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ESCUELA TÉCNICA SUPERIOR DE INGENIEROS DE MONTES

**ANÁLISIS MULTIESCALA DE LA DISPONIBILIDAD Y
CONECTIVIDAD DEL HÁBITAT Y SU APLICACIÓN AL
CASO DEL LINCE IBÉRICO (*LYNX PARDINUS*)**

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Calificación

EL PRESIDENTE

LOS VOCALES

EL SECRETARIO

A mis padres y a mi hermano

“Hay un libro siempre abierto para todos los ojos: la naturaleza”

Jean-Jacques Rousseau

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SUMMARY

This thesis focuses on multiscale habitat availability and landscape connectivity analyses and their application to the endangered Iberian lynx (*Lynx pardinus*) in the Iberian Peninsula. The main goal of this research is to improve our understanding on different facets of functional connectivity and to enhance the potential of these analyses to guide applied landscape management and conservation strategies. For this purpose, the thesis adopts a graph-based approach for landscape connectivity analysis and undertakes a sequential set of methodological steps, each focusing in a different scale and research question.

The first step is to define habitat patches at an appropriate scale as to reflect dispersal processes and/or to adapt them to the resolution of the available data. In particular, it focuses on evaluating how changes in the hierarchical level at which the habitat units are defined (single patches versus aggregations of neighbor patches) affect their position in a ranking of their estimated contribution to the connectivity of the whole landscape, as assessed by different connectivity metrics. Results show that only some metrics are robust in maintaining, for different hierarchical levels, the position of the habitat patches in the connectivity ranking (Chapter 2).

The next step is to understand how individuals respond to the landscape and to what extent behavioral state (dispersing individuals versus territorial individuals) influences the use of the territory. Specifically, a novel dataset of around 40,000 telemetry locations of GPS-collared Iberian lynxes from both stable populations and recent reintroduction areas in the Iberian Peninsula was used. The dataset was divided into two groups corresponding to dispersal data and home range use data. A resource selection function was applied to both groups and mixed conditional logistic regression models with 14 environmental variables were built. The outcomes reveal that dispersing individuals show more plasticity when moving across heterogeneous landscapes than resident individuals (Chapter 3).

Then, building from the previous information and results, corridors among habitat patches can be reliably characterized for the Iberian lynx. In detail, an analysis of the differences in trajectories and effective distances (accumulated cost along the least-cost path) as a function of the behavioral state of individuals is conducted. Although the majority of the trajectories of the least-cost paths obtained from both type of data (dispersing versus resident individuals) overlap, the effective distances of the least-cost paths turn out to be remarkably lower for dispersing individuals than for resident ones. These findings indicate that connectivity assessments based on data of only resident individuals may overestimate the isolation of Iberian lynx populations, as well as potentially the populations of other species if similar data would be used (Chapter 4).

Finally, the fourth and last step consists in assessing the extent to which corridor restoration measures can help to enhance landscape connectivity, and which are the corridors in which those restoration measures should be first concentrated. Concretely, the study simulates the

variation in landscape connectivity produced by corridor restoration measures (by reducing the effective distance to the minimum possible value). Effective distance and centrality of corridors are the factors that most affect landscape connectivity gains after corridor restoration. In addition, management recommendations to address the restoration of the key corridors for the Iberian lynx are presented in order to improve the landscape connectivity for this species (Chapter 5).

To sum up, this thesis shows that the combination of individual movement data with graph-based methods can provide improved connectivity assessments at the landscape scale. The analyses presented significantly contribute to improve our knowledge on the Iberian lynx habitat use, dispersal and connectivity patterns as informed by recent empirical data on the present situation of this emblematic species. The results and methodological approach adopted in this thesis have the potential to be applied to support landscape planning and conservation strategies for a wider set of species and management contexts.

RESUMEN

Esta tesis se centra en el análisis multiescala de la disponibilidad de hábitat y la conectividad del paisaje, y su aplicación al caso del lince ibérico (*Lynx pardinus*) en la Península Ibérica. El principal objetivo es mejorar nuestra comprensión de las diferentes facetas de la conectividad funcional y resaltar el potencial de estos análisis para orientar estrategias aplicadas de conservación y gestión del paisaje. Para ello, la tesis adopta un enfoque basado en grafos para los análisis de conectividad y desarrolla un conjunto secuencial de pasos metodológicos, cada uno enfocado en una escala diferente y en un objetivo de investigación diferenciado.

El primer paso consiste en definir las teselas de hábitat a una escala apropiada para reflejar procesos dispersivos y/o para adaptarse a la resolución espacial de los datos disponibles. En particular, esta primera parte de la tesis se centra en evaluar cómo los cambios en el nivel jerárquico en el que se definen las teselas de hábitat (teselas individuales frente a agregaciones de teselas próximas) afectan a su posición en un ranking de contribución estimada a la conectividad del conjunto del paisaje, evaluado a través de diferentes índices de conectividad. Los resultados muestran que sólo algunos índices son robustos en tanto en cuanto que mantienen, para diferentes niveles jerárquicos, la posición de las teselas de hábitat en el ranking de conectividad (Capítulo 2).

El siguiente paso es comprender cómo responden al paisaje los individuos de una determinada especie y hasta qué punto el estado de comportamiento (individuos dispersantes frente a individuos residentes) influye en el uso del territorio que hacen estos individuos. En concreto, para ello se utilizó un amplio y reciente conjunto de datos de aproximadamente 40,000 coordenadas telemétricas de lince ibérico equipados con collares GPS provenientes tanto de poblaciones estables como de las recientes zonas de reintroducción en la Península Ibérica. El conjunto de datos se dividió en dos grupos correspondientes a dispersión y a uso habitual del hábitat dentro de las áreas de campeo. Se aplicó una función de selección de recursos a ambos grupos de datos, y se construyeron modelos mixtos de regresión logística condicional con 14 variables ambientales explicativas. Los resultados revelan que los individuos dispersantes presentan más plasticidad cuando se mueven a través de paisajes heterogéneos que los individuos residentes, y muestran que el lince ibérico utiliza una mayor variedad de cubiertas que lo que habían descrito estudios anteriores para la especie (Capítulo 3).

Basándose en la información y resultados obtenidos en los Capítulos 2 y 3 es posible caracterizar de forma fiable los corredores entre las teselas de hábitat para el lince ibérico, así como evaluar de manera más detallada el impacto que tiene en los análisis de conectividad el tipo de datos utilizados para caracterizar la permeabilidad del territorio. En concreto, se realizó un análisis de las diferencias en las trayectorias de los corredores y en las distancias efectivas (coste acumulado) a lo largo de los mismos en función del estado de comportamiento de los individuos. Aunque la mayoría de las trayectorias de los caminos de coste mínimo obtenidos de ambos tipos de datos (dispersantes frente a residentes) se superponen, las distancias efectivas resultan ser notablemente menores cuando se estiman a partir de la información

aportada por los individuos dispersantes que cuando se usa la información de los individuos residentes. Estos resultados indican que las estimaciones de conectividad basadas únicamente en datos de individuos residentes pueden sobreestimar significativamente el aislamiento de las poblaciones de lince ibérico, lo que puede ocurrir también para otras especies cuando se usen enfoques y tipos de datos similares (Capítulo 4).

Finalmente, el último paso consiste en estimar el grado en el que las medidas de restauración de los corredores pueden ayudar a aumentar la conectividad de paisaje y cuáles son los corredores que deberían concentrar de manera prioritaria esas acciones de restauración. Concretamente, se estima la variación en la conectividad del paisaje que resultaría de la aplicación de medidas de restauración en cada corredor, simulando dicha restauración mediante la reducción de la distancia efectiva del corredor a su valor mínimo posible. La distancia efectiva y la centralidad de los corredores son los factores que más influyen en el aumento estimado de la conectividad del paisaje tras la restauración de los corredores. Además, se presentan recomendaciones de gestión dirigidas a la restauración de los corredores clave para el lince ibérico, con el objeto de mejorar la conectividad del hábitat y las poblaciones de la especie (Capítulo 5).

En resumen, este trabajo de investigación muestra que la combinación de datos de movimiento de individuos con métodos analíticos derivados de la teoría de grafos puede traducirse en mejoras significativas en la estimación de la conectividad a escala de paisaje y en las recomendaciones de gestión relacionadas. El análisis presentado contribuye significativamente a mejorar nuestro conocimiento del uso del hábitat y los patrones de dispersión y de conectividad del lince ibérico, basándose en datos empíricos recientes que reflejan la distribución y los paisajes utilizados actualmente por esta emblemática especie. El enfoque metodológico y resultados de esta tesis tienen potencial para ser aplicados a un conjunto más amplio de especies y contextos de gestión, pudiendo así contribuir a mejorar la gestión del territorio y las estrategias de conservación de la biodiversidad en paisajes heterogéneos.

CHAPTER 1

GENERAL INTRODUCTION

Photo: Santiago Saura

1.1. GRAPH THEORY AND FUNCTIONAL SCALES FOR MEASURING LANDSCAPE CONNECTIVITY

During the last centuries, the intensification of human activities and the development of infrastructures at a global scale have brought, along with services for society, some negative consequences for biodiversity and nature. This intense increase of activities and infrastructures have been progressively reducing natural areas and fragmenting the landscape in small habitat patches (Wiegand *et al.* 1999; Söndgerath and Schröder 2002; Gonzalez *et al.* 2011; Theobald *et al.* 2011; Sutherland *et al.* 2013). As a result of the habitat loss and fragmentation, and of the degradation of the landscape matrix in between habitat patches, landscape connectivity has decreased substantially (Saunders *et al.* 1991; Fahrig 2003; Ovaskainen 2003; Wiegand *et al.* 2005).

Landscape connectivity can be defined as the degree to which the landscape facilitates or impedes the movement of species and ecological processes among source patches (Taylor *et al.* 1993). The movement of individuals and genes across the territory plays an essential role in enabling species dispersal, migration and colonization; safeguarding genetic and individual diversity; adjusting the distribution of populations in face of climate change; easing recovery from disturbances through relocation; or reducing the risk of extinction (Fahrig and Merriam 1985; Saunders *et al.* 1991; Crooks and Sanjayan 2006). Consequently, maintaining or restoring landscape connectivity has become an important goal for researchers, conservationists, and natural resource managers (Crooks and Sanjayan 2006; Rayfield *et al.* 2011; Luque *et al.* 2012; Kool *et al.* 2012) and strategies for enhancing landscape connectivity have been progressively incorporated into nature conservation policies (Heller and Zavaleta 2009; Rabinowitz and Zeller 2010; Gurrutxaga *et al.* 2011). Yet, evaluating landscape connectivity is complex and multifaceted, and it represents a challenge for scientists and practitioners (Goodwin 2003; Calabrese and Fagan 2004).

Among the breadth of methods for measuring landscape connectivity, graph theory is a middle ground between simple structural metrics and complex metapopulation models (Calabrese and Fagan 2004; Saura 2013). On the one hand, simple structural metrics, based in distance-to-neighbor metrics, have proved to be very simplistic. They are only capable of measuring structural connectivity and often fail to detect significant changes in the landscape (Moilanen and Nieminen 2002). On the contrary, metapopulation models (Hanski 1994; Ovaskainen 2003) are very precise but costly, as they require very detailed biological data that in general are difficult to obtain. Metapopulation models regarding connectivity studies are best suited for small regions or research experiments. However, when seeking management-oriented methodologies with limited available data and covering large areas, a different focus is needed (Calabrese and Fagan 2004). Graph theory (Ricotta 2000) consists in a simple but versatile conceptualization of connectivity which allows the incorporation of a wide variety of input data so that different degrees of complexity can be built in. To better understand how network analysis works, some definitions are required. In landscape ecology, a graph consists in a set of *nodes* provided with geographical coordinates that represent habitat patches. These nodes are

connected or not by *links*, which can be assimilated to the ability of an individual to directly move from one habitat patch to another (Dale and Fortin 2010; Galpern *et al.* 2011). Two nodes are directly connected when there is a link between them (*i.e.* a movement between the two nodes is possible without passing through any other intermediate node). When the link (direct connection) between them is missing, they may be fully isolated or indirectly connected through a path that includes several links and intermediate nodes (Fig. 1.1a). Nodes can be weighted using attributes such as habitat area, habitat quality, probability of occurrence, or population rates (Fig. 1.1b). Links can also be weighted by means of Euclidean distances, least-cost distances, actual movement data, immigration rates, movement probabilities, or similar data (Fig. 1.1c). The input data and the objectives of the analysis will determine how nodes and links are defined, in a way that the more detailed the data are, the more complete the graph will result.

Fig. 1.1. Schematic representation of graph structures: a) Unweighted nodes and links, which is the simplest graph representation; b) Weighted nodes and unweighted links; c) Weighted nodes and weighted links. Size of nodes and width of links represent the value of the weight (attribute) used to define the elements of the graph.

Compared to other approaches, graph-based methods present several advantages. First, they offer a spatially-explicit but tractable representation of landscape intricacy and provide more flexibility to work with a wide range of data types. That is, they can accommodate simple calculations such as assimilating nodes with habitat patches (weighted by the patch area) and links with Euclidean distances or they can incorporate very detailed figures such as immigration rates or genetic distances (Keitt *et al.* 1997; Saura and Rubio 2010). In addition, there are powerful graph-based algorithms for efficient network analysis, which makes it possible to analyze large landscape scales in reasonable processing times (Adriaensen 2003). Finally, methods based in graph theory are considered to have the best benefit to effort ratio considering the data input-output balance (Calabrese and Fagan 2004; Bodin and Norberg 2006). To sum up, these methods allow for an understandable graphical representation of complex landscape analyses supported by coherent and significant numerical results. Hence, the number of studies concerning landscape analysis based on graphs has increased swiftly in

recent years (Bodin and Norberg 2006; Fall *et al.* 2007; Ferrari *et al.* 2007; Jordán *et al.* 2007; Saura and Pascual-Hortal 2007; Minor and Urban 2008; Neel 2008; Zetterberg *et al.* 2010; Gurrutxaga and Saura 2013; Saura *et al.* 2014; Avon and Bergès 2016; Albert *et al.* 2017).

In addition, by the end of the last century the majority of connectivity studies were mainly focused on landscape-level metrics, and indicators of connectivity and fragmentation offered one single value attempting to explain the extent to which certain landscape was connected (McGarigal and Marks 1995; Schumaker 1996; Jaeger 2000; Moilanen and Nieminen 2002). This way, indicators such as patch cohesion or size of habitat patches in the landscape were limited in their ecological interpretability and practical applications, particularly for delivering spatially-explicit management recommendations. To overcome these shortcomings, some graph-based metrics incorporate prioritization capabilities by applying patch-removal experiment techniques in order to quantify the importance of a certain habitat patch or link for the connectivity of the whole landscape (Urban and Keitt 2001; Saura and Pascual-Hortal 2007). This technique calculates, first, the overall connectivity of a network (as quantified by a certain connectivity metric X); then, one habitat patch (or link) k is removed from the network and overall connectivity is calculated again for the whole network ($X_{remove,k}$). The percentage of connectivity loss for the whole network after removing the habitat patch (or link), denoted as dX_k , is the percentage of importance of the patch (or link) to overall connectivity of the whole network, as given by:

$$dX_k = 100 \times \frac{X - X_{remove,k}}{X}$$

As a result, this approach ranks quantitatively all the elements of the landscape according to their contribution to the connectivity of the whole. In this respect, the interpretability and applicability of this type of indicators is evident as researchers and practitioners can value the extent to which losing certain elements of the network would affect the connectivity of the network. They can also include these considerations when planning conservation measures in order to decide, for example, which elements should be preserved.

On the other hand, the most analyzed aspect of connectivity has been the spatial pattern of the landscape (Vasudev *et al.* 2015) despite this type of metrics show relevant limitations in exemplifying how fragmentation and/or connectivity actually affect species or ecological processes (O'Neill *et al.* 1996; Keitt *et al.* 1997; Stevens *et al.* 2004; Urban 2005; Pascual-Hortal and Saura 2006; Baguette and Van Dyck 2007). To overcome some of these hindrances, (Pascual-Hortal and Saura 2006) incorporated the concept of *habitat availability (reachability)* to graph-based connectivity metrics. Habitat availability (reachability) considers a patch itself as a space wherein connectivity occurs as organisms are able to move within the habitat area where they dwell. In this sense, a big although isolated patch would make available more connected area within its own boundaries than a group of small but connected patches if the sum of their areas is smaller than the area of the big although isolated one. This ability confers these indices with coherent skills to properly assess landscape changes better than other indices which do not incorporate this concept (Pascual-Hortal and Saura 2006). Thus, habitat availability (reachability) metrics integrate the area within habitat patches, namely intrapatch

connectivity, with the area made available by the connections between patches, namely interpatch connectivity.

Along with these ideas, functional information has started to be incorporated in connectivity studies more recently in an effort to overcome the over-simplistic results of dealing solely with the spatial configuration of the landscape (Tischendorf and Fahrig 2000a, b; Calabrese and Fagan 2004; Li and Wu 2004; Zollner and Lima 2005). For instance, a more detailed way of analyzing landscape connectivity is to aim for specific species and processes. Functional aspects of connectivity should identify the response of species and processes to a certain landscape pattern (Lima and Zollner 1996; Tischendorf 2001). That is, some landscape configuration can be perceived as totally connected for a species with good dispersal abilities while other species with reduced mobility can perceive the same spatial structure as highly fragmented. Moreover, even just a single species can interact with the landscape in different ways depending on the vital stage of their individuals or the process they are going through. For example, adult females might temporarily reduce their home range while breeding or some birds expand their scale of movement during the migration season. Landscape connectivity therefore involves a multi-scale dimension as each species and each process have their specific functional scale (Urban *et al.* 1987; Lausch and Herzog 2002; Wu 2004; Boitani *et al.* 2007; García-Feced *et al.* 2011). For these reasons, connectivity studies are likely to explain more accurately the response of species and processes to the landscape when approached from different angles so that the multiple scales involved in the phenomenon under study are considered (Shen *et al.* 2004; Uuemaa *et al.* 2005; Pascual-Hortal and Saura 2007; Alhamad *et al.* 2011).

In this sense, many studies are interested in assessing the connectivity of broad-scale ecological processes among distant patches, such as dispersal or migration, and discarding the detailed information of other smaller-scale ecological processes, like breeding or foraging, which usually occur within or among neighbor and not too distant habitat patches. In this case, a reasonable approach to specify the scale of the ecological process (*i.e.* dispersal) would be to aggregate together in a single functional patch all habitat patches that are below a certain threshold distance. Hence, all habitat patches below that threshold would be considered a functional unit (node) and landscape connectivity analysis would be conducted for the existing links between these functional units. This definition of habitat patches incorporates one facet of scale in the process of assessing connectivity by nesting the graph structure in hierarchical levels that characterize different ecological processes. This approach provides a powerful tool to identify critical scales in ecology (Fletcher *et al.* 2013). And it can also simplify connectivity assessments constrained by existing data or computational bottlenecks while focusing on the relevant ecological scale of the process. For example, for planning and management strategies, habitat patches are selected considering additional factors such as administrative or socioeconomic reasons, which may advocate grouping in a single node several habitat patches located within the same management or administrative unit. In other cases, the aggregation of habitat patches in a single node may be inevitable, for instance when data on the landscape area available only at a resolution coarser than the grain of some of the landscape or habitat features. In addition, when analyzing large graphs with a high number of habitat patches and the computational requirements exceed the available processors, nearby patches could be

aggregated in a smaller number of nodes for processing feasibility of the entire network analysis. In order to do so, we must ensure that analyzing connectivity by aggregating habitat patches provides similar results than analyzing the whole network using nodes corresponding to single habitat patches. However, there is a lack of knowledge on whether the aggregation of habitat patches would provide different connectivity results compared to the separate consideration of each of the habitat patches conforming the aggregate, and to what extent the connectivity of the network and related conservation management priorities would be affected by such aggregation.

Once the ecological scale of habitat patches is defined so as to narrow the analysis towards the process of interest (more frequently dispersal processes), subsequent steps in connectivity assessments should focus on the movements among habitat patches represented by these functional units. Movement across the territory is one of the most challenging processes to apprehend and measure, and at the same time it is a crucial element to understand the underlying mechanisms of functional landscape connectivity (Zeller *et al.* 2012). It can be measured in many different ways, but the usual approach has been the assignation of resistance-to-movement values (*i.e.* cost) to each land cover type present in the study area. These values are most commonly designated using expert knowledge and/or general map classifications derived from coarse remotely-sensed data, but often the assigned values are unsupported by field species data (Sawyer *et al.* 2011). For this reason, resistance values frequently fail to explain the movement of individuals through the landscape. Actually, individuals move across the territory following specific targets (*e.g.* foraging, patrolling, hunting, dispersing...) and they would respond to the territory differently according to their specific target. For example, individuals engaged in dispersal processes tend to move faster and more direction-oriented than foraging individuals whose movements tend to be slower and usually follow more tortuous trajectories. This target-specific movement can be assimilated to a certain behavioral state and in order to capture it, movements should be examined at an individual scale, considering the behavior in which each individual is engaged. The ideal input data for evaluating movement among habitat patches at the individual scale would be the geographic coordinates of individuals engaged in dispersal behavior. For example, GPS locations of collared individuals or geographically located genetic samples offer accurate information to assess movement among habitat patches (Cagnacci *et al.* 2010). This combination of individual scale and behavioral state adds another layer to the multi-scale process of assessing functional landscape connectivity. However, the integration of behavioral state (*e.g.* dispersal) into connectivity assessments seems complex and there is still a need of further developing efficient and practical methodologies to incorporate it.

Attaining the available information on how individuals disperse across the territory, resistance-to-movement values (*i.e.* cost) can be assigned to the each element of the landscape. Corridors between habitat patches can at last be demarcated (and quantified) and functional connectivity can be finally inferred at the landscape scale. Corridors are generally defined as areas of minimum cumulative cost between habitat patches (Epps *et al.* 2007; Sawyer *et al.* 2011) and they are characterized by two elements: on the one hand, their trajectory or delineation in the landscape and, on the other hand, the effective distance of their least-cost path (quantification of the accumulated resistance-to-movement along the least-cost path) or

some other similar measure of effective distance. These two elements depend on the resistance values assigned to the each element of the landscape and consequently they are a function of the behavioral state of the individuals (D'Eon *et al.* 2002; Belisle 2005; Zeller *et al.* 2012, 2014). Yet, corridors are most commonly defined by resistance values derived as the inverse of habitat suitability models, which are generally obtained from data of individuals within their home ranges (Killeen *et al.* 2014; Elliot *et al.* 2014; Vasudev *et al.* 2015). However, individuals within their home ranges are engaged in processes other than dispersal and there is no proof of a direct relation between resistance-to-movement values obtained from dispersing individuals and the inverse of resistance-to-movement values obtained from resident individuals (Beier *et al.* 2009). Therefore, it remains to be determined whether the use of one or other type of data when assigning cost values to the landscape affect the delineation and quantification of corridors.

Although corridors are considered one of the landmarks for landscape connectivity improvement, the effectiveness of restoration measures to improve the quality of corridors has not been much explored. For these reasons, the quantification of the extent to which connectivity improves due to the amelioration of the corridor quality might help conservationists and practitioners to better address management actions at the local and at the landscape level. Corridor restoration can be simulated by reducing the resistance-to-movement values of the least-cost path to the minimum possible value that could be achieved after restoration actions. By doing so, the cost values of the least-cost path would represent exclusively the cost of moving of the individual due to intrinsic factors (*e.g.* geographical distance or natural features) and would eliminate the additional cost of moving due to unsuitable land covers along the way. On top, biodiversity conservation actions are most often restrained to financial limitations. Thus, it would also be worthy to have some assessment, even if approximate or indirect, of the extent to which restoration measures for corridors are cost-efficient to enhance connectivity.

1.2. LANDSCAPE CONNECTIVITY OF THE IBERIAN LYNX IN SOUTHWEST IBERIAN PENINSULA

The Iberian lynx (*Lynx pardinus*) is an emblematic medium-size carnivore endemic to the Iberian Peninsula. Prey and habitat specialist, the reduction of rabbit populations (*Oryctolagus cuniculus*) and the loss of Mediterranean woodlands contributed to the continued and intense decline of the population until the late 20th century, together with hunting and poaching (Rodríguez and Delibes 1992; Simón *et al.* 2012). Formerly running wild throughout most of Spain and Portugal, at the beginning of the 21st century the Iberian lynx became the most endangered felid of the world with less than 100 individuals remaining in two isolated populations (Doñana and Andújar) (Fig. 1.2a) (Simón *et al.* 2012). The IUCN Red List

categorized the species as critically endangered (Rodríguez and Calzada 2015), and model predictions suggested that, in the absence of decisive recovery management actions, the species would suffer a collapse and probably would get extinct in less than 50 years (Palomares *et al.* 2011; Fordham *et al.* 2013). Fortunately, the population has experienced a swift upsurge due to an ambitious and continued conservation program which included ex-situ breeding and reintroduction of young individuals (Life+ IBERLINCE 2006; Simón *et al.* 2012). As a result of this program, more than 475 individuals have been censused in 2016 (Fig. 1.2b) (Life+ IBERLINCE 2006).

Fig. 1.2. a) Historic distribution of the Iberian lynx during the 1960s (sightings record-based, modified from (Rodríguez and Delibes 1990) in (Garrote 2014)), the 1980s (sightings record-based, modified from (Rodríguez and Delibes 1990; Castro and Palma 1996) in (Garrote 2014)), and the early 2000s (census-based, modified from (Garrote 2014)). b) Current census-based distribution of the Iberian lynx (modified from (Life+ IBERLINCE 2006)).

In order to accommodate this increase in population size, the conservation program of the lynx Life+ IBERLINCE had selected five habitat patches where young individuals have been reintroduced in the most recent years (Montes de Toledo, Campo de Calatrava/Sierra Morena Oriental, Sierra Norte de Sevilla, Matachel, and Vale do Guadiana) aside from the already existing four population areas (Doñana, Andújar, Guarrizas, and Guadalmellato). While Doñana and Andújar are the population nuclei where Iberian lynx has never disappeared from, Guarrizas and Guadalmellato were the first sites selected for reintroduction purposes back in 2009 and they now hold 70 and 55 censused individuals respectively (Life+ IBERLINCE 2006). All reintroduction areas meet a number of conditions: they are located within the historic distribution of the lynx; they are mainly covered by Mediterranean woodlands; they have medium or high rabbit density; they are large enough to hold a stable population; they benefit from strong support from stakeholders in the region; and/or they hold a protection status. But such a sudden rise in numbers poses challenging questions: previous research suggests that natural expansion is highly limited because of habitat fragmentation and lack of corridors (Guzman *et al.* 2002, 2004) in (Gil-Sánchez and McCain 2011).

For a relatively long time, the Iberian lynx has been the focus of diverse research studies regarding its habitat requirements (Palma *et al.* 1999; Fernandez and Palomares 2000; Palomares *et al.* 2000; Palomares 2001; Ferreras 2001; Fernández *et al.* 2006; Fernandez *et al.* 2007; Gil-Sánchez and McCain 2011). These studies revealed that resident lynxes prefer to dwell in Mediterranean woodlands and areas with short and scattered trees, abundant understory vegetation, and high density of rabbits. On the contrary, dispersing lynxes were observed crossing lower quality landscapes too, such as dense forest plantations, while avoiding open areas (Palomares 2001). In very fragmented landscapes lynxes also use remnants of natural vegetation as “stepping stones” (Ferreras 2001). In these studies, land cover types were categorized in few types, namely, Mediterranean shrublands, forest plantations, riparian vegetation, grasslands with or without remnants of natural vegetation, open areas such as dunes and marshes, and a generic cropland category (Palma *et al.* 1999; Palomares *et al.* 2000). These categorization in land cover types is coarse and combines together very different landscape structures, especially for croplands (*e.g.* irrigated strawberry fields and extensive olive groves are placed in the same class in Palomares *et al.* (2000). This generalization of land cover types might lead to imprecise conclusions regarding the use of the habitat by lynxes. Moreover, these studies focused on relatively small areas and they analyzed only one area at a time: Doñana (Palomares *et al.* 2000; Palomares 2001; Fernandez *et al.* 2003), Andújar (Fernández *et al.* 2006; Gil-Sánchez *et al.* 2011), and Algarve (Palma *et al.* 1999). At present, due to the release of lynxes in the reintroduction areas, the nuclei of population are not restricted anymore to those relatively small areas; therefore, research on the habitat selection of lynxes in their new territories is needed. The analyses of this thesis extend over a broader region compared to previous studies, which focused in Doñana, Andújar or Algarve region solely, to account for the recent expansion on lynxes as a result of the reintroduction of individuals of the Life+ IBERLINCE program. The study area for the connectivity analysis is a buffer of 100km around the nine habitat patches where currently stable populations (Doñana, Andújar, Guarrizas, and Guadalmellato) and reintroduction areas (Montes de Toledo, Campo de Calatrava, Sierra Norte, Matachel, and Vale do Guadiana) are located, while the habitat suitability and landscape permeability models are fitted based on

Corine Land Cover data that are available for both Spain and Portugal and hence can be extrapolated to all the Iberian Peninsula. Farther regions were not considered for the detailed connectivity analyses because, despite some individuals might disperse farther and settle outside this edges, they would probably not represent viable populations nor successful reproduction (gene flow) in the short and medium term.

Additionally, the Iberian lynx has also been the focus of a set of research studies regarding its dispersal behavior (Ferrerías *et al.* 1997, 2004; Ferreras 2001; Revilla *et al.* 2004). For example, a study conducted in Doñana radio-tagged 36 individuals for nine years and reported average daily distances and patrolling distances (Ferrerías *et al.* 1997). Besides, (Ferrerías *et al.* 1997) also specified where exactly some individuals settled after dispersing. The same dataset was also used to thoroughly evaluate dispersal factors such as individual condition, environmental factors, and survival rates (Ferrerías 2001; Ferreras *et al.* 2004). Dispersal extent and distance travelled were also examined, and effective distance (obtained as the inverse of the habitat selection model) resulted the factor that mostly affected interpatch connectivity (Ferrerías 2001). Another study measured steps and turning angles using individual-based modelling and showed similarly accurate results (Revilla *et al.* 2004). Yet, the valuable information obtained from these studies generally involves exhaustive fieldwork for long periods of time, which may not be easy to apply to widespread areas, or demands complex parameterization requiring expert knowledge or detailed biological data acquisition.

Furthermore, the current status and range of the Iberian lynx has noticeably changed since the time of those studies. With the reintroduction program starting in 2009, more than 170 individuals have been breed in captivity and released in the wild (Life+ IBERLINCE 2006). Along with genetic reinforcement and disease control strategies, the population has increased and stabilized (Simón *et al.* 2012). Unforeseen behaviors are detected, like females breeding in olive groves (generally categorized in previous studies as croplands and thus regarded as unsuitable habitats) (Garrote, unpublished data), or dispersing lynxes travelling more than 3.000 km throughout the Iberian Peninsula (Life+ IBERLINCE 2006). In addition, new data have been collected in areas where lynxes are dwelling at present and of which no information existed before. A large dataset of 48 GPS-collared lynxes monitored between 2009 and 2013 has provided more than 44,000 locations across former and new populated areas, including information on dispersal events. Previous studies on lynxes mostly used radio-tracking techniques (Palomares *et al.* 2000; Palomares 2001; Fernandez *et al.* 2003), sighting records (Palma *et al.* 1999), and surveys of feces (Fernández *et al.* 2006; Alda *et al.* 2008). Compared to radio-tracking techniques, these GPS collars are more powerful to infer habitat use and landscape permeability for the Iberian lynx because they systematically deliver geographical locations every 4 hours, allow 24-hour coverage under all kind of weather conditions and across all types of land covers, and reduce the risk of missing records due to unexpected or distant dispersal events (Dickson and Beier 2006; Mateo-Sánchez *et al.* 2014; Elliot *et al.* 2014).

In the light of the recent expansion of the Iberian lynx, and of the availability of recent and detailed GPS data for the species, updated and refined landscape connectivity studies and conservation-oriented management recommendations are timely and needed.

1.3. OBJECTIVES OF THE THESIS AND CHAPTERS' SUMMARY

This thesis focuses on multi-scale habitat availability and landscape connectivity analyses and their application to the endangered Iberian lynx (*Lynx pardinus*) in the Iberian Peninsula. The main goal of this research is to improve our understanding on different facets of functional connectivity and to enhance the potential of these analyses to guide applied landscape management and conservation strategies. For this purpose, the thesis adopts a graph-based approach for landscape connectivity analysis and undertakes a sequential set of steps each focusing in a different scale and research question. Specifically, the objectives of this thesis are:

Regarding habitat patch definition:

- to analyze the extent to which changes in the hierarchical level at which the habitat patches are defined impact the spatially-explicit guidelines provided by different connectivity metrics. This impact was examined in terms of which habitat areas are identified as connectivity priorities and which is the estimated decrease in connectivity that would happen if these areas were lost.

Regarding the response of the species to the landscape:

- to study the extent to which the behavioral state of Iberian lynx individuals (dispersing versus resident) affects the selection of habitat and movement areas, and to assess the degree of plasticity of the species when moving across heterogeneous landscapes.

Regarding the establishment of connections among habitat patches at the landscape scale:

- to delineate corridors and to estimate the effective distances along them, using information from dispersing Iberian lynxes, and to compare them with those obtained from the behavior of resident individuals.

Regarding measures to improve landscape connectivity:

- to assess how landscape connectivity would be improved by the application of corridor restoration measures, and to identify the corridors that are of highest priority to improve long-term landscape connectivity for the Iberian lynx.

By doing so, this thesis attempts to (i) develop multi-scale methodologies for assessing landscape connectivity that have potential of application to guide conservation management for a wide variety of species, as well as to (ii) contribute with new insights on the Iberian lynx landscape selection preferences and connectivity patterns that are adapted to the present situation of the species in the Iberian Peninsula.

CHAPTER 2. DEFINITION OF HABITAT PATCHES IN HIERARCHICAL LEVELS TO REFLECT DISPERSAL PORCESSES

Measuring functional landscape connectivity depends on the scale of the ecological process under study (*e.g.* dispersal). Many studies have assessed the sensitivity of connectivity metrics to changes in spatial resolution or extent. Yet, there is a need of research on how the scale at which habitat units are defined affects the outcomes of landscape connectivity metrics. Therefore, this study evaluated how the hierarchical level at which habitat patches are defined (single habitat patches versus aggregation of multiple neighbor patches) affects: (i) their importance values (percent of decrease in the connectivity of the whole landscape that would occur if the patch was lost), and (ii) their position in a ranking of priority patches for maintaining landscape connectivity. The final aim was to assess whether the habitat patches that are found to contribute most to connectivity at upper hierarchical levels (aggregated patches) also contain the individual patches that are identified as those most important for connectivity at lower hierarchical levels (single patches). Results showed that only some connectivity metrics are robust in maintaining the position in the ranking of priority patches across hierarchical levels. On the contrary, the patch importance values obtained were for all metrics dependent on, and eventually flawed by, the particular scale at which the connectivity analysis was conducted. Thus, certain connectivity metrics are reliable to detect key habitat patches (those that most contribute to maintain current connectivity levels) with little impact of the hierarchical level at which they are defined, but not necessarily to quantify the actual amount of connectivity that would be lost if these patches would be removed from the landscape.

CHAPTER 3. RESPONSE OF INDIVIDUALS TO THE LANDSCAPE ACCORDING TO THE BEHAVIORAL STATE

Measuring functional landscape connectivity also depends on the response of individuals to the landscape as a function of the ecological process they are engaged in (*e.g.* dispersal). A study was conducted for the Iberian lynx in order to disentangle the extent to which the responses to the landscape of resident individuals differed from those of dispersing individuals. Around 40,000 telemetry locations for 48 GPS-collared individuals covering the current Iberian lynx range were analyzed. GPS locations within home ranges (to estimate habitat suitability) and GPS locations corresponding to dispersal or exploratory movements (to estimate landscape permeability) were differentiated using the a-LoCoH methodology. A mixed conditional logistic regression model with 12 land cover classes, terrain slope and roads as predictors was built. Results showed that resident and dispersing lynxes preferred the same type of land cover types (mainly Mediterranean woodlands, but also, although to a lower degree, extensive agricultural tree plantations or crops with natural vegetation remnants). However, broader plasticity for dispersing individuals across different land cover types was evidenced compared to resident individuals and a much weaker avoidance of roads and steep terrain was also found when dispersing than when selecting territories. To conclude, the study

suggests that Iberian lynx conservation and reintroduction plans may be effective in a wider set of landscapes than previously thought.

CHAPTER 4. CHARACTERIZATION OF CORRIDORS BY TRAJECTORY AND EFFECTIVE DISTANCE

Corridors are generally defined as areas of minimum cumulative cost through a resistance surface, and they are characterized by their trajectory and their effective distance (accumulated cost along the least-cost path). The cost values of the resistance surface used in connectivity modelling are typically derived from the inverse of habitat suitability models rather than from data on dispersal or exploratory movements. There is, however, a lack of research on whether resistance values derived from the inverse of habitat suitability models can actually be used as a substitute for resistance values obtained from dispersal data. Thus, in order to define corridors effectively it is crucial to evaluate the extent to which corridor delineation and effective distances vary depending on whether home range locations or dispersal data are used to characterize landscape resistance values. Using the outcomes of the Iberian lynx dataset described in Chapter 2, corridors and effective distances were modeled in three ways: (1) considering only GPS locations within home ranges, (2) considering only locations in dispersal or exploratory movements outside home ranges, and (3) considering all locations together. Results revealed that corridors followed similar trajectories and sometimes overlapped in the three models. Nevertheless, effective distances were 42 % lower in the dispersal-based model than in the model based solely on home range use. Thus, effective distances based on resistance values of resident individuals provide lower connectivity estimates than corridors derived from resistance values of dispersal locations, potentially overestimating the actual isolation of populations in heterogeneous landscapes.

CHAPTER 5. IDENTIFICATION OF STRATEGIC CORRIDORS FOR RESTORATION

Corridor establishment is a usual tool in conservation planning when seeking to enhance species connectivity in fragmented landscapes. Yet, little is known *a priori* on the effects of restoration measures aimed to improve corridor quality. Thus, the objective of this study was to assess the extent to which the restoration of the quality of corridors translates into relevant gains in landscape connectivity, as well as to account in this analysis for a proxy of the restoration cost of the corridor. The amelioration of corridors was simulated by reducing the effective distance of the corridor to the minimum possible value (*i.e.* considering that the corridor is all of optimal quality for the species). Results showed that the effective distance and centrality of the corridors were the main factors behind landscape connectivity gains when restoration measures were applied. While corridors with most centrality are those that are expected to be more frequently used, restoration actions imply larger economic costs when they need to focus in corridors linking habitat patches that are far away from each other. Consequently, when resources for corridor amelioration are limited, they may be most efficiently allocated on corridors that are both short and central. Finally, management

recommendations to enhance connectivity for the Iberian lynx in the Iberian Peninsula are presented. We conclude emphasizing that any recommendation aimed to improve landscape connectivity must necessarily comprise a holistic approach and consider the different scales at which the ecological processes under consideration actually happen.

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CHAPTER 2

DEFINITION OF HABITAT PATCHES IN HIERARCHICAL LEVELS TO REFLECT DISPERSAL PROCESSES

Photo: Sonia Illanas

This chapter reproduces entirely the content of the research paper:

Blazquez-Cabrera S, Bodin Ö, Saura S (2014). Indicators of the impacts of habitat loss on connectivity and related conservation priorities: Do they change when habitat patches are defined at different scales? *Ecological Indicators* 45:704–716. doi: 10.1016/j.ecolind.2014.05.028

ABSTRACT

Delivering indicators of habitat connectivity first requires identifying the habitat units that will be treated as individual entities for spatially explicit analyses. These units can be defined at different spatial scales or hierarchical levels, from single habitat patches to aggregations of multiple neighbor patches. Many studies have assessed the scale sensitivity of landscape-level pattern metrics when changing spatial resolution or extent. However, how patch-level connectivity indicators change across hierarchical levels (independently from modifications in resolution or extent) has been largely overlooked, despite the potentially strong and determinant effects on their outcomes and final uses. We evaluated how the hierarchical level at which habitat units are defined affects two types of outcomes frequently derived from connectivity indicators: (i) the importance values (or estimated amount of decrease in landscape connectivity that would be caused by the loss of certain habitat areas), and (ii) the priority ranking (key areas to conserve to minimize connectivity loss), as given by a selected set of widely used metrics (habitat availability, network centrality, metapopulation capacity). We found that importance values can largely vary depending on how habitat units are defined, suggesting that such results may be flawed by a particular a priori selection of hierarchical levels. However, the identification of which parts of the landscape contain the key connectivity providers (priority ranking) was robust, particularly for those metrics that account for the amount of connectivity within habitat units. We conclude that current connectivity indicators based on patch removals do not allow, considering their scale dependence, to consistently assess the magnitude of connectivity decrease resulting from large-scale habitat loss, but that they can be used with much more confidence for detecting those key areas that most contribute to maintain current connectivity levels.

2.1. INTRODUCTION

Landscape connectivity can be defined as the degree to which the landscape facilitates or impedes the movement of genes, species, and other ecological flows among habitat resources in the landscape (modified from Taylor *et al.* (1993)). It is widely acknowledged that species movements through the landscape play an important role in species genetic variability and persistence, in easing recovery from disturbances through dispersal and recolonization, and in allowing species adaptation to climate changes (Crooks and Sanjayan 2006). Nowadays, large-scale land use intensification is reducing and fragmenting natural areas, consequently decreasing the quality of functional connections among habitats. Henceforth, enhancing landscape connectivity is a major concern increasingly influencing management strategies in nature conservation (Heller and Zavaleta 2009; Rabinowitz and Zeller 2010).

The analysis of landscape connectivity is a complex task for several reasons. First of all, connectivity is related to species movements, but monitoring the movement of species over large spatial and temporal scales is extremely costly and challenging. This has made necessary and increasingly common to use indicators of connectivity, *i.e.*, connectivity metrics that can incorporate available knowledge on species dispersal but do not require from empirical movement data to be specifically gathered for each monitoring or planning application (Hanski and Ovaskainen 2000; Urban and Keitt 2001; Calabrese and Fagan 2004; Pascual-Hortal and Saura 2006; Estrada and Bodin 2008; Vogt *et al.* 2009; Saura and Rubio 2010; Morzillo *et al.* 2010; Foltête *et al.* 2012; Reza *et al.* 2013; Van Looy *et al.* 2014; Liu *et al.* 2014; Saura *et al.* 2014).

Secondly, the selection of an appropriate scale for landscape indicator delivery is crucial, since patterns and processes operate on multiple scales often organized in nested hierarchical levels (Urban *et al.* 1987; Lausch and Herzog 2002; Wu 2004; García-Feced *et al.* 2011). Studies addressing the effects of scale in landscape indicators and metrics have proliferated in the ecological literature over the years (Woodcock and Harward 1992; Lausch and Herzog 2002; Wu *et al.* 2002; Saura 2004; Shen *et al.* 2004; Wu 2004; García-gigorro and Saura 2005; Uuemaa *et al.* 2005; Corry and Laforzezza 2007; Alhamad *et al.* 2011). However, the majority of these studies has focused in landscape level indicators based on structural metrics, and have not evaluated the impacts on connectivity that would result from changes such as habitat loss in individual patches or localized portions of the landscape. Indicators of the impacts of landscape change and habitat loss in particular patches or areas of the landscape are often necessary and widely used to set conservation planning priorities, *i.e.*, to select among many possible locations for particular conservation or restoration measures (*e.g.* Hanski and Ovaskainen (2000); Pascual-Hortal and Saura (2008); Saura and Rubio (2010); Reza *et al.* (2013); Liu *et al.* (2014); Van Looy *et al.* (2014)). In addition, previous studies on landscape indicators have examined changes in scale by modifying the spatial resolution, the extent or both. However, even for a given spatial resolution and extent, it is necessary to define the habitat units among which the connectivity analysis is to be performed, and this definition can be done at different hierarchical levels: for instance, a patch (*e.g.*, a polygon in a vector map or group of contiguous habitat pixels in a raster layer), or an aggregated set of patches or

metapatch (*e.g.*, a set of nearby patches considered as a single functional habitat unit for the focal species) as in Zetterberg *et al.* (2010). These sets of patches can be defined, based on spatial or ecological criteria, at different aggregation distances, with those patches separated by a distance smaller than the specified aggregation distance being considered as part of the same habitat unit. Analyzing variations in patch-level connectivity indicators due to the choice of different hierarchical levels without modifying the spatial resolution or extent remains to our knowledge unassessed.

The choice of a scale or hierarchical level for landscape connectivity indicator delivery may be highly constrained by the degree of detail of available spatial information on landscapes. Connectivity indicators require as an input spatially explicit data that allow adequately representing the distribution of the habitat for focal species. The spatial resolution of the available data will inevitably determine the minimum size of each individual habitat unit (spatial entity) separately considered in the analysis.

Ecological aspects also influence the operational scale or hierarchical level of the analysis. For example, animals can exhibit different movement types at different scales depending on their behavioral state: long distance movements such as natal dispersal or migratory events versus daily movements like foraging or patrolling inside the home range (Blums *et al.* 2003; Fritz *et al.* 2003). Thus, if small scale movements (like foraging or patrolling) occur among patches that are relatively close to each other and the connectivity analysis focuses in broad scale movements (such as dispersal or migration) then it is reasonable to aggregate neighbor patches that fall within the distance assumed for daily movements. This set of aggregated neighbor patches may correspond to a home range and, therefore, would be considered as a single habitat unit with full or very high connectivity (no major movement limitations) within it. The subsequent connectivity analysis and indicators would focus only in the possibilities of movement among different units located at relatively large distances.

Finally, other operational reasons may justify the selection of higher hierarchical levels when defining habitat units for delivering connectivity indicators (*e.g.*, a set of neighbor patches instead of a single patch). For example, computational bottlenecks can make some connectivity analysis cumbersome in large study areas with many thousands of habitat patches due to large processing times. Thus, the number of habitat units could be reduced by considering patches within a relatively short distance as a single habitat unit, if this simplification is reasonable on ecological grounds (home range size, movement behavior of the species, objective of the study).

Whatever the reason is to select a particular scale or hierarchical level (data availability, ecological considerations, or computational bottlenecks), such choice may strongly influence the indicator values and the spatially explicit decision support guidelines derived from it. Two types of outputs can be calculated for habitat units that can be useful as indicators supporting connectivity conservation decision-making, and that are generally obtained from the so-called patch-removal experiments (Bodin and Saura 2010). First, a numerical value for each habitat unit that quantifies the amount of decrease in landscape connectivity that would be caused by the loss of a certain habitat area (henceforth importance values); and second, a position in the ranking of importance values for all habitat units, indicating which of them are the most

important for conserving or enhancing landscape connectivity (henceforth priority ranking). Due to the potential impact of the hierarchical level employed in landscape connectivity indicators, two identical connectivity analyses conducted at different operational scales may provide dissimilar results for the same habitat units in terms of importance values or priority ranking and, consequently, on the ensuing conservation decision making or reported trends. However, these effects remain largely unassessed to date, despite the large and increasing number of ecological studies that rely on this type of connectivity indicators and the spatially explicit results that they provide (*e.g.* Saura *et al.* (2011); Gil-Tena *et al.* (2013); Reza *et al.* (2013); Liu *et al.* (2014); Van Looy *et al.* (2014)).

Therefore, this study aimed to evaluate how changes in the hierarchical level at which the habitat units are defined affect the importance values and the priority rankings for landscape connectivity, as assessed by different widely used connectivity indicators (metrics). For this purpose, and unlike previous scale-related patch-removal studies (*e.g.* Pascual-Hortal and Saura (2007); Townsend *et al.* (2009)), we evaluated modifications in nested hierarchical levels defining habitat units (single patches versus aggregations of patches at different aggregation distances D_{agg}), rather than modifying the size or distribution of habitat units as happens when varying spatial resolution, minimum mapped unit or extent (*e.g.* Saura (2002)).

Our final aim was to assess whether habitat units with high importance values or priority rankings at upper hierarchical levels (habitat units corresponding to set of aggregated patches) contain the same areas that are also of high importance or priority when the indicators are obtained at lower hierarchical levels (habitat units as single patches). In this way, we intended to evaluate the extent to which current connectivity indicators are robust across nested hierarchical levels or, alternatively, may be dependent and eventually flawed by a particular a priori selection of the scale at which the connectivity analysis is conducted.

In our analysis, we focused on operational, pragmatic (non data-hungry) indices widely used in connectivity studies: habitat availability/reachability metrics (Pascual-Hortal and Saura 2006; Saura and Rubio 2010; Baranyi *et al.* 2011), network centrality metrics (Freeman 1977; Estrada and Bodin 2008; Bodin and Saura 2010) and the metapopulation capacity (Hanski and Ovaskainen 2000). All these indices require as inputs a set of habitat units and connections among them portraying, respectively, the distribution of habitat resources in the landscape (patches and aggregation of patches at several D_{agg}) and the movement abilities of the focal species (here given by an array of dispersal distances d_{disp} representing a wide range of species movement abilities). We performed these analyses in two forest landscape networks in Spain and Madagascar. These two networks were selected for this study because (1) they harbor species and services of conservation interest that are severely affected by habitat fragmentation, (2) they have been analyzed in detail in previous studies that provide a good background description of their topology and functional connectivity (Bodin *et al.* 2006; Bodin and Norberg 2006; Pascual-Hortal and Saura 2008; Bodin and Saura 2010; Saura *et al.* 2014), (3) they show very different spatial configurations, which make them appropriate for evaluating the robustness of our results against different landscape structures, and (4) they include scarce and dispersed distributions of patches for which connectivity maybe a major conservation concern.

2.2. MATERIALS AND METHODS

2.2.1. STUDY AREA

The two landscapes analyzed in this study were (i) an agricultural region in southern Madagascar (Bodin *et al.* 2006), and (ii) a forested area encompassing the capercaillie (*Tetrao urogallus*) habitat in northeastern Spain (Estrada *et al.* 2004; Pascual-Hortal and Saura 2008).

The Madagascan landscape has been extensively described and analyzed in previous studies (Bodin *et al.* 2006; Bodin and Saura 2010; Saura *et al.* 2014). It is located in the Androy region, at the very south of Madagascar (Fig. 2.1). Ecosystem functions in this region such as crop pollination by bees (*Apoidea*) and seed dispersal by ring-tailed lemurs (*Lemur catta*) are potentially threatened due to ongoing land use change, and formal protection is generally rare. The study area contains 203 patches scattered in an agricultural matrix and cover barely 3·5% of a total area of approximately 65,000 ha. Patch sizes range between <1 and 95 ha (minimum patch area of 0·5 ha) and are quite evenly distributed in the landscape.

The Spanish landscape comprises the suitable habitat areas for the capercaillie in the region of Catalonia (NE Spain), at the southernmost part of its European distribution (Fig. 2.1). In this region the capercaillie is an endangered species severely affected by habitat connectivity loss, among other conservation threats. An estimate of the probability of capercaillie occurrence was obtained for every 1 km × 1 km cell in Catalonia through field surveys and niche-based modeling (Estrada *et al.* 2004). Here, only those cells with a probability of occurrence of at least 0·2 were considered as habitat, as in Pascual-Hortal and Saura (2008). This yields a total of 522 cells of 1 km × 1 km confined in 131 geographically separated habitat patches.

Fig. 2.1. Location of the study areas and distribution of the habitat patches in S Madagascar (top, adapted from Bodin *et al.* (2006)) and NE Spain (bottom, adapted from Pascual-Hortal and Saura (2008)).

2.2.2. CONNECTIVITY METRICS

The connectivity metrics used in this study are described in Table 2.1. They are based on graph theory (Urban and Keitt 2001; Fall *et al.* 2007; Saura and Rubio 2010; Foltête and Giraudoux 2012) or, in the case of the *MC* (Metapopulation Capacity), derived from metapopulation theory under given assumptions (Hanski and Ovaskainen 2000). *IIC* (Integral Index of Connectivity) and *PC* (Probability of Connectivity) are habitat availability/reachability metrics, that is, they integrate the connected area within habitat units, namely intrapatch connectivity, with the area made available by the connections between habitat units, namely interpatch connectivity (Pascual-Hortal and Saura 2006; Saura and Rubio 2010). These metrics measure connectivity as the amount of reachable habitat.

All metrics analyzed in this study require as an input a set of habitat units (called nodes in graph theory) and connections (called links or edges in graph theory). Habitat units are usually individual patches, but for the purposes of this study other possibilities (sets of multiple nearby patches) are considered here. Habitat units are characterized by an attribute (a_i) (see details in Table 2.1) that will here correspond to the amount of habitat area in the unit. In a probabilistic connection model, there is a probability of direct dispersal (p_{ij}) between each pair of habitat units, generally derived from a negative exponential function of the distance between them (although other dispersal kernels could be used); this probabilistic model applies to *PC*, BC_k^{PC} and *MC*. In a binary connection model, pairs of habitat units are simply connected or not (with no intermediate modulation of the quality, strength or frequency of use of that connection) based on a distance threshold value that usually represents the maximum distance at which dispersal is possible. This model applies to *IIC*, BC_k and BC_k^{IIC} .

The betweenness centrality metrics are patch-level metrics that indicate some aspect of the importance of an individual habitat unit as part of the pathways that need to be followed when moving among other habitat units (BC_k , BC_k^{PC} and BC_k^{IIC}). The rest of the metrics (*IIC*, *PC*, *MC*) are landscape-level metrics, but they are frequently used to assess the importance of an individual habitat unit for connectivity through a one-by-one removal procedure in which the importance of habitat unit k is quantified as the percentage of decrease in the connectivity value after the (hypothetical) removal of that habitat unit (dPC_k , $dIIC_k$, dMC_k). As a result, both these patch-level and landscape-level metrics can rank the landscape habitat units according to their contribution to some aspect of landscape connectivity. Saura and Rubio (2010) showed that the importance values dPC_k and $dIIC_k$ can be partitioned in three fractions measured in the same units, each one representing a specific way in which a habitat unit can contribute to overall connectivity and habitat availability in the landscape: $dPC_k = dPC_{intra_k} + dPC_{flux_k} + dPC_{connector_k}$ and $dIIC_k = dIIC_{intra_k} + dIIC_{flux_k} + dIIC_{connector_k}$ (see Table 2.1 for details). The generalized betweenness centrality metrics BC_k^{PC} and BC_k^{IIC} can be directly compared with those of $dPC_{connector_k}$ and $dIIC_{connector_k}$ respectively (Bodin and Saura 2010) and are measured in the same units. Finally, *MC* is more related to the flux fraction than to any of the other two fractions of dPC_k and $dIIC_k$ (Bodin and Saura 2010).

Table 2.1. Description of the analyzed connectivity metrics.

Metric	Formula	Description and interpretation	References
Probability of connectivity (<i>PC</i>)	$PC = \sum_{i=1}^n \sum_{j=1}^n \frac{a_i \cdot a_j \cdot p_{ij}^*}{A_L^2}$	<i>PC</i> measures the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other, which includes connectivity within and among habitat units. <i>PC</i> accounts for the attributes of the habitat units (a_i) and for stepping stones by calculating the maximum product probability of all paths that can be followed when moving between habitat units (p_{ij}^*) as determined from the probabilities of direct dispersal among them (p_{ij}). Dividing by the squared total landscape area (A_L^2) normalizes the index range of variation from 0 to 1.	Saura and Pascual-Hortal (2007)
Integral index of connectivity (<i>IIC</i>)	$IIC = \sum_{i=1}^n \sum_{j=1}^n \frac{a_i \cdot a_j}{1 + nl_{ij}} \frac{1}{A_L^2}$	<i>IIC</i> is conceptually similar to <i>PC</i> but estimates the possibilities for dispersal between habitat units. Rather than on probabilities of dispersal, <i>IIC</i> is based on a binary connection model in which two habitat units are either connected or not. nl_{ij} is the topological distance, <i>i.e.</i> , the number of links in the shortest path between units i and j . The rest is the same as for <i>PC</i> .	Pascual-Hortal and Saura (2006)
<i>PC</i> and <i>IIC</i> fractions	$dPC_k = dPC_{intra_k} + dPC_{flux_k} + dPC_{connector_k}$ $dIIC_k = dIIC_{intra_k} + dIIC_{flux_k} + dIIC_{connector_k}$	Fraction <i>intra</i> corresponds to the contribution of habitat unit k to overall connectivity in terms of intrapatch connectivity. It represents the amount of reachable habitat area provided by the habitat unit k itself. Fraction <i>flux</i> measures how well habitat unit k is connected to other habitat units in the landscape. This fraction depends both on the attribute (habitat area) of habitat unit k (so that units with more habitat resources produce more flux when the rest of factors remain equal) and on its position within the landscape network. Fraction <i>connector</i> is the contribution of habitat unit k to the connectivity among other habitat units different from k , as a connecting element or stepping stone between them. This fraction is only based on the topological position of k within the landscape network, but it considers the attributes of the other habitat units that are being connected through k .	Saura and Rubio (2010)
Betweenness centrality (BC_k)	$BC_k = \sum_{i=1}^n \sum_{j=1}^n \frac{g_{ij}(k)}{g_{ij}}$	BC_k quantifies how much habitat unit k stands in between other units i and j in a network. It calculates the sum of all shortest paths between all pairs of units i and j that go through k ($g_{ij}(k)$) divided by the sum of all shortest paths between all pairs of units (g_{ij}).	Freeman (1977)
BC_k^{PC} / BC_k^{IIC}	$BC_k^{PC} = \sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^{*k}$ $BC_k^{IIC} = \sum_{i=1}^n \sum_{j=1}^n a_i a_j \frac{1}{1 + nl_{ij}^k}$	BC_k^{PC} and BC_k^{IIC} are generalizations of Freeman's BC_k to account for the attributes of habitat units (a_i) and for the strength of the connections between them (quantified respectively through p_{ij}^{*k} or nl_{ij}^k), so that they are measured in the same units as <i>PC</i> and <i>IIC</i> respectively. p_{ij}^{*k} is the maximum product probability between those pairs of units i and j for which k is included in the shortest path between them (otherwise $p_{ij}^{*k} = 0$). Similarly, nl_{ij}^k is the topological distance between i and j for those cases in which k is included in the shortest path between i and j ($nl_{ij}^k = \infty$ otherwise).	Bodin and Saura (2010)
Metapopulation capacity (<i>MC</i>)	$m_{ij} = a_i a_j p_{ij}$	<i>MC</i> assesses the persistence of a species in a landscape. It is defined as the leading eigenvalue of a landscape matrix with elements m_{ij} , which account for the attributes of the habitat units (a_i , usually area) and for the probability of direct dispersal between habitat units (p_{ij}) calculated as a negative exponential function of distance.	Hanski and Ovaskainen (2000)

2.2.3. CONNECTIVITY ANALYSIS FOR NESTED HIERARCHICAL LEVELS

In both study areas, we followed a three-step procedure to analyze the behavior of the connectivity indicators at different hierarchical levels when defining habitat units:

(1) We created a set of networks based on the original landscape data but with different types of habitat units. The first network in each study area had the same spatial detail as the available landscape data, *i.e.*, each patch in the habitat layer was considered as an individual habitat unit (node). This is the most usual approach in connectivity analyses. The rest of the networks in the set represented higher hierarchical levels so that habitat units were defined as aggregations of patches (metapatches) within a certain aggregation distance D_{agg} , *i.e.*, two patches belonged to the same habitat unit if the minimum Euclidean distance between their edges was not larger than D_{agg} (Fig. 2.2). Within a habitat unit with $D_{agg} > 0$ (that is, an aggregate) species are assumed to be able to move without hindrances or restrictions among patches. Several D_{agg} distances were chosen corresponding to the 5%, 10%, 15%, and 20% of the maximum distance between the two most distant patches in both landscapes. Higher D_{agg} would leave very few habitat units so that a connectivity analysis would be uninteresting. As a result, we obtained five networks for each landscape: the original network ($D_{agg} = 0$) plus four others at different $D_{agg} > 0$. These habitat units defined at different hierarchical levels could correspond to the foraging or patrolling area of different potential species with diverse ecological needs, with higher D_{agg} corresponding to species with larger spatial requirements and home ranges.

(2) Secondly, several dispersal distances d_{disp} were considered in each network. In this study, $d_{disp} > D_{agg}$ by definition. For metrics based on binary connections (IIC , BC_k , and BC_k^{IC}), d_{disp} represented the maximum distance at which dispersal was possible: two habitat units were directly connected (there was a link) if the Euclidean distance between them was not larger than d_{disp} , and unconnected otherwise. For metrics using probabilistic connections (PC , BC_k^{PC} , and MC), d_{disp} corresponded to the mean dispersal distance. The probabilities of direct dispersal (p_{ij}) between habitat units were calculated as a negative exponential function of the Euclidean distance between the edges of the habitat units (d_{ij}), $p_{ij} = e(-(d_{ij})/(d_{disp}))$. The d_{disp} values were chosen to cover a wide range of dispersal abilities, from short d_{disp} for which very few units were linked to large d_{disp} directly connecting most of the habitat units in the whole network; this resulted in different d_{disp} in approximately regular intervals ranging from 25% to 75% of the maximum distance between the most distant patches in both landscapes. Higher d_{disp} were unnecessary because all patches were already connected at those distances. All indices were calculated using a purposefully adapted version of JMatrixNet (Bodin *et al.* 2006), Conefor 2.6 (Saura and Torne 2009), and R (R Development Core Team 2013).

(3) Finally, we evaluated changes in (i) the importance value and in (ii) the priority ranking of habitat units when varying the hierarchical level at which these habitat units were defined. The importance value of habitat unit k was quantified as dPC_k , $dIIC_k$, dMC_k for the landscape-level habitat availability and metapopulation capacity metrics, but was given directly by BC_k , BC_k^{PC} , and BC_k^{IC} for the patch-level betweenness centrality metrics.

- i. In order to evaluate changes in the importance value of habitat units we quantified an Importance Ratio (IR_k) separately for each metric, D_{agg} , and d_{disp} values. IR_k was calculated as the ratio between (a) the importance value of a habitat unit k comprising multiple patches and (b) the sum of the importance values of each of the individual patches that made up k when no aggregation was considered (single patches, $D_{agg}=0$). Only units made up of two or more patches were considered for calculating IR_k (since otherwise $IR_k = 1$ by definition). The closer IR_k is to 1, the more robust a metric is in assessing the importance of different habitat areas across scales. $IR_k = 1$ indicates that the metric is scale invariant, that is, that the connectivity assessment is not influenced by the chosen hierarchical level. This would be the ideal behavior. $IR_k > 1$ means that the connectivity metric indicates comparatively higher importance value for the metapatch than for the single patches that compose that metapatch and vice versa.
- ii. In order to evaluate changes in the priority ranking we computed (separately for each metric, D_{agg} , and d_{disp} values) Kendall's Tau-b (τ_b) coefficient between the importance values of a habitat unit and the sum of the importance values of the individual patches within that habitat unit (single patches, $D_{agg} = 0$). Kendall's Tau-b (τ_b) coefficient is a measure of rank correlation, that is, the similarity of the ordering of two datasets. τ_b ranges between 0 and 1, with higher values indicating more similarity in the connectivity conservation priorities derived at different scales. The results from (i) and (ii) are not necessarily coincident or redundant. For example, τ_b may be equal to 1 (same priority ranking for both the metapatch and the individual patches in it) but IR_k may be considerably different from 1 because a higher importance value is assigned to the loss of a given metapatch ($D_{agg} > 0$) than to the loss of each of the individual habitat patches within that meta-patch ($D_{agg} = 0$). Therefore, for instance, connectivity metrics may indicate largely varying importance values at different hierarchical values but still indicate similar priorities for the same parts of the landscape.

Fig. 2.2. An example of a hypothetical landscape where habitat units are defined at two hierarchical levels. In the lower hierarchical level each of the patches (a_i , b_i , c_i , d_i , e_i) is considered as an individual habitat unit. In the higher hierarchical level habitat units correspond to aggregates A (a_1, a_2, a_3), B (b_1, b_2, b_3, b_4), C (c_1, c_2, c_3), D (d_1, d_2, d_3), and E (e_1, e_2), which consist of sets of nearby patches (metapatches) defined by the aggregation distance D_{agg} .

2.3. RESULTS

2.3.1. IMPORTANCE VALUE OF HABITAT UNITS

In general, the importance values of habitat units varied greatly with the hierarchical level chosen (Fig. 2.3 and 2.4 for metrics based on the probabilistic connection model; and Fig. A.1 and A.2 in the Appendix for metrics based on the binary connection model). In many cases, the quantified importance values of habitat units did not follow a trend across the hierarchical levels considered. The most frequent result was that the quantified importance of the habitat units was higher for an aggregate (*i.e.*, an individual habitat unit made of several patches) than for every patch of that aggregate treated as a separate individual habitat unit ($IR_k > 1$). For metrics based on a probabilistic connection model IR_k values tended to increase with the aggregation distance. The variations were however less pronounced for the Madagascan landscape than for the Spanish one. For the Madagascan landscape, IR_k was below 3, except for a few large peaks found for dMC_k (Fig. 2.3c), which were caused by the almost zero value of these metrics at short d_{disp} when habitat units corresponded to single patches. IR_k was very close to the unity for dPC and $dPCflux_k$ (Fig. 2.3a and e) especially at low aggregation levels (5%, 10% and 15%). On the contrary, in the Spanish landscape IR_k values were above 2 for dPC and $dPCflux_k$ (Fig. 2.4a and e), while values of $IR_k < 1$ were only found for the highest aggregation level (20%) of BC^{PC}_k (Fig. 2.4b). For the metapopulation capacity, dMC_k , results were similar to those of the Madagascan landscape (Fig. 2.4c). Also, $dPCintra_k$ presented $IR_k > 100$ for the highest aggregation level (20%) and highest dispersal distances (Fig. 2.4d). For those metrics based on a binary connection model, results showed that for almost all metrics in Madagascar $IR_k < 2$ at some d_{disp} and D_{agg} (Fig. A.1a–e). The exception is $dIICconnector_k$ whose peaks were caused by the almost zero value of these metrics at short d_{disp} when habitat units corresponded to single patches (Fig. A.1f). On the other hand, in the Spanish landscape values of $IR_k < 1$ were only found for the centrality metrics BC^{IC}_k and BC_k at low d_{disp} and D_{agg} (Fig. A.2b and c). Also, values of $IR_k > 5$ were found for the largest D_{agg} and most of the metrics (Fig. A.2a–f).

2.3.2. PRIORITY RANKING OF HABITAT UNITS

Generally, priority rankings were quite robust for several of the analyzed connectivity metrics with values of τ_b above 0.8. The priority rankings given by dPC_k were only slightly affected by scale, with τ_b above 0.8 in Madagascar and above 0.9 in Spain for all d_{disp} and D_{agg} (Fig. 2.5a and 2.6a). The three fractions of dPC_k reacted however differently to variations in the hierarchical level used. The intra fraction, $dPCintra_k$, showed the highest τ_b (Fig. 2.5d and 2.6d). The flux fraction, $dPCflux_k$, also presented τ_b values above 0.8, except at small d_{disp} (Fig. 2.5e and 2.6e). The connector fraction, $dPCconnector_k$, was the one most affected by changing spatial scales, with τ_b values as low as 0.4 and in a few cases even below (Fig. 2.5f and 2.6f). The betweenness centrality metrics, BC^{PC}_k , (Fig. 2.5b and 2.6b) showed similar high scale sensitivity as

$dPCconnector_k$ (Fig. 2.5f and 2.6f), to whom they are in part conceptually related (Bodin and Saura 2010). The connectivity priority rankings provided by centrality and connector metrics were those that changed most when larger habitat units were used in both landscapes. Priority rankings derived from dMC_k were more sensitive to hierarchical level changes than those given by dPC_k . dMC_k behaved similarly to the flux fraction, $dPCflux_k$ (*i.e.*, lower τ_b values for smaller d_{disp}), although dMC_k was slightly more sensitive to spatial scale than $dPCflux_k$ (Fig. 2.5c and 2.6c). As expected, larger D_{agg} generally resulted in lower stability of the priority positions, particularly for the most sensitive metrics to changes in the hierarchical level, although there were exceptions (Fig. 2.5 (a and d) and 2.6 (a, d and e)). For those metrics based on binary connection models we found similar results as those described above for those based on the probabilistic connection model: $dIIC_k$, $dIICintra_k$, and $dIICflux_k$ were largely robust, with τ_b values above 0.8 except for low D_{agg} in $dIICflux_k$ (Fig. A.3 (a, d, and e) and A.4 (a, d and e)). Betweenness centrality metrics, BC_k and BC^{IIC}_k , presented lower τ_b around 0.6, values at higher D_{agg} (Fig. A.3 (b and c) and A.4 (b and c)). The connector fraction, $dIICconnector_k$, was the one most affected by changing spatial scales, with τ_b values as low as 0.4 and in a few cases even below (Fig. A.3f and A.4f).

Fig. 2.3. Similarity in the connectivity importance values (measured by IR) when the habitat units are defined at different hierarchical levels in the Madagascar landscape. IR is the average of all the IR_k values corresponding to each habitat unit k in the landscape. Results are shown for each of the metrics based on probabilistic connections (PC and its fractions, BC^{PC}_k and MC) as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} . Note the change in scale for the y-axis on the asterisk-marked plots (c). Results for the metrics based on binary connections are shown in Fig. A.1 in Appendix A.

Fig. 2.4. Similarity in the connectivity importance values (measured by IR) when the habitat units are defined at different hierarchical levels in the Spanish landscape. IR is the average of all the IR_k values corresponding to each habitat unit k in the landscape. Results are shown for each of the metrics based on probabilistic connections (PC and its fractions, BC_k^{PC} and MC) as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} . Note the change in scale for the y-axis on asterisk-marked plots (c and d). Results for the metrics based on binary connections are shown in Fig. A.2 in Appendix A.

Finally, τ_b varied more steadily with d_{disp} for metrics based on probabilistic connections (e. g., $dPCconnector_k$, BC_k^{PC} , and dMC_k) than for those based on binary connections (e. g., $dIICconnector_k$, BC_k^{IC} , and BC_k).

2.4. DISCUSSION

2.4.1. HOW RELIABLE ARE THE INDICATORS OF CONNECTIVITY IMPACTS (IMPORTANCE VALUE) AT A GIVEN HIERARCHICAL LEVEL?

We found large sensitivity in the importance values for the habitat units measured by different metrics when changing the hierarchical level at which those habitat units were defined. The importance values estimated from these indicators (*i.e.*, estimated percentage of decrease in overall connectivity by removing a particular portion of the habitat) was found to be generally of little reliability when assessed from the individual importance values of multiple small units (*e.g.*, patches) simultaneously affected by a given habitat loss process. We found however that

the hierarchical level sensitivity was considerably less pronounced in Madagascar than in Spain, due to the different habitat spatial configuration. In Madagascar patches were evenly distributed and comparatively closer to each other while in Spain patches were irregularly distributed and farther apart, which induced larger and more abrupt changes in the indicators with the D_{agg} and/or d_{disp} distance values. In general, our findings indicate that it is difficult to generalize which would be the impact of a given habitat loss in terms of the amount of connectivity lost for different species, since species with different dispersal abilities (as related to d_{disp}) or using territories of different sizes (as related to D_{agg}) are estimated to respond quite differently (as assessed by the analyzed connectivity indicators) to a given modification in the habitat network. Therefore, these results provided by widely used connectivity indicators cannot be generalized across all species and ecological processes; multiple analyses at different spatial scales would be required to match the particular traits of each of the involved species. Generally, the quantified importance values for habitat units at different hierarchical levels was higher for an aggregate than what indicated by the same metrics when every patch of that aggregate was treated as a separate individual habitat unit. This could indicate more prominent and synergistic effects on connectivity for the combined loss of several patches (all considered as a single habitat unit) than for those derived from the sum of the individual effects of single patch removals. This result brings some concern on the degree to which the accumulated and combined effects of multiple habitat losses can be assessed through single patch removal procedures. Therefore, we suggest that further studies should focus in examining the validity of these widely used single patch removal procedures when multiple habitat patch losses occur simultaneously or accumulate through time in increasingly vulnerable landscape networks. This is part of our ongoing research.

2.4.2. HOW RELIABLE ARE THE CONSERVATION PRIORITY RANKINGS DERIVED FROM CONNECTIVITY INDICATORS AT A GIVEN HIERARCHICAL LEVEL?

Unlike the importance values, the priority rankings of habitat units were robust and, for some metrics like dPC_k , largely maintained across the different hierarchical levels at which the habitat units were defined. This result happened in both directions. First, habitat units identified as key connectivity providers at higher hierarchical levels (aggregations of patches) contained those patches that were also critical for connectivity at smaller scales. Conversely, habitat units that were identified as unimportant for connectivity at large scales contained patches that were also not essential for connectivity when smaller hierarchical levels were considered. Because these results occurred in two landscapes with very different configurations, we are confident that these connectivity metrics can be consistently used for identifying critical habitat areas for connectivity and related spatially explicit conservation priorities with little concern for their sensitivity to the spatial scale chosen for indicator delivery.

Fig. 2.5. Similarity in the connectivity conservation priorities (measured by τ_b correlation coefficient) when the habitat units are defined at different hierarchical levels in the Madagascan landscape. Results are shown for each of the metrics based on probabilistic connections (PC and its fractions, BC_k^{PC} and MC) as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} . Results for the metrics based on binary connections are shown in Fig. A.3 in Appendix A.

Fig. 2.6. Similarity in the connectivity conservation priorities (measured by τ_b correlation coefficient) when the habitat units are defined at different hierarchical levels in the Spanish landscape. Results are shown for each of the metrics based on probabilistic connections (PC and its fractions, BC_k^{PC} and MC) as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} . Results for the metrics based on binary connections are shown in Fig. A.4 in Appendix A.

Our results do not omit, even for the robust metrics, the possibility that a key metapatch (aggregation of patches) could include, along with those individual patches that are a priority for connectivity conservation at a lower hierarchical level, other individual patches that are not critical at that lower hierarchical level. However, in practice our results suggest that some of the analyzed connectivity metrics can be applied to deliver conservation priorities that are consistent and valid for multiple species with different dispersal abilities (as related to d_{disp}) and home range sizes (as related to D_{agg}); those priority habitat areas for connectivity identified at larger hierarchical levels include those priority individual patches that are identified at finer spatial scales, even if potentially accompanied by some other non-critical individual patches. In such case, an additional analysis at a finer spatial scale focusing only on the small set of key metapatches could identify (but not miss) which subset of individual patches should be really part of the connectivity conservation priorities for other species with different traits, such as those related to home range size or dispersal abilities.

2.4.3. WHY ARE SOME CONNECTIVITY METRICS MORE SENSITIVE THAN OTHERS TO THE HIERARCHICAL LEVEL AT WHICH THE HABITAT UNITS ARE DEFINED?

There were large differences in the sensitivity of connectivity metrics to the spatial scale at which the habitat units were defined. These differences are related to the ingredients of each connectivity metric, *i.e.*, which components of connectivity they consider or not and the weight of each of these aspects in the final connectivity assessment provided by these metrics. First, it is important to distinguish between metrics that consider connectivity within habitat units and those that do not. The habitat availability/reachability metrics $dIIC_k$ and dPC_k do measure connectivity accounting for both the reachable habitat within and between habitat units. This characteristic provides improved properties and performance in many varied situations as compared to other connectivity metrics, including appropriate prioritization abilities (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010). In this study, these properties and abilities are reinforced by the considerable robustness to spatial scale of the conservation priorities they provide. The intra fraction of these metrics ($dIIC_{intra_k}$, dPC_{intra_k}) quantifies exclusively the amount of reachable habitat within habitat units and resulted in the most robust priority rankings of all analyzed connectivity metrics (Fig. 2.5d and 2.6d). This is a reasonable result, since the total area of reachable habitat within a habitat unit composed of multiple patches will be largely equivalent to the sum of the habitat area of each of the individual patches. The fact that $dIIC_k$ and dPC_k assess connectivity not only among habitat units but also within them (*i.e.*, intra fraction contributes to their values) provides these metrics with stability against scale changes that improves their performance compared to other analyzed metrics. Metrics purely accounting for network topological aspects (*i.e.*, position of a given habitat unit relative to others) were much more sensitive to the spatial scale at which habitat units were defined. This was the case of the connector fraction of the habitat availability/reachability metrics, $dIIC_{connector_k}$, $dPC_{connector_k}$, and of the network centrality metrics, BC_k , BC^{IIC}_k , and BC^{PC}_k , which all quantify

different aspects of how important a given habitat unit is beyond itself for keeping the rest of the habitat well connected. An illustrative example of the sensitivity of these metrics to scale changes is provided in Appendix B. Metrics quantifying how well habitat units are connected to the rest of the habitat resources ($dIICflux_k$, $dPCflux_k$, dMC_k) presented higher sensitivity to scale changes than those considering connectivity within habitat units ($dIICintra_k$, $dPCintra_k$, $dIIC_k$, dPC_k) and lower sensitivity than those specifically focusing on the role of habitat units as providers of connectivity between other habitat areas ($dIICconnector_k$, $dPCconnector_k$, BC_k , BC^{IIC}_k , and BC^{PC}_k). This is so because the amount of connectivity estimated by these metrics depends on two ingredients: (a) the topological position of the habitat units compared to others (with habitat units closer to others being better connected), and (b) the amount of habitat in the habitat units (with larger habitat units assumed to exchange higher number of individuals). The former (a) varies greatly with the spatial scale chosen while the latter (b) is less affected by the hierarchical level at which habitat units are defined: the amount of habitat in an aggregate can be well predicted from the amount of habitat in each of the individual habitat patches. The larger d_{disp} , the better the habitat units are connected to each other (in the extreme case all units would be fully connected to all others); therefore, the expected amount of individuals exchanged will depend to a greater extent (or exclusively, in that extreme case) on their amount of habitat resources. In this case, the weight of the less scale-dependent ingredient (b) would increase, explaining why these metrics showed higher variability to scale at smaller d_{disp} . The sensitivity to scale of $dIIC_k$ and dPC_k was lower than what would be expected from averaging the sensitivity to scale of the three fractions that compose them. This is caused by the reorganization of the values of the fractions when habitat units are defined at different hierarchical scales, so that even if the values of the individual fractions change considerably with scale, variations in one fraction partly compensate or absorb variations in the others, resulting in a considerably robust total $dIIC_k$ or dPC_k value (see Appendix B for an illustrative example). This capacity of the $dIIC_k$ and dPC_k metrics to redistribute the roles of habitat patches at different spatial scales makes these metrics markedly more robust than others like the metapopulation capacity, which does not explicitly consider the type of connectivity that is quantified by the intra and connector fractions (Saura and Rubio 2010; Saura *et al.* 2014). Finally, it is worth noting that connectivity conservation priorities were more robust for metrics based on the probabilistic connection model than for their binary counterparts, given the sharper variations that can occur in the latter as a function of d_{disp} and D_{agg} used in the connectivity analysis (Bodin and Saura 2010).

2.5. CONCLUSIONS

We have tackled important and largely overlooked aspects of widely used procedures for connectivity indicator delivery. Our findings highlight the need to be aware of the effect that a particular choice of hierarchical level may have (even if unintentionally imposed by data availability limitations) in the connectivity indicators used for impact assessments and for

setting conservation priorities. We have found that (1) the amount of connectivity loss by the removal of a given part of the habitat estimated by current connectivity indicators can largely vary depending on the hierarchical level at which habitat units are defined, and that, notwithstanding, (2) the connectivity conservation priorities (*i.e.*, the identification of which parts of the landscape contain the habitat areas whose loss would be most or least detrimental for connectivity) are considerably robust across scales at least for several metrics, particularly those that measure connectivity as the amount of reachable habitat in the landscape (habitat availability metrics). The latter means that aggregates (habitat units comprising several patches) that are important in upholding connectivity at a certain hierarchical level also contain the patches (when these are considered as single habitat units) that are identified as key connectivity providers by these spatial indicators. This conclusion offers scientists and conservationists confidence in using robust spatially explicit indicators that can support decision-making for conserving connectivity in changing landscapes for different species. In summary, the current methods and indicators for analyzing connectivity based on single patch removal experiments at a time do not seem to allow, considering their dependence on hierarchical levels, answering with confidence to the following question: which proportion of the current landscape connectivity will be lost after the removal of multiple habitat patches from the landscape? But these indicators are however much more reliable in answering this other question: which are the habitat areas that need to be prioritized for landscape connectivity conservation?

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2.7. SUPPLEMENTARY MATERIAL

2.7.1. APPENDIX A

Fig. A.1. Similarity in the connectivity importance values (measured by IR) when the habitat units are defined at different hierarchical levels in the Madagascar landscape. IR is the average of all the IR_k values corresponding to each habitat unit k in the landscape. Results are shown for metrics IIC and its fractions, BC_k and BC^{IIC}_k as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} . Note the change in scale for the y-axis on the asterisk-marked plots (f).

Fig. A.2. Similarity in the connectivity importance values (measured by IR) when the habitat units are defined at different hierarchical levels in the Spanish landscape. IR is the average of all the IR_k values corresponding to each habitat unit k in the landscape. Results are shown for metrics IIC and its fractions, BC_k and BC^{IIC}_k as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} . Note the change in scale for the y-axis on asterisk-marked plots (d, f).

Fig. A.3. Similarity in the connectivity conservation priorities (measured by τ_b correlation coefficient) when the habitat units are defined at different hierarchical levels in the Madagascan landscape. Results are shown for metrics IIC and its fractions, BC_k and BC^{IIC}_k as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} .

Fig. A.4. Similarity in the connectivity conservation priorities (measured by τ_b correlation coefficient) when the habitat units are defined at different hierarchical levels in the Spanish landscape. Results are shown for metrics IIC and its fractions, BC_k and BC^{IIC}_k as a function of dispersal distance d_{disp} for different aggregation distances D_{agg} .

Some of the additional examples presented here illustrate here different situations related to connectivity metrics behavior when changing the hierarchical level at which habitat units are defined. These situations are mostly related to the sensitivity to scale of these metrics.

When all habitat units correspond to individual patches ($D_{agg}=0$) and d_{disp} is large enough (Fig B.1a), multiple stepping stone patches (b1, b2, b3, b4) allow moving from patches a2/a3 to patches c1/c2. This means that network centrality and the connector fraction (evaluated against single patch removals) are zero or very low for b1, b2, b3 or b4, because the rest of these patches can still act as single stepping stones when one of them is lost. None of them is an irreplaceable connectivity provider whose individual loss would completely disrupt the connectivity between a2/a3 and c1/c2; therefore, the overall importance of the set of patches b1/b2/b3/b4 will also be low when habitat units correspond to individual patches. However, when considering certain $D_{agg} > 0$ (Fig. B.1b) so that all patches in B (b1/b2/b3/b4) are treated jointly as a single habitat unit, the loss of B would entirely impede movement between A and C by removing the only habitat patches that can act as stepping stones between A and C. Therefore, at this higher hierarchical level of analysis, B is found to be a key connecting element.

Likewise, at short d_{disp} , when $D_{agg}=0$ (Fig. B.2a) each of the individual patches d1, d2, and d3 has a positive connector fraction or network centrality value because losing of any of them would break the chain of stepping stones needed to move from c3 to e1 (no other alternatives to movement exist). The sum of the importance values for each of individual patches d1, d2, and d3 will correspond to three times the amount of connectivity loss due to impeding movement from c3 to e1. When $D_{agg} > 0$ so that patches d1, d2, and d3 are considered as a single habitat unit D (Fig. B.2b), their importance value according to these metrics decreases to one third compared to the previous situation, since the removal of the now only habitat unit between c3 and e1 (D) gets an importance value of only one time the amount of connectivity lost due to movement disruption between c3 and e1.

Another situation is shown in Fig. B.3, where the existing flux fraction at $D_{agg}=0$ among patches a1, a2 and a3 becomes intra fraction within habitat unit A when D_{agg} is large enough so that all these three patches are part of the same unit A. In the example discussed above for patches d1, d2, and d3, an important amount of connector fraction existing at $D_{agg}=0$ (Fig. B.2a) is redistributed and largely absorbed by the intra and flux fractions in the larger habitat unit D ($d1 + d2 + d3$) when considering a certain D_{agg} (Fig. B.2b). This example illustrates that the capacity of the $dIIC_k$ and dPC_k metrics to redistribute the roles of habitat patches at different spatial scales makes these metrics markedly robust to the use of different hierarchical levels when defining habitat units.

Fig. B.1. A hypothetical landscape illustrating the connector fraction sensitivity to the hierarchical level at which habitat units are defined. In (a) each of the patches (a_i, b_i, c_i, d_i, e_i) is considered as an individual habitat unit. In (b) habitat units correspond to aggregates A (a₁, a₂, a₃), B (b₁, b₂, b₃, b₄), C (c₁, c₂, c₃), D (d₁, d₂, d₃), and E (e₁, e₂), which consist of sets of nearby patches defined by the aggregation distance D_{agg} . Red arrows indicate the connections between habitat units for the dispersal distance d_{disp} shown in the graphical scale, and gray lines in (b) bond those patches that are part of the same habitat unit as given by D_{agg} .

Fig. B.2. A hypothetical landscape illustrating the connector fraction sensitivity to the hierarchical level at which habitat units are defined. In (a) each of the patches (a_i, b_i, c_i, d_i, e_i) is considered as an individual habitat unit. In (b) habitat units correspond to aggregates A (a₁, a₂, a₃), B (b₁, b₂, b₃, b₄), C (c₁, c₂, c₃), D (d₁, d₂, d₃), and E (e₁, e₂), which consist of sets of nearby patches defined by the aggregation distance D_{agg} . Red arrows indicate the connections between habitat units for the dispersal distance d_{disp} shown in the graphical scale, and gray lines in (b) bond those patches that are part of the same habitat unit as given by D_{agg} .

Fig. B.3. A hypothetical landscape illustrating a situation of swap of fraction flux into fraction intra as a result of varying the hierarchical level at which habitat units are defined. In (a) each of the patches (a_i, b_i, c_i, d_i, e_i) is considered as an individual habitat unit. In (b) habitat units correspond to aggregates A (a_1, a_2, a_3), B (b_1, b_2, b_3, b_4), C (c_1, c_2, c_3), D (d_1, d_2, d_3), and E (e_1, e_2), which consist of sets of nearby patches defined by the aggregation distance D_{agg} . Red arrows indicate the connections between habitat units for the dispersal distance d_{disp} shown in the graphical scale, and gray lines in (b) bond those patches that are part of the same habitat.

CHAPTER 3

RESPONSE OF INDIVIDUALS TO THE LANDSCAPE ACCORDING TO THE BEHAVIORAL STATE

Photo: Sandra Blázquez

This chapter reproduces entirely the content of the research paper:

Gastón A, **Blázquez-Cabrera S**, Garrote G, Mateo-Sánchez MC, Beier P, Simón MA, Saura S (2016). Response to agriculture by a woodland species depends on cover type and behavioral state: insights from resident and dispersing Iberian lynx. *Journal of Applied Ecology* 53:814–824. doi: 10.1111/1365-2664.12629

SUMMARY

1. Conservation biology faces the challenge of ensuring species persistence in increasingly modified landscapes. Agriculture covers a large proportion of the Earth's surface, but the degree to which crop production is compatible with species use of the landscape is still uncertain, particularly for woodland carnivores with large territories. Here, we focus on the Iberian lynx (*Lynx pardinus*), an emblematic endangered species that has coexisted for centuries with human-modified Mediterranean mosaics, as a case study to unravel habitat and dispersal preferences in heterogeneous landscapes.

2. We estimated species resource selection from $\approx 40\,000$ telemetry locations for 48 GPS-collared individuals covering all the current Iberian lynx range, including more fragmented areas where the species was reintroduced from 2009. We differentiated GPS locations within home ranges (to estimate habitat suitability) and those corresponding to dispersal or exploratory movements (to estimate landscape permeability). We built mixed conditional logistic regression models with 12 land cover classes, terrain slope and roads as predictors.

3. We found that lynx response to agriculture largely depends on the crop type and on the presence of natural vegetation remnants. Lynx largely avoided intensive cultivation areas such as irrigated arable lands when establishing home ranges, but frequently selected permanent crops (olive groves) and/or heterogeneous agricultural lands, which were used with smaller differences to the most preferred shrubland or forest covers than reported in previous studies.

4. Such differences further narrowed down when lynx moved outside home ranges, with some agricultural covers being as permeable as shrublands for lynx dispersal. The species dispersal plasticity was also evidenced by a much weaker avoidance of roads and steep terrain when dispersing than when selecting territories.

5. Synthesis and applications. We conclude that (i) the widespread consideration of all agricultural lands within a single (and usually regarded as unsuitable) class for the study and management of woodland or forest species is not supported and that (ii) the ability of woodland species to use fragmented and heterogeneous agricultural landscapes may have been underestimated, which may mislead conservation measures due to a priori assumptions that do not relate to the actual species responses to heterogeneous land covers. We suggest that Iberian lynx conservation and reintroduction may be successful in a wider set of more heterogeneous areas than previously thought, including mainly well-conserved Mediterranean woodlands but also some extensive agricultural lands with permanent crops and natural vegetation remnants.

3.1. INTRODUCTION

Many formerly pristine regions have been modified, or are being modified, for establishing crops or for other human land uses. An intensive land use only oriented to maximizing yields over large areas may cause the disappearance of many, if not most, of the species originally occupying those areas. In some other landscapes, however, agricultural and artificial lands of different types are interspersed with natural or semi-natural patches of different sizes forming heterogeneous mosaics that may be more multifunctional, providing a wider range of ecosystem services, from crop production to biodiversity conservation (Tscharntke *et al.* 2005). Since pristine areas fully covered by natural habitats are becoming scarcer, understanding and managing species responses to landscape heterogeneity and human modification is one of the top priorities for ecological research and applied conservation management (Fahrig *et al.* 2011).

In many regions, it is unlikely that human activities can be completely excluded over large areas; therefore, species with broad spatial requirements are likely to encounter human-modified and agricultural land uses at least in parts of their territories. This is the case of many top predators such as mammalian carnivores, many of which are endangered species that have suffered large population declines as the combined result of habitat destruction, fragmentation and human persecution (Woodroffe 2000; Dirzo *et al.* 2014). While mortality by direct killing may be largely reduced as a result of social awareness, policy measures and law enforcement, the potential effects of landscape modification are less likely to be reversed, and species may need to adapt to some amount of human land use or otherwise continue to decline in numbers (Dellinger *et al.* 2013).

To provide insights into these important questions, we here focus on studying habitat suitability and landscape permeability for the endangered Iberian lynx (*Lynx pardinus*), an emblematic medium-sized carnivore endemic to Spain and Portugal (Rodríguez and Calzada 2015) that has rabbit *Oryctolagus cuniculus* as its main prey (Delibes 1980; Gil-sánchez *et al.* 2006). Once distributed throughout most of the Iberian Peninsula, the large population decline and range contraction suffered by the Iberian lynx (Rodríguez and Delibes 2002; Simón *et al.* 2012) restricted its presence at the beginning of the 21st century to only two isolated areas (Andújar-Cardena and Doñana-Aljarafe, see their approximate location in Fig. 3.1) with less than 100 individuals in total (Simón *et al.* 2012). This strong decline has been attributed to the combined result of the destruction and fragmentation of its habitat, the decrease in rabbit abundance and hunting or poaching activities (Rodríguez and Delibes 2002; Rodríguez and Delibes 2004; Simón *et al.* 2012). Recent conservation efforts have reversed the decline of the Iberian lynx populations (Simón *et al.* 2012). The most recent census estimates a population size above 300 individuals in 2014 (Life+ IBERLINC 2006). This considerable population size increase in about a decade has been achieved by reinforcing the lynx populations in Andújar-Cardena and Doñana-Aljarafe and since 2009 by reintroducing the species in two other areas within the species historical range (Guarriazas and Guadalmellato) (Fig. 3.1), in both cases with the support of individual translocation, captive breeding and genetic reinforcement strategies (Simón *et al.* 2012; Rodríguez and Calzada 2015).

Our aim was to understand how a wide-ranging woodland species uses heterogeneous landscapes and how it responds to natural (semi-natural) habitats, agricultural areas and other human-made land covers. Our case study features several important characteristics towards this end.

First, the landscape composition in the range of the Iberian lynx has been highly modified by humans for centuries, presenting a mixture of agricultural lands and fragmented Mediterranean woodlands or forests. Secondly, we analyze a large new data set from GPS-collared lynx that allows more powerful inferences on habitat selection and dispersal than previous studies on the species (Palma *et al.* 1999; Palomares *et al.* 2000; Palomares 2001; Fernandez *et al.* 2003; Fernández *et al.* 2006; Gil-Sánchez *et al.* 2011). We analyze these telemetry data with context-dependent resource selection functions (estimated by mixed-effects conditional logistic regression), which can provide improved estimates of habitat preferences and landscape permeability to species movement (Duchesne *et al.* 2010; Zeller *et al.* 2014). Thirdly, we consider all the areas with current presence of the Iberian lynx, which include the two main nuclei with the best habitat conditions in which the species distribution had contracted at the beginning of this century (Doñana-Aljarafe and Andújar-Cardena) but also other more fragmented areas in which the Iberian lynx was reintroduced (Simón *et al.* 2012). In doing so, we cover a large spatial extent and a variety of conditions in land cover composition and heterogeneity and aim to provide models that are applicable to the entire Iberian Peninsula.

We estimated the Iberian lynx preferences for 12 land cover classes, including seven types of agricultural lands, and also accounting for the effect of roads and terrain slope. Because habitat selection may differ between behavioral states or types of activity (Zeller *et al.* 2014), we analyzed separately lynx locations within home ranges (resident individuals) and locations corresponding to exploratory or dispersal movements outside home ranges. We found that the reported or assumed avoidance of agricultural lands by this species (Palomares *et al.* 2000; Palomares 2001; Fordham *et al.* 2013) is not supported and that the Iberian lynx was less reluctant to traverse steep terrain, roads and low suitability covers when dispersing than when establishing home ranges. Woodland patches were clearly those most preferred by the species, but agricultural areas with tree crops and/or with some amount of natural vegetation were frequently selected both by resident and dispersing lynx. Our results suggest that the species' ability to use fragmented and heterogeneous mosaics of human-altered and naturally occurring land cover may have been underestimated. We discuss the reasons underlying this finding and suggest that similar circumstances may apply to other woodland species, with potentially broad implications for informing conservation strategies and management measures in heterogeneous human-modified landscapes.

3.2. MATERIAL AND METHODS

3.2.1. TELEMETRY DATA

GPS-GSM collars provided the location of tracked lynx every 4 hours. GPS locations were acquired between May 2009 and November 2013. We analyzed 44,002 GPS locations from 48 individuals (mean 917, range 150 - 4069) from all four currently stable populations (Fig. 3.1), including a large representation of the more fragmented areas where the species was reintroduced (Guarrizas and Guadalmellato); see Table A.1 in Appendix A (Supplementary material). The large set of tracked individuals comprised males and females, subadults and adults, and animals born in the wild (69% of GPS locations) and others born in captivity and released in the wild (31% of locations). Further details are provided in Appendix A.

3.2.2. SEPARATING HOME RANGE USE AND DISPERSAL

We used the a-LoCoH adaptive method (Getz *et al.* 2007) to separate GPS locations into two groups, each used for fitting a different model: (i) locations corresponding to home range use by resident individuals, which were used to construct the habitat suitability model and (ii) locations corresponding to dispersal or exploratory movements outside home ranges, which were used to construct the landscape permeability model. An example for two lynx is shown in Fig. 3.2. Further details are provided in Appendix B.

All analyses described next were performed separately for the home range locations (habitat suitability model), for the dispersal or exploratory locations outside home ranges (landscape permeability model) and for all locations (home range and dispersal locations together; hereafter joint model). The joint model allowed us to evaluate whether the obtained results hold independently of the decision of partitioning the GPS fixes into two behavioral states (dispersal and home range use subsets). In addition, to discard the possibility that captive-bred individuals ($\approx 31\%$ of all GPS locations) may be affecting our conclusions on the Iberian lynx habitat selection, we also built the habitat suitability and landscape permeability models using only the GPS locations for the individuals born in the wild.

3.2.3. ENVIRONMENTAL DATA

Because current conservation strategies aim at recovering the historical lynx distribution, we built habitat suitability and landscape permeability models for the entire Iberian Peninsula, which is in a comparable manner for all continental Spain and Portugal. We therefore selected 15 explanatory variables that (i) had a plausible causal relationship with habitat selection by the Iberian lynx and (ii) for which homogeneous and spatially continuous information was available for the entire Iberian Peninsula.

These variables included one variable for terrain slope, two variables for high-traffic and low-traffic roads and twelve variables for land cover types. Land cover types were based in CORINE 2006 Land Cover map developed by the European Environment Agency (<http://www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version-2>), which is the same map used in other recent studies on the species at the scale of the Iberian Peninsula (*e.g.* Fordham *et al.* (2013)). The 12 differentiated land cover types (see Table 3.1 and Appendix C for the full list) ranged from unsuitable areas (artificial surfaces, unvegetated areas, water bodies and wetlands) to shrublands (bushy sclerophyllous vegetation) and transitional woodland/shrub (bushy or herbaceous vegetation with scattered trees). Further details on the environmental variables and spatial layers are provided in Appendix C. All variables were rasterized at a spatial resolution of 30 m, which was that of the highest-resolution layer considered (digital elevation model) (Appendix C). This 30-m cell size was used to facilitate the joint processing of all layers with the same format and spatial resolution for subsequent steps, but the resource selection models built from these data were developed at a coarser spatial resolution of 90 m for the used habitat and at an extent of several km for the available habitat (see next section).

Fig. 3.1. Distribution of GPS locations in the southern Iberian Peninsula. The names of the current four stable populations of Iberian lynx are indicated over the map. The locations in the north-west of the study area correspond to a single lynx that dispersed far away from the original Doñana-Aljarafe population.

Fig. 3.2. Example of the differentiation of the GPS locations corresponding to habitat use within the home ranges by resident individuals (brown) and the locations corresponding to exploratory or dispersal movements outside home ranges (green) for two lynx individuals.

3.2.4. RESOURCE SELECTION FUNCTIONS: CONDITIONAL MIXED-EFFECTS LOGISTIC REGRESSION MODELS

We built resource selection functions based on the approach proposed by Zeller *et al.* (2014) to estimate the probability of habitat selection as a function of predictor variables (here land cover and terrain characteristics) for the different behavioral states. This approach is based on comparing the used and available (reachable but not selected) habitat for each GPS location. The used habitat at each GPS location was characterized as the average values of the environmental variables (*i.e.* slope, proportion of roads and of each land cover class) in the nine cells around each location (90 x 90 m window) to account for the actual accuracy of GPS coordinates and for the spatial scale of CORINE land cover data (CORINE is distributed at a similar spatial resolution of 100 m by the European Environment Agency, see <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-3>). For each used GPS location, we defined available habitat (*i.e.* habitat that could be potentially accessed by a tracked individual) as that within a circle with radius equal to the 99th percentile of the observed 4-hour displacement distances. A circle was used because there was no significant

directionality in the 4-hour Iberian lynx displacements (see Appendix D). Every cell inside the circle was considered to calculate the average value of each environmental variable in the available habitat, but the contribution of cells to the average was weighted by distance, giving more weight to the cells closer to the GPS location as they are more likely to be selected according to the observed 4-hour lynx displacements (Fig. D.1 in Appendix D). Weights were obtained (separately for each of the three models) from a generalized Pareto distribution fitted to the empirical distribution of 4-hour displacement distances. See further details in Appendix D.

We fitted conditional mixed-effects logistic regression models with each individual as random effect following the same approach as in Zeller *et al.* (2014) to analyze matched data of used and available habitat. We used *glmer* function in lme4 R package version 0.999375-42 (Bates *et al.* 2011). The estimates of this model are equivalent to those of a conventional conditional logistic regression (Agresti 2002, sect. 10.2.6). Grasslands were used as the reference land cover class, given that this was the cover type with natural or semi-natural vegetation considered less suitable for the Iberian lynx. In conditional logistic regression, there is no model intercept; therefore, the selection probability for the reference class (grasslands) is 0.5. The predicted selection probabilities for each cover class are relative to the reference class, that is a probability above 0.5 for a particular cover type *X* means that when the alternative habitat that may be available for selection by the lynx is grassland, such cover type *X* is preferred.

3.2.5. MODEL VALIDATION

We used a 10-fold cross-validation approach to evaluate model predictive performance considering the ability of the model to discriminate used from available habitat (Pearce and Ferrier 2000). Discrimination ability was assessed using the area under receiver operating characteristic curve (AUC). In our analysis, data are stratified; therefore, the selection of pairs for the calculation of AUC was constrained to be within the same stratum (Pennells *et al.* 2014).

3.3. RESULTS

About 75% of GPS locations for all tracked lynx were classified as resident habitat use within home ranges and the remaining 25% as dispersal or exploratory movements outside home ranges (see Fig. 3.2 for an example). The 99th percentile of lynx displacements in 4-hour periods was 2956 m for resident individuals, 5179 m during dispersal or exploratory movements and 3777 m in the joint model (Fig. D.1 in Appendix D).

The ability of the models to discriminate between selected and available areas was acceptable (AUC = 0.78) for the habitat suitability model and the joint model and high (AUC = 0.91) for the landscape permeability model. The habitat suitability, landscape permeability and joint models showed some common patterns but also several important differences (Table 3.1, Fig. 3.3). In all three models, the transitional woodland-shrub was the most preferred cover (Table 3.1, Fig. 3.3). Artificial and unvegetated areas were largely avoided, and intensive crops (particularly irrigated ones but also agricultural classes 2 and 6, see Table 3.1) were also negatively selected compared to the reference grassland class; the same pattern was found when only lynx born in the wild were considered (Fig. E.1 in Appendix E).

In all three models, there was a large heterogeneity in the Iberian lynx selection of the different cover classes corresponding to or including agricultural lands (classes 2 to 8 in Table 3.1). Some agricultural lands were strongly avoided (such as irrigated crops), but other covers (olive groves, agricultural lands mixed with natural vegetation or agroforestry areas) were used more than the grassland reference class (Table 3.1). The same result was obtained in the model built only for the lynx born in the wild (Fig. E.1 in Appendix E).

Iberian lynx were more selective inside home ranges than when dispersing (Table 3.1, Fig. 3.3). Differences among the most preferred land cover classes, and among woodland and agricultural classes, narrowed down in dispersal compared to home range use (Fig. 3.3); the same happened when only lynx born in the wild were considered (Fig. E.1 in Appendix E). For instance, as shown in Table 3.1, the difference between the coefficient of the transitional woodland-shrub and the next most-selected cover type decreased from 0.3015 within home ranges (significant difference, $P < 0.05$) to 0.088 in dispersal or exploratory movements (non-significant difference, $P > 0.1$). While the Iberian lynx selected against steep terrain when establishing home ranges, slope was not significant in determining the areas traversed in the dispersal or exploratory movements (Table 3.1). Similar dispersal plasticity was found regarding transport infrastructure. While low-traffic roads were avoided when selecting habitat inside home ranges (Table 3.1), these roads were not a significant impediment for lynx dispersal movements (Table 3.1). High-traffic roads had a significant negative effect in the joint model, but they were not significant (despite the largely negative coefficient value) in the habitat suitability model (Table 3.1), which seems to be mostly due to the lack of large transportation infrastructures in nearby home ranges: 90% of the ≈ 3 -km radius of available habitat around the GPS locations of resident individuals had no presence at all of high-density roads, while the same figure decreased to only 6% for low-traffic roads.

Table 3.1. Model summaries, including the estimated regression coefficients, standard errors and significance levels (**<0.001, *<0.01, †<0.1). Estimates for the reference class 10 (grasslands and pastures) are not provided since in conditional logistic regression there is no model intercept; the coefficient for the reference class is 0 (see Materials and methods)

Explanatory variable	Habitat suitability model	Landscape permeability model	Joint model
Terrain slope	-1.53 ± 0.3***	-0.24 ± 0.57	-0.17 ± 0.25
High-traffic roads	-4.27 × 10 ⁶ ± 38.11 × 10 ⁶	-7.08 ± 4.16†	-370.68 ± 11.2***
Low-traffic roads	-1.2 ± 0.25***	-0.07 ± 0.42	-0.76 ± 0.2***
1. Unsuitable areas	-21.34 ± 0.62***	-69.37 ± 2.29***	-26.2 ± 0.54***
2. Non-irrigated and non-tree crops	-3.07 ± 0.31***	-1.9 ± 0.44***	-0.73 ± 0.17***
3. Irrigated arable lands	-52.81 ± 2.11***	-3.66 ± 0.83***	-14.47 ± 0.55***
4. Olive groves	1.35 ± 0.14***	1.55 ± 0.24***	0.97 ± 0.11***
5. Other fruit tree plantations	0.79 ± 0.54	0.1 ± 1.75	-0.88 ± 0.28**
6. Mix of annual and permanent crops	-0.57 ± 0.62	-5.83 ± 0.97***	-1.75 ± 0.27***
7. Agricultural lands mixed with natural vegetation	1.42 ± 0.15***	1.73 ± 0.28***	1.29 ± 0.13***
8. Agroforestry areas	1.59 ± 0.12***	1.44 ± 0.24***	1.39 ± 0.1***
9. Forests	2.11 ± 0.12***	1.72 ± 0.23***	1.78 ± 0.1***
11. Shrublands	2.08 ± 0.14***	1.3 ± 0.26***	1.63 ± 0.11***
12. Transitional woodland/shrub	2.4 ± 0.11***	1.81 ± 0.22***	2.05 ± 0.09***

3.4. DISCUSSION

3.4.1 THE IMPORTANCE OF ACCOUNTING FOR AGRICULTURAL LANDS HETEROGENEITY

Medium and large carnivore mammals generally suffer from high risk of extinction associated with human pressures, and thus, they tend to be more abundant over areas with low human population density (Woodroffe 2000). Consequently, habitat selection studies for these species are in many cases conducted in the more pristine or largely forested areas where the largest populations are found; in these areas, the agricultural land covers may be absent or present only in very small amounts and are hence omitted in the analyses (*e.g.* Carroll *et al.* (2001); Jędrzejewski *et al.* (2004); Nielsen *et al.* (2006); Niedziałkowska *et al.* (2006); Klar *et al.* (2008);

Squires *et al.* (2013)). In many other cases, when agriculture is present and is considered a relevant predictor in models of habitat selection by medium and large carnivores, all agricultural land covers are usually merged in a single class (*e.g.* Kramer-schadt *et al.* (2004); Dickson *et al.* (2005); Northrup *et al.* (2012); Dellinger *et al.* (2013); Zeller *et al.* (2014); Mateo-Sánchez *et al.* (2014)). Such a decision may be related to a priori knowledge or assumptions about the lack of suitability of all crop types, to the actual or assumed homogeneity of agricultural lands (regardless of whether they are suitable or not) in a given study area or to the need of reducing the number of land cover classes to avoid model overfitting problems, particularly when species presence or telemetry data sets are small (Harrell 2001).

Our case study on the Iberian lynx allowed us to provide novel insights on this subject by analyzing a large telemetry data set (40 000 GPS fixes) over a wide spatial extent that covered a diversity of agricultural cover types interspersed with more natural scrubland or forest mosaics. By unravelling the Iberian lynx responses to a set of seven differentiated agricultural covers (as well as to other environmental predictors), we were able to show that agricultural land composition and heterogeneity matter up to the point of dictating largely contrasting selection preferences among crop types. Previous studies on the Iberian lynx habitat selection were conducted in three areas (only one area considered in each study) where the species persisted at the time: Algarve in Portugal (Palma *et al.* 1999), and mainly Doñana (Palomares *et al.* 2000; Palomares 2001; Fernandez *et al.* 2003) and Andújar-Cardena in Spain (Fernández *et al.* 2006; Gil-Sánchez *et al.* 2011). Early resource selection models used a single agricultural land cover class and reported significant avoidance of crops (Palomares *et al.* 2000) or non-significant effects (Palma *et al.* 1999). In subsequent research, crops were omitted in most studies (Palomares 2001; Fernandez *et al.* 2003; Fernández *et al.* 2006) or merged with other classes (Gil-Sánchez *et al.* 2011). The single agricultural class in the Doñana study area of Palomares *et al.* (2000) includes both intensive crops such as irrigated strawberry fields and comparatively more extensive land uses like olive groves. Our results show that lynx strongly avoid intensive crops (such as strawberry fields), but select less intensive agricultural land covers such as olive groves, agro-forestry areas and heterogeneous lands where crops are mixed with natural vegetation remnants at fine spatial scales. This conclusion is reinforced by recent field studies that report at least two lynx females breeding in olive groves in the south-east of the Andújar-Cardena population (G. Garrote unpublished data).

Merging different agricultural classes may lead to underestimating the suitability of the more extensive agricultural lands, as model coefficients would be downweighted by areas of intensive crops that are strongly avoided. Our findings suggest that the previously reported strong avoidance of all agricultural lands by the Iberian lynx (Palomares *et al.* 2000) may be an oversimplification that can propagate into the results of metapopulation models (Ferrerías 2001) and climate change impact assessments (Fordham *et al.* 2013) that are based on those early habitat selection studies. Our results are, however, in agreement with those previous studies on Iberian lynx habitat selection not only in the avoidance of intensive crops, but also in those covers that are most suitable and preferred by the species (particularly transitional woodland-shrub, *i.e.* bushy or herbaceous vegetation with scattered trees).

3.4.2 DIRECT HUMAN-CAUSED MORTALITY OUTSIDE WOODLANDS MAY HAVE BEEN MISINTERPRETED AS A LACK OF HABITAT RESOURCES IN SOME AGRICULTURAL LANDS

Medium and large mammalian carnivores have been actively persecuted in many regions of the world mainly because they compete for prey species with humans (and kill livestock in some cases) and because they are exploited through subsistence or commercial hunting (meat, pelts, etc.). Consequently, avoidance of some human-influenced landscapes may be more related to mortality risk than to the lack of habitat resources in those areas (Corsi *et al.* 1999). Our results suggest that the previously reported avoidance of all agricultural lands by the Iberian lynx might be due to factors other than just the potentially low availability of resources for the species. Killing by people (direct hunting, trapping, poisoning, etc.) has traditionally been by far the greatest source of mortality for the Iberian lynx, threatening the persistence of this species as for many other mammalian carnivores. Non-natural mortality ratios of the Iberian lynx were very high until the 1970s and have decreased since then due to legal protection and changes in game management (Rodríguez and Delibes 2004). Despite this reduction, the majority (>85%) of non-natural deaths were caused by traps or firearms at least until 1990 (Rodríguez and Delibes 2004) and probably this continued to be the main mortality source until the late 1990s (Ferrerías *et al.* 1992, 2004). More recent data for the period 2006-2013 (López *et al.* 2014) based on mortality records for 78 tracked lynx show a significant reduction in the proportion of non-natural deaths caused by poaching (23% of all deaths), with diseases (39%) being the main mortality source in this more recent period.

These changes in human attitudes and mortality causes, which are undoubtedly linked to legal protection, conservation efforts and increased social awareness in recent times, may have also modified the Iberian lynx perception of the mortality risk in some open agricultural areas. Consequently, these changes may have favored the colonization of relatively more human-used areas and caused an adjustment of the species habitat use as observed in other carnivores (Lesmerises *et al.* 2012). If persecution has largely declined in these open or heterogeneous landscapes, the risk of human encounter may now be comparatively better counteracted by the availability of foraging resources such as rabbits in some of these areas. The intermediate suitability of extensive agricultural lands for the Iberian lynx could be related to a significant density of prey favored by the patches of remaining vegetation and fine-scale heterogeneity in such croplands, as observed in other mammalian carnivores (Rajaratnam *et al.* 2007; Dellinger *et al.* 2013). Rabbit availability is vital for the Iberian lynx survival (*e.g.* Palomares 2001; Gil-sánchez *et al.* 2006), and a remarkable rabbit abundance has been reported in some extensive agricultural lands and particularly in heterogeneous mosaic landscapes including scrublands and crops (Virgos *et al.* 2003).

We agree with Dellinger *et al.* (2013) that some mammalian carnivores may select human-altered land cover types if unimpeded by negative human attitudes, thus increasing the likelihood of recovery in areas in close proximity to human activities (Chapron *et al.* 2014), particularly given the current trends of rural land abandonment that are triggering the naturalization of marginal agricultural lands in Europe. The conservation of the Iberian lynx could clearly benefit from such adaptive behavior, as the amount of suitable area clearly increases if some extensive crops are considered, potentially leading to landscape

compensation, or even landscape supplementation responses, as reported for other species in heterogeneous landscapes (Brotons *et al.* 2005). The magnitude of these responses may be in fact a key aspect for determining the likelihood of long-term persistence of the species and the possibility of recovering an important portion of the species' historical range.

Fig. 3.3. Variation in the probability given by the mixed conditional regression model for (a) habitat suitability and (b) landscape permeability as a function of the proportion of land occupied by each land cover class, with the rest of the land being occupied by the grassland reference class (the sum of both proportions is equal to 1) and assuming a flat terrain and no presence of roads. Curves for the reference class (grasslands and pastures) are not plotted because in conditional logistic regression there is no model intercept, which implies that the probability for the reference class is 0.5 (see Materials and methods).

3.4.3 DISPERSAL PLASTICITY AND THE INSIGHTS FROM GPS COLLARS HAS LANDSCAPE RESISTANCE TO MOVEMENT BEEN OVERESTIMATED

We found that the suitability of the less intensive agricultural lands was closer to that of the natural woodlands when dispersing than when establishing home ranges. The dispersal plasticity of the Iberian lynx was also evidenced by a much lower avoidance of roads and steep terrain than when territories were selected by resident individuals. These results are in agreement with the general finding that dispersing animals may use habitats of lower quality than those used by resident individuals, as previously reported for the Iberian lynx (Palomares *et al.* 2000; Palomares 2001) and other species (Selonen and Hanski 2006; Wasserman *et al.* 2010; Elliot *et al.* 2014; Mateo-Sánchez *et al.* 2015). However, unlike conclusions from previous studies on the species (Palomares *et al.* 2000), we found that dispersing Iberian lynx not only use lower-suitability forest areas (*e.g.* dense plantations) but also certain agricultural lands (olive groves, agroforestry areas and heterogeneous lands where crops are mixed with natural vegetation). This discrepancy between our results and those of previous studies on the Iberian lynx may be due, as discussed above, to the wider set of population areas and the more detailed evaluation of multiple agricultural classes we considered. In addition, these new insights may also result from the different type and extent of location data we analyzed. Unlike the GPS collar data used in our analyses, previous studies on the Iberian lynx habitat selection were based on radiotracking (Palomares *et al.* 2000; Palomares 2001; Fernandez *et al.* 2003) and on surveys of feces (Fernández *et al.* 2006) or sighting data (Palma *et al.* 1999). GPS collars are more accurate and less biased than ground-based conventional radiotracking triangulation and allow 24-hour coverage and positioning by night and in bad weather, which is often difficult with radiotracking (Tomkiewicz *et al.* 2010). The continuous and automatic recording of animal locations by GPS collars reduces the risk of contact loss that is frequent in conventional radiotracking, particularly when movements occur through unexpected or distant areas. Consequently, radiotracking studies are more prone to miss long distance dispersal events or movements through areas where these events are, or are assumed to be, less likely (*e.g.* Dickson *et al.* (2005)). This fact may have an impact on the assessments related to population and habitat connectivity, most likely leading to an overestimate of landscape resistance to movement, by assuming a low suitability for dispersal of some cover types that may be in fact significantly used by dispersing individuals, but misrepresented in the available species occurrence records or radiotracking data sets, as shown for other terrestrial mammals (Mateo-Sánchez *et al.* 2014; Elliot *et al.* 2014).

3.4.4 LIMITATIONS AND FURTHER RESEARCH

The Iberian lynx was once widespread throughout most of the Iberian Peninsula, and ongoing conservation efforts for the species aim at recovering a significant portion of this past distribution by consolidating current populations and establishing new ones through reintroduction in selected areas within the historical range in both Spain and Portugal. Therefore, our objective was to produce habitat suitability and landscape permeability models that could be applicable for the entire Iberian Peninsula. Because our models required explanatory variables that were mapped in a comparable manner all throughout Iberia, we

could not directly consider (although they may be in part captured indirectly through other coarser variables) some known drivers of Iberian lynx habitat selection, such as prey density, diseases, non-natural mortality risk, fine-scale forest canopy cover and vegetation height. We believe that the lower AUC for the habitat suitability model compared to the landscape permeability model is likely due to the finer-scale factors (particularly rabbit abundance) determining home range selection as opposed to the broader-scale landscape factors driving dispersal. Some of the considered land cover classes may be relatively broad or may not differentiate some relevant features for the Iberian lynx. For example, olive groves in flatlands are often intensively managed to remove competing understory vegetation, while olive groves in more remote or steeper mountain areas retain more natural herbaceous and shrubby vegetation. This latter type of more extensive olive groves is the one most frequently found in the areas where the Iberian lynx is currently distributed (particularly in Guadalmellato). Therefore, our reported selection probabilities for olive groves may not apply to the more intensive ones in other areas of Spain and Portugal. As in any model, extrapolation to conditions that are not present in the available training data (currently occupied areas) is risky and should be made with much care. Further application of our approach based on higher-resolution local data may improve recommendations for the conservation and reintroduction of this endangered species in some portions of the species' range.

On the other hand, our analyses were based on a 4-hour acquisition frequency. Although this frequency was found to provide a good model performance (not below that of shorter acquisition intervals) by Zeller *et al.* (2014), higher acquisition rates may allow capturing a stronger or significant response for some of the more subtle environmental effects that may remain unreported (or reported as not significant) at longer acquisition intervals (Zeller *et al.* 2014; Carvalho *et al.* 2015), although this is an issue that would require further research. An important trade-off is that higher acquisition intervals reduce the total duration of the tracking periods (due to GPS-GSM battery constraints), which may miss those relatively rare dispersal events over long distances and periods that are important for a good characterization of landscape permeability and for not underestimating species movement abilities (population connectivity).

Finally, we studied habitat selection and dispersal preferences for the Iberian lynx, but we did not perform a population viability or persistence analysis. Our study therefore provides information on relative usage of different land covers by resident and dispersing individuals, but does not evaluate fitness and hence species persistence in different types of landscapes or land cover assemblages. Additional research that evaluates reproductive success and mortality risks (*e.g.* roadkills, disease prevalence) in different land covers and that incorporates this information into habitat models that account for demographic performance (*e.g.* Nielsen *et al.* (2006, 2010); Boitani *et al.* (2007))), would further strengthen our understanding of the viability of Iberian lynx populations in different landscape settings.

3.5. CONCLUSIONS

We provided a broader picture of how an endangered and flagship species uses heterogeneous landscapes by considering a greater variety of land cover conditions than previous studies. We tracked Iberian lynx individuals through GPS collars not only in the traditional population nuclei with higher levels of protection (*e.g.* National Park in Doñana), but also in the more fragmented areas in which the species was historically present and was reintroduced from 2009. The observed contrasting responses to different agricultural covers and dispersal plasticity of the Iberian lynx can provide valuable information for managing and recovering the populations of this species in such mosaic landscapes. First, our models offer a guide to build functional land cover types adapted to both lynx dispersal and home range use (Fahrig *et al.* 2011) and may enhance the assessment of population responses to landscape configuration and habitat fragmentation, explicitly incorporating the matrix quality instead of considering suitable patches as islands embedded in a matrix of unsuitable landscape (Brotons *et al.* 2005). Secondly, our results suggest that the Iberian lynx, together with other species, may benefit from measures to mitigate the intensification of agriculture (*e.g.* the agri-environment schemes introduced by the European Common Agricultural Policy), especially if they are aimed at enhancing or maintaining landscape complexity (Concepción *et al.* 2008). Thirdly, our results provide novel insights and an improved understanding of the Iberian lynx habitat selection that can benefit conservation planning for the species and a suite of other models such as metapopulation models, landscape matrix resistance surfaces and connectivity analyses among population and reintroduction areas.

Overall, our findings suggest that Iberian lynx conservation and reintroduction may be successful in a wider set of more heterogeneous areas than previously thought, including mainly well-conserved Mediterranean woodlands but also some extensive agricultural covers with permanent crops and natural vegetation remnants, which may provide both suitable habitat (*e.g.* foraging resources) and support functional landscape connectivity for the species. Given that the Iberian lynx has been one of the best studied terrestrial mammals, we tentatively suggest that the previous underestimation of the species' actual preferences and ability to use heterogeneous landscapes and some agricultural covers may be relatively widespread and applicable to other mammalian carnivores or woodland species.

3.6. DATA ACCESSIBILITY

The data in the present study have not been archived because they contain sensitive information about home ranges and individual locations of the endangered Iberian lynx. To

request the data, contact Dirección General de Gestión del Medio Natural y Espacios Protegidos (Junta de Andalucía) at dggmnep.secretaria.cmaot@juntadeandalucia.es.

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3.8. SUPPLEMENTARY MATERIAL

3.8.1 APPENDIX A. FURTHER DETAILS ON LYNX TRAPPING HANDLING AND TRACKING THROUGH GPS COLLARS

All individuals were trapped using double-entrance box traps (see López *et al.* (2009)) and transported in stainless-steel transport compression cages. The individuals captured in the wild were transported to the nearest (from 1 to 30 km) Iberian lynx clinic (Simon *et al.* 2013). A complete routine health evaluation was performed for all individuals, which were anesthetized using a mix of ketamine-medetomidine or ketamine- dexmedetomidine; a supplementation with isoflurane inhalatory anesthesia was performed if needed (Martínez *et al.* 2007). Lynx captured in the wild were individually identified on the basis of the patterns of their spots, and their age (in years) was recorded by comparisons with photos of cubs from previous years (see Garrote *et al.* (2010)). Anesthetized Iberian lynx were tagged with GPS-GSM collars manufactured by Microsensory (Spain). Collars weighted 300 g. After handling, all individuals were safely released at the place of capture, translocation or reintroduction. GPS locations were filtered for errors and non-relevant periods (*e.g.* locations within fences during soft release), resulting in a total of 44,002 GPS locations from 48 tracked individuals (mean 917,

range 150 - 4,069). Table A.1 below shows the percentage of GPS locations by sex, age class, origin (born in captivity or in the wild), population area and season. Missed fixes from failure of the collar to record or send a GPS location resulted in a mean number of 4.42 GPS fixes per tracked day (instead of the 6 fixes per day that would result if all the 4-hour fixes were successfully recorded), *i.e.* a successful acquisition rate of 73.6%.

Garrote G, Perez de Ayala R, Pereira P, et al (2010) Estimation of the Iberian lynx (*Lynx pardinus*) population in the Doñana area, SW Spain, using capture–recapture analysis of camera-trapping data. *Eur J Wildl Res* 57:355–362. doi: 10.1007/s10344-010-0440-7

López G, López-Parra M, Fernández L, et al (2009) Management measures to control a feline leukemia virus outbreak in the endangered Iberian lynx. *Anim Conserv* 12:173–182. doi: 10.1111/j.1469-1795.2009.00241.x

Martínez F, Pastor J, Molina I, et al (2007) Inmovilización reversible en el lince ibérico (*Lynx pardinus*) con la combinación de ketamina y medetomidina. In: *Proceedings of the VIII Jornadas SECEM. Sociedad Española para el Estudio y Conservación de los Mamíferos (SECEM)*. Málaga, Spain,

Simon MA, Arenas R, Báñez JA, et al (2013) Ten years conserving the Iberian lynx. Seville, Spain

Table A.1. Percentage and number of GPS locations by sex, age class (age of the lynx individual when first tracked through the GPS collar), origin (born in captivity or in the wild), population area and season. The location of each population area is shown in Fig. 3.1.

		Percentage of GPS locations	Number of GPS locations
Sex	Male	63.2%	27,830
	Female	36.8%	16,172
Age class (when tracking started)	Subadults (1-2 years)	68.1%	29,955
	Adults (> 2 years)	31.9%	14,047
Origin (birth)	Wild	68.7%	30,243
	Captivity	31.3%	13,759
Population area	Andújar-Cardena	13.1%	5,757
	Doñana-Aljarafe	13.3%	5,856
	Guarrizas	33.7%	14,812
	Guadalmellato	39.9%	17,577
Season	Winter	20.1%	8,829
	Spring	30.4%	13,375
	Summer	28.3%	12,438
	Autumn	21.3%	9,360

3.8.2 APPENDIX B. DETAILS ON THE a-LoCoH METHOD FOR SEPARATING HOME RANGE AND DISPERSAL LOCATIONS

The non-parametric a-LoCoH adaptive method (Getz *et al.* 2007) was used to delineate home ranges for each lynx individual and hence separate GPS locations into two groups: (i) locations corresponding to home range use by resident individuals (locations within delineated home ranges), and (ii) locations corresponding to dispersal or exploratory movements (locations outside home ranges). The a-LoCoH method was selected because it has shown to present a better performance in home range delineation than other methods, particularly when (i) hard (sharp) boundaries exist between used and unused areas (*e.g.* roads, water bodies) or when unused holes are present within the home ranges, and (ii) there are many locations available (Getz *et al.* 2007), as is the case for the Iberian lynx telemetry data here analyzed. The a-LoCoH method constructs utilization distributions (Jennrich and Turner 1969; Ford and Krumme 1979) representing the density of space used by animals from the union of convex hulls associated with each point and its neighbors within a variable sphere around a root point such that the sum of distances between these points and the root point is less than or equal to a given value of a (Getz *et al.* 2007). Then, these convex hulls are ordered from the smallest to the largest and progressively grouped upwards until a given percentile $x\%$ of the points is included, which results in a $x\%$ isopleth. Each isopleth contains the densest amount of points up to that percentile and provides an estimation of the density of fixes. We applied three different percentile values to the 48 lynx individuals considering their activity during the tracking period: predominantly territorial (22 individuals, 90% percentile), predominantly exploring or dispersing (9 individuals, 60% percentile), and territorial with important exploratory or dispersal movements (17 individuals, 80% percentile). Using different percentiles was necessary because the GPS-collared lynx differed in their use of the landscape during their particular tracking periods and considering the expert knowledge on their actual territorial behavior in the field. The value of a was selected so that it minimized changes in the home range area as a function of a , as recommended by Getz *et al.* (2007), *i.e.* by selecting the value of a for which the isopleth home range area remained constant before a sharp increase for a larger isopleth value. Getz *et al.* (2007) showed that the a-LoCoH method remains remarkable robust to changes in values of a . The obtained home ranges obtained from the a-LoCoH method were confronted and validated with expert knowledge of the crews involved in lynx tracking and monitoring in the field. The a-LoCoH analyses were performed with R software (R Development Core Team 2015) by using the scripts available at <http://locoh.cnr.berkeley.edu/tutorial>.

Ford RG, Krumme DW (1979) The analysis of space use patterns. *J Theor Biol* 76:125–155. doi: 10.1016/0022-5193(79)90366-7

Getz WM, Fortmann-Roe S, Cross PC, et al (2007) LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2:e207. doi: 10.1371/journal.pone.0000207

Jennrich RI, Turner FB (1969) Measurement of noncircular home range. *J Theor Biol* 22:227–237. doi: 10.1016/0022-5193(69)90002-2

3.8.3 APPENDIX C. FURTHER DETAILS ON THE EXPLANATORY VARIABLES

Terrain slope was obtained from raster digital elevation models (DEM) for Spain (DEM25 from Instituto Geográfico Nacional, with a spatial resolution of 25 meters) and Portugal (DEM for Portugal Continental e Regiões Autónomas, with a spatial resolution of 30 meters). Spatial resolution of both DEMs was homogenized in a single layer with a cell size of 30 meters. Altitude was not included as an explanatory variable in the models because the effect of altitude is not direct but indirect through other variables such as land cover, while slope may indeed have a clearer direct effect (*e.g.* energetic cost for lynx movement). Road spatial layers were the official BCN200 for Spain (Spanish Ministry of Public Works and Transport) and the analogous cartography developed by the Portuguese Army Geographical Institute for Portugal, both in vector format. Both layers were corrected, updated and integrated by SECAD (Servicio de Cartografía Digital e Infraestructura de Datos Espaciales) of University of Extremadura (Vicerrectorado de Investigación, Innovación e Infraestructura Científica, Spain) with the support of Mapa Oficial de Carreteras Interactivo for year 2006 (Spanish Ministry of Public Works and Transport) for Spain and of the images of Campsa Guide for year 2006 for Portugal. Hightraffic roads were defined as those with a maximum speed of at least 100 km/h, a road shoulder, and two lanes in one or both directions. The rest of paved roads were classified as low-traffic roads. Any 30 m cell traversed by a road line (as given by the vector layer) was considered as a road cell (either low or high traffic) for the resource selection models. The twelve land cover classes that were differentiated and reclassified from CORINE Land Cover 2006 are described in Table C.1 below. The distribution of the land cover classes over the study area is shown in Fig. C.1 below. The selection of these classes considered the previous knowledge on Iberian lynx habitat selection and the amount of GPS fixes falling into each land cover type. Land cover types that were widely used by the Iberian lynx (*i.e.* having a large number of GPS locations) were considered separately, while those types with none or few GPS locations were aggregated into broader classes. It should be noted that CORINE Land Cover includes one class corresponding to transport infrastructure (CORINE class 1.2.2, included within class 1 for the models, see Table C.1). This CORINE class, however, only includes roads with a width of at least 100 meters, which excludes almost all the transport infrastructures in Spain and Portugal, which were accounted for in the models by the above-described spatial layers and explanatory variables different from CORINE Land Cover. Burnt areas (CORINE class 3.3.4 in Table C.1) are those identified as such in the year 2006 when CORINE Land Cover was developed (forest fires that occurred in 2006 or three years earlier). We observed however that these areas presented a significant development of woody vegetation (shrubs and/or trees) in the moment in which this study was developed, based on which this class was included within transitional woodland-shrub. The impact of this burnt area class, and of the decision to include it within class 12 in our study, is however minimal for the purposes of the models here developed, since this class 3.3.4 represent less than 0.1% of the total area of the Iberian Peninsula according to CORINE Land Cover, and a much lower percentage in the areas where the Iberian lynx is currently distributed.

Table C.1. Twelve land cover classes considered as independent variables in the model (left column) defined from the combination of one or more CORINE Land Cover 2006 classes (as indicated in the right column). Further details on the CORINE land cover classes and the three-level hierarchical class codes can be found at <http://www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version-2>

Land cover class considered in the model	CORINE Land Cover classes included
1. Unsuitable areas (artificial, unvegetated, water bodies)	Artificial surfaces (all classes 1.x), open spaces with little or none vegetation (3.3.1, 3.3.2, 3.3.3, 3.3.5), water bodies and wetlands (all classes 4.x and 5.x)
2. Non-irrigated and non-tree crops	Non-irrigated arable land (2.1.1), vineyards (2.2.1)
3. Irrigated arable lands	Permanently irrigated land (2.1.2), rice fields (2.1.3)
4. Olive groves	Olive groves (2.2.3)
5. Other fruit tree plantations	Fruit trees and berry plantations (2.2.2)
6. Mix of annual and permanent crops	Annual crops associated with permanent crops (2.4.1), complex cultivation patterns (2.4.2)
7. Agricultural lands mixed with natural vegetation	Land principally occupied by agriculture, with significant areas of natural vegetation (2.4.3)
8. Agroforestry areas	Agroforestry areas (2.4.4)
9. Forests	Broad-leaved forest (3.1.1), coniferous forest (3.1.2), mixed forest (3.1.3)
10. Grasslands and pastures	Pastures (2.3.1), natural grasslands (3.2.1)
11. Shrublands	Sclerophyllous vegetation (3.2.3), moors and heathland (3.2.2)
12. Transitional woodland/shrub	Transitional woodland-shrub (3.2.4), burnt areas in 2006 or earlier (3.3.4)

Fig. C.1. Distribution of the land cover classes in the Southern Iberian Peninsula. The area shown is the same as in Fig. 3.1 in the main text.

3.8.4 APPENDIX D. DETAILS ON TURNING ANGLES AND AVAILABLE HABITAT CALCULATIONS

We initially considered using the turning angle to estimate the weights used for calculating the available habitat around a given GPS location (see methods on resource selection functions in the main text), as animals may have propensity to keep moving in a given direction (e.g. Fortin *et al.* (2005)). We calculated turning angles separately for movements inside home ranges (resident individuals) and outside home ranges (dispersing individuals) and compared the observed distribution to the uniform distribution using a two-sample permutation test (*oneway test* function in coin R package, (Hothorn *et al.* 2008)). The test did not find significant directionality, *i.e.* the distribution of turning angles did not differ from the uniform distribution ($p=0.67$ for resident individuals, $p=0.28$ for dispersing individuals). Direction of a movement segment between two consecutive GPS locations was hence considered independent of the direction that the animal had followed in the previous displacement. Consequently, turning angles were not further considered to weight available habitat estimates; available habitat was quantified through a circle around each GPS location with a circle radius equal to the maximum observed displacement distance. The maximum distance was defined as the 99th percentile of the observed 4-hour displacement distances. A generalized Pareto distribution was fitted to the empirical distribution of 4-hour displacement distances using the POT package in R (Ribatet 2012). A different Pareto kernel was fitted for the habitat suitability, landscape permeability and joint models (see Fig. D.1 below). The contribution of cells inside that circle to the average of each environmental variable in the available habitat was weighted by distance, with more weight to the cells closer to the GPS location as given by the frequency (density) of distances in the fitted Pareto kernels (Fig. D.1).

Fortin D, Beyer HL, Boyce MS, et al (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330. doi: 10.1890/04-0953

Hothorn T, Hornik K, van de Wiel M, Zeileis A (2008) Implementing a class of permutation tests: The coin package. *J Stat Softw* 28:1–23. doi: 10.18637/jss.v028.i08

Ribatet M (2012) Generalized Pareto distribution and peaks over threshold. R package.

Fig. D.1. Frequency (density) distribution of the displacements between consecutive GPS locations (recorded with a time difference of 4 hours) that reached a given distance for the (a) habitat suitability model (GPS locations for resident individuals within home ranges), (b) landscape permeability model (GPS locations for dispersal or exploratory movements outside home ranges) and (c) joint model (all GPS locations). The bars correspond to the observed frequencies while the continuous line shows the Pareto kernel fitted to those observed values. The maximum distance (99th percentile of the observed 4-hour displacement distances) was 2,956 m for the habitat suitability model, 5,179 m for the landscape permeability model, and 3,777 m for the joint model.

3.8.5 APPENDIX E. RESPONSES TO LAND COVER TYPES OBTAINED FOR THE LYNX BORN IN THE WILD ONLY

(a) Habitat suitability model (lynx born in the wild)

(b) Landscape permeability model (lynx born in the wild)

Fig. E.1. Variation in the probability given by the mixed conditional regression model built for the lynx born in the wild only. Results correspond to (a) habitat suitability and (b) landscape permeability as a function of the proportion of land occupied by each land cover class, with the rest of the land being occupied by the grassland reference class (the sum of both proportions is equal to 1) and assuming a flat terrain and no presence of roads. Curves for the reference class (grasslands and pastures) are not plotted because in conditional logistic regression there is no model intercept, which implies that the probability for the reference class is 0.5 (see Material and methods in the main text).

CHAPTER 4

CHARACTERIZATION OF CORRIDORS BY TRAJECTORY AND EFFECTIVE DISTANCE

Photo: Sonia Illanas

This chapter reproduces entirely the content of the research paper:

Blazquez-Cabrera S, Gastón A, Beier P, Garrote G, Simón MA, Saura S (2016). Influence of separating home range and dispersal movements on characterizing corridors and effective distances. *Landscape Ecology* 31:2355-2366. doi: 10.1007/s10980-016-0407-5

ABSTRACT

Context

Corridors are usually delineated as areas of minimum cumulative resistance to movement through a resistance surface and characterized by their effective distance (accumulated resistance along the least-cost path). The results of these assessments depend on resistance values, which are typically derived from the inverse of habitat suitability models or from presence data of individuals within their home ranges, rather than from data on dispersal or exploratory movements.

Objective

Evaluate the extent to which corridor delineation and effective distance estimates may vary depending on whether home range locations or dispersal data are used to characterize species habitat selection and landscape resistance to movement.

Methods

We analyzed a large telemetry dataset (GPS collars) for the endangered Iberian lynx. We modeled corridors and effective distances in three ways: (1) considering only GPS locations within home ranges, (2) considering only locations in dispersal or exploratory movements outside home ranges, and (3) considering all locations together.

Results

Delineated least-cost corridors followed similar trajectories and sometimes overlapped in the three models. The estimated effective distances were 42 % lower in the dispersal-based model than in the model based solely on home range use.

Conclusions

Models derived exclusively from locations within home ranges may provide lower connectivity estimates than models derived from dispersal locations, affecting estimates of resistance to move between habitat areas, even when the most likely movement routes are similar. Although dispersal data are costly to gather, they potentially provide more realistic assessments of the actual isolation of populations in heterogeneous landscapes.

4.1. INTRODUCTION

Enhancing landscape connectivity has long been acknowledged as a way to buffer the effects of global change and cope with the fragmentation and loss of natural habitats due to human development and resource use increase (Crooks and Sanjayan 2006; Rayfield *et al.* 2011; Luque *et al.* 2012; Kool *et al.* 2012). One of the most common approaches to improve landscape connectivity for animal populations consists in the establishment of corridors between habitat patches (Adriaensen 2003; Beier *et al.* 2008). The primary input to a corridor model is the resistance surface, *i.e.* a raster layer with resistance values that capture the difficulty (physiological cost, mortality risk, behavioral aversion, etc.) of an individual traversing each cell (Zeller *et al.* 2012).

Corridors are usually delineated as regions of minimum cumulative resistance to movement connecting patches of suitable habitat within a heterogeneous matrix of more or less unsuitable habitat. The two primary outputs of the corridor model are the predicted location of the least-cost path or corridor, and the effective distance of the path or corridor (accumulated resistance along the least-cost path across a resistance surface between two habitat patches). Both the location of a modeled corridor and its associated effective distance depend on the resistance values of the cells in the landscape. Therefore the parameterization of the resistance surface is a crucial step in connectivity analysis and conservation planning.

It is reasonable to assume that the resistance of a cell depends on whether the individual is foraging, migrating, mating, patrolling, denning, dispersing, or engaged in any other activity (D'Eon *et al.* 2002; Belisle 2005; Zeller *et al.* 2012, 2014). When estimating resistance values to identify suitable corridors, it is best to obtain them from analyses of movements that reflect dispersal activities (as opposed to resource use within home ranges) (Killeen *et al.* 2014; Elliot *et al.* 2014a; Vasudev *et al.* 2015). When GPS location data are available, trajectories that are fast, long and with a dominant direction are often assumed to be dispersal movements, whereas slow, short and tortuous trajectories are assumed to represent activities like foraging (Zeller *et al.* 2014). But some activities within the home range (like searching for a mate or patrolling) might be fast and directional, and dispersing animals may slow their pace to feed or rest (Gurarie *et al.* 2009; Baguette *et al.* 2013). Thus a better approach may be to split the locations of every individual into a territorial subset of locations that fall within a coherent home range and a subset of exploratory or dispersal locations that fall outside the home range, potentially moving through unfamiliar landscape. With this differentiation into home range and exploratory movements, dispersal behavior could be specifically incorporated into connectivity analyses and corridor identification.

There are a few comparative studies on how behavior influences resistance estimates (Morales and Ellner 2002; Van Dyck and Baguette 2005; Baguette and Van Dyck 2007; Trainor *et al.* 2013; Zeller *et al.* 2014; Mateo-Sanchez *et al.* 2015) but to our knowledge, no studies specifically quantify how estimating resistance from movements within the home range versus estimating resistance from exploratory movements influence corridor identification and effective distances, as we do in this study. For this purpose, we focused on a large telemetry

dataset for 48 GPS-collared Iberian lynx (*Lynx pardinus*) tracked between May 2009 and November 2013. The Iberian lynx has been at the brink of extinction, with less than 100 individuals estimated in only two isolated populations in southern Spain (Doñana–Aljarafe and Andújar–Cardeña) by the end of the twentieth century (Guzman *et al.* 2004; Simón *et al.* 2012). Recent conservation efforts, including translocation, captive breeding, genetic reinforcement, and reintroduction into new areas within the historical range have contributed to a notable increase in population size to around 400 individuals (Life+ IBERLINCE 2006; Simón *et al.* 2012). Despite this recent success, the long-term persistence of the species is jeopardized by the isolation of some of the populations and by a limited connectivity with other suitable habitats or reintroduction areas to which the species may expand in the future. This makes the Iberian lynx a particularly appropriate case study for our research, because identifying suitable corridors and estimating effective distances among established populations and potential reintroduction areas can be an important decision making support in landscape management and conservation of this species.

For these reasons, herein we tested the hypothesis that behavioral state (resident individuals within home ranges vs. exploring or dispersing individuals outside their home ranges) affects how animals travel through the landscape and therefore also produces different estimates of connectivity. We used Iberian lynx as our focal species. We predicted that movement data from dispersing individuals produces lower resistance and effective distance estimates, because dispersers may exhibit more plasticity when moving between habitat patches than resident individuals. Consequently, we expected that pooling all movement data and thus, ignoring behavioral states, in landscape connectivity assessments produces higher estimates of the potential isolation of habitat patches.

4.2. MATERIALS AND METHODS

4.2.1. STUDY AREA AND SPECIES

Iberian lynx are distributed among nine habitat patches, each representing a stable population nucleus or a reintroduction site (Fig. 4.1). One stable population is present in the Doñana–Aljarafe area (hereafter Doñana), holding 76 censused individuals (Life+ IBERLINCE 2006). Also, 285 individuals are estimated to inhabit Sierra Morena, with three patches that are spatially disjoint but functionally connected (by dispersing lynx): Andújar–Cardeña (hereafter Andújar), Guadalmellato, and Guarrizas (Life+ IBERLINCE 2006). The two latter populations (Guadalmellato and Guarrizas) were the result of an Iberian lynx reintroduction that started in 2009–2010 and already hold growing populations. In 2014/2015 the LIFE+ IBERLINCE project (LIFE10NAT/ES/570) reintroduced several lynx individuals from captive breeding into new areas in Portugal and Spain within the species historical range, namely Campo de Calatrava,

Matachel, Montes de Toledo, and Vale do Guadiana, and the project plans to reintroduce lynx into Sierra Norte–Valdecigüeñas (hereafter Sierra Norte) in the near future.

Fig. 4.1. Study area for the evaluation of corridors and effective distances. The study area is defined as a 100-km buffer around the four stable population nuclei and the five reintroduction areas of the Iberian lynx in the southern Iberian Peninsula

These reintroduction areas were selected for their habitat appropriateness, prey (rabbit) density, minimum area of 10,000 ha, existing legal protection, social acceptance, and possibility to contribute to a metapopulation (Gil-Sánchez *et al.* 2011). About 43 individuals were estimated in these new reintroduction areas in 2015. Connectivity is emerging as a high

priority for the conservation and management of these populations and reintroduction areas. The study area comprises a 100-km buffer around the nine habitat patches and extends over 165,000 km² of Spain and Portugal (8853052.39400W 37857020.49900N). This is a diverse territory with mountains reaching 2,461 masl, high plateaus, a main primary river (Guadalquivir) with a wide valley, and coastal ecosystems. The main land cover types are agricultural lands (61 %, with 12 % agroforestry, 10 % olive groves, and 2 % agriculture mixed with natural vegetation), shrublands including sparse tree cover (23 %, with 10 % transitional woodland-shrub, 8 % sclerophyllous vegetation, and 5 % natural grasslands), forests with a canopy cover of at least 30 % (12 %), artificial surfaces (2 %), wetlands and open areas (1 %), and water bodies (1 %) (CORINE Land Cover 2006). Humans have extensively and intensively modified the landscapes in the study area since the Paleolithic era. At present, most of the human population lives in cities while rural areas have generally low population densities. However, numerous linear infrastructures such as roads and railways traverse the region. The degradation of the Mediterranean shrublands (the Iberian lynx optimal habitat) and the presence of numerous roads and railways are regarded as important threats for the Iberian lynx survival (Ferreras *et al.* 1992; Palomares 2001; Rodriguez and Delibes 2002; Gil-Sánchez *et al.* 2011).

4.2.2. RESISTANCE SURFACES

We obtained landscape resistance values from three resource selection models developed in Gastón *et al.* (2016), who used 44,002 GPS locations of 48 individuals monitored between May 2009 and November 2013. The GPS–GSM collars provided locations every 4 h. The following explanatory variables were mapped in the resource selection models at a spatial resolution of 90 m: terrain slope, two road variables (high-traffic and low-traffic roads) and twelve land cover types based on CORINE Land Cover 2006 (transitional woodland/shrubland, shrublands, forests, agroforestry areas, agricultural lands mixed with natural vegetation, mix of annual and permanent crops, olive groves, other fruit tree plantations, irrigated arable lands, non-irrigated and non-tree crops, and unsuitable areas). Our resource selection model compared used and available habitat where used habitat corresponded to the actual GPS locations and available habitat was characterized by a circle around each GPS location with radius equal to the 99th percentile of the distances travelled in the 4-h interval between GPS locations. For each circle, the “available” value of each explanatory variable was the average across all 90-m cells, weighted by distance to the GPS location. Resource selection models were fitted in a conditional mixed-effects logistic regression with individuals as random effects (Gastón *et al.* 2016). A tenfold cross-validation approach was used to validate the models. Area Under ROC curve (AUC) was used to measure model predictive performance.

The three resource selection models predicted the probability of selection of each 90 x 90-m cell in the study area using three different input sets of GPS locations, (1) GPS locations within home ranges only (33,153 GPS locations), (2) locations corresponding to exploratory or dispersal movements outside home ranges (10,849 GPS locations), and (3) all GPS locations pooled together.

To classify each GPS location as either inside or outside of a home range, we computed the home range for every lynx individually using the a-LoCoH method (Getz *et al.* 2007), which constructs utilization distributions using a non-parametric local convex-hull. The hull is the union of minimum convex polygons around each location. The a-LoCoH method encompasses the advantages of both minimum convex polygons (*MCP*) and bivariate kernels as it delineates boundaries based on real data while providing density estimates. We preferred the a-LoCoH method over other commonly used methods such as the *MCP* or bivariate kernels because it produces better home range delimitations, particularly when (1) hard (sharp) boundaries exist between used and unused areas (*e.g.* roads, water bodies) or when unused areas (holes) are present within the home ranges, and when (2) many locations are available (Getz *et al.* 2007), as is the case for our data. The a-LoCoH analyses were performed with R software (R Development Core Team 2015) using scripts available at <http://locoh.cnr.berkeley.edu/rtutorial>. Further details are provided in Gastón *et al.* (2016).

The resulting resource selection models obtained from GPS locations within home ranges (habitat suitability model, AUC = 0.78), from GPS locations of exploratory or dispersal movements (dispersal model, AUC = 0.91), and from all GPS locations together (joint data model, AUC = 0.78) yielded estimates of the probability of selection of each cell in the study area. We converted these resource selection models into resistance surfaces by linearly and inversely rescaling their values into a 1-100 range representing the resistance to movement across the landscape. The minimum probability value in each resource selection model (0) was assigned the maximum resistance of 100 units, and the maximum probability value in each model was assigned the minimum resistance of 1 unit, as follows:

$$Resistance(x) = 1 + (99/w_{max}) \times (w_{max} - w(x))$$

where, Resistance (x) = value of each cell in the resistance surface model, $w(x)$ = value of each cell in the model of probability of selection, w_{max} = maximum value of the model of probability of selection across all cells.

We obtained three resistance surfaces, one using locations within home ranges (henceforth, habitat suitability resistance surface), one using locations during dispersal or exploratory movements (henceforth, dispersal resistance surface), and one using all locations (henceforth, joint data resistance surface).

4.2.3. EFFECTIVE DISTANCES AND CONNECTIVITY ANALYSIS

For each of the three resistance surfaces, we determined the effective distances and created a corridor map among all the patches using the Linkage Mapper tool extension for ArcGIS 10.0 (McRae and Kavanagh 2011). The corridor map was the combination into a single mosaic of all individual least-cost paths between any two patches (McRae and Kavanagh 2011). To obtain it, Linkage Mapper first obtains the cost weighted distance rasters from every patch individually. Next, the cost-weighted distance rasters are calculated for each of the two patches considered; for each cell in the landscape this sum represents the effective distance of the lowest-cost inter-patch path passing through that cell. Then the least-cost path is identified as

the set of cells with the lowest effective distance (in cost units). The effective distance would be equal to the Euclidean distance if the traversed areas all corresponded to optimal habitat (*i.e.*, with a cost value equal to 1). The effective distance of the least-cost path is then subtracted from the effective distance associated with each cell to represent the additional cost of moving through the cell relative to the cost of moving through the least-cost path. Finally, all these relative cost maps are combined into a single mosaic composite relative-cost map using the ArcGIS command Mosaic (McRae and Kavanagh 2011). The relative cost associated with each 90 m cell in the mosaicked map represents the cost of moving from one cell to any adjacent cell. To avoid the border effect, the calculation was conducted for the entire Iberian Peninsula and afterwards clipped to the study area.

We also calculated the length of the least-cost path, the mean cost along the least-cost path, and the least-cost path tortuosity. The length of the least-cost path is the distance in meters along the least-cost path between a pair of patches. The mean cost along the least-cost path (cost/m) is the ratio between the effective distance and the length of the least-cost path and gives an estimate of the average resistance per distance unit along the least-cost path. The least-cost path tortuosity, dimensionless, is the ratio between the length of the least-cost path and the Euclidean distance and quantifies the straightness of the least-cost path.

All calculations were performed for the three different resistance surfaces. We compared corridor delineation, effective distances, length of the least-cost path, mean cost along the least-cost path, and least-cost path tortuosity among the three resistance models (habitat suitability, dispersal, and joint data models). We used pairwise Kendall's tau (τ) rank correlation tests to discern whether the relative ranking of effective distances was robust across resistance surface models. All analyses were performed with R software (R Development Core Team 2015).

4.3. RESULTS

4.3.1. CORRIDOR AND LEAST-COST PATH DELINEATION

The corridors (Fig. 4.2) and the trajectories of the least-cost paths (Fig. 4.3) were similar for the three resistance models. Several corridors traverse the central part of the study area, in an East–West strip (axis Vale do Guadiana–Calatrava) where central patches are immersed in a more or less continuous region of low-resistance. On the other hand, the peripheral habitat patches (Montes de Toledo, Doñana, and Matalachel) are surrounded by regions of higher resistance to movement and have fewer low-resistance corridors to other populations. Another common feature of the corridors delineated in all three models is that the Doñana population is connected to the rest of the patches through a narrow bottleneck following the Guadamar river valley (Fig. 4.3). In all the models, the corridor avoids the city of Seville and

the intensely cultivated South side of the Guadalquivir river valley, which is dominated by irrigated arable lands. It is also remarkable that none of the three resistance models identifies a more or less straight corridor linking the Doñana population to the first patch to the West (Vale do Gadiana) (Fig. 4.2). Instead, individuals moving between these two patches are assumed to take a detour through the narrow bottleneck connecting patch Doñana to Sierra Norte and then turn left at a sharp angle to reach Vale do Gadiana. Likewise, there are no straight corridors between patches that are in the periphery of the study area; instead, they all go through the central part of the study area and connect via intermediate patches (Fig. 4.2). For example, patches in the northwest of the study area (Vale do Gadiana and Matachel) are only connected through an intermediate patch (Sierra Norte), and the corridor that links Montes de Toledo and Sierra Norte also goes through an intermediate patch (Guadalmellato).

4.3.2. EFFECTIVE DISTANCES AND RELATED INDICATORS

The dispersal model resulted in effective distances lower than those of the habitat suitability model and those of the joint data model (Fig. 4.4a, b; Table 4.1). Also, effective distances in the joint data model were always lower than those obtained from the habitat suitability model (Fig. 4.4c; Table 4.1). Average effective distance was 42 % (SD 7.20 %, range 29–56 %) lower for the dispersal model than for the habitat suitability model (Table 4.1). Or alternatively, effective distance was 75 % (SD 22.58 %, range 40–125 %) greater for the habitat suitability model than for the dispersal model when connecting the same pair of patches. The mean cost along the path (ratio between the effective distance and the length of the least-cost path) varied among models by nearly identical percentages (Table 4.1). These differences in cost among models are consistent with the observation by Gastón *et al.* (2016) that lynx performing exploratory or dispersal movements readily traverses a wide variety of land cover types, while resident individuals using resources within home ranges were more restricted and selective in their preferences.

Hence, the dispersal model resulted in lower estimates of resistance to movement than the habitat suitability model for each pair of patches. The differences in effective distances between models were larger for pairs of patches separated by longer geographical distances (Fig. 4.4a–c). The higher the effective distance, the larger the difference between models (in Fig. 4.4a–c, dots farther apart from the diagonal line). The highest effective distances were those for least-cost paths linking Montes de Toledo with Vale do Gadiana and Montes de Toledo with Doñana. The least costly of all paths connect patches that are quite close to each other (among Guarrizas, Campo de Calatrava, Andújar and Guadalmellato).

The length of the least-cost paths did not differ among the three resistance models (Fig. 4.4d–f; Table 4.1). Similarly, path tortuosity did not vary among the three models; in each model the mean length of the least-cost path was about 1.59 the Euclidean distance (Table 4.1).

Finally, Kendall's tau (τ) rank correlation test indicated that the relative ranking of values of effective distances between each pair of habitat patches was stable among models ($\tau = 0.911$ for dispersal model against habitat suitability model; $\tau = 0.889$ for the joint data model against the habitat suitability model; $\tau = 0.914$ for the joint data model against the dispersal model).

Fig. 4.2. Relative cost map and trajectories of the least-cost paths (LCPs) among the nine patches for the three resistance models: a dispersal model, b habitat suitability model, and c joint data model. The color ramp characterizes the resistance of a cell relative to the least-cost path; white indicates the minimum cost (LCP cost is set to zero).

Fig. 4.3. Trajectories of least-cost paths resulting from the dispersal model (green), the habitat suitability model (red), and the joint data model (black).

4.4. DISCUSSION

4.4.1. CONNECTIVITY VALUES DERIVED FROM MOVEMENTS WITHIN HOME RANGES ARE LOWER THAN THOSE DERIVED FROM DISPERSAL MOVEMENTS

We found that estimates of the relative cost of travel through the landscape (effective distances) depended strongly on whether one infers resistance from habitat suitability models of locations within the home range, or from models derived from locations of individuals that disperse or explore the landscape. Dispersing individuals that leave one habitat patch and move through the landscape searching for other habitat patches are able to reach them at less cost than indicated by a model based on locations of resident individuals (or all locations). Indeed, in our study, effective distances calculated from dispersers or explorers were lower by 40–125 % (mean 75 %) than effective distances estimated as the inverse of habitat suitability within the home range. Therefore, our results do not support the common approach of using the linear inverse of a habitat suitability model based on locations of individuals in their home

ranges as a proxy for landscape resistance (Graham 2001; Schadt *et al.* 2002a, b; O'Brien *et al.* 2006; Chetkiewicz *et al.* 2006; LaRue and Nielsen 2008; Shirk *et al.* 2010). This approach has been understandably widespread, because until the recent advent of GPS radio-tags, researchers typically were unable to obtain locations during rare, fast dispersal or exploratory movements. But our results show that these estimates yield different effective distances than using locations of exploratory individuals, which would better reflect the cost of travelling through the landscape. We believe that our findings are not contingent on the particular species, study area or dataset we explored, but apply to most organisms and landscape conditions. For instance, effective distances for the brown bear (*Ursus arctos*) using resistance surfaces estimated as the inverse of species habitat suitability model were 37–51 % higher than resistance surfaces inferred from genetic data (Mateo-Sanchez *et al.* 2015).

Fig. 4.4 a–c Comparison of effective distances for the three resistance surface models (habitat suitability, dispersal and joint data model). Dots represent the 36 least-cost paths connecting the pairs of habitat patches of the Iberian lynx. The straight diagonal line in each plot corresponds to the scenario in which the two models provide the same values ($y = x$). The higher the effective distances, the larger the differences in effective distances between models (dots farther apart from the straight diagonal line). d–f Comparison of lengths of the least-cost path for the three resistance surface models (habitat suitability, dispersal and joint data model). Dots represent the 36 least-cost paths connecting the pairs of habitat patches for the Iberian lynx. The straight diagonal line in each plot corresponds to the scenarios in which the two models would provide the same values ($y = x$). The three models resulted in similar lengths of least-cost paths for almost all pair of patches

However, we caution that cost-distance values have no direct ecological interpretation. For example if one path has an effective distance half the effective distance of another path, it does not necessarily follow that twice as many individuals will use the less-costly path, and does not guarantee it will be actually used by any individual. In fact, actual travelling costs can only be accurately estimated a posteriori (*e.g.* genetic distance). Nonetheless, connectivity maps derived from dispersal data suggest a higher likelihood of reaching distant patches than connectivity maps derived from resident individuals. Less accumulated cost of movement could also mean reaching nearby areas in better physical condition, or better chances of survival and reproduction of dispersers (With *et al.* 1997; Graham 2001; Stevens *et al.* 2004; Drielsma *et al.* 2007). Thus, how values of resistance to movement through the landscape are estimated could have important practical implications. For instance, resistance values specifically obtained from dispersal data could yield more optimistic assessments of whether a potential reintroduction site could be genetically or demographically connected to other populations, compared to resistance values obtained from information for resident individuals. Similarly, acceptance of a broader range of habitat conditions by dispersing individuals (dispersal plasticity) provides managers with more flexibility in where a low-cost corridor might be located, potentially reducing the risk of conserving a single low-cost corridor, particularly if located in an area where practical implementation of conservation measures may be complicated by conflicting land uses.

Therefore, when possible to do so, we recommend connectivity assessments should use data from dispersal or exploratory movements, despite the greater expense of acquiring such data. Nonetheless, locations of exploratory movements were generally environmentally similar to locations within home ranges, although exploratory movements showed tolerance of a wider variety of environmental conditions. Also, the Kendall's tau (τ) rank correlation tests indicated the relative ranking of effective distances remained robust across models. Therefore, when dispersal data are unavailable, habitat suitability resistance surfaces would delineate similar corridor areas. Habitat suitability models could also provide the most suitable estimates of resistance to determine the location for a road-crossing structure on a road passing through a large continuous habitat patch. Thus, the selection of methodology should be based on the specific objectives of the study.

4.4.2. SEPARATING HOME RANGE AND DISPERSAL MOVEMENTS

Many estimates of resistance to landscape features rely solely on home range locations, or ignore the animal's behavioral state (Beyer *et al.* 2010; Sawyer *et al.* 2011; Squires *et al.* 2013). However, we have shown that the landscape presents lower resistance to exploratory or dispersal individual movements than suggested by resistance models based on habitat suitability in the home range. Our results confirm the hypothesis that behavioral state influences how animals respond to landscape features and the degree of potential isolation of habitat patches (Morales *et al.* 2004; Cagnacci *et al.* 2010; Zeller *et al.* 2014; Gastón *et al.* 2016; Keeley *et al.* 2016).

Table 4.1 Comparison of four connectivity-related indicators, each calculated as the mean of the 36 potential corridors connecting every pair of patches

The connectivity-related indicators are the effective distance, the length of the least-cost path, the mean cost along the least-cost path, and the path tortuosity, for the three resistance models (dispersal model, habitat suitability model, and joint data model)

^a Calculated as $100 \times (\text{dispersal model value} - \text{habitat suitability model value}) / \text{habitat suitability model value}$

^b Calculated as $100 \times (\text{habitat suitability model value} - \text{dispersal model value}) / \text{dispersal model value}$

	Dispersal model	Habitat suitability model	Joint data model	% Increase for dispersal model ^a	% Increase for habitat suitability model ^b
Effective distance (cost)	484,100	827,436	609,563	-42 % SD 7.2 % [-56 %, -29 %]	75 % SD 22.6 % [40 %, 125 %]
Length of the least-cost path (m)	223,259	219,816	238,675	0.50 % SD 6.6 % [-5.4 %, 25.7 %]	-0.11 % SD 5.8 % [-20.4 %, 5.8 %]
Mean cost along the path (cost/m)	2.54	4.33	3.14	-42 % SD 6.8 % [-53.8 %, -29.5 %]	76 % SD 20.8 % [41.9 %, 116.4 %]
Path tortuosity	1.43	1.42	1.54	0.50 % SD 6.6 % [-5.4 %, 25.7 %]	-0.11 % SD 5.8 % [-20.4 %, 5.8 %]

There are several ways to identify behavioral states using appropriate types of input data. Procedures to identify dispersal and exploratory movements include analyses of movement distances and turning angles (Morales *et al.* 2004; Zeller *et al.* 2014), dividing individuals in groups according to their sex or age (Trainor *et al.* 2013; Elliot *et al.* 2014b, a), applying fractals (Fritz *et al.* 2003), and relating life-history traits with dispersal (Whitmee and Orme 2013). These procedures may also identify behaviors like predation and feeding (Ruth *et al.* 2010; Wilmers *et al.* 2013) or denning and communication behaviors (Allen *et al.* 2014). However, analyzing behavior following those approaches can be time-consuming and cumbersome, especially if the objective of the study does not require a high level of specificity. In this study, we used a relatively simple procedure appropriate for GPS locations that assigns locations to one of two bins: first, home ranges were delineated for each lynx using the a-LoCoH method and then all lynx locations falling within their corresponding home range were allocated in one bin and all lynx locations falling outside their corresponding home range were allocated in another bin. Consequently, locations within the home range would reflect behaviors such as resting and foraging and locations that are outside the home range would reflect behaviors like exploring and dispersing through unfamiliar landscapes.

4.4.3. THE IBERIAN LYNX CASE STUDY AND MANAGEMENT IMPLICATIONS

Estimates of the effective distances or degree of isolation among habitat patches were highly sensitive to the resistance model. We recommend the use of dispersal and exploratory movements to build suitability and resistance models that will be used to assess effective distance and degree of isolation. These models will suggest that individuals could arrive at habitat patches that might appear unreachable if the resistance model were based on home range locations. In the context of the Iberian lynx, an endangered species with few small and restricted habitat patches but with a growing population, this result could help managers to consider the conservation value of some peripheral or small patches of potential habitat that might otherwise be dismissed. Taking this broader perspective may ultimately improve the species conservation status.

The continuous map (Fig. 4.2a) of the relative costs among nine Iberian lynx population nuclei covering the whole study area shows a sharp decrease in connectivity in the South (the valley of the Guadalquivir river, dominated by irrigated crops and other agricultural lands) and to the Northeast (high plateaus dominated by arable lands). This suggests that it is less likely lynx would expand in those directions. The abrupt reduction in connectivity could help to identify major barriers to movement. On the contrary, range expansion may be more feasible to the West, Northwest, or East. Consequently, conservation and management resources could be focused in those areas. For instance, conservation attention could be focused on ameliorating the bottleneck restricting the flow of lynxes to and from the Doñana population. Likewise, conservation and management efforts could include delineating corridors of low resistance among habitat patches (the fact that the locations of the least-cost paths were similar in all three resistance models can provide managers confidence in corridor delineations), improving width and habitat quality of the corridors, ameliorating the habitat quality of occupied or potential habitat patches that are well connected to current populated areas, minimizing road kills by constructing wildlife passages and fencing roads traversing those corridors, promoting public campaigns to enhance support from social stakeholders, or strengthening collaboration among governance sectors.

4.5. CONCLUSIONS

In this study we presented the consequences of using three resistance models based on different behavioral states (habitat selection within the home range, dispersal and exploratory movements, and the combination of both states) in the identification of corridors and in the quantification of effective distances for assessing landscape connectivity. The three resistance models identified similar corridors and least-cost paths among every pair of habitat patches but produced strikingly different estimates of effective distances between patches. We

conclude that estimating resistance as the inverse of habitat suitability models within the home range consistently provides lower values of connectivity between patches and indicates less potential for range expansion than using dispersal data. Given the results of this study, when estimates of connectivity and cost of travelling through the landscape are desired, we recommend acquiring data from exploratory and dispersing individuals, despite the greater cost of such data, to provide more realistic assessments of dispersal behavior and connectivity patterns.

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CHAPTER 5

IDENTIFICATION OF STRATEGIC CORRIDORS FOR RESTORATION

Photo: Javier Pereira

This chapter reproduces entirely the content of the research paper:

Blazquez-Cabrera S, Ciudad C, Saura S, *et al.* (in preparation). Identification of strategic corridors for restoration: a case study for the Iberian lynx.

ABSTRACT

The conservation or creation of ecological corridors stands out as a strategic measure to support the persistence of species distributed in fragmented populations. However, there is little guidance on where to focus the restoration measures to improve the quality and functionality of ecological corridors. Focusing on the emblematic Iberian lynx (*Lynx pardinus*) as the target species and using a resistance surface parameterized through detailed telemetry data for the species, we applied a modelling approach targeted to assess the extent to which the restoration of different alternative corridors is beneficial for landscape connectivity. The restoration benefits for connectivity were quantified as the increase in the Probability of Connectivity index (*dPC*) that results in the entire network after reducing the effective distance along a particular corridor to its minimum possible value as a result of restoration, and as *dPC* normalized by an estimate of the total restoration effort required in each corridor. Results showed that the connectivity benefits of restoring each of the corridors were related to their effective distance (accumulated cost for movement along the corridor) and centrality (potential frequency of use by dispersing individuals) in the current landscapes. The Iberian lynx corridors that would benefit more from restoration measures would be those in the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava, in which conditions are relatively good currently but where significant connectivity gains could be still obtained with a relatively low restoration cost, and those in the axis Doñana-Sierra Norte-Matachel, which would require more ambitious, larger-scale restoration projects. The adopted methodological approach can be applied to potential corridors linking future reintroduction areas of the Iberian lynx, to case studies in other study areas and with other focal species, or to evaluate the impacts of the degradation or loss of corridors due to land use changes and other pressures. The applied approach is a powerful tool to estimate how landscape connectivity for any given species may be affected when changes in the landscape are planned or can be predicted, as long as sufficiently reliable information on species habitat use and movement preferences is available.

5.1. INTRODUCTION

Ecological corridors stand out as a strategic conservation measure to support species persistence, especially when species are characterized by fragmented populations dwelling in discontinuous habitats (Crooks and Sanjayan 2006; Chetkiewicz *et al.* 2006). Corridors contribute to mitigate the negative effects of habitat fragmentation (Hilty *et al.* 2006), reduce the risk of stochastic local extinctions (Reed 2004), promote genetic exchange among distant populations (Mech and Hallett 2001), maintain and regulate ecological processes in anthropogenic environments (Haddad and Tewksbury 2006; Hilty *et al.* 2006), or grant species the opportunity to relocate in response to global change (Channell and Lomolino 2000). Many authors also highlight potential downsides or limitations of ecological corridors (Hilty *et al.* 2006; Gilbert-Norton *et al.* 2010; Astrom and Part 2013) like, for example, that individuals may use or not the established corridors to move among habitat patches (Chetkiewicz *et al.* 2006); that the edge effect originated from the usual long and narrow shape of corridors might act as an ecological trap (King *et al.* 2009; Johnson and Haddad 2011); or that invasive species and epidemic diseases may spread along corridors with negative impacts on native species (Simberloff *et al.* 1992; Sullivan *et al.* 2011; Resasco *et al.* 2014). There are however evidences showing that the benefits of corridors largely outweigh their downsides (Gilbert-Norton *et al.* 2010), which therefore calls for further efforts in the conservation or establishment of corridors at the landscape and regional scale.

Despite ecological corridors are considered one of the flagships for biodiversity conservation and landscape connectivity enhancement, little effort has been done to assess the effectiveness of restoration measures to improve corridor quality. To date, the common approaches to improve landscape connectivity have mainly focused on the identification and delimitation of habitat patches that could potentially be reached by dispersing individuals (Soberon and Peterson 2005); the restoration of areas that do not provide habitat at present but that could do so in the future (Thomson *et al.* 2009); or the delineation of the corridors connecting currently populated habitat patches and potentially reachable ones (Vasudev *et al.* 2015). Furthermore, restoration measures generally focus on ameliorating habitat patch quality, but usually leave aside corridor quality or even the matrix environment (but see Williams and Snyder (2005)). In this sense, practitioners are in need of tools to assess to what extent landscape connectivity would increase if restoration measures for corridors were implemented, including the prioritization of the connectivity benefits of different corridors in which restoration efforts could be focused on. Given that biodiversity conservation actions are, more often than not, limited to budgetary constraints, such corridor restoration assessments also need to consider the extent to which the planned measures are cost-efficient to mitigate the negative effects of habitat fragmentation.

Corridors can be defined as ecological features, encircling structural and functional characteristics, that connect two or more habitat patches (or populations) in a way that individuals found in one habitat patch are able to reach the other patch moving along the corridor without encountering barriers to movement (Hilty *et al.* 2006; Chetkiewicz and Boyce 2009). They can have many forms, ranging from linear structures such as riparian forests to a

widespread landscape matrix whose land cover does not offer high resistance to movement albeit not having optimal conditions such as the preferred habitat for the species (Beier *et al.* 2008; Chetkiewicz and Boyce 2009). Such landscape matrix may also include intermediate elements like a set of stepping stones helping to connect the habitat patches. Structural and functional characteristics of corridors are generally entangled. For instance, two patches being close enough to allow individuals to assume the physiological cost of travelling from one to the other implies a structural characteristic (distance between patches) and a functional aspect linked to that structure (the mobility and scope of movement of the species). Similarly, the land cover within ecological corridors should be somehow continuous *e.g.* absence of barriers or insurmountable gaps (structural aspect) and, at least, tolerated (if not preferred) by the species to be able to use it (functional aspect).

A common approach to depict corridors is to delineate least-cost paths derived from resistance-to-movement values (Etherington and Penelope Holland 2013; Parks *et al.* 2013). Least-cost paths identify the paths with lowest cumulative resistance between each pair of habitat patches (Adriaensen 2003). They are characterized by a structural aspect, their trajectory in the landscape, and by a functional aspect, their effective distance (accumulated cost along the least-cost path). The lower the accumulated cost, the better the corridor quality is and the higher the connectivity they are likely to endow. Thus, a corridor of low quality would weakly contribute to connectivity among habitat patches, which could be alleviated by restoration measures improving corridor quality. In addition, just like habitat patches can be prioritized according to their importance for enhancing landscape connectivity, so corridors can. Therefore, a methodological approach that prioritizes habitat patches according to their contribution to the connectivity of the whole can also be similarly applied to corridors in order to quantify the extent to which they strengthen the connectivity of habitat patches.

In order to demonstrate the potential of this approach we focus on the Iberian lynx (*Lynx pardinus*), an endangered felid species inhabiting the southern Iberian Peninsula which is distributed in nine separate areas (hereafter referred to as patches), including currently stable populations and recent reintroduction areas. These populations, and particularly the recently reintroduced ones, are generally small and have connectivity as one of the main targets of the conservation efforts for ensuring their long-term persistence and the expansion of the Iberian lynx ranges in Spain and Portugal. This population and conservation context makes the Iberian lynx case study particularly interesting and informative for the purposes of the approach here adopted. In addition, in our study we could benefit from considerably detailed information on the resistance of different land covers to species movement, as assessed through GPS-GSM collars and quantified in habitat selection (habitat suitability) and dispersal/landscape permeability models for the Iberian lynx (Blazquez-Cabrera *et al.* 2016; Gastón *et al.* 2016).

Our aim was to assess how landscape connectivity would be affected if corridor amelioration and cost-efficient restoration measures were applied. Specifically, the objectives of this study were:

- 1) to determine the key corridors in which to concentrate the restoration efforts to improve landscape connectivity, including an assessment of the cost-effectiveness of corridor restoration alternatives,

2) to assess the degree to which the connectivity benefits of restoring a particular corridor are related to some characteristics of the corridor in the current landscape and network context, such as its effective distance (accumulated cost of moving across the landscape using that corridor) or centrality (expected frequency of use by dispersing individuals moving between habitat patches).

3) to provide priorities for the strategies aiming to enhance the connectivity of the Iberian lynx, thereby contributing to the consolidation, persistence and range expansion of this emblematic species in Spain and Portugal.

5.2. MATERIALS AND METHODS

5.2.1. STUDY AREA AND SPECIES

The study area is bounded to a 100-km buffer around the nine patches of the Life+ IBERLINCE program (LIFE10NAT/ES/570), which are either currently populated by Iberian lynxes (Doñana, Guadalmellato, Andújar, and Guarrizas) or selected for reintroduction (Vale do Guadiana, Sierra Norte, Matachel, Montes de Toledo, and Campo de Calatrava/Sierra Morena Oriental) (Fig. 5.1). Based on CORINE 2006 Land Cover Map, the landscape is composed of transitional woodland-shrub (10 %), sclerophyllous vegetation (7.9 %), forests (12 %), non-irrigated arable lands (21.2 %), irrigated arable lands (4.8 %), annual and permanent crops (0.6 %), agricultural lands mixed with natural vegetation (2.3 %), complex cultivation patterns (6.2 %), agroforestry areas (12.4 %), olive groves (10.1 %), other fruit tree plantations (3.1 %), grasslands and pastures (5.1 %), unvegetated areas (2.2 %), and artificial covers (1.9 %). Detailed information on land cover types can be found in (Gastón *et al.* 2016). The region is crisscrossed by a great number of linear transport infrastructures with several degrees of use intensity.

The Iberian lynx is an endangered endemic species included in the IUCN Red List of Threatened Species (IUCN 2016). It is a territorial species and habitat specialist, preferring to dwell on Mediterranean woodlands and areas with scattered trees and abundant understory vegetation where rabbits, its main prey, can be found. However, lynxes can also use, particularly in their dispersal movements, other land covers, such as tree plantations, permanent wood crops (*e.g.* olive groves), and heterogeneous arable lands with remnants of natural vegetation (Gastón *et al.* 2016). Despite being critically jeopardized in the past, several recovery projects and reintroduction programs in the last years have accomplished a substantial increase in the number of individuals up to around 400 individuals according to the last census (Life+ IBERLINCE 2006). Nowadays the species shows a growing population trend and a metapopulation structure. Previous connectivity studies for the species modeled diverse routes representing the least-cost path and other low-cost strips across the study area (Fig.

5.1; Blazquez-Cabrera *et al.* 2016). For all these reasons, it is a very suitable species to analyze how connectivity is affected when improving corridor quality.

Fig. 5.1. Study area with the nine patches, the 36 least-cost paths corresponding to the connections between each of the pairs of patches, and the corridor map for the Iberian lynx developed in Blazquez-Cabrera *et al.* (2016) and derived from the landscape permeability model developed in Gastón *et al.* (2016).

5.2.2. DATA ANALYSIS

We calculated the *variation in the Probability of Connectivity index (dPC)* for each link (least-cost path) connecting every pair of patches when the effective distance along the path decreases from its present value ($lcp_{present}$) to the lowest possible effective distance ($lcp_{optimal}$).

In order to do so, we computed the Link Change option for the Probability of Connectivity index (*PC*) with the Conefor software (Saura and Pascual-Hortal 2007; Saura and Torne 2009; Saura and Rubio 2010). The Link Change option calculates the variation of overall connectivity (as measured by the Probability of Connectivity *PC*) that results from two different values for the same path. Note that the *PC* for a link (path) only corresponds to the *connector* fraction ($dPC_{connector}$), because links are defined as connecting elements that do not contain habitat area (Saura and Rubio 2010; Saura and Torne 2012). The effective distances of the least-cost paths in the present state ($lcp_{present}$) were obtained from the corridor raster map developed in Blazquez-Cabrera *et al.* (2016). In this corridor raster map (Fig. 5.1) each cell represents the cost of moving from one patch of the study area to another patch according to the model of landscape permeability for dispersing lynxes developed in (Gastón *et al.* 2016). The effective distance of the least-cost path with the highest possible path quality value ($lcp_{optimal}$) was obtained by assigning the minimum cost value (1 cost unit) to every cell traversed by the least-cost path in the corridor raster map, which was equivalent to assume that all the corridor was composed of optimal land cover for the Iberian lynx dispersal. We defined the attribute of the patches as the total area of the patch weighted by their average quality value obtained from the habitat suitability model for the Iberian lynx developed in (Gastón *et al.* 2016).

We also computed $dPC_{restore}$, defined as the *variation in the Probability of Connectivity normalized by the restoration cost* required to improve each least-cost path from their present state ($lcp_{present}$) to an optimal state characterized for the lowest possible effective distance ($lcp_{optimal}$). The restoration cost was assumed to be proportional to the difference between $lcp_{present}$ and $lcp_{optimal}$, as we assume that the larger the difference between present and optimal states, the higher the restoration costs will be. This was calculated as:

$$dPC_{restore} = (10^6 \times dPC) / (lcp_{present} - lcp_{optimal})$$

In addition, we also estimated the *mean restoration cost per length unit* ($Cost_{unit}$) as the difference between $lcp_{present}$ and $lcp_{optimal}$ divided by the length of the least-cost path (lcp_{length}):

$$Cost_{unit} = (lcp_{present} - lcp_{optimal}) / lcp_{length}$$

This index is strongly influenced by the length of the least-cost path. The product of the length of the least-cost path by the mean restoration cost per length unit provides the difference between the effective distances of $lcp_{present}$ and $lcp_{optimal}$ (which is the restoration cost).

In order to evaluate which factors were associated to the connectivity gains obtained after the restoration of a corridor (as quantified by dPC and $dPC_{restore}$ as defined above), we characterized the corridors using two indices. These indices assessed the condition or importance of the corridor in the current network, before any restoration action. They do not assess the connectivity gains after restoration but may be hypothesized to be related to them even if indirectly.

The first index is the *number of times each of the least-cost paths was used* to move from any of the patches to any other patch within the study area (*Centrality*), *i.e.* the number of patch pairs whose maximum product probability path is different from zero (as measured by the Probability of Connectivity *PC*) and uses that link.

Secondly, we calculated the *sum of the product of the attributes of any pair of patches by all their maximum product probabilities (SumPaths)*. This index measures the probability of use of all paths connecting *patch i* and *patch j* weighted by the attribute of each patch (Saura and Pascual-Hortal 2007). This index gives us an idea of the potential lynx's traffic density along every path. It can be thought of as a habitat-weighted and probability-weighted centrality metric for links. It is calculated as follows:

$$SumPaths = Sum (a_i \times a_j \times p^{*}_{ij})$$

where,

a_i and a_j represent the attribute (area $\times$ mean habitat quality) of *patch_i* and *patch_j* respectively.

p^{*}_{ij} represents the maximum product dispersal probabilities of the all paths connecting of *patch_i* and *patch_j* (that is the estimated likelihood of movement between *patch_i* and *patch_j*): see Saura and Pascual-Hortal (2007) and Saura and Rubio (2010) for further details on p^{*}_{ij} .

In all these analyses and indices, we omit the results of Guarrizas - Campo de Calatrava because they are adjacent patches. We performed these calculations using the batch processing tool of Conefor software (Saura and Torne 2012) that allow calculations for a wide range of effective dispersal distances. Effective dispersal distances d_{disp} ranged from 1,000 to 100,000 cost units at 1,000 cost units interval steps. Effective dispersal distances for Iberian lynx previously obtained in Ferreras (2001) comprises values that range from 4,000 to 131,600 km. However, the resistance surface was derived from the inverse of a habitat suitability model, which has shown to provide resistance values up to 75 % higher than resistance surfaces obtained from dispersal models (Blazquez-Cabrera *et al.* 2016) as we used in this study. In Ferreras *et al.* (2004) the calculated total distance travelled ranged between 8,200 to 28,000 m and in Ferreras *et al.* (1997) average daily distances travelled varied from 6,400 to 38,600 m. Recent data from GPS-collared lynxes show even higher dispersal distances for some individuals, thus it is of interest to perform the calculations for an ample range of dispersal distances. The rest of the calculations were computed using R and ArcGIS (R Development Core Team 2015; ESRI 2017).

5.3. RESULTS

Major differences between present and optimal least-cost paths obviously occurred between patches that were farther apart or, to a lesser extent, between those whose least-cost path was surrounded by the least preferred land cover for dispersing lynxes (Table 5.1). Likewise, minor differences between the present and the optimal least-cost path happened between patches that were proximal.

Table 5.1. Cost values of $lcp_{present}$ and $lcp_{optimal}$ and mean restoration cost per length unit ($Cost_{unit}$) for every least-cost path between the nine patches.

From patch	To patch	$lcp_{present}$	$lcp_{optimal}$	$Cost_{unit}$
Andújar	Doñana	546176·06	274840	0·99
Andújar	Guadalmellato	61718·90	27438	1·25
Andújar	Guarrizas	34174·80	17234	0·98
Andújar	Montes de Toledo	456551·16	188732	1·42
Andújar	Matachel	447066·91	163066	1·74
Andújar	Campo de Calatrava	46338·20	29682	0·56
Andújar	Sierra Norte	293118·91	157269	0·86
Andújar	Val do Guadiana	701725·63	387584	0·81
Doñana	Guadalmellato	429940·88	226550	0·90
Doñana	Guarrizas	644360·63	332263	0·94
Doñana	Montes de Toledo	1051636·88	469504	1·24
Doñana	Matachel	691467·88	166866	3·14
Doñana	Campo de Calatrava	655923·38	345149	0·90
Doñana	Sierra Norte	218439·58	101752	1·15
Doñana	Val do Guadiana	294161·53	183399	0·60
Guadalmellato	Guarrizas	159903·64	84861	0·88
Guadalmellato	Montes de Toledo	569835·19	240844	1·37
Guadalmellato	Matachel	383766·00	134286	1·86
Guadalmellato	Campo de Calatrava	171466·56	97747	0·75
Guadalmellato	Sierra Norte	176884·63	108979	0·62
Guadalmellato	Val do Guadiana	585492·31	339293	0·73
Guarrizas	Montes de Toledo	548517·63	249681	1·20
Guarrizas	Matachel	545251·38	220489	1·47
Guarrizas	Sierra Norte	391303·47	214692	0·82
Guarrizas	Val do Guadiana	799910·56	445006	0·80
Montes de Toledo	Matachel	717208·44	244183	1·94
Montes de Toledo	Campo de Calatrava	545865·44	250650	1·18
Montes de Toledo	Sierra Norte	798580·00	351933	1·27
Montes de Toledo	Val do Guadiana	1207187·88	582195	1·07
Matachel	Campo de Calatrava	556814·50	233375	1·39
Matachel	Sierra Norte	284188·13	16661	16·06
Matachel	Val do Guadiana	836379·06	264815	2·16
Campo de Calatrava	Sierra Norte	402866·81	227578	0·77
Campo de Calatrava	Val do Guadiana	811473·56	457893	0·77
Sierra Norte	Val do Guadiana	361812·56	200733	0·80

The **mean restoration cost per length unit** ranges between 0·56 (Andújar and Campo de Calatrava) and 16·06 (Sierra Norte and Matachel). The latter is noticeably high in comparison with the rest of the restoration costs per length unit despite Sierra Norte and Matachel are relatively close to each other in relation to the study area (Fig. 5.1). This high value of $Cost_{unit}$ is mainly caused by the agricultural fields that surround those two patches, mainly non-irrigated arable lands, which are among the least preferred land uses of dispersing lynxes (Gastón *et al.* 2016). Some small and scattered patches of olives groves and agro-forestry areas are present too and could act as stepping stones between the two patches. With the exception of this

particular case, the mean restoration cost per length unit ranges between 0.56 (Andújar and Campo de Calatrava) and 3.14 (Doñana and Matalchel). Higher values of $Cost_{unit}$ correspond to those corridors whose paths are in part shared with the corridor between Sierra Norte and Matalchel.

The *variation in the probability of connectivity (dPC)* when the quality of each least-cost path improves from their present state ($lcp_{present}$) to the highest possible quality value ($lcp_{optimal}$) became noticeable from dispersing distances of 25,000 cost units and onwards for the majority of the least-cost paths. For those cases, the variation in the probability of connectivity grew with a soft increasing trend that remained below 6 % at all distances. However, five out of the 36 least-cost paths presented different trends in their dPC values (Fig. 5.2a). First, the least-cost path linking Sierra Norte and Matalchel resulted in the greatest dPC value (14 % of variation in the probability of connectivity). The Sierra Norte-Doñana least-cost path presents a similar but dimmer trend (7.5 % of variation in the probability of connectivity) and it also crosses Matalchel patch. Thus, considering an average dispersal distance of $d_{disp} = 20,000$ cost units, the axis comprised by the least-cost paths linking Doñana-Sierra Norte-Matalchel is the corridor whose amelioration would contribute the most to enhance connectivity among patches (Fig. 5.4a).

On the other side, the dPC of the least-cost path linking Andújar and Guarrizas grows with a steep slope until it reaches $d_{disp} = 22,000$ cost units to decrease slowly afterwards. The effective distance of this least-cost path is 34,000 cost units (length of the least-cost path ≈ 17 km) and it is the one with lowest cost. The importance of this link in relation to the rest of the connectivity network decreases with increasing d_{disp} as other patches become available (Fig. 5.2a). Similar but weaker behavior can be found in least-cost paths connecting Andújar with its two closer neighbors (link Andújar-Campo de Calatrava and link Andújar-Guadalmellato). That way, considering an average dispersal distance of $d_{disp} = 20,000$ cost units, the least-cost paths linking Guadalmellato-Andújar-Guarrizas-Campo de Calatrava constitute a second axis susceptible of restoration measures, which would help to further reinforce connectivity among the three biggest and closest populations at this moment (Fig. 5.4a).

When estimating the *variation in the Probability of Connectivity of the effective distances accounting for the restoration cost of improving the quality of the path ($dPC_{restore}$)*, we found that those least-cost paths whose amelioration would most cost-efficiently contribute to an increased connectivity of the landscape were basically the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava ($dPC_{restore} > 100$ between 15,000 and 45,000 cost units); the axis Doñana-Sierra Norte-Matalchel ($dPC_{restore} > 50$ from 90,000 cost units and onwards); and also the link Sierra Norte-Guadalmellato ($dPC_{restore} > 50$ from 90,000 cost units and onwards) (Fig. 5.2b and Fig. 5.4b). The $dPC_{restore}$ of the rest of the least-cost paths experimented a slightly growing trend with increasing dispersal distance, but their effect on the connectivity of the landscape can be considered negligible ($dPC_{restore} < 50$ for all distances).

Centrality was highest for the links connecting Guarrizas-Andújar, Andújar-Guadalmellato, and Guadalmellato-Sierra Norte with values between 14 and 19 times used (Fig. 5.3a). The number of times each of the least-cost paths was used depended on the dispersal distance considered. The index reaches an asymptote at a $d_{disp} = 8,000$ cost units. This distance is the minimum

required distance to connect the whole network of patches based on the corridor raster map considered. Some of the corridors were used more often at shorter distances than at larger ones (Sierra Norte-Guadalmellato, Sierra Norte-Doñana, and Andújar-Montes de Toledo). This is due to the fact that at larger dispersal distances, longer least-cost paths become available connecting directly the source and destination patches, replacing a concatenation of shorter paths that had some of these other patches as intermediate stepping stones.

The *sum of the product of the attributes of any pair of patches by all their maximum product probabilities (SumPaths)* showed that the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava was the region with higher probabilities to be traversed by lynxes (*SumPaths* $\approx 1.0 \times 10^9$ at high dispersal distances for Guadalmellato-Andújar and *SumPaths* $> 2.2 \times 10^9$ at high dispersal distances for Andújar-Guarrizas) according to the corridor raster map used (Fig. 5.3b). These patches were relatively close to each other in relation to the rest of the study area and in general yield high attribute values (mean habitat quality weighted by the area). Least-cost paths joining Sierra Norte-Doñana and Sierra Norte-Guadalmellato obtained values of *SumPaths* ranging from 0.3×10^9 and 0.5×10^9 at high dispersal distances. For the rest of the least-cost paths, *SumPaths* $< 0.1 \times 10^9$ in all cases.

Fig. 5.2. a) Results of the variation in the Probability of Connectivity (dPC) when the quality of each least-cost path improves from their present state ($lcp_{present}$) to the highest possible quality value ($lcp_{optimal}$) in relation to the dispersal distance. Some of these least-cost paths are really long and their amelioration might not provoke perceptible changes in the connectivity of the landscape. Thus, for the sake of clarity they are not included in the figures. Only the highest five results are shown. b) Results of the variation in the Probability of Connectivity of the effective distances accounting for the restoration cost ($dPC_{restore}$) of improving the quality of each least-cost path from their present state ($lcp_{present}$) to the highest possible quality value ($lcp_{optimal}$) in relation to the dispersal distance. Only values of $dPC_{restore} > 50$ are shown (the rest of results are practically indistinguishable from zero).

Fig. 5.3. a) Results of the *number of times each of the least-cost paths was used* to go from any of the patches to any other one within the study area (*Centrality*) in relation to the dispersal distance. Only the least-cost paths that were used more than five times are shown. b) Results of the *sum of the product of the attributes of any pair of patches by all their maximum product probabilities (SumPaths)* in relation to the dispersal distance. Only the results above 0.1×10^9 are shown (the rest of results are practically indistinguishable from zero).

Fig. 5.4.a) Values of dPC (% of overall connectivity increase by the restoration of each of the least-cost paths) at an average dispersal distance of $d_{disp} = 20,000$ cost units. b) Values of $dPC_{restore}$ (% of overall connectivity increase by the restoration of each least-cost path normalized by the estimated restoration cost) at an average dispersal distance of $d_{disp} = 20,000$ cost units.

5.4. DISCUSSION

5.4.1. APPLICABILITY OF THE METHODOLOGY AND SIGNIFICANCE OF THE RESULTS

The amelioration of corridors was emulated by reducing the value of the movement cost of crossing each cell of the least-cost path to just 1 cost unit (the minimum possible value that eliminates the cost provoked by crossing unsuitable land cover, *i.e.* simulating that the land cover of the corridor is all optimal for the species dispersal). In the case study of the *Iberian lynx*, this proxy allows to simulate the effect on the connectivity of the species of converting unsuitable land cover types along the corridors (for instance, irrigated arable lands or annual crops) into the preferred land cover type for lynxes to disperse (transitional woodland/shrub) (Gastón *et al.* 2016). This proxy is a simple way to represent the effect of a restored corridor in terms of movement cost and its application to any species is straightforward. Practitioners could simulate which corridors are susceptible of restoration measures and to what extent they would enhance landscape connectivity for a given species in the most cost-effective manner. The methodological approach of estimating the variation in the probability of connectivity of corridors when their quality changes (dPC) might be also used to assess other scenarios such as the degradation or complete loss of corridors due to land use changes or new urban developments. In these cases, the effective distance of the least-cost paths in their present state ($lcp_{present}$) would be calculated as usual. The effective distance of the degraded corridor would be calculated by increasing the effective distance of present least-cost paths to the effective distance estimated after the land use change or the urban development has taken place ($lcp_{degraded}$). The complete loss of a corridor would be represented by $lcp_{degraded} \approx \infty$. In this sense this methodological approach can be a powerful tool to estimate how much connectivity for any given species would be affected when changes in the landscape are planned or can be predicted.

The length of the least-cost path was revealed as the main variable affecting the connectivity gains when reducing the effective distances of present least-cost paths ($lcp_{present}$) to emulate optimal least-cost paths ($lcp_{optimal}$). In terms of cost units, dispersal is a cumulative process, thus the farther the distance travelled the higher the dispersal cost (Bonte *et al.* 2012). In this sense, corridors connecting patches that are far away might not be the most suitable paths for restoration as the increase in connectivity would be small and the restoration costs could result very high. On the other hand, corridors connecting patches that are relatively close to each other in relation to the study area contributed the most to increase landscape connectivity when their effective distance decreased from $lcp_{present}$ to $lcp_{optimal}$. Additionally, when longer dispersal distances were considered, the increase in landscape connectivity became less prominent as effective distances decrease from $lcp_{present}$ to $lcp_{optimal}$. This is basically due to two reasons. First, the fact that the longer the dispersal distance considered, the higher the number of patches that become reachable and the higher number of alternative movement pathways that can be used, therefore diminishing the relative importance of an individual corridor. Second, species with greater dispersal capabilities are able to travel farther

and through a wider variety of land covers and, consequently, they are less affected by changes in corridor quality (Bodin and Saura 2010). When several alternative corridors become available, corridors located in central positions would be used more frequently because distances are shorter and the cost of movement lessens accordingly. This is why the number of times each corridor was used (*Centrality*) may be more related to its central position and not that much related to the quality of the path itself or that of the paths around them. If this is the case, central corridors might be the most appropriate targets for restoration measures because they are likely to be more frequently used and their amelioration could imply a more substantial increase in the effective connectivity of the whole. Likewise, short corridors of low quality but strategically positioned between high quality patches would also be appropriate targets for restoration measures as their amelioration is cost-effective and the increase in landscape connectivity may be substantial.

However, the assessment of the degree to which the connectivity of the landscape would be affected by increasing the quality of the corridors or the patches needs to consider that dispersing individuals can use habitat types of lower quality than those used by resident individuals. This is because, when dispersing, individuals do not need to fulfill all their biological requirements (e.g. breeding or other activities that require high physiological costs) (Palomares *et al.* 2000; Bonte *et al.* 2012) and the patches selected to settle might be the result of a set of other factors and intrinsic behaviors such as avoidance of conspecifics, mate searching, etc. Factors such as habitat resources relevant to survival and reproduction or the intrinsic attributes of dispersing individuals should be carefully considered to assess in detail the variables that affect the connectivity of corridors and patches and, ultimately, dispersal success (Vasudev *et al.* 2015). Here we already incorporated some of these considerations in the study because the corridor map used to identify least-cost paths and effective distances were the result of a landscape resistance model derived from the preferences of collared dispersing individuals (Gastón *et al.* 2016). Factors related with environmental constraints for dispersal, such as the effects of roads on movement or the protection provided by the land cover were included in the landscape resistance model (Zeller *et al.* 2012; Gastón *et al.* 2016). Likewise, the intrinsic characteristics of individuals were also implicitly included in the landscape resistance model. Notwithstanding these considerations, unforeseen dispersal behaviors could always happen and these special situations might be difficult to introduce in a model (Bélisle *et al.* 2001; Zollner and Lima 2005; Vasudev *et al.* 2015). As an example, two remarkable cases of dispersing lynxes that behaved unpredictably have been recently reported. Kahn and Kentaro, two lynx siblings born and raised in captivity as a part of the Life+ IBERLINCE ex-situ reintroduction program and released in Montes de Toledo reintroduction area in 2015 with GPS-GSM collars, dispersed more than 1,000 km in opposite directions for unknown reasons. The distances went over by these two individuals have not been previously documented for the species, whose average dispersal distance was estimated to be around 20 km in Doñana area using radio-tracking techniques (Ferrerías *et al.* 2004), although recent studies indicate that the species can disperse farther (Life+ IBERLINCE 2006). The extent to which these long-distance, and possibly low-frequency, dispersal events could influence long-term persistence of the species is an open question that should be further examined.

Natural expansion of Iberian lynxes from already populated patches to recolonize areas of the historic distribution may be limited due to habitat fragmentation and lack of dispersal corridors (Gil-Sánchez and McCain 2011). Fortunately, as a result of the reintroduction efforts of the last years, some increase in the exchange of individuals is being reported as populations are growing and stabilizing in the area (Life+ IBERLINCE 2006). Consequently, management actions on corridors and connectivity enhancement are at this point required. Among the recommendations for managers, those regarding the spatial configuration of the landscape are in general focused on habitat and corridor amelioration according to the species requirements. However, species requirements are more often than not in opposition with some primary land uses, especially intensive agriculture practices. The extent to which primary land uses are compatible with species requirements would determine the degree of implementation of effective restoration measures for habitat amelioration. In this sense, Gastón *et al.* (2016) provided essential and useful insights in the compatibility of land uses with the habitat requirements and dispersal preferences of Iberian lynx. Bearing in mind this knowledge, management recommendations regarding the amelioration of corridors to enhance landscape connectivity would focus on two main restoration projects.

First, if the restoration project suffer from budgetary constraints, the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava (see Fig. 5.4b) would be the best target. Consolidating the connectivity along this axis of corridors, which link the patches with more number of individuals so far, would help to ensure a fluid exchange of lynxes among these populations. The region yields the best prospects for further expansion of the current connectivity levels. Hence, restoration measures that facilitate the exchange of individuals while reducing mortality risks provoked by non-natural causes would surely benefit the recovery of the species.

Second, a most ambitious restoration project would concentrate in the axis Doñana-Sierra Norte-Matachel (Fig. 5.4a). If resources are available, this project would contribute to reconnect these areas and would allow individuals from Doñana, the second population in number of lynxes, to disperse. Doñana is very isolated and efforts to diminish the isolation of the patch would favor the species on the whole. Also, the link Sierra Norte-Matachel is central and short, but the landscape around it is composed by some of the least preferred land covers for dispersing lynxes, such as non-irrigated arable lands. Management actions to restore this corridor would strengthen connectivity between two central patches that might be key elements in the movements of the lynxes across their distribution range the near future.

Nevertheless, a question remains regarding to what extent it is required to apply restoration measures in order to increase connectivity. That is to say, it is still to be determined the level of connectivity, as assessed through the methods and metrics here adopted, that would be necessary to guarantee a sufficient exchange of individuals and genes. Above that level of connectivity, restoration measures may not have a significant additional effect on the genetic exchange among populations and on the genetic variability within them. In such case, restoration measures would be more beneficial for the Iberian lynx population as a whole when allocated in corridors that are clearly below that level. For instance, corridors along the

axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava might already be above such a level of connectivity that secures genetic exchange among patches in the long term given the observations of GPS-collared individuals moving across the area. Hence, from this perspective, it might be more beneficial to focus on the axis Doñana-Sierra Norte-Matachel for the application of connectivity restoration measures.

As an additional note, once these two restoration projects are secured, the amelioration of the corridor linking Sierra Norte and Guadalmellato (Fig. 5.4a, b) would contribute to connect these two important lines of expansion. As a result, connectivity in the East-West direction and in the North-South direction would be reinforced allowing individuals to move across most of its present distribution range. Such an improved scenario would provide the growing lynx population with more space and mobility to adjust to eventual deleterious effects of global change, given the exposure of Mediterranean woodlands to climate warming, land use modifications and urban developments (Gil-Tena *et al.* 2013).

Corridors like the Guadiamar River, close to the Doñana patch (Fig. 5.1), are crucial elements for enhancing connectivity in fragmented and degraded landscapes and for that reason they require special attention (Ferrerías 2001). Conserving and restoring their habitat quality is highly encouraged as well as implementing management actions for broadening their width when possible (Ferrerías 2001; Rodríguez and Delibes 2003). In all cases, trade-offs between cost-effective restoration measures and the degree of connectivity improvement need to be balanced carefully. The methodological approach of this study could lend a hand to practitioners in decision-making processes in order to allocate budget efficiently. The identification of “black points” in existing and potential corridors is also key for improving corridor quality. We defined “black points” as those locations where corridors cross linear infrastructures like roads and railways and that are collision-prone due to a high risk of wildlife-traffic crash. This is part of our ongoing research. Linear infrastructures have considerable disadvantages for numerous species: not only collisions, but also noise, light, pollution, and the barrier effect (D’Amico *et al.* 2015). In the case of the Iberian lynx, traffic collisions are one of the most frequent causes of death in recent years (Simón *et al.* 2012). Besides, the barrier effect is affecting lynxes in Doñana not only in highways, but also in secondary and not paved roads (D’Amico *et al.* 2015). Thus, some restoration measures to take into account for ameliorating connectivity across linear infrastructures are the creation of under- and overpasses, fencing, reflective lights, and reduced vehicle speed in the “black points” and surrounding areas (Simón *et al.* 2012). These strategies have proven to be successful in reestablishing and improving connectivity for some species (Sawaya *et al.* 2013; Ascensão *et al.* 2013), as well as in some previously implemented actions for the Iberian lynx.

5.5. CONCLUSIONS

Previous studies on the use of the landscape by dispersing Iberian lynxes and on corridor delineation in the area make appropriate and timely this study on the effects of corridor restoration alternatives to increase landscape connectivity. Corridor length and centrality were the main factors affecting landscape connectivity among patches when restoration measures to improve the quality of the corridors are applied. The methodology presented can be also used to estimate the effect on landscape connectivity when corridors are lost or degraded due to land use changes. Results showed that, in general, potential amelioration measures moderately affect landscape connectivity at the scale of the entire Iberian range here considered, although two recommended lines of action emerged for the Iberian lynx as a result of the study. First, if budgetary constraints are considerable, a restoration project of the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava could strengthen connectivity among these neighbor patches, at least until a fluid movement of individuals between patches secures the required levels of genetic exchange among the subpopulations. Second, a most ambitious project would focus in ameliorating the quality of the axis Doñana-Sierra Norte-Matachel, where connectivity is considerably restrained, in order to provide more dispersal routes for future expansion of the species. With these two restoration projects, connectivity of current populations on the direction East-West and on the direction North-South would be reinforced allowing the exchange of individuals across most of the distribution range of the species, with exception of the most distant patches (Vale do Guadiana in the West and Montes de Toledo in the North), the connectivity of which should be tackled, but possibly with less priority according to our analyses, in other restoration projects in the future.

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CHAPTER 6

GENERAL DISCUSSION

Photo: Sonia Illanas

6.1. CONNECTIVITY ASSESSMENTS CONSIDERING FUNCTIONAL SCALE AND INDIVIDUALS' RESPONSE TO THE LANDSCAPE

The functional scale of dispersal processes and the individuals' response to the landscape are essential aspects to be considered in connectivity assessments (Dunning *et al.* 1995; Zollner and Lima 1997; Wiegand *et al.* 1999; Tyre *et al.* 2001; Dickson *et al.* 2005; Schtickzelle *et al.* 2006; Ewers and Didham 2006; Mueller and Fagan 2008; Hagen *et al.* 2012). This research attempts to incorporate them within a methodological framework that is composed of three main steps. First, defining habitat patches in a way that matches the functional scale of the process and that makes subsequent connectivity analyses ecologically relevant and computationally feasible. Second, capturing the response of dispersing individuals to heterogeneous landscapes. Third, conducting the connectivity analyses with appropriate graph-based metrics that reflect the dispersal preferences of the species considered. The proposed methods were applied to the emblematic Iberian lynx, an endangered species with a fragmented population structure and limited movements between populations. This application for the Iberian lynx provides a compelling case study illustrating that, as long as appropriate input data can be gathered on the species and landscapes, similar connectivity assessments for other species and environments are feasible and able to provide valuable results for both scientists and practitioners alike.

Even so, the definition of habitat patches according to the functional scale of species-specific dispersal processes can be a difficult task. Previous connectivity studies sometimes incorporated scale sensitivity analyses in their assessments by modifying grain or extent (Wiens and Milne 1989; Wiens *et al.* 1997; Mayer 2003; Saura 2004; Urban 2005; Corry and Laforzezza 2007). Yet, to our knowledge, bringing together the scale of the habitat patches and of the ecological process considered in dispersal analyses has not been considered so far. Some studies have proven that the aggregation of patches in functional units can help to capture the ecological scale of processes regardless the grain or extent of the study area (Fletcher *et al.* 2013). However, in these studies the relevance of patch aggregation in connectivity assessments constitutes one of the results instead of an input for the analysis (Fletcher *et al.* 2013). In contrast, in this research the aggregation of patches in hierarchical levels was defined intentionally so as to represent functional units resembling the areas of departure, arrival and/or stepping stones used by dispersing individuals. As well, the impacts of this aggregation on the results of the connectivity analyses were specifically investigated. The possibility of defining aggregated but functionally relevant habitat patches overcomes some difficulties and presents some advantages of practical and ecological nature.

To begin with, in heterogeneous landscapes with multiple land uses, the definition of habitat patches as each of the individual polygons with suitable or optimal habitat for the species could result in an atomization of patches in the region. That is, habitat patches would eventually consist of a large number of small areas of the most frequently selected habitat for the species interspersed in a mosaic landscape of other land cover types. Following this

approach, graph-based landscape connectivity analyses may end up being computationally unfeasible, due to the vast computational requirements given by the combinations of pairs of habitat patches involved in the calculations, which increase at a rate of $n(n-1)/2$ with n being the number of patches. Thus, the selection of these single small habitat areas as patches for graph-based dispersal studies might not be computationally efficient. In addition, these approach might not be of ecological usefulness either. Such small areas of high quality habitat might not even contain the home range of a single individual. Territorial species require certain amount of habitat and resources to establish home ranges (Ferrerias *et al.* 1997; Palomares 2001; Dickson and Beier 2002; Dellinger *et al.* 2013). Consequently, it is logical that in heterogeneous landscapes home ranges contain multiple fine-scale habitat patches, landscape features and land covers, all of which jointly meet the requirements of the species. Accordingly, a population of a territorial species would contain at least several home ranges comprising small areas of high quality habitat along with others that are suboptimal or not so frequently selected. Within these land cover mosaics representing home ranges, individuals' movements would be associated to resident behavior, *e.g.* activities like patrolling, hunting, or resting (Cagnacci *et al.* 2010). However, when individuals initiate a dispersal event in search of other territories to settle in, they would move through unknown areas shifting their movement patterns from home range use behavior to dispersal behavior (Palomares *et al.* 2000; Dekker *et al.* 2001). For these reasons, in order to analyze dispersal processes it is practical and reasonable to construct a network of patch aggregates representing tightly connected patches that work as a single functional units (each corresponding to an individual subpopulation or groups of neighbor home ranges) and that are weakly connected to other patches or patch aggregates (Fletcher *et al.* 2013). Movement within aggregates (tightly connected patches through routine movements by resident individuals) would represent home range use behavior within a subpopulation, while movement between aggregates (comparatively weakly connected patches) would represent dispersal behavior. This network structure offers a clear and simple visualization of dispersal processes in metapopulation structures in spite of the heterogeneity of land cover types of the landscape that helps to understand at first sight subsequent connectivity analyses as exclusively movements between aggregates are considered (Brandes *et al.* 2006).

Other reasons for considering aggregates of patches as functional units in connectivity assessments can be driven by administrative, socioeconomic or management factors. For instance, protected areas are hardly ever composed of a homogeneous land cover nor circumscribed to the home ranges of a target species. They are generally managed as a conservation entity (although different lines of action may be taken inside them), in comparison with the landscapes outside their boundaries which may be unmanaged or managed for different purposes (Bennett *et al.* 2006; Lindenmayer *et al.* 2006; Geneletti and van Duren 2008). Likewise, collaboration among administrative or political authorities of different regions might prompt connectivity projects among distant areas of high conservation value (*e.g.* the Natura 2000 network), which may comprise different habitat types. Other connectivity projects might also aim to link disjoint areas inhabited by a given target species, but which may contain a variety of land covers. In this case, the functional units for the connectivity analysis might be composed of heterogeneous land mosaics as long as the target species is present. This is the case of the Iberian lynx, where the selected patches have been

designated by the Life+ IBERLINCE program as key areas for the Iberian lynx conservation (Life+ IBERLINCE 2006). Patches represent populated regions, where Iberian lynxes are already dwelling (current presence of already stable populations), and recent reintroductions areas, where individuals of the species have been recently released or where they will be released soon (potential presence in the near future). The selection of the reintroduction sites was the result of a multi-criteria procedure that carefully considered the following variables: habitat structure, prey availability, minimum area, possibility of integration in the current metapopulation structure, possibility of potential expansion to other suitable areas, social support, and threats such as illegal persecution pressure (Simón *et al.* 2009).

The level at which these patches were defined as a result of the multi-criteria selection procedure might contain one or more than one habitat patches and/or home ranges, although this information was not necessarily used in the connectivity assessments of dispersal processes. Nonetheless, both populated regions and selected reintroduction areas will certainly be the sources of dispersal of individuals towards other regions, leaving aside the characteristics of the patches, because lynxes are already present or will be present in the near future. Therefore, the network structure built to analyze landscape connectivity for the Iberian lynx case study considered these current populations and reintroduction areas as the functional units that would become the starting point, and probably the final destination and/or stepping stones, of dispersal processes. Hence, according to the results obtained from the analysis of the dependence of the hierarchical level at which habitat patches are defined in connectivity assessments, it is possible for the Iberian lynx case study to focus exclusively in the movements between distant aggregates (Doñana, Guadalmellato, Andújar, Guarrizas, Campo de Calatrava/Sierra Morena Oriental, Montes de Toledo, Matachel, Sierra Norte and Vale do Guadiana) independently of their internal configuration as long as a landscape-scale process (*e.g.* dispersal) remain the objective of the study. In addition, by doing so, the outcomes of the connectivity analyses provide results at the scale that is more relevant for the management and conservation efforts for the species. At this level, the connectivity analyses provide a synoptic pattern of the dispersal and connectivity at the relatively broad scale at which they actually happen and at which they are most needed. This result is more useful and practical than a detailed and overcomplicated network analyses focused on a more local scale at which there are no significant limitations to the species movements, or at which these movements are insufficient to promote the desired flow of genes and individuals between populations in the Iberian Peninsula.

However, it is important to note that not all graph-based connectivity metrics responded equally to changes in the scale used to define the patches. Only metrics capable of capturing both intrapatch connectivity and interpatch connectivity (habitat availability) were able to identify with confidence which were the key elements, whether patches or corridors or both, that ensure and enhance landscape connectivity with little sensitivity to the scale of patch definition. By using metrics such as the Probability of Connectivity (*PC*) and the Integral Index of Connectivity (*IIC*) and their fractions (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010), the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava and the axis Doñana-Sierra Norte-Matachel would continue to be identified as the key ones for connectivity conservation and restoration even if other levels of aggregation would have been used to define the patches. On the other side, if the interest of the study was

focused on dispersal events happening at a regional scale (*e.g.* long-distance dispersal events) so that, in the extreme, the chosen hierarchical level considers Guadalmellato, Andújar, Guarrizas and Campo de Calatrava as one aggregate, this aggregate would also be the most important element to conserve (in this case including both patches and corridors) in order to ensure or promote the likelihood of long-distance dispersal events of lynxes across the whole Iberian Peninsula. For these reasons, and based on the results on the effects of patch aggregation on connectivity prioritization, it is possible to confidently conclude that the management recommendations for the Iberian lynx obtained in this thesis remain valid and pertinent regardless these scale issues.

Once the habitat patches have been defined according to the functional scale of the dispersal process, the next step is capturing the individuals' response to the landscape. Factors like land composition and spatial configuration (*e.g.* vegetation structure, proportion of different land cover types, barriers), environmental conditions (*e.g.* season, population dynamics, resources), or the intrinsic state of individuals (*e.g.* health condition, age, body mass) affect how the landscape is utilized by a species (Vasudev *et al.* 2015). Some of these factors can be extracted from mapping environmental variables and combining them with movement data of individuals and its associated metadata. For this research, an extensive dataset of GPS-GSM collared Iberian lynx individuals was available. In accordance with previous studies that pinpoint the drawbacks of using the inverse of habitat availability models derived from home range use for analyzing dispersal processes (Elliot *et al.* 2014b; Killeen *et al.* 2014; Vasudev *et al.* 2015), GPS data was divided according to the behavioral states of interest (resident versus dispersing) to generate different models of landscape use. In order to assign GPS locations to one or other type of behavioral state, the home range of every individual was delimited and then, locations falling inside them were placed in the home range use group and locations falling outside were included in the dispersal group.

Likewise, when GPS data are available (geographic locations, the time and date, and the unequivocal identification of each individual), the possibilities of capturing alternative behaviors are numerous. The method used to discriminate data derived from home range use and from dispersal data can also be used to extract other types of behaviors and to address different hypothesis regarding movement across the landscape. For example, extracting the locations of females with cubs at the breeding season could be used to map how reproductive females with calves utilize the landscape. Similar studies on the topic have already been published by several authors (Fernandez and Palomares 2000; Fernandez *et al.* 2002, 2003, 2007). However, these studies were mostly conducted exclusively in Doñana, while the recent status of the Iberian lynx has changed substantially both in numbers and in distribution. This method also offers a new perspective on examining the relation between processes and landscape patterns. Not only connectivity patterns in general can be mapped but also other different or more specific ecological processes such as long-distance dispersal events, breeding spots, accident-prone zones, or post-dispersal settlement preferences. The challenge of this method is being able to accurately discriminate data in order to capture the behavior that is more appropriate to the ecological process of interest (Benz *et al.* 2016).

After discriminating data derived from home range use and data from dispersing individuals, the application of recently developed modelling approaches for characterizing resource

selection provided a more detailed insight into the habitat and dispersal preferences of Iberian lynxes. The habitat suitability and the landscape permeability maps offered comprehensive information with regards to the spatial configuration of the landscape and the environmental characteristics, and they may have also captured individuals' intrinsic conditions implicitly. The validation of the model threw high performance for the landscape permeability model (AUC = 0.91), and more moderate for the habitat suitability model (AUC = 0.78). A hypothesis to explain the reasons of the slightly lower performance rate of the habitat suitability model is that home range use involves activities happening at a different functional scale than dispersal processes, and that finer-scale inputs are necessary to capture more accurately the home range landscape preferences of lynxes. Fortunately GPS data for the species is continuously being recorded and adjustments of the parameters of the model with fine-scale environmental variables to improve the model performance would be possible in the future. Lynxes are nowadays expanding through areas from where they disappeared a long time ago and knowledge of the factors driving dispersal and settlement of wild lynx individuals in these new territories is still incipient because current range expansion is assisted through active reintroduction. However, the results of this thesis and the ongoing research and monitoring of the species is contributing to consolidate this understanding.

For example, resource selection models showed a remarkable dispersal plasticity for the Iberian lynx: dispersing individuals consistently used more often the habitats or land covers that resident individuals tended to avoid, and they also exhibited less reluctance to cross roads. This lower resistance to movement confirms that estimates of dispersal costs are more accurate when they are obtained exclusively from data of dispersing individuals (Cagnacci *et al.* 2010; Morales *et al.* 2010). In addition, the results from the resource selection models suggest that future (and ongoing) Iberian lynx reintroductions may be viable in more heterogeneous landscapes than previously thought. These landscapes may include a relatively wider variety of habitat types (up to a certain limit, and always with the leading presence of Mediterranean woodlands), as well as high quality habitat patches that were previously tagged as isolated when surrounded by certain land covers that are now shown to be less resistant to species dispersal movements than what suggested by previous assessments. In this sense, conservation strategies for the Iberian lynx may expand their potential range of successful action. This flexibility of land cover use has also been recorded for other species (Jopp and Reuter 2005; Shaw *et al.* 2014; Elliot *et al.* 2014a; Christie and Knowles 2015; Panzacchi *et al.* 2016) bolstering the hypothesis of wider plasticity of movement during dispersal processes for species in general. The consequences of overlooking these emerging evidences would imply the underestimation of the potential for expansion of the Iberian lynx and other species, given that they may move farther than expected, or reach in better physiological conditions new patches of suitable habitat.

After apprehending the Iberian lynx individuals' response to the landscape, a step forward in the research, and in the methodological framework, consists in studying the effective benefits of corridor restoration measures for an increased landscape connectivity. Short and central corridors are those that would most easily increment connectivity as a result of restoration measures, particularly when the associated restoration cost is taken into account. Other longer corridors, but still with a central position in the landscape network, are interesting candidates for larger-scale restoration projects with more resources and area of land involved. For the

Iberian lynx population context, corridors linking Guadalmellato, Andújar, Guarrizas, and Campo de Calatrava on the one side, and corridors linking Doñana, Sierra Norte, and Matachel on the other side, are the axes where amelioration measures should be preferentially targeted. The restoration measures to improve connectivity would include actions not only along the corridors but also around the populations and the wider landscapes in which they are embedded. Along the corridors in the first axis (Guadalmellato-Andújar-Guarrizas-Campo de Calatrava), relative gains in connectivity could be achieved by applying restoration measures with relatively little effort, compared to other regions. For the second axis (Doñana-Sierra Norte-Matachel), a more challenging restoration project implementing actions in larger and more heterogeneous tracts of land (including areas that are currently less permeable to Iberian lynx movements) would be required to increase connectivity. Such a project would be however essential to connect all existing populations and thereby to contribute to the long-term, self-sufficient viability of the species in the Iberian Peninsula. The approach to evaluate connectivity gains as a result of applying restoration measures along corridors is likely to be of applied potential for other species, areas, and contexts, provided that certain key aspects are considered and appropriately quantified. These aspects are the spatial configuration of the landscapes in the study area, the habitat suitability conditions of the patches, the individuals' responses to the landscape when dispersing, and the role and characteristics of landscape elements (patches and corridors) involved in the current and potential dispersal events.

6.2. MANAGEMENT RECOMMENDATIONS FOR THE IBERIAN LYNX

As shown by previous results, general management recommendations for improving landscape connectivity would include a series of actions comprising habitat patches, corridors and surrounding matrix, centering the actions in the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava, along the East-West direction, and particularly in the axis Doñana-Sierra Norte-Matachel, along the North-South direction, where more ambitious and potentially beneficial projects would be needed.

First, general management actions would need to focus in restoring the adjacent areas of the high quality habitat patches containing stable populations. In order to ensure the viability of the species, a minimum area is required to be able to harbor a stable population. Ferreras *et al.* (2010) stated that the home range of an adult lynx occupies between 500 ha and 1,500 ha and signaled a minimum of 10-12 breeding females in order to constitute a healthy to moderate-sized population. Thus, at least 5,000 ha of suitable habitat is necessary to yield a viable population, and larger areas would be preferable if possible. The restoration of the areas around the high-quality habitat patches already populated by Iberian lynx would help to ensure the minimum area required. Securing adjacent areas would also improve intrapatch connectivity and would reduce the effective distance between habitat patches, enhancing

interpatch connectivity, which is especially relevant for considerably fragmented habitats (Pascual-Hortal and Saura 2006). Attention should be paid to landscape features surrounding habitat patches, such as edges of optimal habitat or barriers, as they have proven to condition the initial movements of dispersing individuals of Iberian lynxes (Ferrerías 2001). Therefore, landscape configuration immediately surrounding stable populations can indirectly affect connectivity through individuals' decisions taken during the start of dispersal. Hence, it is essential to identify critical locations nearby high quality habitat patches that currently do not provide habitat or that restraint dispersal processes, and to assess whether amelioration measures would improve the quality of adjacent areas (Thomson *et al.* 2009). In addition, prey availability should be preserved or improved in habitat areas as lynx populations are highly dependent on rabbit population status. Because different diseases have caused the decline of rabbit abundance, these actions are a priority (Life+ IBERLINC 2006, 2016; Fernández and Molina 2007).

Second, the delimitation of new patches that are susceptible to host the species and facilitate individuals' settlement is recommended. This selection should consider both current and projected habitat suitability in prevision of climate change forecasts (Fordham *et al.* 2013). From the landscape permeability model developed in this thesis, major barriers to movements are located southwards Guadalquivir valley and towards agricultural plateaus located northeast. In contrast, regions to the west, northwest, and east are most likely to accommodate the range expansion of the species. Consequently, it is suggested that new suitable areas should predominantly be located towards those directions. Other methodologies or complementary criteria are available and need to be considered when selecting new suitable habitat patches: for example using the historic distribution when land use changes have not substantially modified the landscape; selecting habitat patches that are similar to those of the stable populations; or identifying areas suitable for hosting emblematic species by applying a predicted rarity-weighted index (Fordham *et al.* 2013; Albuquerque and Beier 2016). Within already populated areas, prey availability is a key element of potential habitat patches and its provision is an important part of the management of the species (Life+ IBERLINC 2006). Ideally, suitable habitat patches would be located within the dispersal range of the species, that is, preferably not more than 40-45 km far away from the nearest population (Rodríguez and Delibes 2003; Simón *et al.* 2009), although recently recorded dispersal events of the Iberian lynx are suggesting that the species may be able to disperse further than previously thought. If some patches are located far from others, as in some of the recent Iberian lynx reintroduction patches, introduction of individuals might be an alternative option to consider (Fernández and Molina 2007; Simón *et al.* 2012), and the investments in the improvement of connectivity with other areas through the permeation of the intermediate landscapes should focus particular attention.

Indeed, the next (third) objective would be the delineation of suitable corridors in order to connect currently or potentially occupied patches with high habitat quality. As natural expansion may be significantly restricted due to habitat loss and fragmentation (Gil-Sánchez and McCain 2011), efforts in restoring or establishing corridors are required. By using a landscape resistance model informed by the observed movement preferences of the species, corridors can be delineated locating low-cost areas in the landscape, and their effective distances can be calculated. Other methods to delineate corridors include genetic distances to

find successful dispersal routes (Mateo-Sanchez *et al.* 2015), circuit theory approaches (McRae and Beier 2007), the inverse of habitat suitability models (Keeley *et al.* 2016) or expert knowledge among others. Validation of existing corridors with real data is also mandatory. For example, the corridor joining Guadalmellato-Andújar-Guarrizas has been verified to be functional and active by the observation of numerous individuals released in one habitat patch and tracked in another. Some individual exchanges have been also observed, although with a lower frequency, between Doñana (Spain) and Vale do Guadiana (Portugal), suggesting that there is the potential to establish or reinforce a corridor between those patches (Life+ IBERLINCE 2006), despite the difficulties for movement through some of these areas that is suggested by the landscape permeability model. In any case, the empirical observation of individual exchange is essential to confirm the critical functional corridors that are identified with the support of landscape connectivity modelling approaches.

Fourth, the restoration of corridors connecting high quality areas (axes Guadalmellato-Andújar-Guarrizas-Campo de Calatrava and Doñana-Sierra Norte-Matachel) would enhance connectivity of the whole landscape, eventually up to a level in which all these patches would function as a single effective population. Corridors, apart from linking populations, are also aimed to allow floaters to colonize of new areas. The amelioration of the habitat conditions in and around these corridors would increase the survival of dispersing individuals (Rodríguez and Delibes 2004; Palomares *et al.* 2011; Rodríguez *et al.* 2012). Corridors should ideally be integrated with habitat patches and eventually become, in the longer term, part of the habitat of the lynx (even if suboptimal), particularly if the species continues to expand its range in the next decades. However, restoring the habitat quality of these areas can be a daunting task due to the large extent of their cover and their degree of habitat deterioration in some sectors (Fernández and Molina 2007). Given that lynxes can use lower quality habitats to disperse than those that they prefer as residents, as proven by this work in accordance with previous studies (Palomares *et al.* 2000; Ferreras 2001), low-intensity and soft management may be a suitable option. Such management may include, for example, reducing the impacts of traffic and urban/industrial developments, enforcing predation control and game regulations, or including tax incentives for small game management (Life+ IBERLINCE 2006; Rodríguez and Calzada 2015). These measures are in general compatible with primary land uses or human-related activities and they can be easily adjusted to future land use and societal changes. Adaptive and extensive management over larger areas as opposed to intensive management in smaller patches could improve the chances of the species to survive (Palomares *et al.* 2011).

Fifth, conflicting spots in both existing and potential corridors should be identified. Conflicting spots refer to those locations ("black points") along ecological corridors that are crossed by roads or railways. Wildlife-vehicle collision risk is high at the conflicting spots and appropriate actions should be taken. During the 1980s, 5 % of the 1,258 non-natural lynx deaths were provoked by traffic accidents (Fernández and Molina 2007). However, this percentage has substantially increased in the 1990s and 2000s probably caused by the development of the transportation network and the expansion of the Iberian lynx range, and in parallel to the decreases of other mortality sources (Life+ IBERLINCE 2006; Simón *et al.* 2012). Plans for new linear infrastructures should take into consideration the distribution of lynx populations and the potential corridors among them so that lynxes are not significantly disturbed by vehicle traffic impacts such as noise, light, the barrier effect, or collisions (Simón *et al.* 2012; D'Amico

et al. 2015). Basic management recommendations for alleviating these disturbances could be fencing, implementation of reflective light systems, enforcement of reduced speed for vehicles, construction and maintenance of under- and over-passes on existing roads, and avoid paving dirt roads (Fernández and Molina 2007; D'Amico *et al.* 2015).

Nonetheless, strategies for enhancing species persistence in fragmented landscapes must necessarily comprise an holistic approach, including not only actions over the spatial configuration of the landscape (habitat patches, corridors and matrix) but also considering the impacts of anthropogenic activities or current legislation; species traits, like fitness or dispersal abilities; and other factors, like genetic drift or global change predictions (Ferrerías *et al.* 2001; Fordham *et al.* 2013; Vasudev *et al.* 2015). As a part of this comprehensive program, management recommendations for the recovery and conservation of the emblematic Iberian lynx should involve planning at different scales and across multiple sectors (Simón *et al.* 2012; Gurrutxaga San Vicente 2013; Fordham *et al.* 2013). Landscape-scale measures may include reintroduction of individuals in new habitat patches; amelioration of the areas adjacent to the population nucleus; agreements with landowners in areas with suitable habitat for lynxes; or rabbit supplementation in zones with low density of prey (Life+ IBERLINCE 2006; Fernández and Molina 2007; Ferrerías *et al.* 2010; Simón *et al.* 2012; Fordham *et al.* 2013). Individual-scale measures may comprise checking individuals' fitness and genetic status regularly; controlling disease outbreaks by extracting unhealthy individuals; or monitoring individual movements in order to analyze behavior (Life+ IBERLINCE 2006; Fernández and Molina 2007; Palomares *et al.* 2011; Simón *et al.* 2012). Planning across multiple sectors refers to actions not specifically related to the conservation of the Iberian lynx but wherefrom the species could benefit. These actions may include measures such as regulations for road and railway infrastructure design in order to mitigate future impacts on landscape connectivity for wildlife in general; agricultural policies to promote sustainable practices by combining primary land uses with natural vegetation fragments while delivering multiple ecosystem services; or campaigns for raising social awareness in areas where vulnerable and endangered species dwell (Life+ IBERLINCE 2006; Ferrerías *et al.* 2010; Palomares *et al.* 2011; Simón *et al.* 2012; Fordham *et al.* 2013). Finally, the conservation of an umbrella species like the Iberian lynx could foster the implementation of measures that could benefit many other species, as well as create synergies that would contribute to restore ecosystems like the Mediterranean woodlands, help to deploy green infrastructure, and strengthen the resilience of our landscapes in the long term (Cushman *et al.* 2013).

6.3. FUTURE RESEARCH

FURTHER ADJUSTMENTS OF THE RESOURCE SELECTION MODEL

Lynxes are nowadays occupying territories that were never monitored before. It is likely therefore that new management challenges, as well as somehow different species preferences and behaviors, may arise as lynxes explore and use these recently reconquered landscapes. Fortunately, fresh data is continuously becoming available due to the ongoing monitoring of GPS-collared lynxes, so that model results could be further contrasted with evidence-based data. In this sense, further research aimed to fine-tune the resource selection model is required to incorporate new variables and to adjust the current ones so as to apprehend an increasingly more precise response of individuals to the environment. Mapping prey availability, non-natural mortality risks, distribution shifts caused by climate change, or fine-scale land cover structure is challenging. However, these variables might help to better understand how lynxes move through the territory and what factors drive their behavior and performance. Additionally, other scale-dependent behaviors different from dispersal or home range use (*e.g.* post-dispersal settlement or breeding) could also be extracted from the monitoring data and applied to the model to shed light on the relation of the Iberian lynx with its environment. Finally, the results from the resource selection models should also be considered together with other important factors for the viability of Iberian lynx populations, such as disease prevalence, genetic variability, or the attitudes and engagement of rural populations and landowners in their conservation.

WILDLIFE-VEHICLE COLLISION MAPPING FOR IBERIAN LYNXES

One of the most important current threats for the Iberian lynx is the non-natural deaths provoked by collisions with vehicles. Despite all the important efforts to conserve and protect the species, the proportion of non-natural deaths provoked by traffic accidents has considerably increased in the last years, mainly as a consequence of the larger areas now occupied by the Iberian lynx and the reduced rabbit density in some of these areas. Given the small size of the Iberian lynx populations, reducing mortality rates due to traffic collisions is crucial to ensure long-term viability of the species. Of special concern are the roadkills that happen at the intersection of ecological corridors with linear infrastructures, which could be identified with the help of the habitat suitability and landscape permeability models described in this thesis. These locations are conflictive because it is likely that they might be crossed by lynxes more frequently than other points of the transportation network. Therefore, identifying these “black points” (*i.e.*, intersection of ecological corridors with roads and railways) is of high priority. Future research could focus in mapping high-mortality roads and in pinpointing the conflictive spots where preventive measures could be applied as to more efficiently minimize Iberian lynx roadkills.

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CHAPTER 7

CONCLUSIONS

Photo: Javier Pereira

1. The methodological approach presented in this thesis has the potential to be applied in improved landscape connectivity assessments that consider the functional scale and the behavioral state of individuals for a variety of species, study areas and management contexts. Such methodological approach entails three main steps: defining habitat patches at a scale that reflects the ecological process under study (usually dispersal), separately capturing the response of resident and dispersing individuals to landscape heterogeneity, and incorporating the dispersal behavior in habitat availability indices based on graph theory.
2. Habitat connectivity metrics, considering their dependence on the hierarchical level at which patches are defined, do not allow answering with confidence to the following question: which proportion of the current landscape connectivity will be lost after the removal of multiple habitat patches from the landscape? However, some of the connectivity metrics, particularly those that are based in quantifying habitat availability (reachability) in the landscape, are much more reliable in answering this other question: which are the habitat areas that need to be prioritized for landscape connectivity conservation?
3. Species show a remarkable dispersal plasticity, as evidenced for the case of the Iberian lynx through the analysis of an extensive dataset obtained from GPS-GSM collars. Dispersing individuals use suboptimal habitats more frequently, show a considerably weaker avoidance of roads and of some agricultural lands, and are able to use a wider variety of land covers than resident individuals.
4. Iberian lynx conservation and reintroduction may be successful in a wider set of more heterogeneous areas than previously thought, including mainly well-conserved Mediterranean woodlands but also some extensive agricultural covers with permanent crops and natural vegetation remnants, which may provide both suitable habitat (e.g. foraging resources) and support functional landscape connectivity for the species.
5. Estimating resistance as the inverse of habitat suitability (as modelled using data of resident individuals within home ranges) consistently provides lower values of connectivity than directly using dispersal data. Acquiring data from exploratory and dispersing individuals is recommended to provide more realistic assessments of travelling costs, of range expansion or colonization potential, and of the actual degree of isolation of habitat patches and populations.
6. Length and centrality of corridors are the main factors determining the landscape connectivity gains that result from the application of corridor restoration measures. In the case of the Iberian lynx, two main axes for connectivity restoration were identified. First, the axis Guadalmellato-Andújar-Guarrizas-Campo de Calatrava, where conditions are already relatively good (compared to other areas) and significant gains in effective connectivity could still be achieved with relatively small restoration investments. Second, the axis Doñana-Sierra Norte-Matachel, where the conditions are currently

more restrictive for connectivity and more ambitious larger-scale restoration projects would be needed.

7. The approach to assess the relative connectivity gains of corridor restoration actions, here applied to the case of the Iberian lynx, has the potential to support more broadly the evaluation of the impacts of landscape changes on the connectivity of other species, populations or habitats. The assessment of the benefits of restoration management actions focusing on landscape permeability and corridor quality must comprise the different key aspects involved. These aspects include the spatial configuration of the landscape, the species-specific responses to land covers, the habitat suitability in and around each current or potential population, and the role of each habitat area and corridor in the entire ecological network comprising the species range (including the areas of potential species reintroduction or colonization).