donnelly, 2006). More than a binary concept of suitable versus hostile habitat, some agricultural landscapes can be seen as a mosaic of habitats with different degree of permeability, which differs for each species.

All three species in our study system showed a positive response to woody cover within patches in the form of shrubs, trees, or the dense structure of riparian vegetation associated with streams. The Egyptian mongoose, however, was the only specie sensitive to patch area, suggesting that it is the species with highest requirements of shrub cover.

The incidence of badgers and mongooses was also benefited from the proportion of shrubby linear elements around the patch. Although badgers can use cereal crops (Skinner and Skinner, 1988;Kruuk, 1989), and olive groves as food sources (Kruuk and de Kock, 1981), the presence of shrubby refuges (like hedgerows and verges) in the surroundings of patches may not be essential for their colonisation but may promote their regular use by resident individuals. Genets can use hollow trees as bedding sites or breeding dens (Palomares and Delibes, 1994), so they may be less constrained by cavities in old trees present in patches, provided that these refuges are abundant in surrounding olive groves.

Corridors can be defined as linear structures embedded in the matrix connecting two or more habitat fragments (Beier and Noss, 1998), but this definition excludes linear habitats that do not physically connect patches but, however, can offer valuable resources as to maintain resident individuals (CHAPTER 3) or to act as stepping stones guiding and favouring the diffusion of carnivores through the agricultural mosaic. Hedgerows in agricultural lands can support relatively rich communities of small mammals and birds, thus providing potential prey for the three carnivores we consider here. Moreover, prey density in hedgerows may be higher than in the core of patches or in open fields (Rodenhouse et al., 1992;Gelling et al., 2007). Hedgerows allow foraging close to a refuge (Macdonald, 1995), and can act as important communication and hunting routes as well (Whittingham et al., 2005;Macdonald et al., 2007).

The amount of independent variance explained by patch context compared with patch quality for badger occupancy (68% of the explained variance) was higher than for the incidence of genets (26%) and mongooses (23%). This supports our initial hypothesis that the species less tolerant to fields and with lower colonization ability (the Egyptian mongoose) would be more dependent on patch area and patch quality.

If resource supply in patches were insufficient for the establishment of carnivore home ranges, then individuals may use additional patches to fulfil their resource requirements, a process called supplementation by (Dunning et al., 1992). If so, individuals should use the matrix frequently (as genets in olive groves), or even should use it for foraging, as could be the case of badgers during the short growing season of cereals. The apparent use of patch surroundings by animals implies that agricultural matrix may not always be as inhospitalable as previously considered (MacArthur and Wilson, 1967;Wu and Vankat, 1991;Martin and Heske, 2005). Patch occupancy by carnivores with moderate tolerance to agricultural fields, such as badger and genet, may use the incorrectly called "matrix" frequently and, consequently, its presence would be influenced by the attributes of those agricultural habitats; whereas less tolerant species presence, such as the Egyptian mongoose, would be almost exclusively dependent upon the area and quality of patches. A suitable spatial configuration (not far away from each other) and well connected with linear structures such as hedgerows will favour the functional connectivity of landscape for all three species.

ACKNOWLEDGEMENTS

This research was funded by the Consejería de Innovación, Ciencia y Empresa (grant P06-RNM-1903), and Consejería de Medio Ambiente, Junta de Andalucía, as well as by CSIC (grant 200830I195). MP was supported by Ministerio de Educación, Cultura y Deporte

through a FPU fellowship (AP2003-2370). Linda Swankie, Juan C. Rivilla and Sonia Alís helped with the field work. I thank the helpful advices of Javier Seoane about the statistical approach.

CAPÍTULO 2

Ecología espacial y comportamiento de la gineta y el meloncillo en un paisaje agrícola Mediterráneo

Spatial ecology and behaviour of the common genet and the Egyptian mongoose in an agricultural Mediterranean landscape

RESUMEN

La preservación de las especies forestales en paisajes agrícolas se está convirtiendo en un objetivo crucial para el mantenimiento de la biodiversidad. Los mamíferos carnívoros deben ser especialmente sensibles a la transformación de los hábitats dados sus grandes requerimientos de superficies forestales. Hemos estudiado algunos atributos de la biología, ecología espacial y comportamiento de un grupo de carnívoros de mediano tamaño, ginetas y meloncillos, habitando un paisaje agrícola altamente transformado. Hemos testado la hipótesis de que los carnívoros forestales que vivan en paisajes agrícolas reflejarán su estrés energético en su estado físico y atributos de su comportamiento. Esperamos que estos índices sean más desfavorables que en el caso de poblaciones de paisajes forestados más continuos, y predecimos mayores áreas de campeo para los individuos del agrosistema comparadas con la de individuos en paisajes menos fragmentados.

Nuestra hipótesis inicial de que los individuos del agrosistema estarían incurriendo en mayores costes dadas la dispersión o escasez de recursos no se pudo mantener con las diferencias en tamaño corporal, ni condición física o reproductiva de los individuos muestreados. De la misma forma, estos individuos no necesitaron dedicar mayores periodos de actividad en el paisaje fragmentado para abastecerse de los recursos necesarios. Contrariamente a lo esperado, las áreas de campeo de las ginetas y meloncillos en el paisaje agrícola fueron significativamente menores que en el caso de individuos del Parque Nacional de Doñana. Esto sugiere que tanto ginetas como meloncillos pueden obtener suficientes recursos en un paisaje agrícola con mínima cobertura forestal, y enfatiza la importancia de la conservación de estos remanentes para la conservación e las poblaciones de estas dos especies en los sistemas agrícolas mediterráneos.

ABSTRACT

Preservation of forest species in agricultural landscapes is becoming crucial for the maintenance of biodiversity. Mammalian carnivores may be especially sensitive to habitat transformation because their requirements of large forest areas. We studied some attributes of the biology, spatial ecology and behaviour of a group of medium-size carnivores, the common genet and the Egyptian mongoose, living in a highly transformed agricultural landscape. We tested the hypothesis that forest carnivores living in an agricultural landscape would reflect their energetic stress in indices of fitness and attributes of behaviour that should be lower than those of populations living in more continuous forest landscapes, and predicted larger home ranges for individuals living in the agroecosystem compared to those in less fragmented landscapes.

Our initial hypothesis that individuals living in the agoecosystem incur in higher cost due to the dispersion or scarcity of resources was not supported by differences in body size, body condition or reproduction. Likewise individuals did not need to devote longer activity periods to achieve the necessary resources in the fragmented landscape. Contrary with our expectations, home ranges of genets and mongooses in the agricultural landscape were significantly smaller than those in Doñana National Park. This suggests that genets and mongooses can obtain enough resources in an agricultural landscape with very little forest left, and highlight the importance of conserving these remnants for the maintenance of populations of these two species in Mediterranean agricultural lands.

INTRODUCTION

Human land uses in general, and agriculture in particular, alters landscape pattern through the processes of habitat loss and habitat fragmentation (Lindenmayer and Fischer, 2006). Vegetation clearance for agriculture reduces forest area and patch size, increases the number of patches, edge lengths, and the distance between patches (Fahrig, 2003). As a result, agricultural landscapes are frequently unfavourable to forest species, and usually cause declines in population size and species diversity (Wilcox and Murphy, 1985;Andrén, 1994;Attwood et al., 2009;Ludwig et al., 2009).

Agricultural lands have become one of the largest terrestrial biomes occupying around 40% of the land surface (Foley et al., 2005). Therefore, preservation of forest species in agricultural landscapes is becoming crucial for the maintenance of biodiversity. Mammalian carnivores may be especially sensitive to habitat transformation because they require large forest areas (Noss et al., 1996;Carroll et al., 2001;Constible et al., 2006;Frey and Conover, 2006;Huck et al., 2010). Additionally, predators can indirectly promote biodiversity at local and regional scales through the diversification of prey species and the control of meso-predators (Kareiva, 1987;Crooks and Soule, 1999;Miller et al., 2001;Soule et al., 2005;Letnic et al., 2009;Wallach et al., 2009). Forest species tend to disappear in landscapes with less than 20% forest left (Andrén, 1994;MacDonald and Kirkpatrick, 2003;Swift and Hannon, 2010). It is assumed that this results from a gradual process (Lomolino and Perault, 2004), probably non-linear (Radford et al., 2005), preceded by ecological processes that occur at the individual level. For example, living in a highly fragmented landscape prompts behavioural changes that entail higher energetic costs to compensate the lower availability and higher dispersion of resources (Rosenzweig, 1981;Russell et al., 2003). The increment in the energetic cost of foraging could decrease both body condition and body size (Hewison et al., 2009), as well as lower fecundity and survival rates (Lambrechts et al., 2004) which finally can translate at the population level into lower growth rates. On the other hand, behavioural flexibility would allow some organisms to survive in suboptimal landscapes (Henein et al., 1998).

Our main objective is to study some attributes of the biology, spatial ecology and behaviour of a group of medium-size carnivores, the badger (*Meles meles*), the common genet (*Genetta genetta*) and the Egyptian mongoose (*Herpestes ichneumon*), living in an highly transformed agricultural landscape, and to compare these attributes with reference values obtained in a neighbouring forest landscape.

We hypothesise that forest carnivores living in an agricultural landscape reflect their energetic stress in indices of fitness and attributes of behaviour that should be lower than those of populations living in more continuous forest landscapes. In the agricultural landscape we predict that a) adults will weigh less and will exhibit lower body condition, b) a lower frequency of reproduction sign during the breeding season, c) that the circadian period of activity will be longer, d) that home ranges will be larger and their shape will be constrained by the spatial configuration of forest remnants, e) a larger proportion of resting places in suboptimal habitat, and f) a higher frequency of agonistic encounters with conspecifics and heterospecifics due to increased competition for scarce resources.

METHODS

Species

The Egyptian mongoose (*Herpestes ichneumon*) and the common genet (*Genetta genetta*) are two carnivores of medium size which share an Ethiopic origin (Delibes, 1982), while badger present a wide distribution in the Palaeartic region (Revilla and Palomares, 2002b). The Egyptian mongoose, the only mongoose living in Europe, is restricted to the south-west of the Iberian Peninsula (Delibes, 1982) but it is also present in most of Africa and the Middle East (Corbet, 1984), while the common genet occurs in south-western Europe and northern Africa (Dobson, 1998). The Eurasian badger Meles meles occurs in Europe, northern Asia and the Middel East. The Egyptian mongoose and the common genet are considered trophic generalists and feed mostly on vertebrates of small and medium size (Delibes, 1974;Palomares and Delibes, 1991a;Virgós et al., 1999). The Eurasian badger feed on small vertebrates too, but its diet is wider including fruits and cereals found in agricultural landscapes (Kruuk and Parish, 1985;Wilson, 1993;Roper and Lups, 1995;Balestrieri et al., 2004;Rosalino et al., 2005). In the Mediterranean region, the three species have shown to be dependent on woody cover, especially scrubland (Palomares and Delibes, 1990;Palomares and Delibes, 1994;Virgós and Casanovas, 1997;Revilla et al., 2000).

Study area

We conducted our study in a 800 km2 agroecosystem of the Guadiamar river, SW Spain (37º23’ N, 6º13’ W; Figure 1). The climate is Mediterranean subhumid, with mild, wet winters and hot, dry summers. Farmland covers 94.6% of the landscape, whereas remnants of forest, scrubland, and pine or eucalyptus plantations sum up to a mere 2.4%. Three main types of farmland can be distinguished: herbaceous crops (mainly cereals) predominate, followed in extent by olive groves and dehesa, an agroforestry system that combines pastures or cereal with scattered oak trees and little or no understorey (Joffre et al., 1988). Forest, often with a layer of shrubs, appears as small woodlots, riparian forest and hedgerows. The landscape contains six towns and seven smaller housing aggregations with a total of 31000 people.

Farmland types are not homogeneously distributed across the landscape. Cereal crops abound in the northern half, where very little forest remains, while in the south olive groves dominate the mosaic and the proportion of forest is above the average (Figure 1). Preliminary mammal surveys detected mongooses and genets regularly in the south, but rarely in the north (Rodríguez and Delibes 2003). Therefore, we defined our study area as a square landscape sample of 79.2 km2 in the southern half (Figure 1). This area contains 7.7% of forest, 3.0% in the form of woodlots and 4.7% of scrubland, most of it associated to two streams that run from northwest to southeast. Most fields, groves and dehesas are bounded by thin woody hedgerows.

Trapping and radiotracking

We recorded the presence or absence of mongoose, genet and badger in 55 forested patches of the Guadiamar agro-ecosystem during two consecutive years (CHAPTER 1). Among all fragments, two groups of adjacent patches with high occupancy probability for the three species were selected, and checked again before the trapping period. In the last survey, selected patches were prospected by foot and the number and location of signals were recorded. We decided to trap in the pool of patches in which the frequency of signals of the three species was highest. Bait stations, 1 m diameter circles of smoothed sand (Figure 2), were set in subjectively suitable places and baited with sardines, chicken pieces or fruits (apple and peanuts) in order to record visits of the three species which were identified by their footprints. The purpose of pre-baiting was to choose the best potential locations of traps and to determine the relative attraction of the three species to different baits, in order to maximize the success of the trapping sessions. Twenty three bait stations were set in five forested patches and were checked daily during 10 consecutive days. After an overall effort of 350 station-nights mongooses visited bait stations more often than genets and badgers (21, 8 and 6 times, respectively). Mongooses and genets only visited stations baited with sardines or chicken, while badgers were not recorded in stations baited with chicken (Table 1).

Taking into account to the placement of the bait stations most frequently visited, boxtraps (2.0 x 0.5 x 0.5 m) were placed adjacent to watercourses or hedgerows, and baited with sardines, chicken, or fruit. These baits were used during a single continuous trapping session of 41 days, with a total trapping effort of 820 trap-nights. During this session we only caught a female mongoose in a trap baited with chicken. Given these preliminary results thereafter we decided to employ live domestic pigeons as bait in subsequent trapping sessions to test whether trapping success was higher.

Figure 1. Study area in the Guadiamar river basin (SW Spain).

Table 1. Visiting rates of carnivores (100*nº visits/ total nights) to bait stations. A) Visits have been grouped for stations located in the same zone (identified by a letter) within a patch (denoted by an identification number) that were baited with the same bait. Total survey effort (bait station-nights) is summarized for each bait type, and the average visiting rate (%) is shown for each species. B) Total visits have been grouped for the entire study area by bait type.

A) Patch Id	*Bait*	*Bait stations-nights (n)*	*Badger*	*Genet*	*Mongoose*
60-a	Chicken	10	0	20	0
60-a	Fruit	20	0	0	0
60-a	Sardines	40	0	5	10
60-b	Chicken	10	0	0	0
60-b	Fruit	20	10	0	0
60-b	Sardines	10	0	0	0
62-a	Chicken	10	0	0	20
62-a	Sardines	20	0	0	35
64-a	Chicken	10	0	0	0
64-a	Fruit	10	0	0	0
64-a	Sardines	20	0	10	5
64-b	Chicken	10	0	10	0
64-b	Sardines	20	5	0	0
64-c	Chicken	20	0	0	0
64-c	Fruit	10	0	0	0
64-c	Sardines	30	6	3	10
81-a	Chicken	10	0	0	0
81-a	Fruit	10	0	0	0
94-a	Chicken	20	0	0	35
94-a	Sardines	20	0	0	0
81-a	Sardines	20	5	0	0

B) TOTAL	*Bait*	*Bait stations-nights (n)*	*Badger*	*Genet*	*Mongoose*
	Chicken	100	0.00	3.00	9.00
	Fruit	70	2.86	0.00	0.00
	Sardines	180	2.22	2.78	6.67

Animals were captured from June 2005 to March 2007 during seven trapping sessions. Traps were checked daily and pigeons were supplied with water, food and shade all the time. The duration of each session varied depending on its success. We immobilized carnivores with tiletamine-zolazepam (Zoletil, Virbac, Spain). We recorded sex and body weight, and estimated age according to tooth wear. We measured head and –body length, tail length, hinder foot length, and shoulder height. A simple index of body condition was calculated as the ratio between body weight and head and body length. In females we assessed pregnancy and the number of fetuses through abdomen palpation. We only tagged adults which were equipped with transponders and VHF radio-collars containing activity sensors (Biotrack, Wareham, UK).

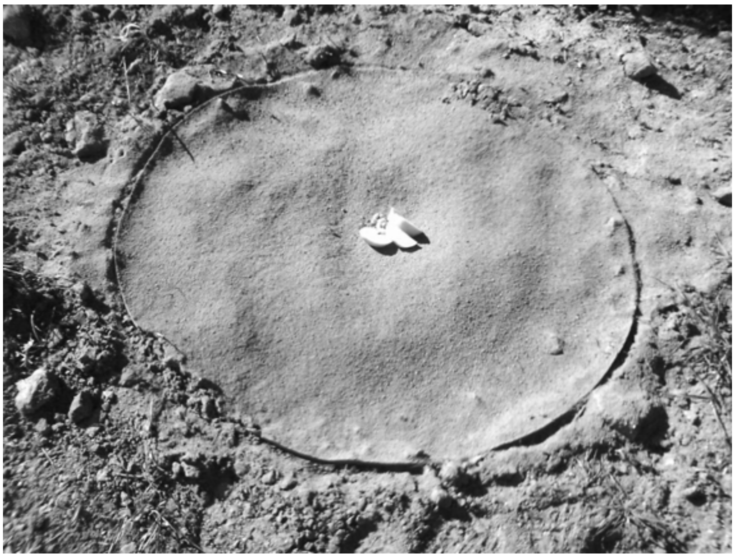


Figure 2. Station baited with apple and peanuts

We collected animal positions following two different schedules: a) one daily location at random times assumed to produce a set of independent locations used to estimate the size and shape of home ranges, and b) continuous radio-tracking sessions of variable duration. The continuous sessions took place mostly during the activity period of each species. Animals were followed by foot and at a short distance but without disturbing them (the homing technique, (Mech, 1983), to minimize the error associated to triangulation and to determine the microhabitat at each location. New fixes were taken every time the animal switched from active to inactive, or viceversa. To standardize the number of locations per unit time, and to make the structure of our data comparable with published information in the area of reference, we recalculated the position of the animals at fixed intervals of 15 minutes. The binomial activity value (either active or inactive) of the previous fix taken in the field was assigned to each of these estimated positions.

From continuous tracking sessions and occasional observations we recorded the behaviour of marked individuals in every encounter with conspecifics or heterospecifics. We also recorded the position and attributes of resting sites outside patches of dense cover.

Table 2. Duration, number of boxtraps used, and number of genets and mongooses caught per trapping session. The ratio female:male (f:m) is shown into brackets.

Session	Starting date	Duration (days)	Traps	Bait	Genets (f:m)	Mongooses (f:m)
1	10/05/2005	41	20	Chicken, fruit, sardines	0	1 (1:0)
2	21/06/2005	4	20	Pigeons	2 (1:1)	3 (2:1)
3	20/09/2005	3	10	Pigeons	2 (1:1)	2 (2:0)
4	13/03/2006	3	10	Pigeons	2 (2:0)	4 (2:2)
5	13/11/2006	3	10	Pigeons	2 (0:2)	2 (2:0)
6	13/12/2006	6	10	Pigeons	6 (3:3)	3 (2:1)
7	07/02/2007	3	6	Pigeons	3 (1:2)	2 (1:1)
total		63	86		17 (8:9)	17 (12: 5)

Data analysis

Activity

Daily activity patterns were described by tabulating the percentage of active locations at each hourly interval, using independent daily fixes and standardized data from periods of intensive tracking.

Home ranges

In landscapes with neat borders between habitat types, like the streams and hedgerows of our study area, convex-hulls methods have demonstrated to estimate the extent and limits of home ranges better than other techniques because they reduce the amount of non-used areas (Getz and Wilmers, 2004). Therefore, home ranges were estimated as Nearest Neighbour Convex Hulls (NNCH-5) using independent locations from daily fixes and one random location per day sampled from periods of intensive tracking. Minimum Convex

Polygons (MPCs) were also estimated for comparative purposes with published data. MCPs and NNCHs were calculated with the ArcView extensions Animal Movement (Hooge et al., 1999) and LoCoh (Getz and Wilmers, 2004), respectively.

We calculated an index of home range shape as the ratio between the perimeter of the home range and the minimum perimeter of a circle with the same area (Patton, 1975;Forman and Godron, 1986).

The overlap between the home ranges of two individuals was calculated using the Cole's index of concordance (Cole, 1949), defined as:

$$C = 100 \cdot 2 \cdot A12 / (A1 + A2),$$

where A12 is the area of overlap, and A1 and A2 are the areas of home ranges. We calculated overlap only for home ranges of individuals tracked during the same temporal window.

When possible, data have been compared to published data of mongooses and genets populations within the Doñana National Park, which lies 10 km apart of the study area.

RESULTS

We captured 34 different carnivores on 44 occasions during seven trapping sessions. On average each trapping session lasted 3.7 days and the total trapping effort was 1166 trap-nights (Table 2). We caught 17 genets and 17 mongooses, but no badger. Five genets and three mongooses were recaptured once and one genet was recaptured twice.

Nine adult genets (1M: 1.25F) and 13 adult mongooses (1M: 2.25F) were tagged with radio-collars. The collar fitted to two genets (male M3 and female F4; table 2) and those fitted to two mongooses (male M1 and female F1) failed during the firsts days of tracking. A few days after marking one female genet (F2) was found dead due to unknown causes and one female mongoose (F7) drowned in a stream as a result of a heavy rainfall. Excluding these cases, we recorded enough positions from six genets (1M: 1H) and 10 mongooses (1M: 2.3H) with a total amount of intensive tracking of 16,215 and 26,205 minutes, respectively (Table 3).

Table 3. Tracking effort, expressed as the number (n) of independent locations and the number (N) and duration (T) of continuous tracking sessions, and estimates of home range size using the Minimum Convex Polygon (MCP) and convex-hulls for (a) genets and (b) mongooses in the Guadiamar study area. The independent locations number (one per day) and the total and mean time (T) dedicated to intensive tracking are shown. Home ranges are estimated as for each individual.

a)	*Independent locations*			*Intensive tracking*		
	n	MCP (ha)	Convex-hull (ha)	N	T total (min)	T mean (min)
F1	25	843.0	327.4	10	1710	171
F2	1	-	-	0	-	-
F3	34	46.4	24.8	20	3735	187
F4	3	-	-	0	-	-
F5	33	114.0	62.2	18	3030	168
M1	14	192.0	176.8	4	765	191
M2	61	44.4	5.8	21	3180	151
M3	3	-	-	0	-	-
M4	44	226.0	107.7	22	3795	173
Total				95	16215	171

b)	*Independent locations*			*Intensive tracking*		
	n	MCP (ha)	Convex-hull (ha)	N	T total (min)	T mean (min)
F1	8	-	-	0	-	-
F2	15	51.1	34.1	5	720	144
F3	39	296.0	39.5	31	5325	172
F4	54	194.2	42.7	34	6735	198
F5	25	74.3	27.6	20	3570	193
F6	31	45.8	31.5	21	3870	184
F7	3	-	-	0	-	-
F8	14	12.9	6.2	7	1230	176
F9	29	84.1	44.1	18	2925	163
M1	8	-		1	240	240
M2	10	-	-	0	-	-
M3	5	-	-	2	300	150
M4	9	-		8	1290	161
Total				131	26205	200

Biometry

The mean body mass of adult genets was 2.11 kg for males (SD=0.10, range= 1.95-2.20, n=5) and 1.84 kg for females (SD=0.28, range= 1.45-2.20, n=6). The mean weight of adult mongooses was 3.11 kg for males (SD=0.24, range= 2.90-3.50, n=5) and 2.97 kg for females

(SD=0.56, range=2.25-3.75, n=8). No sexual differences were found either in body measurements or the index of body condition for genets or mongooses. The only exception was a trend for male genets to have on average a larger shoulder height than females (Table 4a).

The mean weight of adult genets in Doñana National Park was 1.90 kg for males (SD=0.82, range= 1.90-2.00, n=4) and 1.87 kg for females (SD=0.13, range= 1.78-1.96, n=2; (Palomares and Delibes, 1994). The mean weight of adult mongooses in Doñana was 3.14 kg for males (SD=0.38, n=8) and 2.82 kg for females (SD=0.18, n=11; (Palomares and Delibes, 1992b). We did not find significant differences in the mean body weight between Guadiamar and Doñana populations, either for genets (males: t= 0.879, df= 7, p=0.408; females: t= 0.141, df= 6, p= 0.893) or mongooses (males: t= 0.157, df= 11, p=0.878; females: t= 0.838, df= 17, p= 0.413).

Table 4. Body measurments for adult (a) common genets and (b) Egyptian mongooses in the Guadiamar agricultural landscape.

a)	Males		Females			
	Mean (n=5)	SD	Mean (n=6)	SD	t	p
Body mass (g)	2110	102.5	1841.7	278.2	2.03	0.073
Head-body (mm)	516	15.2	496.7	22.5	1.63	0.138
Tail- base (mm)	424	37.8	400.8	94.8	0.51	0.622
Hinder foot (mm)	95	14.2	93.8	21.7	0.103	0.92
Shoulder height (mm)	222	17.6	197.7	9.1	2.968	**0.016**
Index of body condition	4.1	0.1	3.7	0.6	1.421	0.189

b)	Males		Females			
	Mean (n=5)	SD	Mean (n=8)	SD	t	p
Body mass (g)	3110	238.2	2975	562.5	0.503	0.625
Head-body (mm)	545	15.8	524.8	19.8	1.925	0.080
Tail- base (mm)	439	30.3	410.3	47.6	1.196	0.257
Hinder foot (mm)	94.6	3	95.1	12.8	-0.089	0.931
Shoulder height (mm)	216.4	18.2	216	15	0.043	0.966
Index of body condition	5.7	0.3	5.7	1	0.076	0.941

Activity

Genets were mostly nocturnal, starting their activity period on average two hours before sunset, ending it on average one hour before sunrise, and showing a peak of activity between 2100 and 0300 h GMT (Figure 3). Mongooses were mostly diurnal, starting its activity period on average just after sunrise, but ending it up to three hours after sunset (Figure 3). We observed two peaks of activity in mongooses, between 0700 and 1200 and between 1400 and 1600, with a 65%-90% decrease in activity between 1200 and 1400 (Figure 3). These activity patterns do not differ from those described for genets (Palomares and Delibes, 1994) and mongooses (Palomares and Delibes, 1992a) in Doñana.

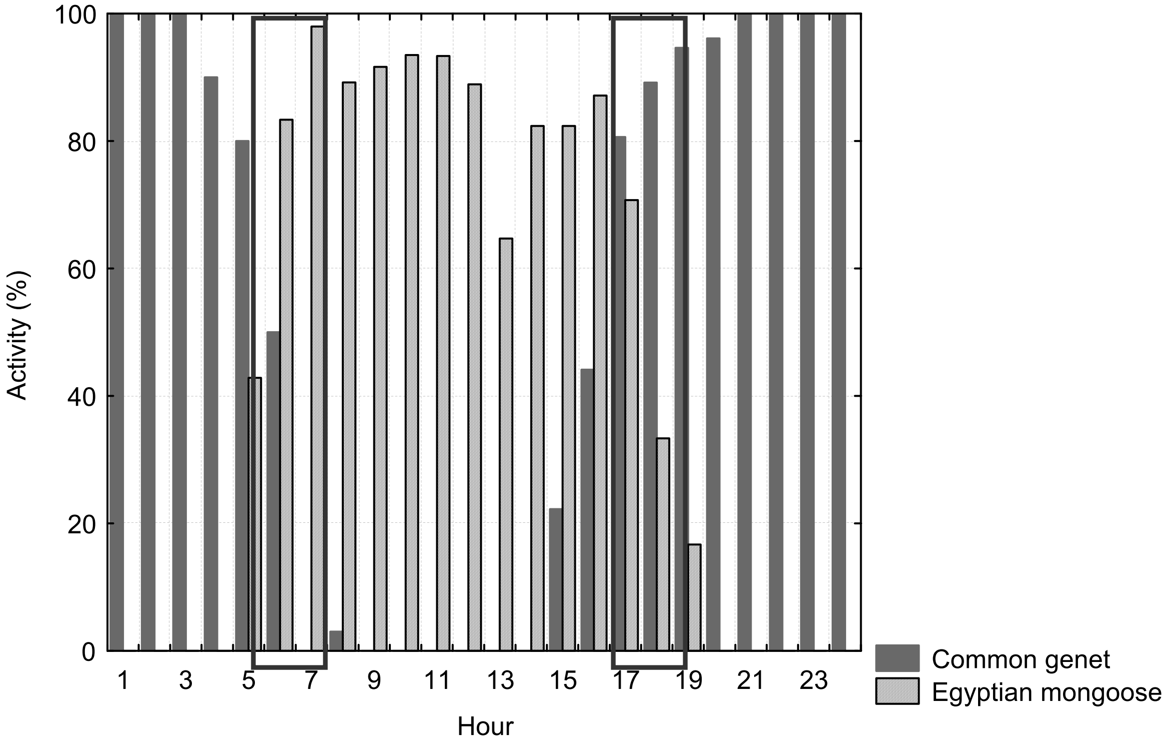


Figure 3. Circadian distribution of activity in adult common genets and Egyptian mongooses of in the Guadiamar basin (SW Spain). The sunrise and sunset time (GMT) is indicated by empty rectangles.

Home ranges

The mean size of home ranges, estimated as NNCH, was 117.4 ha (range= 6 -327 ha) for genets. We did not find significant sexual differences in home range size (Mann-Whitney U test, n=6, Z=-0.245, p=0.806; Table 3). The mean size of convex hulls for the seven mongooses was 32.3 ha (range= 6-44 ha).

Contrary to our expectations, the mean size of genet home ranges in the Guadiamar population (male: mean= 1.54 km2, SD= 0.96, n= 3; female: mean= 3.34 km2, SD= 4.41, n= 3) was smaller than in the Doñana population (male: mean= 6.18 km2, SD= 3.86, n= 3; female: mean= 5.79 km2, SD= 1.01, n= 4; (Palomares and Delibes, 1994). However we did not find significant differences either for males (t= 2.02, df= 4, p=0.113) or females (t= 1.11, df= 5, p= 0.318), probably due to the large variance in the data.

Likewise home ranges of female mongooses living in the Guadiamar basin (MCP mean=1.08 km2, SD=1.00) were significantly smaller (t= 5.12, df=16, p<0.001) than those of female mongooses living in Doñana (MCP mean=3.09 km2, SD=2.43, n=11; (Palomares, 1994a).

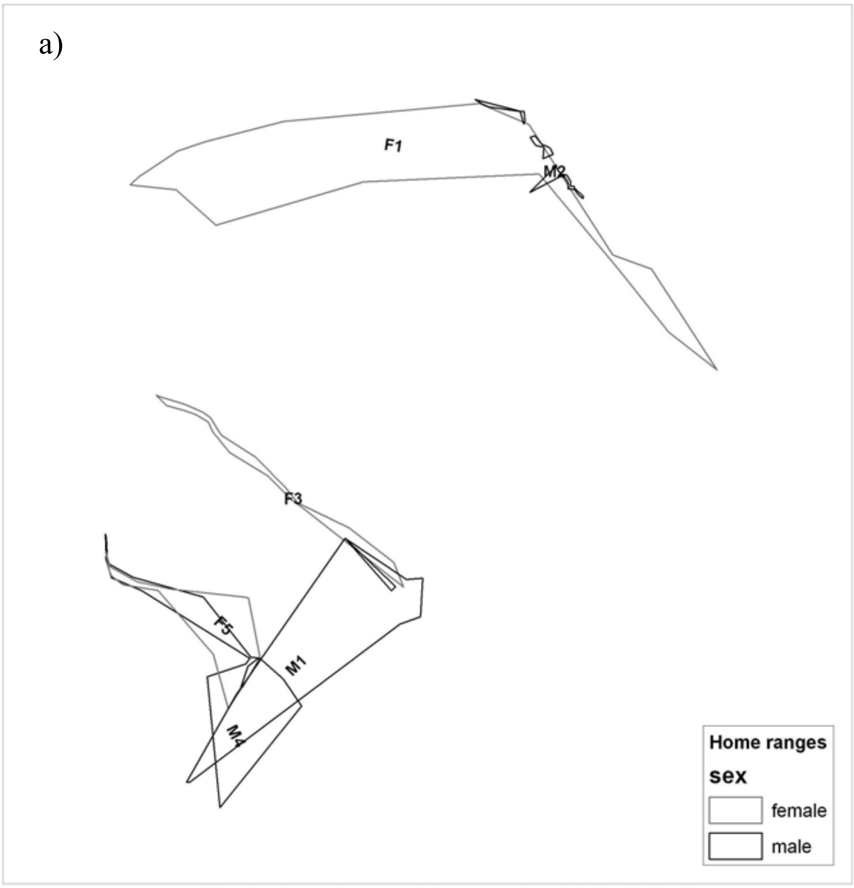
The shape of NNCH home ranges tended to be elongated for most individuals of both species (Figure 4). The mean shape index was 2.7 (range=1.8-4.3) for genets and 2.6 for mongooses (range= 1.8- 3.8), being 1 for a circular home range.

The overlap between home ranges was in general small for the two species (Figure 4). Only two pairs of genets coexisted in space and time: M4 and F5, which usually encountered each other, shared 35.7% of their home ranges; the home ranges of M1 and F3 overlapped only 3.4%. In the case of mongooses, only two females, F3 and F4, shared 1.1% of their home ranges. Females F5, F6 and F8 were tracked simultaneously in the riparian forest associated to a stream and their home ranges did not overlap.

Resting places

Mongooses utilized thickets and dense scrubland as resting places, both during the night and diurnal siestas. The use of burrows under dense cover was detected through an abrupt change in the reception of the radio-signal during continuous tracking. Exceptionally, used burrows were placed in open areas but not far from dense cover. Female F4 utilized a huge rabbit warren in open dehesa 25 m apart from the scrubland during 7.3% of tracking days. Female F2 used a burrow dug in a ditch adjacent to a small road that was 400 m away from the scrubland during 6.2% of tracking days.

While resting, genets were often located in dense vegetation, either in patches or hedgerows. However three individuals were detected resting during the day in trees far away from scrubland. Male M2 rested once in 60 days (1.6%) on an oak in dehesa, 228 m from the nearest scrubland patch. M4 and F5 rested in an olive tree 582 m away from cover 9.0 and 8.8% of their tracking days, respectively.



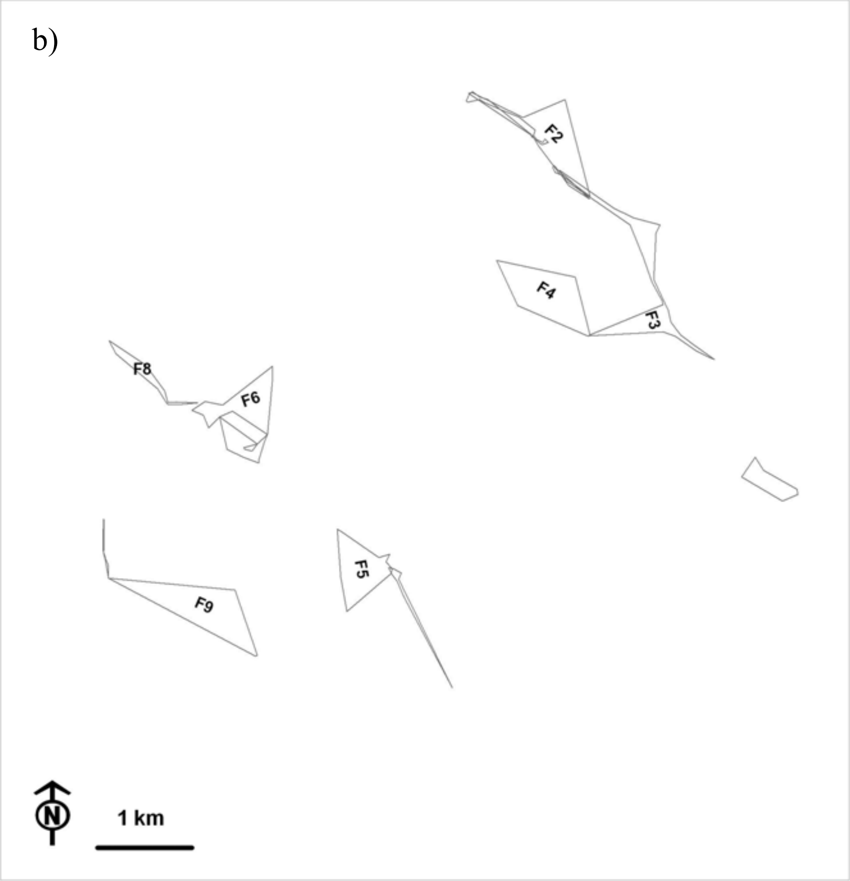


Figure 4. Home ranges, calculated as convex-hulls, of adult common genets (a) and Egyptian mongooses (b) in the Guadiamar basin (SW Spain).

Reproduction

All female mongooses captured between March and May were pregnant: F1 and F5 carried three fetuses each and F6 had two fetuses. One of two female genets captured between March and May (F4) was pregnant of three fetuses. While tracking female F6 in the first days of June we heard vocalizations of kittens, suggesting that F6 was also pregnant during the previous month.

Social and interspecific interactions

Individuals were observed occasionally during sessions of continuous tracking. Male mongooses M1 and M4 and female F9 were observed once, whereas females F4 and F5 were seen 7 and 5 times, respectively, all of them alone. Female F3 was seen 13 of 19 times (68%) together with other two unmarked adults. Female F6 was seen twice accompanied by another adult. In one of these cases, after growling for a while, F6 went apart from the other individual. A small cub was observed moving in and out through the wire mesh of the boxtrap where F2 was trapped; the cub hided in close cover when it detected our presence. Thirty days after capture F2 was seen once again accompanied by three cubs.

Four genets (F1, F5, M2, and M4) were seen during continuous tracking sessions. Female F1 and male M2 were always seen alone (3 and 13 times, respectively), except for a single encounter of F1 with an unmarked conspecific. F1 met another genet while moving along a hedgerow across an olive grove, and started fighting on the ground, then climbed a tree and the fight continued in the canopy. The unmarked genet disappeared but a few minutes later it came back and F1 ran away very quickly. We followed F1 on foot for more than 1 km but the genet was so fast that we lost the signal. Two days after the fight, F1 was found dead on a highway, 200 m away from its last location. Female F5 and male M4 met the 70% of continuous tracking sessions and often travelled together during periods of variable length, but never for the entire night. Both genets used the same portion of hedgerow and the hollow of an old olive tree as resting places during the day (9.0 and 8.8% of resting periods of M4 and F5, respectively), but never bedded together. During the remaining resting periods, both genets used a single hedgerow placed between an olive grove and a dehesa.

Although there was a high interspecific spatial overlap we did not observe any interaction between genets and mongooses during the tracking sessions.

DISCUSSION

Body size of genets and mongooses living in the agricultural landscape was not smaller than the mean body size of these species in the Doñana National Park, suggesting that the availability and/or dispersion of resources in the agroecosystem are not so extreme to increment the energetic cost of foraging and provoke a physic decay of individuals.

Contrary to what we expected if animals were ecologically stressed in the agricultural landscape, female mongooses and genets trapped between March and May were all pregnant. Although we recorded only fragmentary data about reproduction, these observations agree with what has been described in Mediterranean forest landscapes. Mongoose mating in Doñana occurs between February and June, and litters are born between April and August. Young become active about two months after birth (Palomares and Delibes, 1992b). A peak in genet mating seems to take place between February and March, while births occurs between March and November (Calzada, 2002).

Activity

No differences were found between the activity pattern of mongooses and genets of the agricultural landscape and the pattern reported in less fragmented landscapes. Genets activity wase almost exclusively nocturnal, as has been described in Doñana (Palomares and Delibes, 1994), where only one female exhibited a high degree of diurnal activity (Palomares and Delibes, 1988). Mongoose activity was mainly diurnal, as seems to be the rule in Doñana (Palomares and Delibes, 1992a). We could observe a decrease of the activity around midday with a peak at 1300, which matches the diurnal resting siestas inferred by (Palomares and Delibes, 1992a) from a decrease in the mean distance travelled during these hours by mongooses in Doñana National Park.

Home range

The hypothesis of resource dispersion (Macdonald, 1983) predicts that territories need to encompass a minimum area of key habitats, which will be larger when habitat are dispersed. Therefore, in the agroecosystem we predicted larger home ranges than in less fragmented landscapes that feature a higher proportion of habitat with a more aggregated configuration. In contrast we found that home ranges of genets and mongooses in the agricultural landscape were significantly smaller than those in Doñana National Park, even when this comparison was made with MPCs, which overestimate home range sizes in our study area.

Although home range sizes were also estimated with the convex hull method, which removes a large fraction of non-used areas from the home range in the agricultural landscape, a large variability was found in the home range size in both species. The largest home range was more than 50 times larger than the smallest home range for the genet, and more than 6 times larger for the mongoose. This noticeable variability could arise if individuals with larger home ranges included habitats of poor quality and therefore needed larger areas to obtain the necessary resources. In addition, home range shape tended to be elongated for most individuals of both species. The largest home ranges of genets, those of

F1 and M1, were also the less elongated. Most individuals appeared to place their home ranges in one or more streams or hedgerows (Figure 1). This would agree with the hypothesis that landscape structure determines home range size and shape. This question will be addressed in detail in CHAPTER 3.

Resting places

In the continuous forested habitat of the Doñana National Park, mongooses used thickets and rabbit warrens as main resting places (Palomares and Delibes, 1990;Palomares and Delibes, 1993b;Palomares and Delibes, 1993a) whereas genets were described to used preferably thickets and hollow trees (Palomares and Delibes, 1994). In the agroecosystem, genets and mongooses still chose thickets and dense cover as main resting places despite the scarcity of this habitat type, indicating a strong selection of riparian forest and hedgerows, and suggesting the importance of their conservation for the maintenance of these carnivore populations.

Social behaviour

We observed very little intraspecific overlap between home ranges in both species, according to their territorial character (Palomares and Delibes, 1993c;Virgos and Casanovas, 1997). Only two genets (M4, F5) shared a significant portion of their home ranges (36%). These genets, probably mates or part of the same family, were seen together several times and shared some resting places (an olive tree and specific portions of a hedgerow) although they did not use them at the same time. M4 and F5 used to move along a shrubby hedgerow and the linear character of the hedgerow could have favoured frequent contacts between these individuals. We did not observe any two other genets moving together, which agrees with the description of this species as solitary (Palomares and Delibes, 2000).

According to the description of the Egyptian mongoose as a territorial species, the contiguous home ranges of three female living in the same stream were perfectly delimited and separated without any overlap. Moreover one of these females showed an aggressive display against another unmarked adult that approached her, which again supports the hypothesis of strong territoriality. At least one of the radio-tracked mongooses made part of a stable familiar group. In other populations foraging family groups, mainly composed of an adult female, young and/or an adult male has been commonly reported (Palomares and Delibes, 1993c). Our data concur in that the Egyptian mongoose is not a truly solitary carnivore.

Genets and mongooses are trophic generalists, and feed on a similar set of small vertebrate species. They also seem to select dense vegetation despite its scarcity in the study area. Although both species are temporally segregated, they still share a fraction of time at the beginning and end of their respective activity periods (Figure 3). Considering that both species exploit similar resources, we could expect interspecific competition for space. However, no spatial segregation existed between these two carnivores, and no aggression was recorded during continuous tracking sessions. Elsewhere genets and mongooses seem to suffer interference from larger carnivores like the Iberian lynx Lynx pardinus and the red fox Vulpes vulpes (Palomares and Delibes, 1991b;Palomares et al., 1996), but no reference of aggressions between mongooses and genets has been reported.

Conclusions

Although we expected changes in the spatial organization and behaviour of populations living in the agricultural landscape with regard to nearby populations inhabiting forest habitats, we only found marked differences in home range size, and the sign of these differences was against our expectations. Our initial hypothesis that individuals living in the agoecosystem incur in higher cost due to the dispersion or scarcity of resources was not supported by differences in body size, body condition or reproduction. Likewise individuals did not need to devote longer activity periods to achieve the necessary resources in the fragmented landscape. The selection of shrubby landscape is demonstrated in CHAPTER 3. This suggests that genets and mongooses can obtain enough resources in an agricultural landscape with very little forest left, but also that these resources were found mostly in the scarce remnants of scrubland present along streams and in the form of hedgerows. Our results highlight the importance of conserving these remnants for the maintenance of populations of these two species in Mediterranean agricultural lands.

ACKNOWLEDGEMENTS

This research was funded by Consejería de Innovación, Ciencia y Empresa (grant P06-RNM-1903), and Consejería de Medio Ambiente, Junta de Andalucía, which also authorized animal capture, handling, and tagging in compliance with regulations in force. MP was supported by the Ministry of Education through a FPU fellowship (AP2003-2370). I thank Miguel Solís and the Lazo family who let us work in their properties; Juan Carlos Rivilla, María Viota, Marcello D'amico and Jose Vicente López-Bao for their help with the bait-stations and boxtraps transport and settlement; and Jolies Dortland and Luis León for field assistance.

CAPÍTULO 3

Importancia de la conservación de remanentes leñosos lineares para dos carnívoros forestales en un paisaje agrícola Mediterráneo

Conservation value of linear woody remnants for two forest carnivores in a Mediterranean agricultural landscape

The content of this chapter has been published as:

Pereira, M., and A. Rodríguez. 2010. Conservation value of linear woody remnants for two forest carnivores in a Mediterranean agricultural landscape. Journal of Applied Ecology **47**:611-620.

RESUMEN

La pérdida de biodiversidad a causa de la expansión de la agricultura puede ser contrarrestada mediante la adopción de estrategias agrícolas respetuosas con la flora y fauna nativas, y mediante la expansión de una red de reservas naturales. Los beneficios potenciales de la extensificación de la agricultura, representadas en Europa por escenarios agro-ambientales, aún siguen difusos. En particular, la efectividad de la preservación de vegetación leñosa linear para retener carnívoros forestales en agrosistemas ha recibido una atención limitada. Documentamos el valor de lindes y estrechas franjas de bosquetes riparios para el meloncillo (*Herpestes ichneumon*) y la gineta (*Genetta genetta*). En un mosaico agrícola del suroeste de España, conteniendo un 4.7% de vegetación leñosa, hemos testado la hipótesis de que el papel de los elementos lineales y tres tipos de cultivos agrícolas difieren en la cantidad, calidad y estructura de la cobertura leñosa. Hemos analizado la influencia de los elementos lineales sobre la localización y utilización de las áreas de campeo mediante la combinación de análisis composicional y métodos numéricos.

Los meloncillos y ginetas seleccionaron fuertemente la vegetación linear leñosa. Todos los tipos de cultivos, incluidos los campos abiertos, dehesa y olivares, fueron evitados, sugiriendo que ambas especies dependen estrictamente de la cobertura leñosa nativa. La mayoría de individuos hicieron uso regular de las lindes, e incluso algunos de ellos las usaron como la única fuente de cobertura leñosa en sus áreas de campeo. La distribución de las áreas de campeo sugirió que los individuos componen una población continua, en lugar de discreta, en un hábitat espacialmente estructurado. Una distribución regular de la red de lindes a lo largo de la matriz agrícola podría impedir la fragmentación de las poblaciones.

ABSTRACT

The loss of biodiversity due to agricultural expansion can be countered by adopting wildlife-friendly farming strategies and by expanding the network of nature reserves. The potential benefits of agricultural extensification, represented in Europe by agri-environmental schemes, still remain unclear. In particular, the effectiveness of preserving linear woody vegetation to retain forest carnivores in farmland has received limited attention. We document the value of hedgerows and narrow strips of riparian forest for the Egyptian mongoose (*Herpestes ichneumon*) and the common genet (*Genetta genetta*). In an agricultural mosaic of southern Spain containing 4.7% of woody vegetation we tested hypotheses about the role of linear elements and three farmland types differing in the amount, quality, and structure of woody cover. We analysed the influence of linear elements on the placement and utilisation of home ranges by combining compositional analysis and numerical methods.

Mongooses and genets strongly selected linear woody vegetation. All types of farmland, including open fields, dehesa and olive groves, were avoided, suggesting that both species strictly depend upon native woody cover. Most individuals made regular use of hedgerows, and some individuals used hedgerows as the only source of woody cover in their home ranges. The distribution of home ranges suggested that individuals made up a continuous, rather than discrete, population in a spatially structured habitat. An evenly distributed hedgerow network across the intervening agricultural matrix could prevent population fragmentation.

INTRODUCTION

The increasing need for food by the growing human population make the conversion of natural areas into agriculture a major threat to biodiversity (Tilman et al. 2002). This can be compensated for by increasing the amount of land protected in nature reserves or by adopting wildlife-friendly farming (Green et al. 2005). Extensive farming methods may alleviate species loss (Knop et al. 2006), but may fail to conserve sensitive species (Donald 2004; Kleijn et al. 2006) and net biodiversity gains may be limited (Kleijn et al. 2001; Feehan, Gillmor & Culleton 2005; Whittingham et al. 2007). Moreover, the reduced yield of extensive farming may result in more land being converted to agricultural production (Green et al. 2005). More research is needed to properly assess the potential of low-intensity agriculture as a global conservation option (Kleijn & Sutherland 2003).

In Europe over the last decades, extensification has been widely applied in the form of agri-environment schemes (AES) (Kleijn & Sutherland 2003). Among other measures, AES include the restoration of woody cover in farmland, often in the form of hedgerows or similar linear elements, typical of extensive agricultural landscapes in the temperate region (Fritz & Merriam 1996; Baudry, Bunce & Burel 2000; Herzog et al. 2005). Conserved or restored lines of woody cover often increases the diversity and abundance of a variety of taxa (Hinsley & Bellamy 2000; Aviron et al. 2005; Hannon & Sisk 2009), but this has not been found everywhere (Bates & Harris 2009).

Implementation of AES at small spatial scales (single farms or small groups of farms) may partly explain their limited performance in restoring species of conservation concern (Whittingham 2007). The benefits of linear woody vegetation have been reported for small organisms including plants, invertebrates, and vertebrates with low mobility (Corbit, Marks & Gardescu 1999; Jehle & Artzen 2000; Thomas et al. 2001). However, little information exists about the role of woody linear features for larger and more mobile organisms that are unlikely to find sufficient resources within a single hedgerow or similar feature (Redpath 1995).

We studied the habitat use of the Egyptian mongoose (*Herpestes ichneumon* L.) and the common genet (*Genetta genetta* L.) in a Mediterranean agroecosystem where woody cover is scarce and occurs mainly as linear remnants (riparian forest and hedgerows). These species are considered to be forest carnivores, but their ecology is almost unknown in agricultural mosaic landscapes. Therefore, we first tested the hypothesis that resident mongooses and genets must obtain their resources in woody vegetation, and that adjacent farmland was unsuitable due to low prey abundance or insufficient cover. We expected a positive selection of woody cover and a negative selection of farmland patches.

Secondly, taking into account the scansorial habits of common genets (Larivière & Calzada 2001), we tested the hypothesis that resident genets, but not mongooses, would exploit and positively select farmland with high tree cover.

Thirdly, we examined the value of linear landscape features, including hedgerows, tree rows and grassy field margins. We tested the null hypothesis that these structures do not offer enough resources for resident mongooses and genets to use them regularly. This hypothesis predicts that 1) the density of linear landscape features within home ranges will be, at best, proportional to their availability in the landscape; 2) the proportion of animal locations outside riparian forest that fall in linear landscape features will be equal to, or lower than, the availability of such structures within home ranges; and 3) the spatial distribution of animal locations in open farmland will be independent of the proximity of linear landscape features.

Fourthly, we measured the amount of woody vegetation within the home ranges of resident individuals in order to establish a threshold, and to explore whether hedgerows may substitute for riparian forest as a source of woody cover. If cover quality was similar in hedgerows and riparian forest, we would expect home ranges including only hedgerows (lower cover density) to be larger than those including also riparian forest. An inverse correlation between the extent of hedgerows and that of riparian forest would also be expected within home ranges.

Finally, we tested two null hypotheses reflecting the quality of linear landscape features: 1) hedgerows and grassy lines were used with similar intensity, and 2) the intensity of use was independent of the length and width of the linear element, as well as of the degree of human disturbance in their surroundings.

MATERIALS AND METHODS

Model species

In Europe the Egyptian mongoose (mean adult weight: 2.9 kg) is restricted to the southwest of the Iberian Peninsula, has diurnal habits, prefers dense cover for resting, and actively avoids open areas (Palomares & Delibes 1993). The common genet (mean adult weight: 1.8 kg) also occurs in southwestern Europe, exhibits nocturnal activity, forages both on the ground and in the tree canopy and has been reported to select dense cover for breeding and resting (Palomares & Delibes 1994). Both species feed upon small vertebrates, mostly mammals (Palomares & Delibes 1991).

Study area and landscape structure

We conducted our study in the lower Guadiamar basin, SW Spain (37º23' N, 6º13' W; Figure 1). We corrected the position, size, shape and content of polygons in a land cover layer (Junta de Andalucía 1999) through comparison with orthophotographs and field surveys. We then simplified cover types that shared a similar vegetation structure into four categories (Table 1). All landscape measurements were made on ArcView GIS 3.2 and ArcMap 9.0 (ESRI, Redlands, California, USA).

Remnant woody vegetation was structurally similar in all landscape elements (including hedgerows): a continuous association of tall shrubs (*Rubus*, *Pistacia*, *Phyllirea*, *Myrtus*) interspersed with trees (*Quercus*, *Fraxinus*, *Salix*, *Populus*). Since shrub was the dominant vegetation layer, we used 'scrubland' to denote patches, riparian strips of native woody cover, and hedgerows. Scrubland made up 1.6% of the landscape. We distinguished three types of farmland: crops (cereals and sunflower *Helianthus annuus* L.), olive (*Olea europaea* L.) groves, and dehesa. Dehesa is an agroforestry system that combines pastures or cereal with scattered holm oaks (*Quercus ilex* L.) and cork oaks (*Q. suber* L.) and little or no understorey (Joffre et al. 1988). The distribution of farmland types was not homogeneous. Cereal crops abound in the northern half of the study area, where very little scrubland remains, while in the south olive groves dominate the landscape mosaic and the proportion of scrubland is above the average (Figure 1). Preliminary mammal surveys reported mongooses and genets in the south, but rarely in the north (Rodríguez & Delibes

2003). Therefore, we defined our study area as a square landscape sample of 79.2 km2 in the southern half of the Guadiamar agroecosystem (Figure 1). This area contains 4.7% of scrubland (Table 1), most of it associated with three streams that run from northwest to southeast (Figure 1). Some fields, groves and dehesas are bounded by hedgerows (Figure 2), which made up 6.7% of total scrubland.

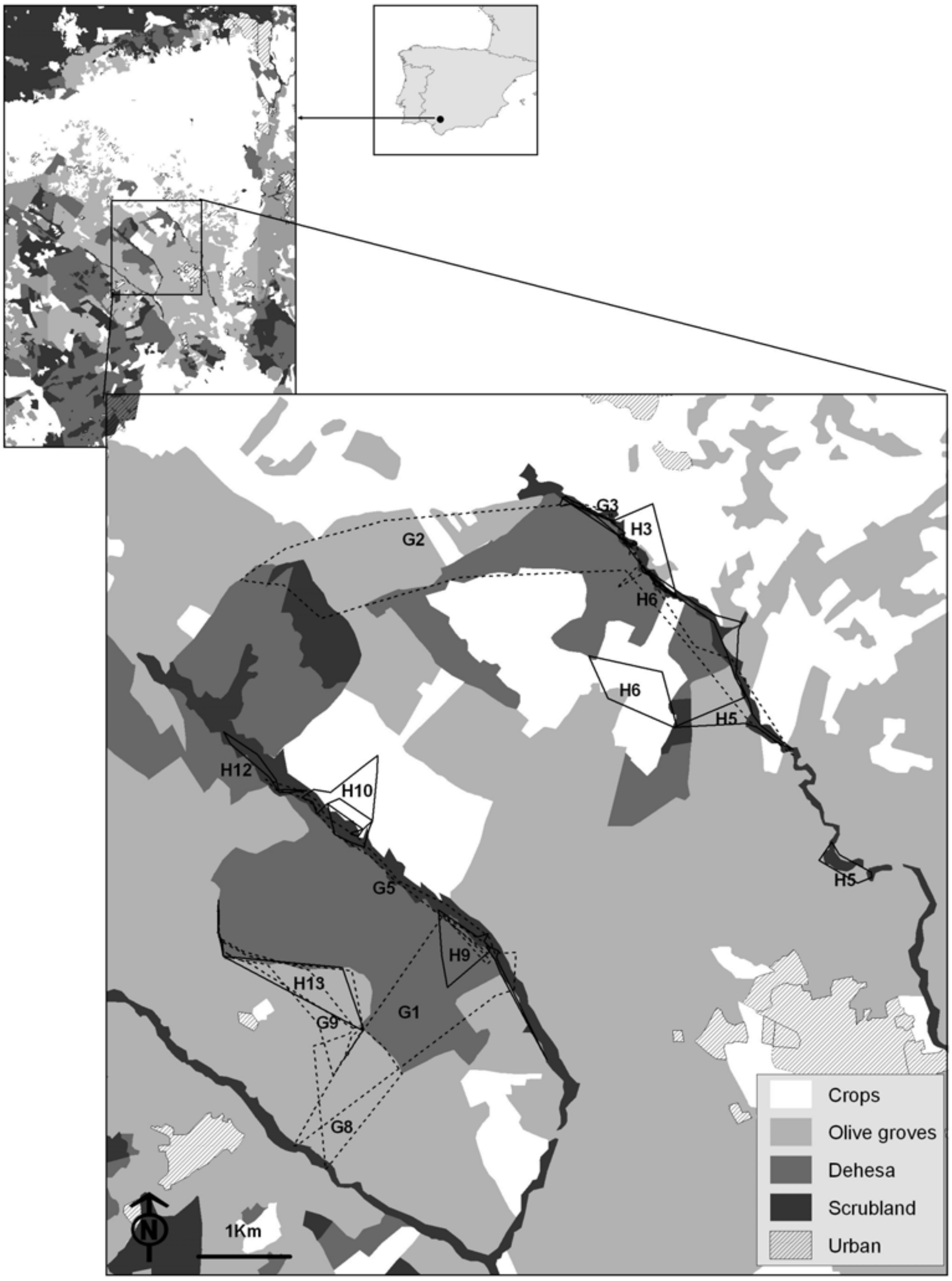


Figure 1. Location of the study area (square) in the Guadiamar agroecosystem and habitat map. Home ranges (nearest-neighbour convex-hulls) for seven Egyptian mongooses (H, solid line) and six common genets (G, broken line) are shown.

On orthophotographs we detected, digitized and characterized 187 linear elements that were subsequently checked in the field. Their overall length was 73 km (density: 0.92 km km-2), of which 55% were hedgerows (0.51 km km-2), 38% grassy lines (0.35 km km-2), and 7% tree lines. We estimated the mean width of linear elements on orthophotographs by taking 3-16 measurements at random points along each line. Most hedgerows were narrow (frequency in width classes: <5 m, 31%; 5-10 m, 57%; 10-15 m, 6%; >15 m, 6%) and did not have physical connections with scrubland patches. The mean width (±SE; n=20) of the riparian forest along the eastern, central, and western streams was 49±3 m, 133±12 m, and 41±4 m, respectively (Figure 2).

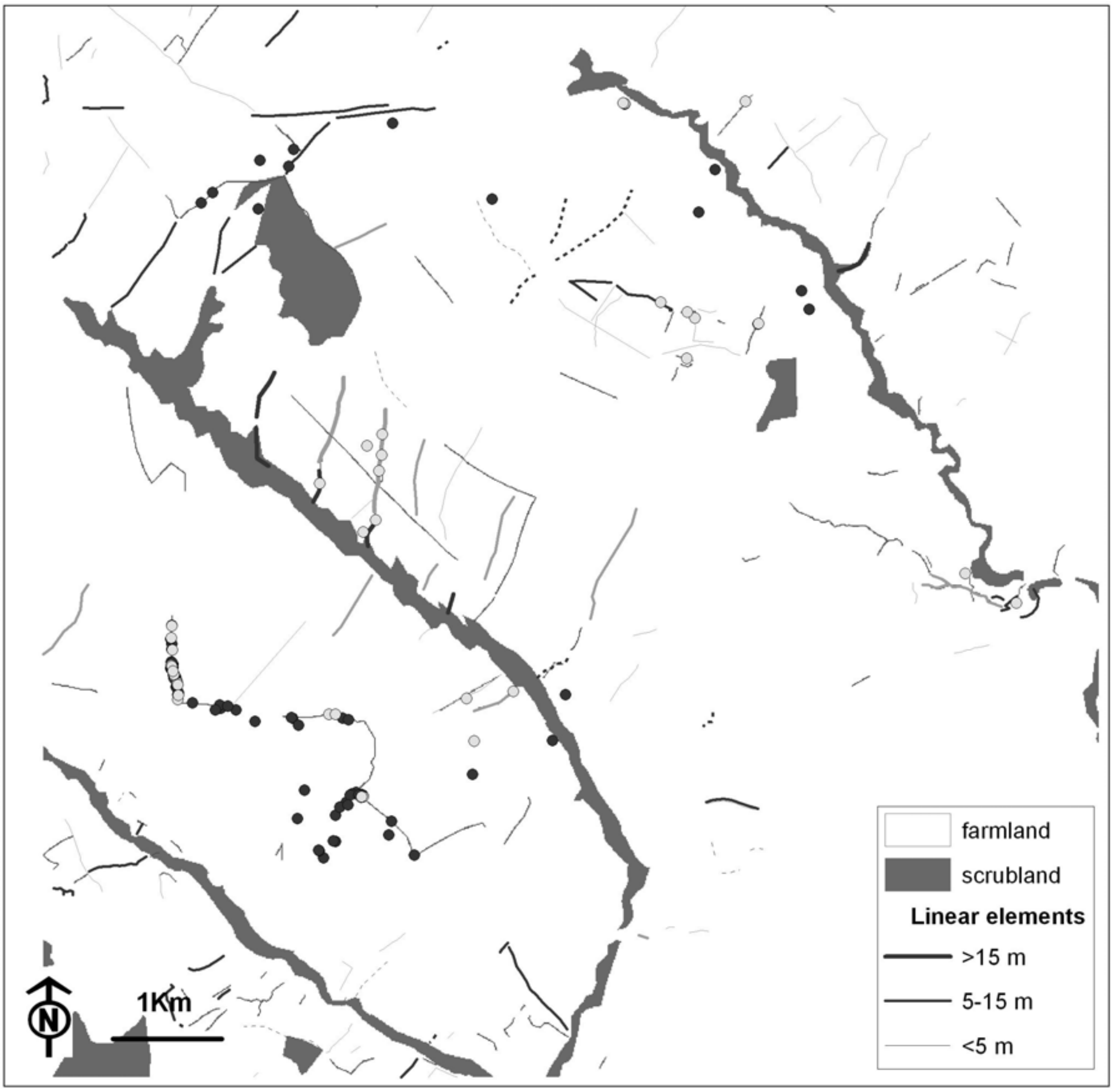


Figure 2. The distribution of scrubland (shaded) in the study area. Black lines: hedgerows; broken: tree lines; grey: grassy lines. Dots: independent radio locations of seven Egyptian mongooses (light, *n*=51) and six common genets (dark, *n*=92) >30 m away from scrubland.

Field methods

Seventeen mongooses (13 adults) and 17 genets (9 adults) were caught with boxtraps (2.0 x 0.5 x 0.5 m) from June 2005 to March 2007. We immobilized animals with tiletamine-zolazepam (Zoletil, Virbac, Spain) and determined their age from body weight, tooth wear, and signs of reproductive activity. All adults were equipped with radiocollars (Biotrack, Wareham, UK). We used the homing technique (Mech 1983) and a GPS unit (Garmin, Olathe, Kansas, USA) to locate tagged animals. We accurately established whether animals were inside or outside linear elements. Animals were located on average every three days (range 1-17 days), at random times, and we assumed that these positions represented independent samples of habitat use during activity and inactivity periods.

Home range estimates

Tracking periods were evenly distributed throughout the year and their mean length was 15 weeks (range 6-24 weeks). We calculated minimum convex polygons (MCP) with the ArcView extension Animal Movement (Hooge & Eichenlaub 2000) as estimates of home ranges. We considered an animal as resident if the increase of MCP area plotted against the number of radio locations decelerated and reached a plateau (mean=28 radio locations), and analyses were restricted to resident individuals. Home ranges were also estimated with Nearest-Neighbour Convex Hulls (NNCH; parameter k=5), an extension of the MCP technique that merges a set of local, smaller MCPs constructed with clusters of locations (Getz & Wilmers 2004). Compared with other estimates, convex hulls reduce the amount of unused areas within the home range, and are useful when the configuration of habitat elements may force non-convex ranges (Getz & Wilmers 2004), as may be the case with the elongated structures of our landscape. NNCH were calculated with the ArcView extension LoCoh (Getz & Wilmers 2004).

Habitat selection

We used compositional analysis (Aebischer, Robertson & Kenward 1993) to determine habitat selection in the placement of home ranges. Availability was the proportion of each habitat type in the study area and animal usage was the respective habitat proportions included within individual NNCH home ranges. Compositional analysis was also employed to analyse habitat use within home ranges. At this level of selection, availability was defined as the proportion of each habitat type within each MCP home range and animal usage was the proportion of independent radio locations that fell in each habitat type. Zero usage was replaced by the value 0.001. We performed compositional analysis with the free software Resource Selection (Fred Leban, University of Idaho, Moscow, USA). We calculated the geometric mean selection ratio in order to estimate selection at the population level (Pendleton et al. 1998).

Use of linear elements

We used Monte Carlo simulations to assess the value of linear elements. To test whether the density of linear elements within home ranges was proportional to their availability in the landscape, for each NNCH home range we generated 99 random convex hulls with identical area and shape whose centroids were random points within the study area. Simulated convex hulls were rotated at a random angle. In actual and simulated ranges we calculated the density of hedgerows, tree lines, and grassy lines. For each home range, the 100 values were ordered, the highest value being assigned rank 1. The rank value/100 was the probability that the density of linear elements was equal or lower than its availabilty (ranking test, Manly 1997). We took the individual as the sampling unit and compared the mean density of linear elements in simulated ranges with the observed density using the Wilcoxon matched pairs test to examine whether a pattern of selection emerges at the population level.

We computed the number of radio locations outside riparian forest and generated 99 groups of the same number of random locations for each MCP to test whether linear elements of different type were used proportionally to their availability. In actual and simulated ranges we calculated the number of positions that fell within hedgerows, tree lines and grassy lines, and the distance from each position to the nearest linear structure of each type. We also tested whether hedgerow quality influenced its usage. We counted how many radio locations fell in hedgerows; simulated 99 sets of the same number of locations randomly placed along available hedgerows within each MCP, and measured hedgerow width. The ranking test was used to assess the significance of selection. Means were compared across individuals with the Wilcoxon test.

We estimated disturbance levels at linear elements by considering their distance to the nearest paved road. We used generalised linear mixed models (GLMMs) to examine the effects of type, length, mean width, and disturbance of linear elements contained in at least one MCP. Individual identity was included as a random variable. We analysed whether each linear element was ever used (models with binomial error) and the number of radio locations that it contained (models with Poisson error). Species identity was included in all models as a fixed factor.

RESULTS

Dependence upon woody cover

We found considerable variability in habitat composition of mongoose home ranges (Figure 1, Table 1), in spite of which standardized selection ratios indicated that scrubland was strongly preferred over any farmland habitat type at the home range level ($-N \ln(\lambda)=9.911$, n=7, P=0.019; Table 2 & Figure 3). Positive selection of scrubland was also evident when habitat use, indicated by radio locations, was compared with its availability within home ranges ($-N \ln(\lambda)=10.338$, n=7, P=0.016; Figure 3). On average, mongooses were located in scrubland 90% of the time (Table 1) and scrubland use was significantly higher than the use of other farmland habitat (Table 2). Within home ranges, individual variability in habitat use was quite low (Table 1).

Common genets included little or no crops within their ranges but variability in the proportion of other habitats was substantial (Table 1). Standardized selection ratios showed that scrubland and dehesa were preferred by common genets over olive groves and crops at the landscape scale ($-N \ln(\lambda)=13.228$, n=6, P=0.004; Figure 3). Within their home ranges, all genets were located in scrubland over 71% of the time, indicating a clear preference for this habitat, while <12% of radio locations were recorded in farmland habitats (Table 1). No genet radio location was found in crops. The positive selection of scrubland and the negative selection of farmland within home ranges were significant ($-N \ln(\lambda)=15.006$, n=6, P=0.002; Figure 3). The differences in preference were significant for the scrubland-dehesa and scrubland-crops pairs (Table 2).

Table 1. Proportion of each habitat type in the study area. Habitat availability in the study area (urban excluded) is compared with mean (±SE) habitat content in nearest-neighbour convex hull (NNCH) estimates of home range for adult resident Egyptian mongooses (n=7) and common genets (n=6). Likewise, mean (±SE) habitat availability within minimum convex polygon (MCP) estimates of home range is compared with the mean (±SE) proportion of fixes in each habitat type.

	Study area	Availability study area	NNCH	Mean availability MCP	Locations
Egyptian mongoose					
Olive groves	0.546	0.568	0.24 ± 0.14	0.21 ± 0.09	0
Crops	0.236	0.245	0.29 ± 0.14	0.26 ± 0.11	0.05 ± 0.03
Dehesa	0.131	0.137	0.15 ± 0.11	0.26 ± 0.09	0.05 ± 0.02
Scrubland	0.047	0.049	0.32 ± 0.12	0.27 ± 0.12	0.90 ± 0.03
Urban	0.040				
Common genet					
Olive groves	0.546	0.568	0.44 ± 0.17	0.38 ± 0.16	0.16 ± 0.04
Crops	0.236	0.245	0.02 ± 0.02	0.07 ± 0.05	0
Dehesa	0.131	0.137	0.26 ± 0.09	0.36 ± 0.10	0.06 ± 0.03
Scrubland	0.047	0.049	0.28 ± 0.16	0.20 ± 0.12	0.83 ± 0.04
Urban	0.040				

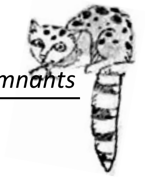


Table 2. Compositional analysis of habitat preference by Egyptian mongooses (*n*=7) and common genets (*n*=6) in the Guadiamar agroecosystem, SW Spain. Habitat ranking matrices represent selection ratios at two levels: 1) habitat content of NNCH estimates of home range vs. habitat availability in the landscape sample, and 2) habitat at animal radio locations vs. habitat availability in MCP estimates of home ranges. Signs denote a positive or negative departure from random use between habitat pairs, followed in brackets by the *P*-value of a *t*-test (Aebischer *et al*. 1993). Ranks range from 3 (most used) to 0 (least used).

	Habitat content of home ranges				Habitat at fixes			
Use	Availability in the landscape				Availability in the home range			
	Dehesa	Olive groves	Crops	Rank	Dehesa	Olive groves	Crops	Rank
Egyptian mongoose								
Scrubland	+ (0.053)	+ (0.062)	+ (0.039)	3	+ (0.031)	+ (0.008)	+ (0.027)	3
Dehesa		+ (0.133)	+ (0.275)	2		+ (0.306)	− (0.481)	1
Olive groves			+ (0.926)	1			− (0.041)	0
Crops				0				2
Common genet								
Scrubland	+ (0.834)	+ (0.275)	+ (0.006)	3	+ (0.027)	+ (0.052)	+ (0.001)	3
Dehesa		+ (0.192)	+ (0.007)	2		− (0.398)	+ (0.280)	1
Olive groves			+ (0.240)	1			+ (0.053)	2
Crops				0				0

Use of farmland with trees by common genets

Olive groves were used less than expected from their availability at the two levels of selection we examined. Out of 210 independent genet locations, only 5% were assigned to dehesa, whose availability in MCPs ranged between 10% and 71%. This avoidance of dehesa was unexpected given that genets included relatively large amounts of dehesa within their home ranges. It is possible that this result could be an artefact of the landscape structure in our study area, i.e. the spatial association between dehesa and scrubland (Figure 1). To test this hypothesis, we calculated the proportion of dehesa in 1-km circles around 99 random points and the distance of its centre to the nearest scrubland. This demonstrated that the proportion of dehesa and the distance to scrubland were negative and significantly correlated (rs=-0.353, P<0.001), whereas the association with scrubland was positive and weak for the proportion of olive groves (rs=0.141, P=0.163) and crops (rs=0.181, P=0.073) in simulated home ranges.

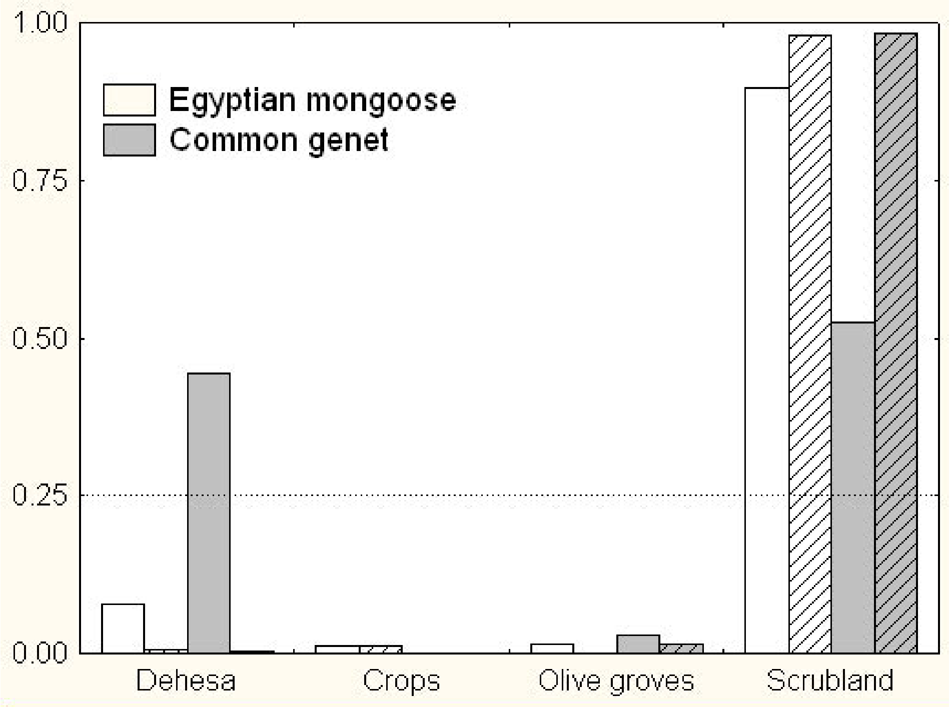


Figure 3. Standardized selection ratios for seven Egyptian mongooses and six common genets at two levels: 1) habitat content of NNCH estimates of home range vs. habitat availability in the landscape sample (open columns), and 2) habitat at animal fixes vs. habitat availability in MCP estimates of home ranges (striped columns). The dotted line indicates random selection.

Use of linear elements by Egyptian mongooses

With the exception of H12, whose home range contained riparian forest almost exclusively (Figure 1), the proportion of scrubland in mongoose convex hulls did not reach 30% (Table 3). The density of hedgerows in mongoose home ranges was 6-22 times higher than the mean density of hedgerows in simulated, random home ranges (Table 3), and these differences were significant (Wilcoxon test, Z=2.201, n=6, P=0.028). No tree row was observed within mongoose home ranges and mean density of tree lines in simulated convex hulls was in the range 0.6-0.8 m ha-1. The density of grassy linear elements was negligible in the home ranges of three mongooses but significantly higher than in random ranges for three other individuals (Table 3). Since the densities of grassy lines and hedgerows were independent in observed (rs=0.522, n=6, P=0.288) or simulated convex hulls (mean values, rs=0.574, n=6, P=0.234), the positive selection of grassy lines could be ecologically meaningful. However, the overall differences between observed and available density of grassy lines within mongoose home ranges were not significant (Wilcoxon test, Z=0.943, n=6, P=0.345).

The size of mongoose convex hulls increased significantly as the proportion of scrubland decreased (rs=-0.786, n=7, P=0.036). All mongooses whose ranges contained <30% scrubland used farmland with a density of hedgerows ≥14 m ha-1 (Table 3); such high densities occurred only in 16% of simulated home ranges (Figure 4). The relationship between the proportion of scrubland and hedgerow density was indeed negative (Figure 4). Mongoose convex hulls contained 0.5-17.4 ha of woody vegetation, of which 0.0-0.9 ha corresponded to hedgerows. One resident mongoose (H13) did not use the riparian forest at all, and lived exclusively in hedgerows covering 0.53 ha (Table 3, Figure 4).

Table 3. Proportion of scrubland and density of hedgerows and grassy lines in NNCH estimates of home ranges. The mean density (m/ha) of hedgerows and grassy linear elements in 99 randomly placed convex hulls of the same size and shape is given. P: probability that the density of linear elements in observed home ranges was lower than that of simulated ranges (ranking test)

		Density of hedgerows (m ha^{-1})			Density of grassy lines (m ha^{-1})		
Individual	Scrubland	Observed	Simulated	P	Observed	Simulated	P
Egyptian mongoose							
H3	0.24	14.0	2.4	0.01	0.0	1.6	1.00
H5	0.17	18.3	3.2	0.01	0.0	2.1	1.00
H6	0.07	20.1	2.2	0.01	20.9	2.1	0.01
H9	0.15	26.3	1.9	0.01	32.3	1.1	0.01
H10	0.29	48.9	2.2	0.01	6.5	1.3	0.03
H12	0.97	0.0	1.1	1.00	0.0	0.9	1.00
H13	0.01	37.5	2.0	0.01	0.4	1.8	0.40
Common genet							
G1	0.04	8.4	2.8	0.12	5.8	4.2	0.14
G2	0.10	6.0	3.5	0.22	0.9	3.9	0.82
G3	0.63	0.0	1.8	1.00	0.0	1.0	1.00
G5	0.89	0.0	3.3	1.00	2.0	1.7	0.28
G8	0.01	16.0	3.4	0.01	0.5	1.9	0.61
G9	0.01	20.0	2.2	0.01	0.4	1.7	0.44

We recorded 43 independent mongoose locations in farmland >30 m away from the scrubland edge. For mongooses whose ranges contained linear elements, locations fell in them more often than expected. Farmland radio locations were significantly closer to linear elements than expected from their availability (Table 4), and these differences were significant across individuals (Wilcoxon test, Z=2.201, n=6, P=0.028).

Five mongooses were found 47 times in 12 different hedgerows whose mean (±SE) length was 574±165 m, and whose mean width was 8.1±2.1 m. During the study period H13 lived in a set of one grassy linear element and three hedgerows 1.2-1.5 km long and 3.1-4.7 m wide. This individual selected stretches of hedgerow wider than expected from random (mean width: 7.8 m; Table 4). Mongooses that used hedgerows occasionally also chose spots wider than expected (6-24 m; Table 4; Wilcoxon test, Z=1.826, n=4, P=0.068).

Use of linear elements by common genets

Two genets (G3 and G5) lived mostly in the riparian forest (Figure 1). Their home ranges did not contain hedgerows (Table 3). Farmland was the dominant habitat (≥90%) within the ranges of the other genets, but hedgerow density was 2-10 times higher than the mean density in home ranges distributed randomly (Table 3). Genets that used large portions of farmland tended to place their home ranges in areas where hedgerow density was higher than random (Wilcoxon test, Z=1.826, n=4, P=0.068). Tree lines within genet convex hulls were scarce or absent, while in simulated ranges mean tree row density ranged between 0.7 and 1.0 m ha-1. Densities of grassy lines did not differ significantly between observed and simulated home ranges (Table 3; Wilcoxon test, Z=0.730, n=4, P=0.465).

The size of genet home ranges tended to increase as the proportion of scrubland decreased (rs=-0.493, n=6, P=0.321). Genets whose ranges contained <10% of scrubland used farmland with a density of hedgerows ≥6 m ha-1 (Table 3). This threshold density was found in only 24% of simulated ranges with <10% scrubland (Figure 4). A significant negative correlation existed between hedgerow density and the proportion of scrubland within home ranges (Figure 4; rs=-0.971, n=6, P=0.001). This relationship held even when two individuals that did not use hedgerows (Table 1) were removed from the analysis (rs=-0.949, n=4, P=0.051). The amount of woody vegetation within genet convex hulls varied in the range 0.4-32.1 ha, of which 0.0-0.7 ha appeared as hedgerows. Two genets (G8 and G9) placed their home ranges along hedgerows (0.48 and 0.42 ha, respectively).

We recorded 92 genet radio locations in farmland beyond 30 m of the scrubland boundary. Three genets contained linear elements in their ranges, and their radio locations in farmland were located in linear elements significantly more often that expected (Table 4).

When in farmland, these genets were recorded at distances significantly closer to linear elements than expected (Table 4). Excluding genets G3 and G5, recorded mostly in riparian forest, farmland radio locations tended to be close to linear elements in spite of the small sample size (Wilcoxon test, Z=1.826, n=4, P=0.068).

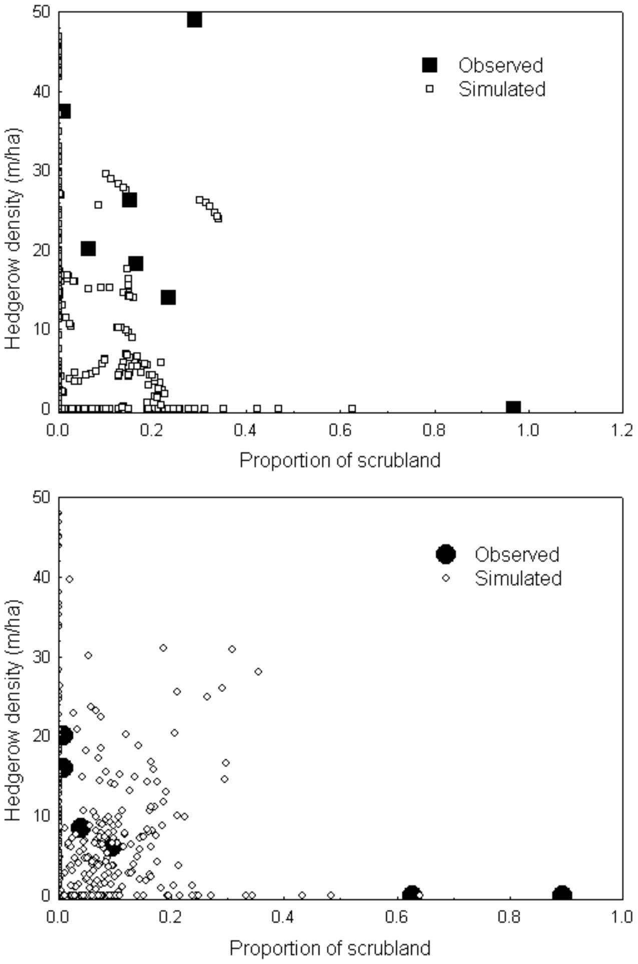


Figure 4. Relationship between density of hedgerows and proportion of scrubland in observed (large symbols) and simulated (small symbols) home ranges (convex hulls) for Egyptian mongooses (top) and common genets (bottom). Y-axis was truncated at 50 m ha^{-1} (a few larger simulated values occurred at X=0).

Three genets were found 67 times in 5 different hedgerows whose mean (±SE) length was 1200±170 m, and whose mean width was 3.9±0.3 m. During the study period, G8 and G9 lived almost exclusively in three hedgerows 1.2-1.5 km long and 3.1-4.7 wide. These genets selected stretches of hedgerow wider than expected from random (mean width ±7.0 m). G2 was also found in spots wider than expected (Table 4).

Table 4. Number of radio locations in linear elements, mean width of hedgerows at the radio location, and mean distance of radio locations in farmland to the nearest linear element. Mean values are given for 99 replicates of an equal number of random radio locations within MCPs or, for widths, the hedgerows they contain. *P*: probability that observed values were lower (number of radio locations, width) or higher (distance) than in simulated ranges. Radio locations within 30 m of scrubland were excluded from the analyses.

	Radio locations in linear elements			Hedgerow width				Distance to hedgerow (m) for radio locations in farmland			
Individual	Observed	Simulated	*P*	*n*	Observed	Simulated	*P*	*n*	Observed	Simulated	*P*
Egyptian mongoose											
H3	0	0						1	10	189	0.02
H5	4	0.5	0.01	4	12.9	8.2	0.1	2	48	305.1	0.01
H6	6	2.6	0.05	6	5.8	3.6	0.01	9	277.9	357.3	0.13
H9	2	0.9	0.19					3	108.3	228.4	0.07
H10	9	4.4	0.05	6	23.6	14.1	0.01	7	31.7	88.4	0.01
H12	0	0.3									
H13	29	2.5	0.01	29	7.8	4.5	0.01	29	2.8	163.9	0.01
Common genet											
G1	0	0.5						4	386.3	228	0.98
G2	7	1.4	0.01	7	5.8	4	0.02	10	205.1	403	0.03
G3	0	0						2	465.5	411.6	0.79
G5	0	0.3									
G8	32	1.3	0.01	32	7.5	4.5	0.01	42	50.3	266.6	0.01
G9	28	1.8	0.01	28	7	4.6	0.01	34	32.5	212	0.01

Table 5. Generalised linear mixed models of linear element use (left; binomial error), and use frequency (right; Poisson error), by Egyptian mongoose and common genet. Reference levels for factors Species and Type were 'mongoose' and 'hedgerow', respectively.

	Occurrence in linear elements				Number of fixes in linear elements			
Predictor	Estimate	SE	$F_{1,47}$	p	Estimate	SE	$F_{1,47}$	p
Intercept	-13.19	4.90			-6.71	2.48		
Species (genet)	-3.61	3.75	0.92	0.342	-0.11	0.49	0.05	0.823
Type (grassy)	-8.14	1.79	20.69	<0.001	-1.93	0.71	7.44	0.009
Length	3.59	0.81	19.89	<0.001	1.52	0.33	20.95	<0.001
Width	0.60	0.11	30.66	<0.001	0.10	0.03	9.12	0.004
Distance to road	-1.36	0.40	11.46	0.001	-0.49	0.11	21.36	<0.001

Attributes of linear elements

The sign and significance of predictors were consistent in mixed models of occurrence and intensity of use (Table 5). Genets and mongooses did not differ in their selection of linear elements. Hedgerows were likely to be used at least once, and were used with higher frequency, than grassy lines (Table 5). Longer and broader linear elements were preferred within the range of values available (Table 5). Greater use was made of linear elements relatively close to paved roads (Table 5); this result can be explained by the location of a single highly used hedgerow about 100 m from a secondary road suggesting that moderate disturbance by traffic did not affect the use of hedgerows by both carnivore species.

DISCUSSION

Egyptian mongooses and common genets depended upon the scarce remnants of woody cover still present in the Guadiamar agroecosystem. These carnivores were able to establish enlarged home ranges outside riparian forest (the main source of woody cover) provided that a sufficient density of hedgerows was available. Both species used hedgerows preferentially suggesting that they provide valuable cover.

A variety of farmland habitats were avoided, including dehesa and olive groves that are rich in old trees but contain little understorey. Open farmland with high canopy cover may not provide enough food or shelter, when compared to shrub cover. Therefore, matrix or unsuitable habitats for mongooses and genets can be defined as the absence of a layer of native shrubs in this landscape. Our results agree with circumstantial evidence indicating that genet latrines occur mostly in dehesas with understorey (Virgós & Casanovas 1997; Costa & Santos Reis 2002) where grazing might have been temporarily abandoned. In the southwest of the Iberian Peninsula, dehesa is a widespread agroforestry system covering >3 million ha (Díaz, Campos & Pulido 1997). Dehesa may preserve some mammal species of Mediterranean forests (Díaz, Pulido & Marañón 2003), but its value for forest carnivores is unclear.

The scarcity of non-linear scrubland did not prevent genets and mongooses from inhabiting the Guadiamar agroecosystem. Whereas spatially structured habitats often result in spatially structured populations (Thomas & Kunin 1999), these carnivores were able to establish a continuous population, with adjacent home ranges, in a landscape containing as little as 4.7% of suitable habitat. We propose four explanations for this observation.

First, resident adults of both species included a high density of linear elements within their home ranges. Small vertebrates abound in riparian vegetation and hedgerows (Hinsley & Bellamy 2000; Maisonneuve & Rioux 2001) and therefore provide suitable foraging habitats for carnivores. Although many carnivores use woody, elongate landscape features regularly (Beier 1995; Tigas, van Vuren & Sauvajot 2002), they rarely rest or stay in them for long, suggesting that they may not provide sufficient shelter. This clearly was not the case for genets and mongooses in our study whose home ranges were entirely in hedgerows. Human activity in our study area was limited to farming and hunting, with little disturbance from traffic due to the distances (>100 m) of the occupied hedgerows from roads. Negative edge effects (risk of predation by dogs or humans) might be similar in hedgerows and riparian strips, despite their mean widths differing by one order of magnitude (4-40 m). The preference for relatively broad segments along hedgerows may be related to better refuge quality.

Secondly, most individuals in our study used several isolated linear elements suggesting that they could travel across the farmland matrix and may perceive the landscape in a fine-grained manner. This indicates that the agricultural mosaic was perceived as functionally continuous by our study animals.

Thirdly, physical connectivity, or the relative proximity of linear woody features in the landscape, may also play a role. In the study area, streams and associated riparian forest are <4 km apart and individuals could move between them, often making use of the hedgerow network. Hedgerows were distributed quite evenly across the area used by the study animals. The spatial distribution of hedgerows could be as important as their overall density since it determines the distance of open farmland gaps that animals have to cross. A regular distribution of hedgerows may allow a fairly even distribution of home ranges across the agricultural landscape and, therefore, continuous rather than structured carnivore populations. In turn, an even distribution of home ranges would facilitate a quick detection and refill of territory vacancies and the maintenance of a continuous occupation of the landscape. It is unclear whether a more clumped hedgerow distribution, while keeping constant hedgerow density, would allow animals to occupy adjacent home ranges. Neither species occurs in the northern sector of the Guadiamar plain where hedgerows are absent and riparian vegetation is scarce (Rodríguez & Delibes 2003).

Finally, at the regional scale, genets and mongooses occupy a pine forest block 5-10 km southwest of the study landscape (Rodríguez & Delibes 2003). We found no evidence that the study population was sustained by immigration, but this forest could be a source of immigrant animals.

The length and density of hedgerows are constrained by field size. As in other Mediterranean agroecosystems (Concepción, Díaz & Baquero 2008), in our study area hedgerows were longer (up to 1.9 km) and field sizes larger (up to 541 ha) than in traditional bocage landscapes of northern Europe with average field sizes of 0.5-3.0 ha and mean hedgerow lengths of 0.1-0.2 km (Deckers, Hermy & Muys 2004; Aviron et al. 2005). Therefore, in the typical agricultural landscapes of central and southern Spain, hedgerow density cannot reach the high values recorded in temperate Europe by simply restoring hedges along every field margin. However, our results may guide the design of specific agri-environment schemes for carnivores in Mediterranean agricultural landscapes characterised by large fields. Specifically, in a landscape with <5% of native woody vegetation, mostly in the form of riparian strips, an overall hedgerow density of 5 m ha-1 can support resident populations of common genet and Egyptian mongoose. A hedgerow density of 10-50 m ha-1 within landscapes containing <20% of riparian forest allows mongooses and genets to cross open farmland and to establish stable home ranges. Suitable hedgerows ranged between 0.5 and 2.0 km long, and between 4 and 10 m wide, provided that stretches broader than 7 m occur in most hedge lines. Hedgerows should consist of native shrubs and may contain native trees, but tree lines without understorey are not suitable. A regular spatial distribution of hedgerows is preferable to an aggregated distribution (and may be crucial).

Hedge width can be manipulated more easily than length. Mean width of well preserved hedgerows approach 10 m (Fritz & Merriam 1996; Deckers, Hermy & Muys 2004), but those created under AES are seldom broader than 3 m (Tattersall et al. 2002; Bates & Harris 2009; Lye et al. 2009). While narrow hedges may favour arthropods and small vertebrates (Jehle & Artzen 2000; Thomas et al. 2001; Tattersall et al. 2002), broader hedges were inhabited by resident genets and mongooses in our study.

The protection and restoration of linear remnants of native woody cover in farmland benefits some carnivores and many smaller organisms (Herlin & Fry 2000; van der Ree & Bennett 2003; Herzog et al. 2005), probably without raducing habitat quality for open land species. We conclude that, if enough linear elements are retained and their quality preserved, resident populations of two forest carnivores could live in an agroecosystem with a proportion of woody cover well below 10%. The tolerance of genets and mongooses to such open agricultural landscapes has not been reported previously. We note, however, that the survival of wild carnivores in agroecosystems requires habitat management at the landscape scale. Hedgerow management over large tracts of farmland may therefore resemble the ‘protected area’ approach (Whittingham 2007) within the wildlife-friendly farming solution to the global problem of agricultural expansion.

ACKNOWLEDGEMENTS

This research was funded by Consejería de Innovación, Ciencia y Empresa (grant P06-RNM-1903), and Consejería de Medio Ambiente, Junta de Andalucía, which also authorized animal capture, handling, and tagging in compliance with regulations in force. MP was supported by the Ministry of Education through a FPU fellowship (AP2003-2370). I thank Miguel Solís and

the Lazo family who let us work in their properties, Jolies Dortland and Luis León for field assistance, and the Associate Editor of the *Journal of Applied Ecology* and two anonymous reviewers for helpful comments.

CAPÍTULO 4

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*Deconstruyendo áreas de campeo: patrones de movimiento de la gineta (*Genetta genetta*) en un paisaje agrícola*

Deconstructing home ranges: movement pattern of the common genet (*Genetta genetta*) in an agricultural landscape

RESUMEN

La transformación del hábitat por la agricultura no sólo reduce la vegetación natural, sino que también altera la configuración de los elementos del paisaje. El uso de los paisajes agrícolas por la fauna salvaje local dependerá de la configuración de los hábitats naturales remanentes, así como del grado de dependencia de cada especie en los parches forestados. Hábitat es un concepto específico de especie y no debe de ser confundido con la simple visión antropogénica de los tipos de coberturas vegetales. Proponemos la hipótesis de que los patrones de movimiento deben reflejar parcialmente la variación espacial en la calidad del hábitat tal como es percibido por el individuo y, por tanto, podemos usar los cambios en el comportamiento para modelar la utilización del espacio para cada especie en lugar de asumir esas funciones de la apreciación subjetiva del paisaje. Hemos utilizado diferencias en los patrones de movimiento de la gineta (*Genetta genetta*) para distinguir zonas dentro de las áreas de campeo y, posteriormente, hemos identificado atributos del paisaje que podrían estar influenciando esos cambios.

Las ginetas se comportaron de forma diferente dependiendo de la intensidad de uso dentro de sus áreas de campeo: movimientos lentos en el núcleo, velocidad media en zonas intermedias, y movimientos más rápidos en la periferia de las áreas de campeo. La estructura del paisaje parece influenciar el uso de determinadas regiones dentro de las áreas de campeo. Las áreas núcleo de las ginetas fueron establecidas en zonas donde la cobertura arbustiva fue al menos del 5%. La presencia de elementos lineares arbustivos aumentó la probabilidad de uso de esas zonas por gineta. Ninguna otra variable de hábitat aparte del matorral (en forma de parches o elementos lineales) fue seleccionada, sugiriendo que los patrones de movimiento son diferentes en los cultivos, independientemente del tipo de los mismos.

ABSTRACT

Habitat transformation by agriculture reduces natural vegetation area but also alters the configuration of landscape elements. The use of these agricultural landscapes by wildlife shall depend on the configuration of the remnants of natural habitat as well as on the degree of dependence of focal species on forested patches. Habitat is a species-specific concept that should not be confounded with an anthropocentric vision of cover types. We hypothesize that movement pattern may reflect in part the spatial variation in habitat quality as perceived by the individual and, therefore, we can use behavioural changes to model the space use by each species, rather than assuming these functions from the subjective appreciation of the landscape. We have used differences in movement pattern of the common genet (*Genetta genetta*) to distinguish between different zones within home ranges and, subsequently, we have identified landscape attributes that could be influencing those changes.

Genets behaved differently depending on the intensity of use of their home ranges: Slow movements in their core area, medium velocity within intermediate areas and fast movements within the home range periphery. Landscape structure seems to influence the intensity of use of regions within the home range. Genet core areas were established in areas where scrubland cover was as low as 5%. The presence of shrubby linear elements also improves the probability of use of an area by a genet. No other habitat variable different from scrubland (in the form of patches or linear elements) has been selected, suggesting that the movement pattern is different in farmland, irrespective of farmland type.

INTRODUCTION

Most ecosystems in western Europe have been highly modified and most of the land transformed into agriculture (Matson et al., 1997), which is the most relevant cause of human induced fragmentation of formerly dominant native vegetation (Burgess and Sharpe, 1981). The development and expansion of agriculture results in the reduction of the total amount of natural habitats, and generate homogeneous blocks of land subjected to one specific management regime, sometimes separated by narrow linear strips of unmanaged land. Therefore, habitat fragmentation in agricultural landscapes is characterized not only by the reduction in size and the increasing separation of remnants of natural vegetation, but also by the modification of their shape, and the formation of a system of interconnected linear strips along the boundaries of cultivated fields.

The use of agricultural landscapes by wildlife may depend on the configuration of the remnants of natural habitat (Aberg et al., 1995), as well as on the degree of dependence of focal species on forested patches (McIlroy, 1978;Salek et al., 2009). The differential use of the space should be reflected on the movement pattern and, finally, on the shape of animal home ranges (Magrini et al., 2009). Therefore, in agricultural landscapes, wildlife species depending on natural vegetation and ranging over wide areas tend to have reticular home ranges, containing large holes of unsuitable habitat (Rondinini and Boitani, 2002;Macdonald and Rushton, 2003). Alternatively, less restrictive species may spend more time in the altered, suboptimal habitats surrounding remnants (i.e. the matrix) during their displacements or foraging activities (Lindenmayer et al., 1999).

Some predators occupying high trophic levels in terrestrial food webs, depending also on forest cover, having relatively wide ranges and typically occurring at low densities, such as carnivores, are often among the species that go extinct first where human activity fragments natural systems (Beier, 1993;Primm and Clark, 1996;Mac Nally and Bennett, 1997). The extinction of wild carnivores in agricultural landscapes may have consequences for community structure through the disruption of top-down processes in which they are involved (Terborgh et al., 1999;Miller et al., 2001), and should be avoided wherever possible.

Conservation management deals with protecting sites or habitats within the landscape in which species of conservation concern are found. But habitat is a species-specific concept that does not have to match exactly a given vegetation type, as perceived

by the human eye (Lindenmayer et al., 2007). What defines a patch from a human perspective might not be particularly meaningful for a particular taxon or species assemblage (Lindenmayer et al., 2008). Indeed, its value or suitability can be markedly different to that usually assumed (Manning et al., 2004). Habitat patches need to be assessed and managed within the context of landscape mosaics and the entire landscape. One key to success in animal conservation lies in being able to predict the conditions that will favour the persistence of animals (Macdonald and Rushton, 2003), rather than their simple presence. Investigations about the details of space use by carnivores can increase our understanding of which elements of the landscape are important to preserve them and their ecological role in the food webs of agroecosystems (Marzluff et al., 2001).

Our aims are 1) to describe the patterns of movement behaviour of a carnivore, the common genet (*Genetta genetta*), inhabiting a highly modified agricultural landscape, paying special attention to avoid an anthropocentric perspective of habitat classification, and 2), to identify the attributes of landscape elements that appear to influence these behavioural patterns.

We assume a correlation between the behaviour of resident genets and the quality of habitat, and hypothesize that their movement pattern may reflect in part the spatial variation in habitat quality. Therefore, we expect to find differences in the movement parameters between areas of different habitat quality within the home ranges of genets. We predict that, in a landscape where the preferred habitat of genets is scattered in small patches, activities like foraging, eating and resting, presumably characterized by slow and sinuous movements, will be restricted to these scarce areas of relative high quality. Activities as exploration or relatively long displacements between patches rich in resources, will probably feature faster and straight movements (Zollner and Lima, 1999), which will be expected in habitats of suboptimal quality within the home range. We shall subsequently examine whether distinct movement patterns correspond to a specific configuration of landscape elements.

METHODS

Model species

The common genet (mean adult weight: 1.8 kg) is present in south-western Europe, exhibits nocturnal activity and forages on small mammals, birds and insects both in the ground and in the tree canopy (Delibes, 1974;Palomares and Delibes, 1991a). In southern Spain, it has been reported to select dense scrubland for breeding and resting (Palomares and Delibes 1994), even if this habitat type is present as narrow linear elements like hegderows (CHAPTER 3).

Study area

The study was conducted in a square landscape sample of 79.2 km^2 in the agroecosystem of the Guadiamar river, SW Spain (37º23' N, 6º13' W; Figure 1). We obtained basic information about landscape composition from a land cover layer by Junta de Andalucía (1999), and checked and corrected the position, size, shape, and content of polygons in this layer through comparison with orthophotos (Junta de Andalucía 2001) and field surveys.

Farmland covers up to 88.3% of total area, from which three main types can be distinguished: olive groves (54.6%) predominate, followed by herbaceous crops (mainly cereals and sunflower, 23.6%) and dehesa (10.1%). Dehesa is an agroforestry system that combines pastures or cereal with scattered oak trees and little or no understorey (Joffre et al. 1988). Native woody vegetation (7.7%) appears as small woodlots (3.0%), riparian forest and hedgerows. Most Mediterranean woody cover (4.7% of the landscape) was associated with three streams that run from northwest to southeast (Figure 1). Urban use covers 4.0% of the area.

The distribution of scrubland and the three main types of farmland are shown, as well as the presence of shrubby linear elements (dark grey lines). Home range, calculated as 50% and 95% kernels, has been drawn for each individual.

Cover types sharing a similar vegetation structure were simplified into four main categories that were named after the dominant component: olive groves, crops, dehesa and scrubland. Some fields, groves and dehesas without understorey are bounded by thin woody hedgerows. We defined linear structures as the landscape features disproportionably longer than it is wide, composed by trees, bushes or dense herbaceous vegetation. Within the study area we detected, digitized and characterized 187 linear structures on aerial photographs that were checked in the field. Their overall length was 73 km, of which 55% were covered by shrubs. We estimated the mean width of linear elements on aerial photographs by taking 3-16 measurements at random points along each line (n=708 measurements). Ninety-four percent of the 40 km of woody vegetation corresponded to linear structures narrower than 15 m, 88% to hedgerows <10 m wide, and 31% to lines <5 m thick. Most narrow lines in this network do not have physical connection with larger forest parches.

All landscape measurements were made on ArcView GIS 3.2 and ArcMap 9.0 (ESRI, Redlands, California, USA).

Field methods

Seventeen genets were caught with boxtraps (2.0 x 0.5 x 0.5 m) from June 2005 to March 2007 during seven short trapping sessions (mean duration: 9 days). Traps were baited with domestic pigeons, supplied with water, food and shade, and were checked daily. Animals were immobilized with tiletamine-zolazepam (Zoletil, Virbac, Spain). The age class (adult, subadult or juvenile) was determined from body weight, tooth wear, and signs of reproductive activity (CHAPTER 2). Only adults (9 individuals) were marked with radiocollars equipped with an activity sensor (Biotrack, Wareham, UK). Genets were released at the trapping place once recovered from sedation.

Animals were tracked by foot during its activity period with continuous tracking sessions of variable duration. Position of tagged animals was determined using the homing technique (Mech 1983) with the aid of a GPS unit (Garmin, Olathe, Kansas, USA), indicating the habitat type they were in. New fixes were taken every time the animal switched from active to inactive, or viceversa, or significantly change its spatial location (mean interval: 6.8 min) in order to maximize the accuracy of the movement path. To standardize the number of locations per unit time, we recalculated the position of the animals at fixed intervals of 15 minutes.

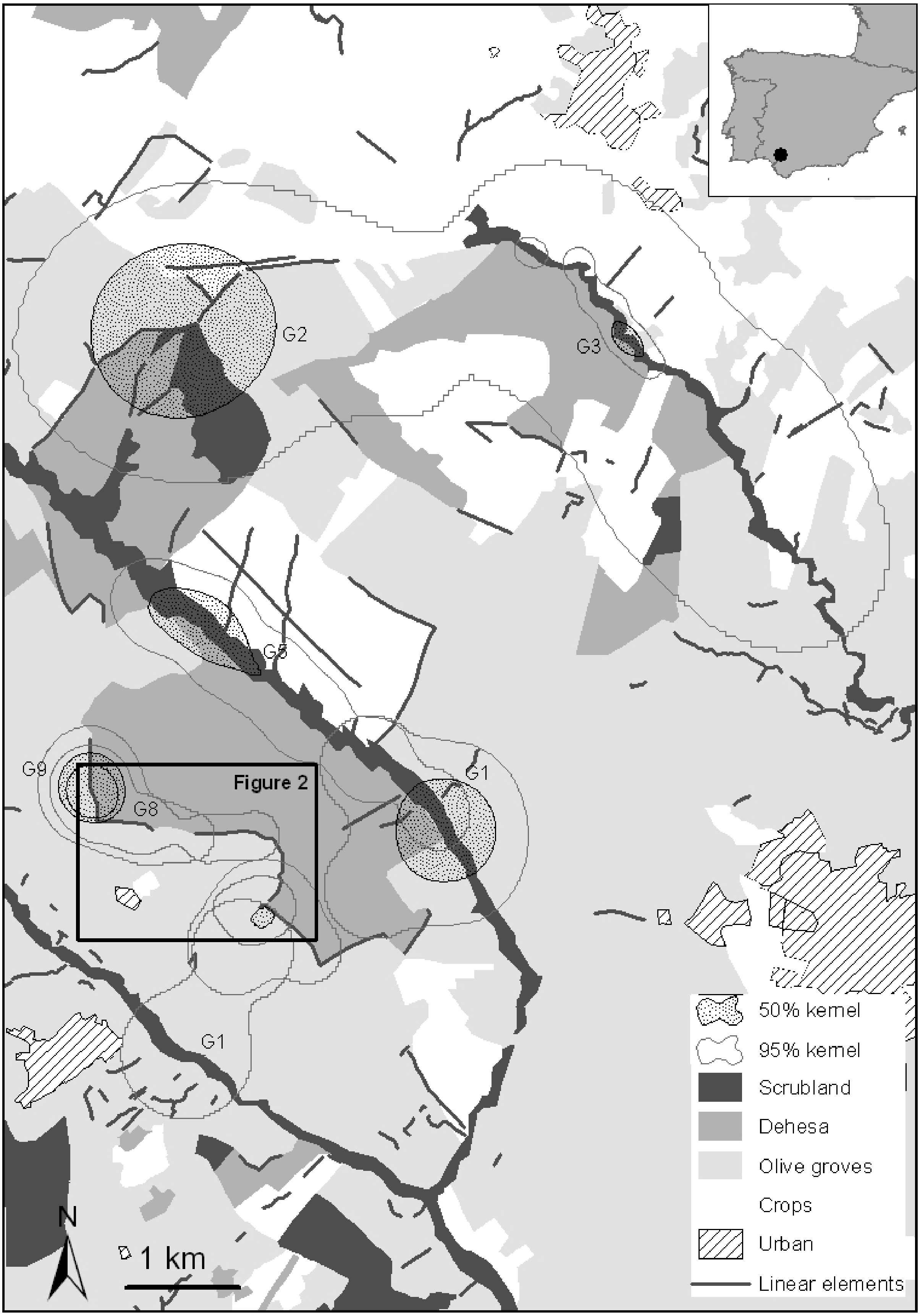


Figure 1. Study area in the Guadiamar agroecosystem, SW Spain.

Analysis

Home range estimation

Analyses were restricted to resident individuals. We checked whether MCP estimates of home range size stabilized with increasing number of fixes (Kenward 2001) and considered an animal as resident if the increase of MCP area plotted against the number of fixes decelerated and reached a plateau. To assess whether this apparent stabilization was reliable, we calculated the mean size and associated SE of 100 MCPs built with bootstrap samples for each number of positions >3. MCPs were calculated with the ArcView extension Animal Movement (Hooge and Eichenlaub 2000). The SE/mean ratio of the bootstrap samples was <0.05 above 25 fixes for all animals. One genet whose signal were lost prematurely was considered resident because its SE/mean ratio was relatively low (<0.15).

Areas of different utilization density within each home range were estimated as different kernels, with the Arcview extension Home range (Rodgers and Carr, 1998), taking one random location per day from the total pool of each individual.

Movement attributes

A path or trajectory was conformed by all straight segments linking successive locations, during a continuous tracking session. Instant velocity was calculated for each pair of consecutive fixes. We interpolated the instant velocity values at each location to estimate the position of the animal at each time unit (1 minute), and re-sampled positions with 15 minutes of separation in order to homogenise the duration of each trajectory segment (Figure 2). We called *step* to each path segment defined by two estimated locations with 15 minutes of difference (Figure 2). Each step has been characterized by its velocity and turning angle, which is the angle formed by the change of direction between two consecutive steps.

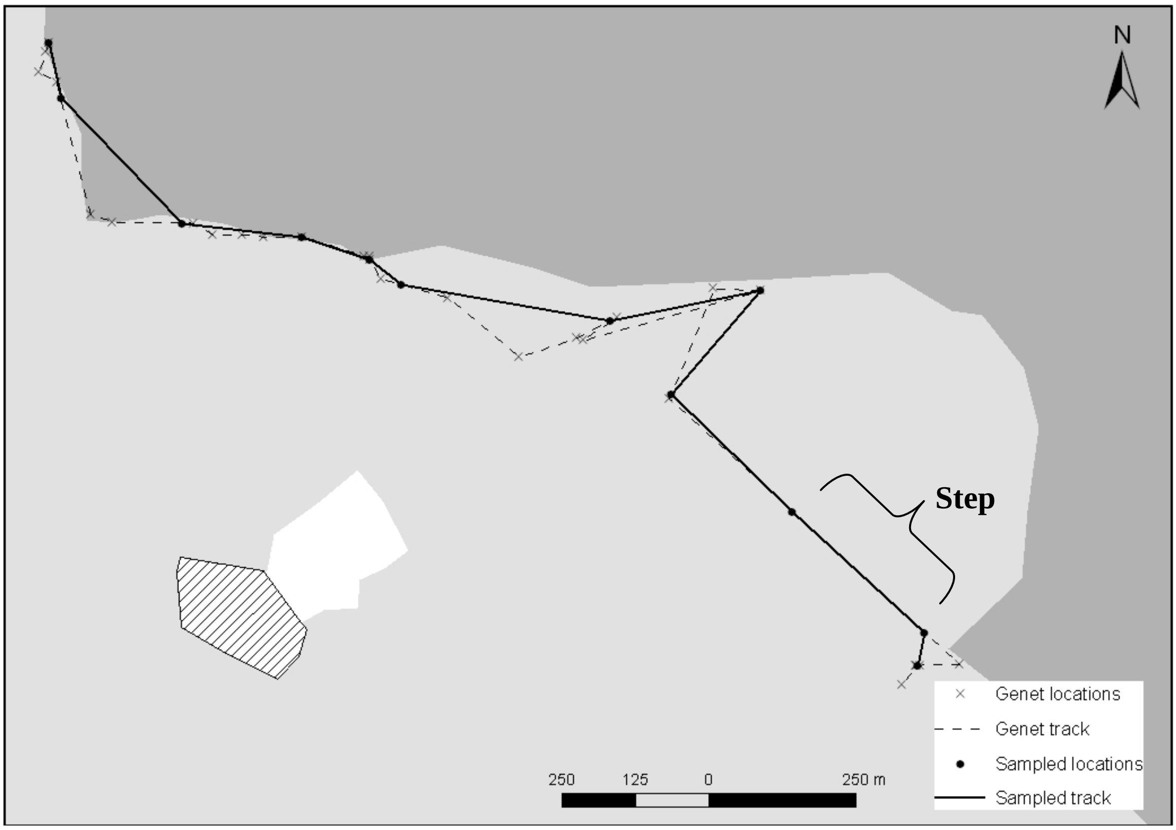


Figure 2. Example of conversion of movement field data. Crosses and broken lines denote the locations and track of a genet (G8) taken in the field; points and black lines represent the sampled locations and the resultant track, after recalculation of position per unit time and resample every 15 minutes.

All steps with velocity lower than 0.5 m/min (7.5 m length, close to GPS error range: <10 m in the study area) were considered as stops, independently of the activity performed by the genet (resting, foraging), and were not taking into account for the subsequent analysis to avoid interferences with the displacement periods. Velocity was normalized by taking logarithms.

Movement parameters were examined at different home range concentric rings with irregular shapes defined by the kernels of 50%, 65%, 80%, 95%, or 100%. Differences in mean velocity and turning angle among kernel levels were explored by means of analysis of variance (ANOVA) and Mardia Watson-Wheleer test for circular variance, respectively. Kernel classes were grouped when nor significant difference in mean velocity could be found in *post hoc* Tukey HSD tests, neither significant difference in turning angles was found using Mardia Watson-Wheleer paired tests for circular distributions. Uniform distribution or, alternatively, auto-correlation of turning angles (mean turning angle= 0º) were contrasted with Rayleigh's and V tests.

Landscape attributes

The proportion of olive groves, crops, dehesa and scrubland, and the density of hedgerows (total length per unit area) were calculated in circular areas with centre in each sampled location and radius equal to the average step length of genets (90 m). These local landscape samples were used as an estimate of the environment perceived by genets at each location. Distance to the nearest shrubby patch or linear element was also measured from the initial point of each step.

The probability of a genet using each kernel ring, defined by significant changes in movement behaviour, was modelled as a function of the landscape attributes (habitat proportion and hedgerow density at the genets' influence area, and distance to nearest scrubland) through multinomial logistic regression. Models predict the probability of animals being in each home range ring as:

$P(y=1)=1/(1+e^{X\beta(2)}+...+ e^{X\beta(n)})$
$P(y=2)= e^{X\beta(2)}/(1+e^{X\beta(2)}+...+ e^{X\beta(n)})$
...
$P(y=n)= e^{X\beta(n)}/(1+e^{X\beta(2)}+...+ e^{X\beta(n)})$,

where X and β are vectors of predictors and their coefficients, y is the home range ring (1= reference area), and $\Sigma_{y=1}^{n}$ (P)=1 (Hosmer and Lemeshow, 2000). Three sets of models have been constructed depending on the landscape variables included as predictors: a) Habitat type: proportion of each habitat type and density of hedgerows in the 90 m radius buffers; b) Distance: distance to the nearest scrubland patch or hedgerow; c) Both: habitat and distance variables. The best model was selected based on the differences in Akaike Information Criterion (ΔAIC=0), but those with $\Delta_i<2$ were considered good alternative models (Sugiura, 1978). Model selection was evaluated by means of the calculation of Akaike weights, ω_i, defined as

$\omega_i= \exp(-1/2\Delta_i)/\Sigma^{R}_{r=1} \exp(-1/2\Delta_r)$.

Akaike weights provide a measure of whether model *i* is the best of a set of models (Burnham and Anderson, 2002). Models were constructed with the R libraries VGAM and nnet (R, 2008).

RESULTS

Trapping and radio-tracking

Animals were tracked during periods whose mean length was 15 weeks (range 6-24 weeks), evenly distributed throughout the year. We obtained 95 movement paths from six genets (3M: 3H), with an average duration of 2.83 h each (Table 1).

Home range area classification by movement attributes

Mean velocity of genet steps increased with the distance of the initial point of the step to the home range core (ANOVA, F(4, 807)=10.524, p=0.000; Figure 3), from 5.01 m/min within the 50% kernel to 12.07 m/min in the outer ring between 95% and 100% kernels. Velocity differences were significant only between the steps within the 50% and the 95% rings, and between the steps within the 100% ring and the rest of kernel rings.

Table 1. The number and mean duration of continuous tracking sessions. We also show the total tracking time per individual.

Individual	*Sex*	*N*	*Mean (min)*	*SD*	*Range*	*Total (min)*
G1	M	4	191.3	105.6	105-345	765
G2	F	10	171.0	89.2	60-345	1710
G3	M	21	151.4	41.1	60-240	3180
G5	F	20	168.3	18.2	135-180	3735
G8	M	22	172.5	47.4	90-270	3795
G9	F	18	205.7	53.9	90-315	3030
Total		95	170.7	52.7	60-345	16215

Table 2. Genet home ranges size estimated as kernels of 50% and 95%. Home ranges were calculated for N independent locations obtained at random times, one per day.

Individual	*Sex*	*N*	*Kernel 50% (ha)*	*Kernel 95% (ha)*
G1	M	14	62.8	444.5
G2	F	25	192.6	1720.6
G3	M	61	5.5	44.2
G5	F	34	41.1	136.0
G8	M	43	30.7	231.9
G9	F	33	16.8	261.0

The distribution of turning angles between successive steps differed depending on their position within the home range (Mardia-Watson-Wheeler test, W=23.27, p=0.003; Figure 4). Only movements in the outer ring, between the 95% and the 100% kernels, had a uniform distribution of turning angles (Rayleigh test, Z=0.196, p=0.825). For the rest of classes, turning angles were significantly auto-correlated (V test for mean angle=0º, p<0.000).

Combining both the frequency distribution of speeds and turning angles, we decided to group kernels in three zones within the genet home range differentiated by the movement behaviour: core area (defined as a 50% kernel, Table 2), intermediate area (50%-95% kernel, Table 2) and home range periphery (95-100% kernel).

The proportion of effective displacements, a quantity inversely related with the time spent in stops, was 82% in the core and 81% in the intermediate area. No stop was recorded in the home range periphery. Mean velocity (±SE) increased from the core area (5.01 ±0.21 m/min), through the intermediate zone (9.80 ±0.60 m/min), to the periphery of the home range (12.07 ±1.18 m/min; Figure 2). Mean velocity differed significantly between the three home range rings (ANOVA, F(2, 809)=18.981, p=0.000) and between each pair of groups (Tukey test, p<0.002 for all pairs). Variability in velocity also increased from the core to the periphery (Figure 3). The distribution of turning angles differed between the three home range rings (Mardia-Watson-Wheeler test, W=12.84, p=0.012), although the differences were only significant between movements within the periphery and the other two rings (Mardia-Watson-Wheeler paired-test, p<0.005). The distribution of turning angles was uniform in the range periphery (Rayleigh test, Z=0.196, p=0.825), but highly correlated in the core and intermediate areas (V test, mean angle =0º, p<0.000; Figure 4).

In summary, genet movements were slow and highly autocorrelated within the core area, autocorrelated and with medium velocities within intermediate areas, and faster with random turning angles in the home range periphery.

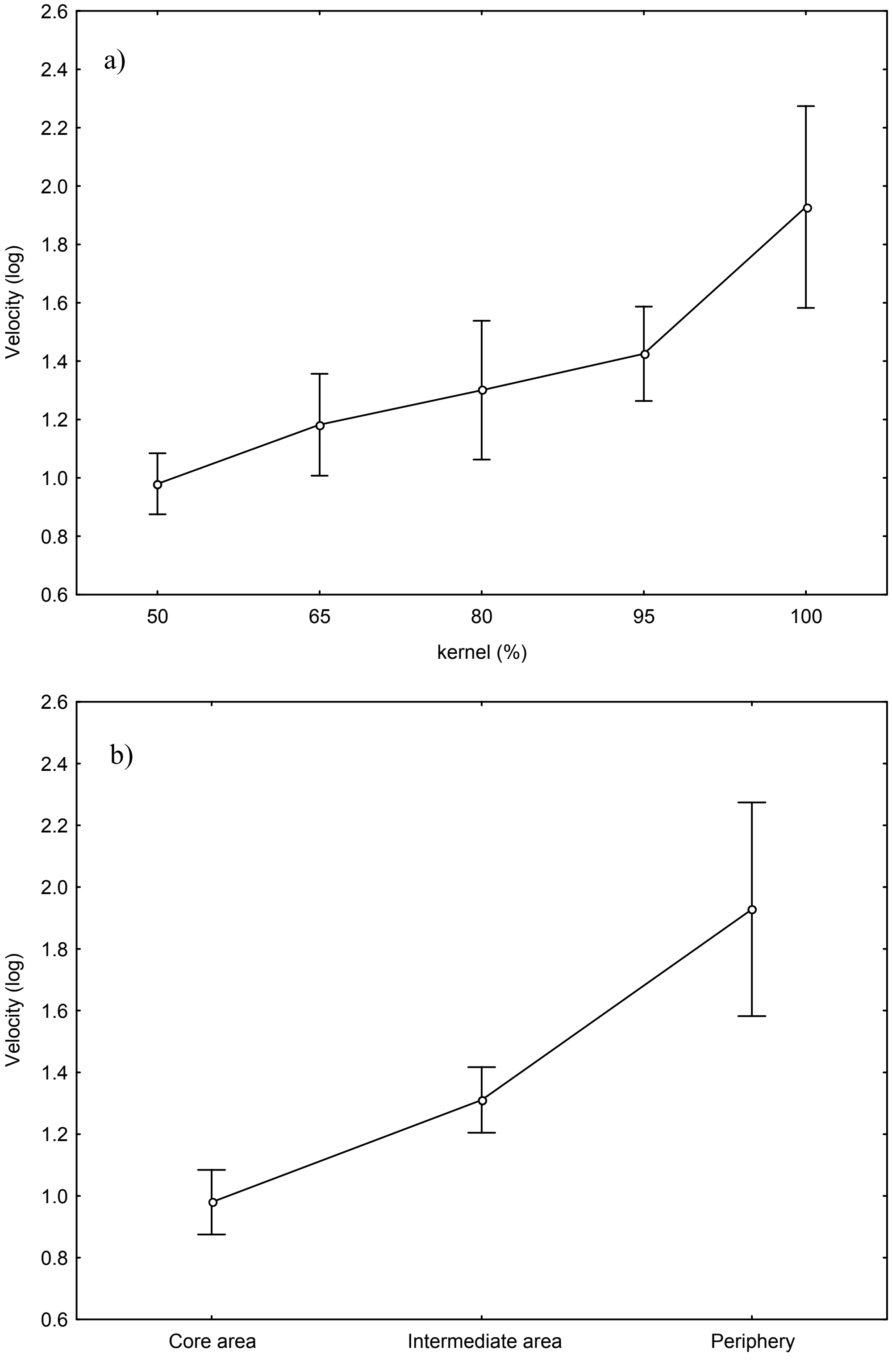


Figure 3. Log-transformed velocity values (mean and 95% confidence intervals) of the common genet steps in different zones of the home range: a) 50%, 65%, 80%, 95% and 100%; b) final simplification of kernels in three differentiated categories: core area (50%), intermediate area (50- 95%) and periphery (95%-100%).

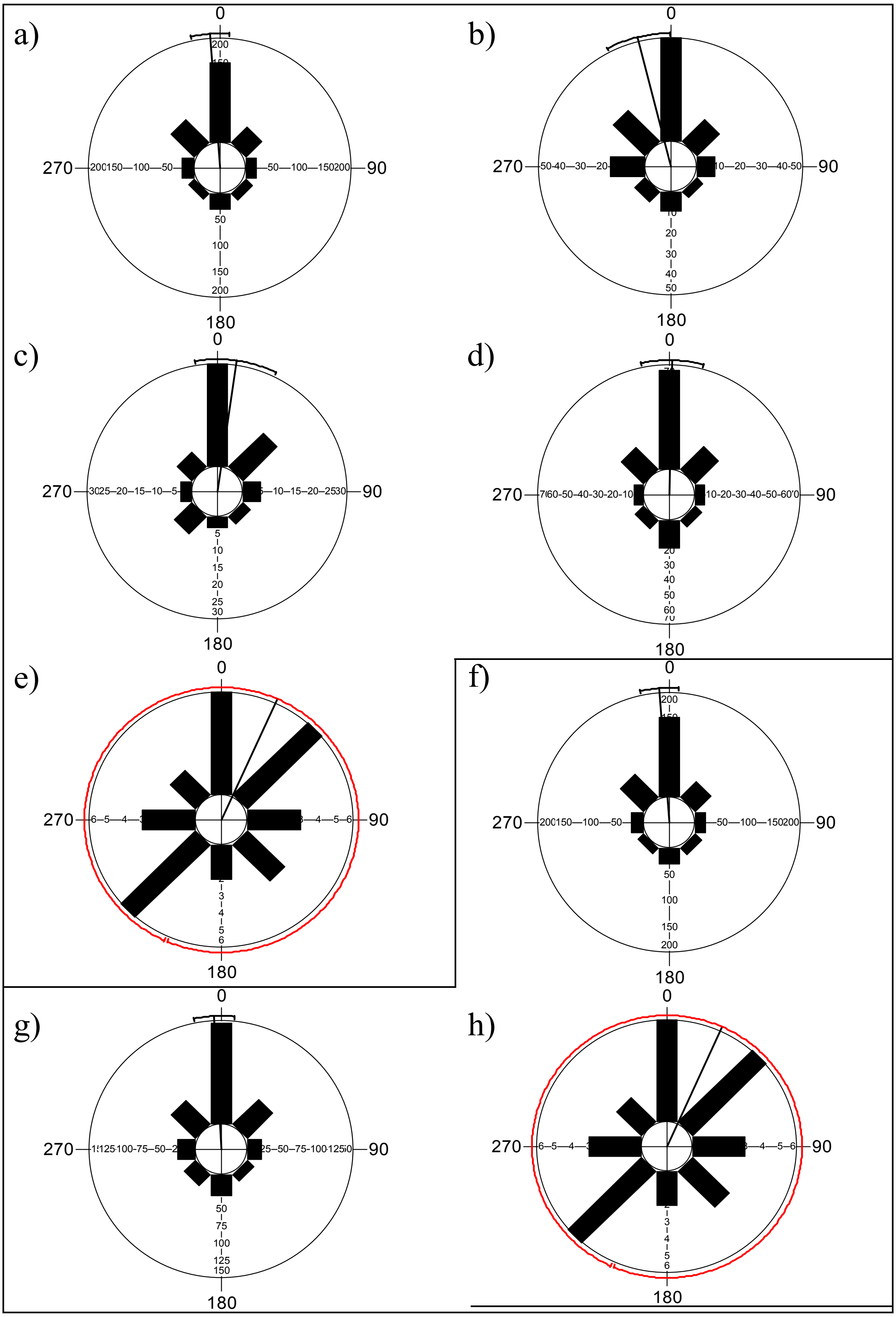


Figure 4. The distribution of turning angles between two consecutive steps, for different rings within the home ranges of common genets: a-e) 50%, 65%, 80%, 95% and 100%; f-h) final simplification of kernels in three differentiated categories: core area (50%), intermediate area (50%-95%) and home range periphery, respectively. Mean angle and 95% confidence intervals are shown as a thin radius and an arc segment. Angles were grouped in eight 45º classes.

Home range areas models by landscape attributes

The most parsimonious model describing the probability of an area being used by a genet as part of its home range included as predictors the proportion of scrubland and the density of linear elements within 90 m as well as the distance to the nearest shrubby structure (AIC= 1109.4, ω_i=0.999; Table 3).

Using home range periphery as the reference class, the probability that a given area makes part of a genet core area increases with the proportion of scrubland and the density of linear elements, and decrease with the distance to nearest scrubland structure (Table 4). We found the same trend for the probability that an area belonged to the home range intermediate area, but the strength of the landscape variables was lower compared with the core area (Table 4).

Table 3. Multinomial regression models for the probability of an area being part of a genet home rage (core area or periphery) in the Guadiamar agroecosystem. Models have been ordered based on the Akaike Information Criterion difference (ΔAIC) and model weight (ω_i). Scrubland, dehesa, olive groves and crops have been calculated as the proportion of each habitat type at 90 m around each animal location. Linear element is the shrubby linear structures density (m/ha) within the 90 m buffer. Distance makes reference to the separation (m) to the nearest shrubby patch or linear element.

	LL	K	AIC	ΔAIC	ω_i
1. Habitat					
Scrubland	-603.3	4	1214.7	105.3	0.0000000
Dehesa	-622.9	4	1253.7	144.4	0.0000000
Olive groves	-603.0	4	1214.1	104.7	0.0000000
Shrubby linear elements	-619.1	4	1246.3	136.9	0.0000000
2.Distance to scrubland or shrubby elements					
Distance	-576.8	4	1161.5	52.2	0.0000000
3. Habitat and distance					
Scrubland, Distance	-568.7	6	1149.4	40.0	0.0000000
Olive groves, Distance	-568.8	6	1149.7	40.3	0.0000000
Scrubland, Distance, Linear elements	-546.7	8	1109.4	0.0	0.9999997
Olive groves, Distance, Linear elements	-561.7	8	1139.5	30.1	0.0000003

Table 4. Selected model for the probability of an area being part of a genet home rage (core area, intermediate area or periphery) in the Guadiamar agroecosystem. Home range periphery has been used as the reference level.

	Core area			*Intermediate area*		
	Coefficient	SE	p	Coefficient	SE	p
Constant	-0.134	0.588	0.8204	1.275	0.473	0.0070
Scrubland (%)	6.728	1.330	0.0000	4.232	1.221	0.0005
Distance (m)	-0.013	0.006	0.0290	0.001	0.002	0.8046
Linear elements density (m/ha)	0.040	0.009	0.0000	0.016	0.008	0.0457

Model predictions were calculated in the range of observed values for each parameter in our study area (Table 5). Local circular buffers containing as less as 5% of scrubland have an almost 100% probability of being used as part of a genet core area (Figure5 a), as well as areas with more than 200 m/ha of shrubby linear elements (Figure 5 b). In the absence of scrubland patches, the probability of a circular buffer being part of the genet core area diminishes with the density of linear elements, favouring its use as intermediate are or home range periphery (Figure 5 b). For genet locations farther than 300 m from the nearest shrubby structure, the probability of use as intermediate area was low but higher than the probability of establishing core areas (Figure 5 c).

Table 5. Observed variation in the values of landscape variables at genet positions or in 90 m circular areas around them. Scrubland, dehesa, olive groves and crops (%) have been calculated as the proportion of each habitat type at 90 m around each animal location. Linear element is the density of shrubby linear structures (m/ha) within the 90 m buffer. Distance makes reference to the separation (m) to the nearest shrubby patch or linear element.

	Mean	SD	Mínimum	Máximum
Scrubland	30.6	34.2	0.0	100.0
Dehesa	28.9	21.1	0.0	100.0
Olive groves	38.7	34.0	0.0	100.0
Crops	1.8	6.3	0.0	54.2
Distance	30.9	95.2	0.0	798.0
Linear elements	33.3	38.2	0.0	201.1

DISCUSSION

Habitat is a species-specific concept that should not be confounded with an anthropocentric vision of cover types (Lindenmayer et al., 2007). Some authors defend the use of behaviour based methods to model the habitat use by each species rather than assuming these functions from the subjective appreciation of the landscape (Johnson et al., 2002;Morales et al., 2004;Frair et al., 2005;Chetkiewicz et al., 2006;Graves et al., 2007). We have used behavioural changes in genet movement to distinguish between different zones within home ranges and, subsequently, we have identified landscape parameters that could be influencing those changes.

Genets behaved differently depending on the intensity of use of their home ranges: Slow movements in their core area, medium velocity within intermediate areas and fast movements within the home range periphery. This pattern is consistent with the idea that individuals perform most of their daily activities, such as foraging, in their core area, which also used to be the area with more suitable resources (Mitani, 1989;Stirrat, 2003;Aiyadurai and Jhala, 2006;Plowman et al., 2006;Sarmento et al., 2006). Genets prey mostly upon small mammals and birds, whose density is also related to woody cover in agricultural habitats (Tattersall et al., 2002;Osbourne et al., 2005;Silva and Prince, 2008). In the intermediate areas, faster and directed movements could be indicating that animals are using these known zones in their displacements to most suitable patches within the home range. Fastest movements are produced in the home range periphery, coinciding with the scarcity or absent of scrubland or shrubby linear elements. This behaviour agrees with the hypothesis that individuals will move at higher velocities while crossing hostile habitats (Zollner and Lima, 2005). Another possible explanation complementing this movement pattern is the necessity for territorial species to maintain scent marking, especially near the boundaries of their home ranges, where conspecific territorial neighbours may live. This behaviour is a common form of intraspecific communication in mammal species (Allen et al., 1999;Stewart et al., 2001). Territory holders probably have to make a great effort to maintain signals in their territory periphery (Roper et al., 1993;Sillero-Zubiri and Macdonald, 1998), and they could be moving at higher velocity to cover and mark the relatively large peripheral area.

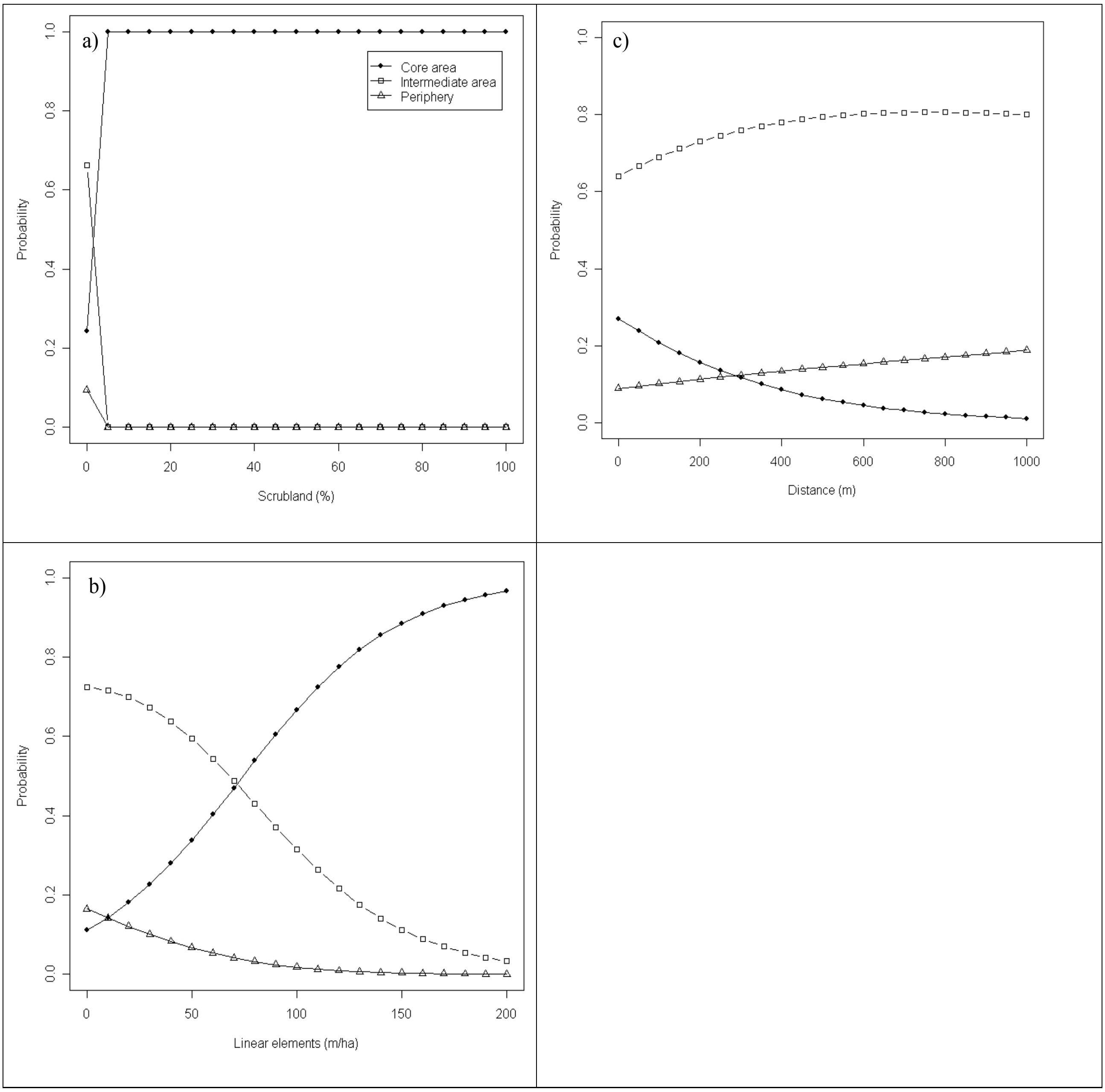


Figure 5. Predicted probability that a circular area of 2.45 ha (radius: 90 m, corresponding to the mean step of genets) belongs to different sections of a genet home range (core area, intermediate area or periphery) based on landscape parameters: proportion of scrubland (a), shrubby linear elements density (b) or distance to the nearest shrubby structure (c). Probabilities have been calculated in the range of values observed for each parameter in the study area. For probabilities based on scrubland proportion, the other model parameters were set to their mean value. For probabilities based on the density of shrubby linear elements and distance to the nearest shrubby patch or linear element, scrubland proportion was set to 0%.

Although slow movements, related to foraging and eating behaviour, were expected to be more sinuous than faster trajectories (Crist et al., 1992;With, 1994;Zollner and Lima, 1999), no difference was found between core and intermediate areas in the distribution of turning angles, where movement paths were strongly auto-correlated. This could be partly explained by the configuration of the landscape and, more specifically, by the distribution of scrubland. Dense shrubby vegetation is an essential resource for genets as it has proven to be strongly selected by this species (CHAPTER 3), but in the study area scrubland presence is in short supply and appears as linear elements such as streams and hedgerows that divide adjacent fields. The distribution and configuration of scrubland patches and linear elements may constrain the movement pattern of genets within their preferred habitat, where the expected movement was more sinuous. Consequently, directionality in the paths of genets may not be a consequence of the habitat composition, but may be imposed by the specific landscape structure of the study area. In contrast, movements within the home range periphery showed a more sinuous pattern.

When animals move in the periphery of their home ranges, in less suitable habitats, their movements may be free of the structural constraints imposed by linear structures, showing paths with a random distribution of turning angles. In addition, this behaviour could be the result of a scent marking strategy with the objective of maximizing the area covered. The greater variability in velocity shown in these peripheral areas suggest a mix of different behaviours, as displacements between suitable patches within the home range at high velocity, as well as exploration and territory marking at medium velocities.

Landscape structure seems to influence the intensity of use of regions within the home range. Genet core areas were established in areas where scrubland cover was as low as 5%. The presence of shrubby linear elements also improves the probability of use of an area by a genet, being equal in core and intermediate areas at about 70 m/ha, and increasing with the density of linear elements in core areas, especially above a density of 200 m of shrubby elements per ha. The selected model has not retained any other habitat variable different from scrubland (in the form of patches or linear elements), suggesting that the movement pattern is different in farmland, irrespective of farmland type. In agreement with habitat selection analysis by genet in the same study area (CHAPTER 3), linear scrubland appears as a key resource for this species in our agricultural landscape, either as riparian vegetation or as hedgerows. This strong dependency for dense cover is also shown in the

maximum distance of genets to these shrubby structures, which in all cases has been shorter than 800 m. Therefore, genets can live in highly managed agricultural lands if enough dense scrubland is preserved as remnant patches, or as a system of linear elements of good quality. But a good structural connectivity of the complete system of patches and hedgerows is necessary to assure the connectivity between local populations in such a fragmented landscape.

In summary, animal behaviour and more specifically movement pattern can be used to define areas of different importance for the specie's conservation. The utilization of landscape attributes in the animal context, including landscape configuration, should help us to avoid an anthropogenic classification of habitats that, in some cases, could lead us to false conservation decisions.

ACKNOWLEDGEMENTS

This research was funded by the Consejería de Innovación, Ciencia y Empresa (grant P06-RNM-1903), and Consejería de Medio Ambiente, Junta de Andalucía, as well as by CSIC (grant 200830I195). MP was supported by Ministerio de Educación, Cultura y Deporte through a FPU fellowship (AP2003-2370). Jolies Dortland and Luis León helped with the field work. Eloy Revilla suggested the title and gave valuable advices about the statistical approach. I specially thank Ruben Pardo for the design of the *Triangulator* and *Eseguimiento* software tools for the movement data treatment.

CAPÍTULO 5

*Patrones de movimiento del meloncillo (*Herpestes ichneumon*) en dos diferentes paisajes Mediterráneos*

Movement patterns of the Egyptian mongoose (*Herpestes ichneumon*) in two different Mediterranean landscapes

RESUMEN

La fragmentación de los hábitats naturales y la pérdida de heterogeneidad afectan a la conexión estructural del paisaje. Sin embargo, la conectividad funcional implica que los parches de hábitat se encuentran conectados por el movimiento de los animales, siempre que estos sean capaces de cruzar la matriz y, por tanto, estará determinada por el comportamiento animal. Proponemos la hipótesis de que el comportamiento animal, y especialmente los patrones de movimiento, diferirá entre paisajes con diferente composición y configuración espacial de los hábitats naturales. Hemos estudiado los patrones de movimientos del meloncillo (*Herpestes ichneumon*) en dos paisajes vecinos en el suroeste de España, con marcadas diferencias en la configuración y cantidad de su hábitat preferenet (matorral): un paisaje agrícola y el Parque Nacional de Doñana. Posteriormente hemos determinado la importancia de la proporción de matorral y la heterogeneidad del paisaje a diferentes escalas espaciales, para cada parámetro del movimiento.

En el agrosistema, la escasez y aislamiento del matorral es severa a escala regional, pero está altamente conectado a escala local. En Doñana, el matorral es abundante pero fraccionado, mientras que la matriz es menos inhóspita que en el agrosistema, por lo que los movimientos en hábitat subóptimos son más comunes. Como resultado, las trayectorias de los meloncillos de Doñana mostraron un mayor desplazamiento neto medio, mayor velocidad media, y una mayor proporción de paradas que los meloncillos del paisaje agrícola. Con independencia del área de estudio, el desplazamiento neto, la longitud total y la velocidad del mismo parecen ser influenciados por el matorral y la heterogeneidad presentes tanto en el contexto inmediato y el más amplio de las localizaciones del meloncillo.

ABSTRACT

Fragmentation of natural habitats and loss of heterogeneity affect the structural connectedness of a landscape. However, functional connectivity implies that habitat patches are connected by animal movement, provided that animals are capable to cross the matrix and, therefore, will be determined by animal behaviour. We hypothesize that animal behaviour, and specifically movement pattern, will differ between landscapes differing in the amount and spatial configuration of natural habitat. We have studied and compared the movement patterns of the Egyptian mongoose (*Herpestes ichneumon*) in two neighbouring areas of southwestern Spain, but with marked differences in configuration and preferred habitat composition (scrubland): an agricultural landscape and Doñana National Park. Subsequently we have determined the importance of proportion of scrubland and heterogeneity of landscape at different spatial scales, for each movement parameter.

In the agroecosystem, lack and isolation of scrubland is severe at the regional scale, but highly connected at the local scale. In Doñana, the scrubland is abundant but patchy, and the matrix is less inhospitalable than in the agroecosystem, so movements into suboptimal habitat may be more common. As a result, paths of mongooses living in Doñana showed higher mean net displacement, higher mean velocity and higher mean proportion of stops than those of mongooses inhabiting the agroecosystem. With independence of the study area, net displacement, total path length and velocity appeared to be influenced by scrubland and heterogeneity at both immediate and wider context of the mongoose location.

INTRODUCTION

With the development of agriculture, natural vegetation has been, and is still being, highly modified. One of the effects of the clearing of native vegetation is the increasing isolation and fragmentation of remnants, resulting in the majority of wild species finding their preferential habitat as patches immersed in a matrix of degraded agricultural or urban land (Forman and Godron, 1981;Forman and Godron, 1986). Commonly, agriculture transformation also implies the geometrization of land, decreasing the variability and heterogeneity of habitats compared to natural landscapes (Forman and Godron, 1986).

Both fragmentation of natural habitats and loss of heterogeneity affect the structural connectedness of a landscape, understood as the physical links between the remnant elements. However, functional connectivity implies that habitat patches are connected by animal movement, provided that animals are capable to cross the matrix even in the absence of structural connections between habitat patches (With et al., 1999). Yet the degree with which connectivity differs between landscapes may largely rely on their structure and the spatial configuration of fragments of natural vegetation as well as on how animals perceive, use and move between these fragments. Therefore connectivity is a species-specific attribute largely determined by animal behaviour, specifically the frequency of interpatch movement in a specific landscape configuration.

The heterogeneity level of a landscape is basically determined by the distribution and spatial arrangement of essential resources. Heterogeneity, therefore, should influence animal behaviour (Martin et al., 2001), which is expected to maximize the ratio between fitness benefit and energy cost of foraging as well as the patterns of other types of movement (Wiens et al., 1995). Patterns of movement can be characterized by quantitative attributes such as net displacement or tortuosity (Crist et al., 1992;Wiens et al., 1997;McIntyre and Wiens, 1999;With et al., 1999). It has been hypothetised that animals will move more slowly and sinuously in good quality habitats, while faster and straighter movements will be observed in relatively hostile habitats (Crist et al., 1992;With, 1994;Zollner and Lima, 1999).

Some authors have proposed that patterns of animal movement may emerge both from decisions at a small scale, as a response to the composition and heterogeneity of resources, and decisions at larger spatial and temporal scales (With, 1994) that may reflect the organism's perception of the landscape and their spatial memory (Lima and Zollner, 1996;Olden et al., 2004). This perception is expected to vary among individuals as well as among species (With, 1994;Crist and Wiens, 1995;Diffendorfer et al., 1995;Wiens et al., 1997;Haddad, 1999)

We have studied the movement patterns of the Egyptian mongoose (*Herpestes ichneumon*) in two neighbouring areas of southwestern Spain. These areas largely differ in the composition and structure of their landscapes and, more specifically, in the amount and spatial distribution of scrubland, which is the preferred habitat of mongooses in Mediterranean ecosystems (Palomares & Delibes 1990, 1993). One landscape is dominated by agriculture while the other is dominated by scrubland.

Our aim was to assess differences in movement attributes of mongooses living in these highly contrasting landscapes in order to determine the importance of landscape structure on mongoose behaviour at three spatial scales. We hypothesize that 1) movement patterns of individuals will differ between the two landscapes differing in the amount and spatial configuration of scrubland; 2) in the agricultural landscape mongooses will cover more distance in their foraging movements to achieve suitable resources in patches more separated than in the forest landscape, 3) in the agricultural landscape the probability that mongooses will cross open habitats between forested patches during their daily movements will be higher than in the more continuous and homogeneous forest landscape and, 4) in the forested landscape the movement of mongooses will be slower, and more continuous and tortuous than in the agricultural landscape.

As dense scrubland is scarcer and fragmented in the agro-ecosystem landscape, we expect that mongooses living in Guadiamar would need to cover more distance (total path length) to achieve the necessary resources than mongooses living in the National Park; to move frequently among shrubby patches, increasing its net displacement; and to move at higher velocity and less sinuosity in their displacements, spending more time in the stops when they find a suitable refuge.

METHODS

Study area

We conducted our study in two areas of southwestern Spain only 10 km away but with marked differences in landscape structure, habitat composition, and intensity of anthropogenic use. We defined our first study area as a square landscape sample of 79 km^2 in the Guadiamar basin (37º2’N, -6º21’W; Figure 1) where the most common habitat types are cultures, mainly olive groves and cereal crops (78%, *open habitats* in Table 1). Forest cover occurs as dehesas and Mediterranean scrubland, mostly associated with three streams. Some fields, groves and dehesas are bounded by thin woody hedgerows (88% of hedgerows <10 m wide).

We selected a landscape sample of 70 km^2 in Coto del Rey, a plain region with sandy soils in northern Doñana National Park (37º9’N, -6º26’W; Figure 1). Forest cover includes patches of pinewood and eucalyptus with scarce shrubby vegetation, riparian forest, and blocks masses of dense shrubs, mainly *Pistacia lentiscus*, interspersed with small patches of open pastures. Larger pasture patches occur in the south and southeast, bordering the marshes, and dehesa with low tree density occurs in the west.

We obtained basic information about landscape composition from a land cover layer by Junta de Andalucía (1999), corrected through comparison with orthophotos (Junta de Andalucía 2001) and field surveys (Fernandez et al., 2003). Cover types that shared a similar vegetation structure were simplified into three main categories based on the presence and density of woody cover: scrubland (with or without trees), woodland (with little or no understorey) and open habitats (Table 1).The woodland class encompassed pinewood, eucalyptus patches and dehesas, whereas the open class included pastures and agricultural lands. Urban areas and water bodies were considered as unsuitable habitats and, then, subtracted from the total area.

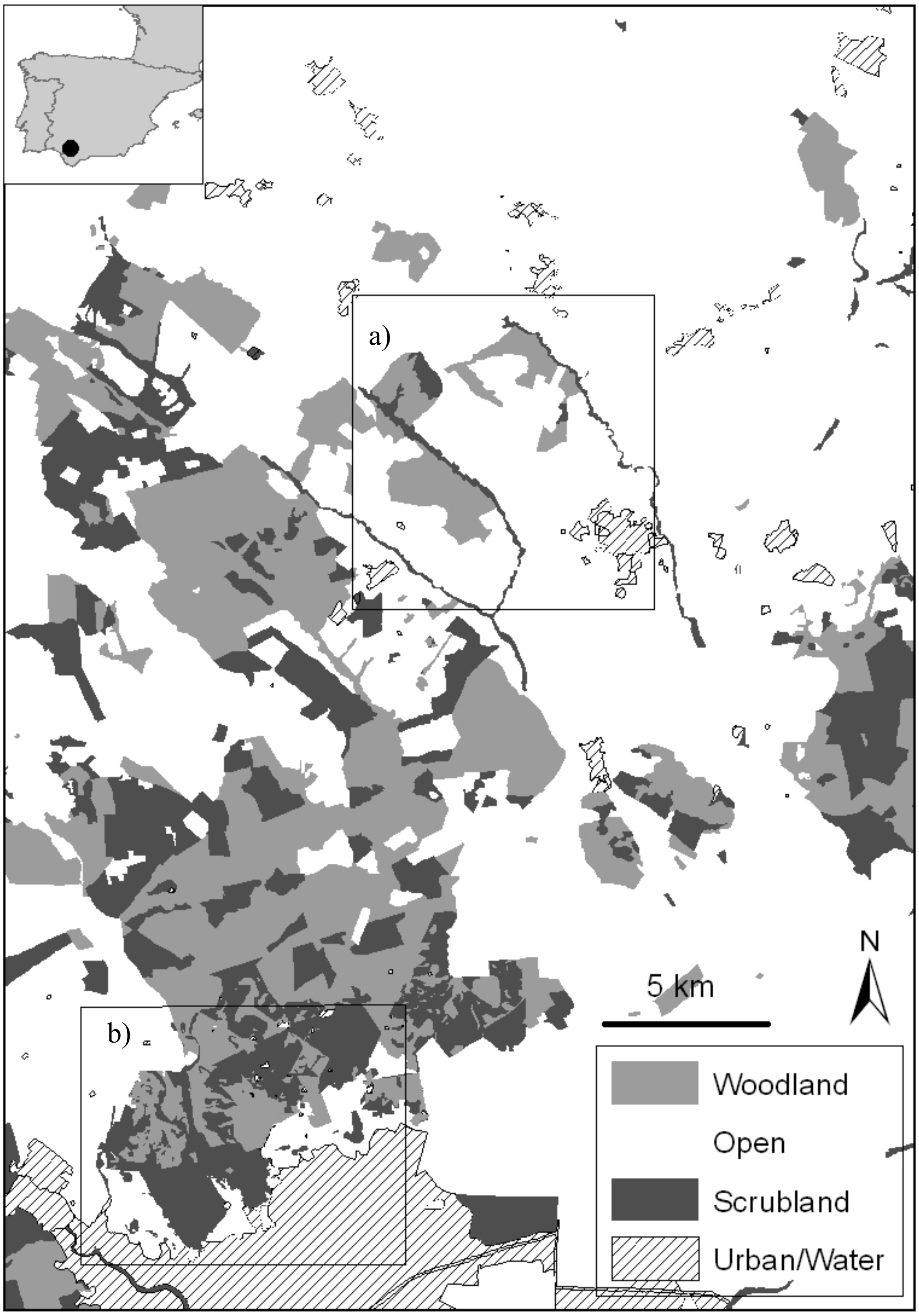


Figure 1. Location of the two study areas: Guadiamar agroecosystem (a) and Coto del Rey (Doñana National Park) (b), SW Spain. Habitats types have been classified in scrubland, woodland and open habitats. Urban and watershed are considered unavailable for the Egyptian mongoose.

Table 1. Landscape attributes of the agricultural landscape (Guadiamar) and the forest landscape (Doñana). The mean proportion and standard deviation (SD) of habitat types in the wider context (a 200 m wide strip at both sides of the path) and the immediate context (linear path) of mongooses is shown in the lower panel. Number of sample paths: n= 86 in Guadiamar; n= 39 in Doñana. Non-parametric comparisons between the two study areas (Wald-Wolfowitz test; Z approximation and significance level, p) are shown.

STUDY AREA	Guadiamar		Doñana		Wald-Wolfowitz Test	
Area (km2)	79.2		69.9			
Scrubland (%)	4.7		33.6			
Woodland (%)	13.3		21.5			
Open (%)	78.4		44.9			
Heterogeneity	152.0		546.0			
Connectance	1.1		2.7			
WIDER CONTEXT	**Mean**	**S.D.**	**Mean**	**S.D.**	**Z**	**p**
Scrubland (%)	31.4	12.6	53.4	22.6	-2.653	0.0080
Woodland (%)	24.0	17.5	24.5	22.6	0.070	0.9438
Open (%)	45.1	22.9	21.9	25.6	-3.909	0.0001
Heterogeneity	5.9	1.7	16.7	8.2	-8.099	0.0000
Connectance	54.3	39.3	34.1	35.8	-2.024	0.0429
IMMEDIATE CONTEXT						
Scrubland (%)	85.8	24.4	53.1	32.6	-5.376	0.0000
Woodland (%)	2.7	10.4	16.9	25.7	-2.338	0.0194
Open (%)	7.9	20.8	28.8	33.9	-1.396	0.1966
Heterogeneity	1.9	1.1	6.5	4.6	-6.423	0.0000

Within the Guadiamar study area we detected, digitized and characterized 187 linear structures on aerial photographs that were subsequently checked in the field, of which 55% were made of shrubs. In order to estimate the area covered by shrubby linear elements we assigned them an arbitrary width of 10 m and integrated them into the general cover map. No linear element was detected in the Doñana study area.

Summing up all patches and linear elements, the proportion of forest in general, and scrubland in particular, in Doñana was seven times higher than in Guadiamar (34% versus 5% of scrubland, respectively; Table 1).

All landscape measurements were made on ArcView GIS 3.2 and ArcMap 9.0 (ESRI, Redlands, California, USA).

Field methods

Mongooses were caught with boxtraps (2.0 x 0.5 x 0.5 m) from 1988 to 1995 in Doñana, and from 2005 to 2007 in Guadiamar. Ten individuals (3M: 7F) in Guadiamar and 14 (2M: 12F) in Doñana were marked with radio-collars equipped with an activity sensor (Guadiamar: Biotrack, Wareham, UK; Doñana: Wildlife Materials, Inc., Illinois, USA).

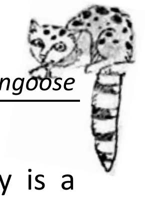
Egyptian mongooses are diurnal (Palomares and Delibes, 1992a) and tracking sessions took place during their activity period, between 0600 and 1900 GTM on foot and at short distances, but without disturbing them. This method allowed us to check the habitat at each location and to minimize the error associated with triangulation. All tagged mongooses were adults and showed stable home ranges.

The radio-tracking schedule varied between study areas. In Doñana intensive tracking sessions lasted the whole activity period and were performed taking one fix every 15 minutes. In Guadiamar continuous tracking sessions were shorter (200 min on average) and a new fix was taken every time the animal moved. Positions in Doñana were recorded in a map through triangulation or observation at short distance, whereas in Guadiamar positions were estimated with a GPS receiver once the animal had left the place. To standardize the temporal scale and to ease comparisons between the two data sets, we recalculated the animal position of the Guadiamar mongooses every 15 minutes (cf. Chapter 4), and took random sub-samples of 10 consecutive locations in each daily movement path of individuals living in both study areas.

Movement characterization

Each path sample was composed of 10 locations and 9 steps. We called *step* each path segment between two consecutive locations, taken with 15 minutes of difference. We considered that the animal *stopped* when step length was lower than 7 m, as this distance approaches the measurement error of the GPS or the triangulation error from bearings taken at short distances.

The following attributes of paths were measured: net displacement (euclidean distance between the initial and final location), path length (sum of all steps length), mean velocity (total length per total displacement time, without stops), proportion of stops (percentage of time without displacement respect the total path duration) and sinuosity, as



an index of the curvature and complexity degree of the movement path. Sinuosity is a measure of deviation of a path length from the shortest possible path, calculated as the ratio between path length and net displacement.

Landscape characterization

The composition and structure of habitat has been characterized at three levels corresponding to three increasing spatial scales at which mongoose movement was considered: immediate context, wider context, and landscape. We defined the mongoose immediate context as the habitat intersected by the trajectory composed of 9 steps in each movement sample. The wider context was defined as an influence strip 200 m wide at both sides of each trajectory. Finally, we called landscape to the landscape samples defined by the study areas in Doñana and Guadiamar.

We calculated the proportion of shrub, tree and open cover along the immediate context and within the wider context for each movement sample. The number of linear segments, defined by transition points at the interface between two different and adjacent habitat types, was used as an index of heterogeneity at the immediate context scale, while the total number of patches was used to describe heterogeneity at the wider context scale.

An index of connectance (*connect*) was calculated to evaluate the structural connection between shrubby patches in each landscape as well as within strips of the wider context around path surroundings. The index *connect* was defined as the number of functional joinings between patches of the same type, where each pair of patches is either connected or not based on a user-specified distance criterion (10 m at the wider context scale, 200 m at the landscape scale). The index is reported as a percentage of the maximum possible connectance given the number of patches (McGarigal and Marks, 1995):

$$\mathrm{CONNECT}= [\Sigma\ c_{ij} / (n\ (n-1)^{*}/2)]^{*}100$$

where c_{ij} indicates whether a joining exists between patch i and j (1 = joined, 0 = unjoined) of the same patch type (scrubland); and n is the number of scrubland patches in the landscape unit.

Landscape indices were calculated with the ARCGIS extension Hawth's Analysis Tools v.3.27 (Beyer, 2002) and the program of spatial analysis FRAGSTATS (McGarigal and Marks, 1995). Vectorial habitat file was rasterized into a 10 m pixel raster file in order to use FRAGSTATS software.

Statistical Analysis

Net displacement and sinuosity were normalized by calculating their decimal logarithm, and the percentage of stops was normalized by taking the arcsine of its square root (Zar, 2004). As an exploratory approximation, we compared the values of each movement parameter between the two study areas by means of a t-test.

The influence of landscape attributes on each of the movement parameters defining mongoose paths was modelled through Generalized Linear Mixed Models (GLMMs) with gaussian errors and specifying individual identity as a random effect. The study area (landscape type) was fitted as a dichotomic factor that was kept in all alternative models, being Guadiamar the reference level. We used the proportion of *scrubland* and *heterogeneity* indices at immediate and wider context as predictors.

For each movement parameter, we built and compared the following set of models: a) scrubland and heterogeneity in the immediate context; b) scrubland and heterogeneity in the wider context; c) scrubland and heterogeneity at both immediate and wider context, simplified by removing the non-significant variables (Crawley, 2002), and d) only landscape type.

Statistical analyses were carried out with the programs STATISTICA 6.0 and R (R, 2004).

RESULTS

Whereas the scrubland proportion is higher in Doñana at landscape and mongoose's wider context scale, this relationship reverses at the mongoose's immediate context (Table 1). In both study areas, the proportion of shrubby habitats increased at the wide context with respect to the total availability in each study area: 6.7 times (from 5% to 31%) higher in Guadiamar, and1.6 time higher (from 34% to 53%) in Doñana. The scrubland proportion at the immediate context (53%, Table 1) was similar to the availability at the wider context scale for the Doñana samples, but increased till 86% in the case of Guadiamar linear paths (18 times higher than scrubland availability at landscape scale). Landscape heterogeneity

decreased with the spatial scale, and was always higher in Doñana than in Guadiamar (Table 1).

The structural connectance of scrubland increased from the landscape to the wider context scale, for both study areas. Scrubland is better connected in the National Park than in the agro-ecosystem at landscape scale, but when the spatial resolution increases (till mongooses wider context) the relationship changed, being the connectance in Guadiamar significantly higher than in Doñana (Table 1; Figure 2).

Although the mean total length of path samples did not significantly differ between mongooses living in both study areas (mean values around 560 m; Table 2), the mean net displacement in Doñana (559 m) was significantly higher than the mean net displacement in Guadiamar (312 m; Table 2). In contrast with our expectations, the mean velocity of mongooses in Doñana (13.6 m/min) was significantly higher (Table 2) than their mean velocity in Guadiamar (4.8 m/min). In Doñana, the mean proportion of time spent in stops (39%) was significantly higher (Table 2) than in Guadiamar (14.3%). There was no significant difference in the mean sinuosity index between both landscapes (values in the range 0.8-0.9; Table 2).

Table 2. Description of the movement parameters (average and standard deviation-SD-) of the trajectories of the sampled mongooses in Guadiamar and Doñana. Number of sample paths: 86 and 39 in Guadiamar and Doñana, respectively.

	Guadiamar		Doñana		T-test	
	Average	SD	Average	SD	t-value	p
Net displacement (m)	311.6	307.3	559.1	419.8	-4.063	0.0001
Total path length (m)	566.0	402.3	558.4	420.8	0.097	0.9227
Velocity (m/min)	4.8	3.1	13.6	7.0	-9.782	0.0000
Stops (%)	14.3	18.0	39.0	23.5	-6.135	0.0000
Sinuosity	0.9	0.9	0.8	0.6	0.797	0.4271

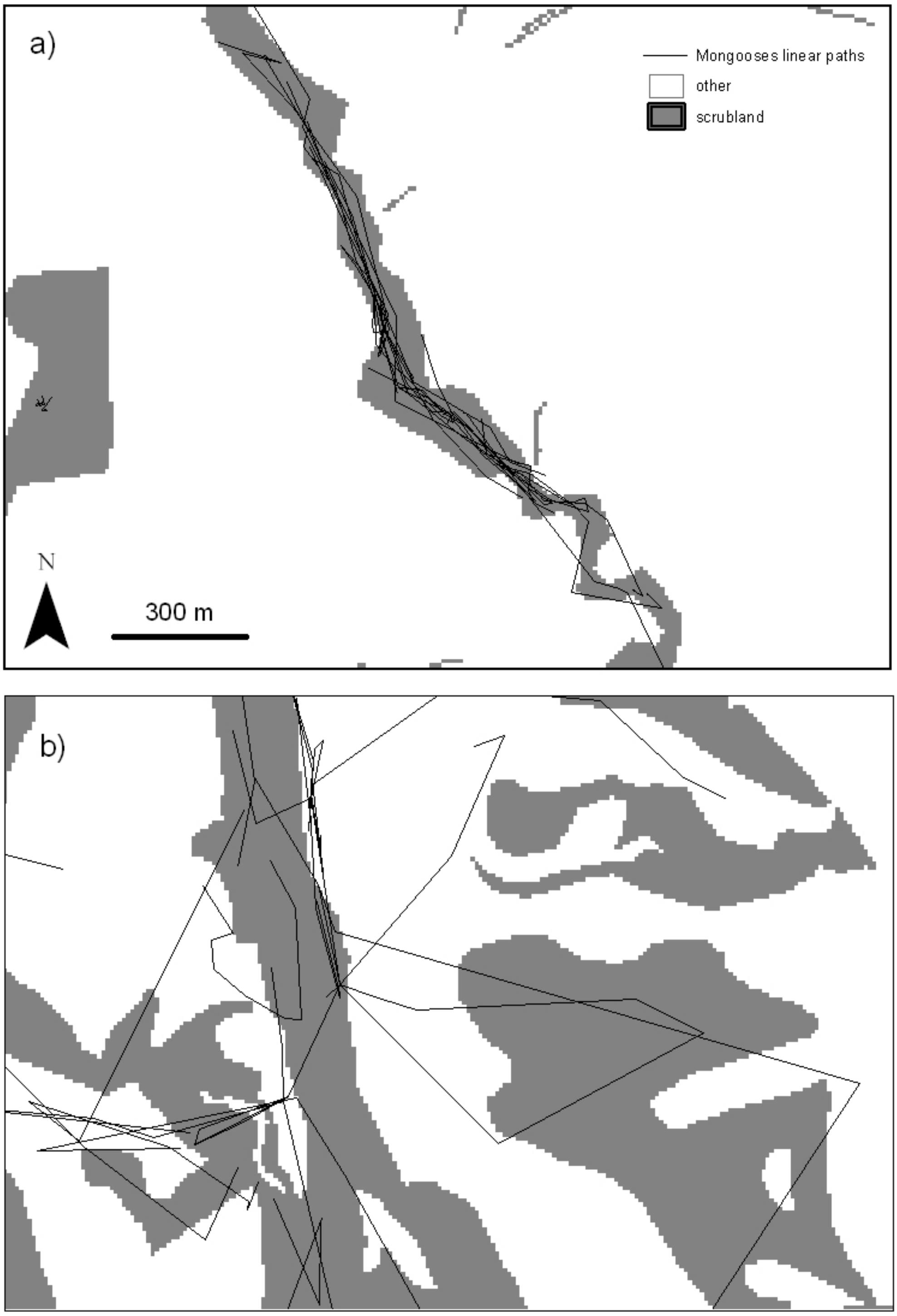


Figure 2. Detail of scrubland (grey) and other habitat types (white) distribution in Guadiamar (a) and Doñana (b) study areas. A few trajectories are shown (black lines).

Net displacement was higher in Doñana than in Guadiamar, but this relationship changes when the effect of scrubland proportion and heterogeneity is controlled in the model (Table 3a). Differences in net displacement between the two study areas lost its significance when the model included landscape attributes at lower spatial scales. As expected, net

displacement increased with habitat heterogeneity at both immediate and wider context. Only when both spatial scales were combined, the negative effect of the proportion of scrubland on net displacement was significant.

Although differences in total path length between study areas were not significant (Table 2), the effect of landscape type (Guadiamar vs. Doñana) acquired significance in the simplest mixed model (Table 3b) once inter-individual variation was controlled for by specifying mongoose identity as a random factor. The effect of landscape disappeared again with the addition of landscape parameters at immediate or wider context: total path length increases with the heterogeneity at both spatial scales, and decreases with the scrubland proportion at the wider context scale.

Contrary to what we expected, the mean velocity of displacements in Guadiamar was significantly lower than in Doñana for all models, decreasing with the proportion of scrubland in the wider context, and increasing with the heterogeneity at both immediate and wider context scales (Table 3c).

The proportion of time that mongooses spend in stops was significantly higher in Doñana than in Guadiamar for all models, and decreased with the heterogeneity in the immediate and wider context. Only marginally, the proportion of scrubland during the trajectory had a negative effect on the time spent in stops (Table 3d).

No landscape variable, not even the landscape type, had a significant effect on path sinuosity (Table 3.e).

For all movement parameters models, the trend of the landscape attributes (scrubland proportion and heterogeneity) agreed for both immediate and wider context scales.

Table 3. Generalized Linear Mixed Models for each movement parameter (a) Net displacement; b) Total length; c) Velocity; d) Stops, and e) Sinuosity) based on: 1) Landscape (Guadiamar-reference level-, Doñana); 2) Landscape and mongoose's immediate context, defined as the linear path; 3) Landscape and mongoose's wider context, defined as a 200 m buffer around the path; and 4) TOTAL: Landscape and mongoose's immediate and wider context. Landscape (study area) is kept in all models. Coefficients and standard error of variables are shown.

	1) Landscape			*2) Immediate context*			*3) Wider context*			*4) TOTAL*		
	Estimate	Std. Error		Estimate	Std. Error		Estimate	Std. Error		Estimate	Std. Error	
a) NET DISPLACEMENT												
Landscape	0.721	0.362	*	-0.003	0.385		-0.238	0.412		-0.745	0.420	•
Scrubland- wider context							-0.012	0.007	•			
Heterogeneity- wider context							0.116	0.022	***	0.115	0.022	***
Scrubland- immediate context				-0.003	0.004					-0.009	0.004	**
Heterogeneity- immediate context				0.141	0.040	***						
Variance (%)	0.9			4.2			7.0			7.6		
b) TOTAL LENGTH												
Landscape	725.310	148.220	***	-39.578	164.801		-194.303	180.000		-206.359	170.280	
Scrubland- wider context							-13.164	2.673	***	-7.832	3.010	**
Heterogeneity- wider context							113.545	7.591	***	69.369	15.096	***
Scrubland- immediate context				1.737	1.392							
Heterogeneity- immediate context				188.752	13.398	***				85.012	25.512	***
Variance (%)	0.7			6.5			6.8			7.4		
c) VELOCITY												
Landscape	9.026	1.454	***	4.965	1.509	***	5.711	1.535	***	5.711	1.535	***
Scrubland- wider context							-0.127	0.024	***	-0.127	0.024	***
Heterogeneity- wider context							0.567	0.068	***	0.567	0.068	***
Scrubland- immediate context				-0.026	0.013	•						
Heterogeneity- immediate context				0.764	0.130	***						
Variance (%)	7.8			7.6			10.9			10.9		

	1) Landscape			*2) Immediate context*			*3) Wider context*			*4) TOTAL*		
	Estimate	Std. Error		Estimate	Std. Error		Estimate	Std. Error		Estimate	Std. Error	
d) STOPS												
Landscape	0.349	0.057	***	0.411	0.075	***	0.555	0.083	***	0.555	0.083	***
Scrubland- wider context							-0.002	0.002		-0.002	0.002	
Heterogeneity- wider context							-0.015	0.006	**	-0.015	0.006	**
Scrubland- immediate context				-0.002	0.001	•						
Heterogeneity- immediate context				-0.025	0.010	**						
Variance (%)	25.4			39.9			43.1			43.1		
e) SINUOSITY												
Landscape	-0.128	0.161		-0.230	0.212		-0.239	0.237		-0.128	0.161	
Scrubland- wider context							-0.002	0.005				
Heterogeneity- wider context							0.009	0.016				
Scrubland- immediate context				0.002	0.003							
Heterogeneity- immediate context				0.026	0.027							
Variance (%)	0.5			0.1			0.6			0.5		

p-value: '***'<0.001, '**'<0.01, '*'<0.05, '•'<0.1
Variance (%): proportion of the data variance explained by the model

DISCUSSION

The movement pattern of the *Egyptian mongoose* differed between the two study areas but, contrary to our expectations, paths of mongooses living in Doñana had higher mean net displacement, higher mean velocity and higher mean proportion of stops than those of mongooses inhabiting the Guadiamar agroecosystem. Also contrary with our spectations, the mean total path length and mean path sinuosity were similar in both landscapes.

Models for each movement parameter but sinuosity included landscape attributes with significant effects in the immediate and wider context of the mongoose path, showing

that landscape structure and composition are influencing the movement pattern of this specie at both spatial scales (Table 3).

Landscape heterogeneity appeared significant in all models, at both immediate and wider context scales. The increase of landscape heterogeneity was associated with an increase in the net displacement, total path length and velocity, while the proportion of stops decreased. The increase in heterogeneity at those spatial scales could mean a higher use of non-preferred habitats by the mongoose, where the movement is expected to be faster and straighter than within the scrubland. The easiness to find suitable habitats as refuge in the proximity of animal locations when the heterogeneity was high can facilitate the use of scrubland and adjacent open habitats in Doñana. Otherwise, in the Guadiamar landscape the preferred habitat for the mongoose is scarce and concentrated in a few patches, and this could constrain their movements to be inside these patches due to a potentially avoidance to use larger tracts of open land.

Net displacement in Doñana was significantly higher than in Guadiamar, but the differences between study areas disappeared with the inclusion in the model of landscape variables at immediate or wider context scale, suggesting that the structure of landscape at this high spatial resolution may cause this effect. Net displacement increased with the heterogeneity at the immediate and wider context scales, and decreased with the proportion of scrubland across mongoose trajectories. Some matrix habitats may oppose less resistance to movement than others, favouring connectivity (Ricketts, 2001). Despite its scarcity in Guadiamar, scrubland was used more frequently than in Doñana (86% and 53% of steps, respectively). This may indicate a greater reticence of mongooses to use the Guadiamar agricultural matrix in comparison with the pasturelands of Doñana and, therefore, a higher functional connectivity in this last, where the matrix of non-preferred habitats may offer less resistance to the movement between patches. This higher inclusion of non-preferred habitats in the daily movements is in agreement with the larger home range size of the mongooses of Doñana respecting to those inhabiting the Guadiamar agroecosystem (CHAPTER 2).

There were no differences in mongoose total path length between the two study areas. We expected that, if the resources in the agroecosystem were scarcer than in the forest landscape, mongooses should need to cover more distance in their foraging movements. However, scrubland in the Guadiamar landscape is composed mainly of linear structures, as streams and hedgerows, which could support a relatively high abundance of small prey (birds, insects, small mammals) by virtue of edge effects, i.e. favoured by the adjacency of crops, as it has been found in other mosaic landscapes (Holland and Fahrig, 2001;Whittingham et al., 2005;Sullivan and Sullivan, 2006). High prey abundance in linear elements may help reduce both foraging time (hence the length of movements) within them and the frequency of transfer between them.

Models for the immediate and wider context scales showed that velocity of displacements increases with the heterogeneity (and non-preferred habitats indeed), and decreases with the proportion of scrubland at the surroundings, in accordance with general expectations. The study area variable remains significant in the models for velocity and proportion of stops, accounting for differences between both landscapes not considered in the selected variables, like prey density, predation pressure or motivational aspects (reproduction, breeding or competition).

As a result of the spatial configuration of the study areas, although scrubland patches connectance is larger in Doñana at landscape scale (Table 1) this relationship reverses at local scale, at which animals decide how to move. At this scale, scrubland is structurally better connected in the agroecosystem due to the linear character of most of the shrubby patches. In Doñana, the availability of scrubland is much larger than in Guadiamar (34% and 5%, respectively) but is distributed in heterogeneous patches of different sizes within the whole area, while in Guadiamar the scrubland is concentrated almost exclusively in the riparian vegetation and hedgerows. Mongooses living in the agroecosystem avoid the use of the agricultural lands and dehesas that surround them (CHAPTER 3) and, therefore, are constrained to these narrow shrubby strips. In Doñana, where the suitable habitat is present in larger quantity and free of structural constrains, animals can move more freely across space, resulting in a higher utilization of open habitats.

Summarizing, we have appreciated two different effects of fragmentation: habitat loss and habitat isolation. In Guadiamar, habitat loss is considerable and isolation of the remaining scrubland is remarkable at the regional scale, but the suitable habitat is highly connected at the local scale. Therefore, animals are restricted to few but structurally connected habitat patches (rivers or hedgerows), while other types of habitat are used marginally (CHAPTER 3). In Doñana, the suitable habitat is abundant and the matrix is less inhospitalable than in the agroecosystem, so movements into suboptimal habitat are more

common (Figure 2b). At a local scale, in Doñana scrubland is naturally patchier than in Guadiamar, increasing habitat heterogeneity and favouring longer net displacements.

ACKNOWLEDGEMENTS

This research was funded by the Consejería de Innovación, Ciencia y Empresa (grant P06-RNM-1903), and Consejería de Medio Ambiente, Junta de Andalucía, as well as by CSIC (grant 200830I195). MP was supported by Ministerio de Educación, Cultura y Deporte through a FPU fellowship (AP2003-2370). I thank Paco Palomares for the Doñana data and reviews of the initial manuscript.

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CONCLUSIONES

1. En un paisaje fragmentado, como es el agrosistema del Guadiamar, la presencia de tejón, gineta y meloncillo dependió tanto de la calidad del parche o fragmento forestado, como de las características del espacio circundante.

2. La probabilidad de ocupación de un parche por tejón aumentó con la proporción de cobertura arbórea y arbustiva del mismo, así como con la densidad de elementos lineales en los alrededores del fragmento, presencia de corredores estructurales entre distintos fragmentos o una de las fuentes de dispersión, y la heterogeneidad en los tipos de cultivos de la matriz.

3. La probabilidad de ocupación de un parche por gineta aumentó de forma notable con la presencia de arroyos en el mismo, así como con la proporción de olivares en los alrededores. Los disturbios ocasionados por la actividad humana en la zona tuvieron un efecto negativo sobre la presencia de la especie.

4. La probabilidad de ocupación de un parche por meloncillo aumentó con el área del parche, el porcentaje de cobertura arbórea y arbustiva del mismo, la presencia de arroyo, y la densidad de elementos lineales en los alrededores. Las molestias causadas por la actividad humana y la distancia a la fuente de dispersión más cercana afectaron de forma negativa a la presencia de esta especie.

5. La importancia relativa de la calidad del parche respecto a las características del contexto fue más relevante para la ocupación de un parche por meloncillo y gineta que para el tejón, probablemente por la capacidad de este último de explotar recursos de la matriz agrícola.

6. Los individuos de meloncillo y gineta muestreados en el agrosistema agrícola no presentaron diferencias significativas en tamaño corporal, condición física o reproducción, respecto a poblaciones viviendo en medios menos transformados y mayor porcentaje de cobertura forestal, como es el Parque Nacional de Doñana.

7. Las áreas de campeo de los individuos de meloncillo y gineta viviendo en el paisaje agrícola del Guadiamar fueron significativamente menores que las de los individuos del

Parque Nacional de Doñana, lo que sugiere que ambas especies son capaces de obtener suficientes recursos en el agrosistema sin incorporar grandes porciones de hábitats secundarios en sus campeos.

8. En el agrosistema del Guadiamar, meloncillos y ginetas seleccionaron fuertemente hábitats con vegetación leñosa natural, tanto en la forma de parches arbustivos como de elementos lineales (principalmente arroyos y lindes arbustivas). Ambas especies evitaron el uso de todo tipo de hábitats modificados, incluyendo las dehesas.

9. Una red adecuada de elementos lineales podría favorecer el mantenimiento de poblaciones de carnívoros en paisajes como los agrosistemas donde la disponibilidad de coberturas naturales es muy baja.

10. La detección de cambios en el comportamiento y, más concretamente, diferencias en los patrones de movimiento de las ginetas, pueden ser utilizados para diferenciar áreas de distinta intensidad de uso dentro de las áreas de campeo de los individuos.

11. La estructura del paisaje influenció la intensidad de uso de las ginetas en el agrosistema, dentro de sus áreas de campeo. La presencia de matorral y densidad de lindes arbustivas favoreció el uso de determinadas regiones como núcleos del área de campeo.

12. Los patrones de movimiento del meloncillo difirieron entre dos paisajes con diferente composición y estructura de matorral, su hábitat preferente. En el Parque Nacional de Doñana el desplazamiento neto de los individuos y la velocidad media a la que se movieron fue mayor que para los individuos del paisaje agrícola, mientras que invirtieron más tiempo en las paradas que estos últimos.

13. En general, la proporción de matorral y la heterogeneidad del paisaje influyeron en los parámetros del movimiento como del meloncillo, como el desplazamiento neto, longitud total de la trayectoria y velocidad.

AGRADECIMIENTOS

En este puñado de papeles va una parte de mi vida. No puedo decir si mejor o peor que otras, porque me gusta conservar la esperanza de que lo mejor siempre está por venir... pero, sin lugar a dudas, una de las más relevantes. Han sido unos años de transición, de la juventud a la madurez (el paso a los 30 deja una huella indeleble), de la universidad al primer trabajo, y de experiencia de vida en general. Los años pasados en la EBD han marcado mi personalidad, y el recuerdo del campo, la oficina, los compañeros... me acompañarán mientras viva.

El principal responsable de haber podido disfrutar de esta oportunidad ha sido, por supuesto, mi director de tesis. Resulta imposible dejar de agradecerle todo el apoyo que me ha brindado a lo largo de todos estos años. Sin duda su ayuda ha sido valiosísima.

Ha sido un enorme honor formar parte de la EBD durante estos años. Por los dos edificios que he tenido el placer de habitar (Pabellón de Perú y Cartuja) he visto pasar a gente maravillosa, de la que siempre es posible aprender algo. Es inútil que los nombre, porque la lista no tendría fin.

El grupo de carnívoros ha sido como una pequeña familia, no sólo para mí sino para todo el que lo ha necesitado. Aunque siempre he estado un poco ausente, me encantaba escucharles discutir sobre temas diversos en los desayunos del Chile, hace ya un tiempo de aquello. Y, como no, destacar a mis pequeñas carnívoras, con las que tanto me he reido. Nunca olvidaré las charlas y el té en Los Machu Pichus. Ahora que todo concluye, me doy cuenta de que he pasado menos tiempo del que hubiera podido en compañía de gente tan maravillosa. Ahora que la mayoría de la gente más cercana empieza a desperdigarse por el mundo, es cuando compruebo lo importante que fueron para mí. Espero que sigan siéndolo.

En cuanto a la familia... ¡cómo han debido de aguantarme! Reconozco haber pasado por rachas... llamémolas regulares, y he acabado estrellando mi mal humor sobre los más cercanos. Tengo que agradecer a mis padres y mi hermana el mantener continuo su cariño y comprensión. Especialmente por evitar preguntarme “¿cuándo vas a acabar la tesis?” tanto como a ellos le hubiera gustado.

Y, por supuesto, no hubiese podido acabar la tesis jamás sin ayuda de Rubén. Él ha estado presente en todas y cada una de las fases de la misma: trabajo de campo, análisis de datos, estancias breves... y ha sido mi apoyo incondicional. No tengo palabras para decir todo lo que le debo.