Evaluation of ecosystem services and conflicts associated with native and exotic wild ungulates

Evaluación de servicios ecosistémicos y conflictos asociados a los ungulados silvestres nativos y exóticos

Roberto Pascual Rico
PhD Thesis

Doctorado en Medio Ambiente y Sostenibilidad

Director: José Antonio Sánchez Zapata
Codirector: Francisco Botella Robles

UNIVERSITAS Miguel Hernández

Evaluation of ecosystem services and conflicts associated with native and exotic wild ungulates

Evaluación de servicios ecosistémicos y conflictos asociados a los ungulados silvestres nativos y exóticos

Roberto Pascual Rico

PhD Thesis

Elche, 2019

RECOMMENDED CITATION:

Pascual-Rico, R. 2019. Evaluation of ecosystem services and conflicts associated with native and exotic wild ungulates. PhD Thesis. Universidad Miguel Hernández, Elche.

Cover design by Roberto Pascual-Rico

Backcover photograph: aoudad group in Sierra Espuña by Sergio Eguía

Programa de Doctorado en Medio Ambiente y Sostenibilidad

Evaluation of ecosystem services and conflicts associated with native and exotic wild ungulates

Evaluación de servicios ecosistémicos y conflictos asociados a los ungulados silvestres nativos y exóticos

Director: José Antonio Sánchez Zapata

Codirector: Francisco Botella Robles

Tesis Doctoral presentada por Roberto Pascual Rico en la Universidad Miguel Hernández de Elche para la obtención del título de Doctor del Programa de Doctorado en Medio Ambiente y Sostenibilidad.

Elche, 2019

PUBLICACIONES INCLUIDAS EN ESTA TESIS DOCTORAL

Chapter 4

Pascual-Rico, R., Pérez-García, J.M., Sebastián-González, E., Botella, F., Giménez, A., Eguía, S., Sánchez-Zapata, J.A. 2018. Is diversionary feeding a useful tool to avoid human-ungulate conflicts? A case study with the aoudad. European Journal of Wildlife Research 64: 67. DOI: 10.1007/s10344-018-1226-6.

Chapter 5

Pascual-Rico, R., Morugán-Coronado, A., Botella, F., García-Orenes, F., Sánchez-Zapata, J.A. 2018. Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain. Applied Soil Ecology 127: 136-143. DOI: 10.1016/j.apsoil.2018.03.017.

AUTORIZACIÓN PARA LA PRESENTACIÓN DE LA TESIS DOCTORAL POR COMPENDIO DE PUBLICACIONES

Dr. José Antonio Sánchez Zapata, Profesor Titular de la Universidad Miguel Hernández de Elche y Dr. Francisco Botella Robles, Profesor Titular de la Universidad Miguel Hernández de Elche

AUTORIZAN

La presentación de la Tesis Doctoral por D. Roberto Pascual Rico, titulada "Evaluation of ecosystem services and conflicts associated with native and exotic wild ungulates", en la modalidad de compendio de publicaciones.

En Elche, a 12 de junio de 2019.

Director:

Dr. José Antonio Sánchez Zapata

Universidad Miguel Hernández

Codirector:

Dr. Francisco Botella Robles

Universidad Miguel Hernández

PROGRAMA DE DOCTORADO EN MEDIO AMBIENTE Y SOSTENIBILIDAD

José Navarro Pedreño, Coordinador del Programa de Doctorado en Medio Ambiente y Sostenibilidad de la Universidad Miguel Hernández de Elche

CERTIFICA

Que la tesis doctoral presentada por Roberto Pascual Rico, titulada “Evaluation of ecosystem services and conflicts associated with native and exotic wild ungulates”, dirigida por Dr. José Antonio Sánchez Zapata de la Universidad Miguel Hernández de Elche y codirigida por Dr. Francisco Botella Robles de la Universidad Miguel Hernández de Elche y se ha desarrollado dentro del Programa de Doctorado en Medio Ambiente y Sostenibilidad, se encuentra en condiciones de ser leída y defendida ante el correspondiente tribunal en la Universidad Miguel Hernández de Elche.

Lo que firmo en Elche, a los efectos oportunos, a 12 de junio de 2019.

José Navarro Pedreño

Coordinador del Programa de Doctorado en Medio Ambiente y Sostenibilidad

This thesis was supported by a pre-doctoral grant (FPU13/05460), as well as a mobility grant (EST16/00229) from Spanish Ministry of Education and Professional Training, and another grant (Resolution 1008/16) from Miguel Hernández University. In addition, the thesis was partly financed by a project (CGL2015-66966-C2-1-R) of the Spanish Ministry of Economy and Competitiveness and the European Regional Development Fund.

GOBIERNO DE ESPAÑA
MINISTERIO DE ECONOMÍA Y COMPETITIVIDAD

GOBIERNO DE ESPAÑA
MINISTERIO DE EDUCACIÓN Y FORMACIÓN PROFESIONAL

A la madre que me parió

Caballos, asnos y onagros se repartían el espacio y el alimento en las tierras bajas; muflones, rebecos y cabras monteses se dividían los terrenos más altos. Los antílopes saiga recorrían las planicies. […] venados de todas las variedades, desde el gamo manchado y el tímido corzo al alce, el ciervo y el reno.

J.M. Auel. *Las llanuras del tránsito*

CONTENT

ABBREVIATIONS AND ACRONYMS

AS	Aggregate Stability
BD	Bulk Density
BSR	Basal Soil Respiration
C	Contour Area Soil
DFS	Diversionary Feeding Stations
EC	Electrical Conductivity
EEZA	Estación Experimental de Zonas Áridas
ENM	Environmental Niche Model
ES	Ecosystem Service
ESP	Ecosystem Service Provider
FS	Feeding Station Soil
GLM	Generalized Lineal Model
GLMM	Generalized Lineal Mixed Model
GPS	Global Position System
GSM	Global System for Mobile Communication
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
MEA	Millennium Ecosystem Assessment
NCP	Nature’s Contribution to People
PCA	Principal Component Analysis
PLFA	Phospholipid Fatty Acids
RS	Reference Soil
USDA	United States Department of Agriculture

Summary

SUMMARY

Ecosystem functioning includes all cycling materials and energy, the interactions among organisms and the abiotic system. This functioning has been modified due to human activities, especially the biodiversity, which has provoked alterations of interactions among species. Currently the scientific community has recognized a biodiversity crisis because of human activities, which could affect negatively to human wellbeing by means of losing ecosystems and its components. All those benefits that people obtain from ecosystems are ecosystem services (ES), as for example food, tools, maintenance of habitats or even cultural aspects.

Historically, our species has been linked to many species and among them ungulates deserve a chapter of their own. Ungulates are animal species closely related with human societies. Relations between humans and wild ungulates vary depending of the context. In developing countries ungulate populations are declining whereas in developed countries they are increasing in abundance and distribution. This rewilding process has contributed to the rise negative interactions between humans and between wild ungulates, as for example agriculture or silviculture damage. To avoid or mitigate these conflicts people use different management tools such as fencing or supplementary feeding. So, research about ungulates and their relations with people should be done from a social-ecological perspective.

This thesis focuses on the human-ungulate relations, both positive and negative interactions, and the evaluation of management tools employed to mitigate those negative impacts. Specifically this thesis aims to assess: i) the state of the art of research in human-ungulates relations (Chapter 1); ii) the services and disservices provided by wild ungulates for two stakeholders: scientists and shepherds (Chapter 2); the niche overlap and potential competition between the native Iberian ibex (*Capra pyrenaica*) and the exotic aoudad (*Ammotragus lervia*) as a paradigm of conservation conflict (Chapter 3); the effects of supplementary feeding effects on the target species

(aoudad), other non-target species and soil properties (Chapters 4 and 5). Finally, in Chapter 6, the results of previous chapters are discussed.

First (Chapter 1), we reviewed scientific publications to establish the state of the art about human-ungulate relations. We showed that most scientific publications approach this relations from the perspective of conflicts, being the ES less considered in that studies. Also, most of the publications included environmental managers and hunters as the main social actors regarding human-ungulate relations. Moreover, management tools employed to mitigate ungulate damages to human interests rarely were evaluated, and lethal control and the use of barriers were the main strategies recommended to mitigate or avoid damages.

In Chapter 2, we approached to the human-ungulate interactions from the perspective of researchers and shepherds and the framework of ecosystem services based on the categories of beneficial nature's contributions to people (NCP; Díaz et al., 2018) . We examined and compared scientific research and shepherds' perceptions regarding the provision of NCP by wild ungulates. We reviewed scientific articles of NCP provided by ungulates in Spain and conducted questionnaires regarding NCP to shepherds in farming systems of Spain where domestic and wild ungulates cohabit. Then, we compared whether the scientific priorities match with those perceived by shepherds. Both stakeholders highlighted more detrimental than beneficial NCP, there were some mismatches between scientific priorities and shepherds' perceptions. Regarding detrimental NCP, soil alteration, damage to silviculture, human safety, traffic collision and human-human conflicts were frequently studied but not mentioned by shepherds. In contrast, shepherds mainly considered vegetation damage, grazing competence, damage to animals with economic interests, crop damage and disease transmission to livestock as important detrimental NCP. Concerning beneficial NCP, whilst hunting was prominent in the publications, shepherds did not conceived it as an important beneficial contribution and considered the regulation of other organisms as an important benefit. These results can have twofold implications. The emphasis on detrimental NCP can reinforce the idea that ungulates can threaten humans rather than contribute to societies' wellbeing. The fact that research does not address the interests of shepherds can affect the social tolerance towards ungulates as the damages experienced or perceived by shepherds are not studied. Our results show the relevance of considering local knowledge systems of shepherds, something highlighted by the NCP approach.

Regarding Chapter 3, we evaluated the potential competition between the native Iberian ibex and the exotic aoudad measuring the niche overlap under cohabit conditions in the Iberian Peninsula. To do that, we compared the trophic niche by using the content of stable isotopes δ15N and δ13C in the hair, and the environmental niche by modelling habitat based on fine-scale presence records. Then we assessed both species' co-occurrence to test for spatial segregation. Our results indicated that both species shared a similar trophic niche, showed a similar distribution of suitable areas and that their environmental niches were similar. Moreover, negative spatial association was found between the aoudad and Iberian ibex. So, both species are ecologically similar and suggest that spatial segregation might have favoured their co-existence in semiarid Mediterranean mountains where they cohabit.

In order to clarify the effect of diversionary feeding (i.e. specific use of supplementary feeding to avoid crop damage), in Chapter 4 we evaluated its effect in the spatial behaviour of the aoudad. Also, we assessed the use of the diversionary feeding stations (DFS) by non-target species. Nine aoudads were tracked with GPS/GSM collars to establish their home ranges and the visits to the DFS. We compared the home ranges and the number of GPS locations in the DFS before and meanwhile food was available at them. Moreover, eight DFS were monitored with camera traps to identify which other species used the DFS. We found that home ranges varied for some individuals and that not all the tracked animals used the DFS. The number of locations in the DFS increased when food was available. Furthermore, other fifteen non-target species of birds and mammals used DFS, especially the wild boar. Aoudads and wild boars segregated temporally in their use of the DFS. These results suggest that diversionary feeding had little effect on the spatial behaviour of the aoudad and benefited other conflictive species.

Continuing with the diversionary feeding as a management tool, we evaluated the effect of this tool on semiarid Mediterranean mountain soils, because physicochemical and biological soil properties can be altered due to the concentration of wildlife in areas where food is deposited (Chapter 5). We collected soil samples from three DFS and compared soil characteristics from three areas: feeding stations (FS), contour area (C; surrounding the feeding stations) and a reference soil (RS; not influenced by feeding stations). Our results suggested no effects on soil physical properties. However, we found that diversionary feeding altered electrical conductivity, nutrient concentration, microbial activity and microbial communities at FS, but effects were weaker in the C. Soil functionality could change due to these alterations of soil dynamics.

Finally, Chapter 6 discusses the results presented in this thesis, the limitations of each chapter and the biodiversity conservation implications and future perspectives about wild ungulates and human relations.

Resumen

RESUMEN

El funcionamiento de los ecosistemas incluye todos aquellos ciclos de materia y energía, así como la interacción entre los organismos. El funcionamiento natural ha sido alterado por las actividades humanas, especialmente la biodiversidad, provocando la modificación de las interacciones entre las distintas especies. Actualmente, la comunidad científica ha reconocido una crisis de biodiversidad por causas antropogénicas asociada a la extinción de especies o la introducción de especies exóticas. Esta pérdida de biodiversidad puede desembocar en efectos negativos sobre el bienestar humano, ya que dicho bienestar está asociado con los ecosistemas y sus componentes (las sociedades obtienen beneficios de los ecosistemas). Todos aquellos beneficios que los humanos obtienen de los ecosistemas son servicios ecosistémicos, como por ejemplo alimentos, herramientas, el mantenimiento de hábitats o incluso aspectos culturales relacionados. Uno de los grupos taxonómicos más relacionado con los humanos es el de los ungulados.

Sin embargo, las relaciones entre los humanos y los ungulados silvestres dependen del contexto. En los países en vías de desarrollo las poblaciones de ungulados silvestres están en descenso, mientras que en los países desarrollados sus poblaciones están creciendo tanto en abundancia como en distribución. Este proceso, denominado “rewilding” en inglés y que podríamos traducir como reconstrucción de los ecosistemas, ha favorecido la aparición de interacciones negativas entre los humanos y los ungulados silvestres, como por ejemplo los daños a la agricultura y a la silvicultura. Para evitar o mitigar estos conflictos se emplean distintas herramientas de gestión como el vallado o los aportes suplementarios. Por lo tanto, la investigación sobre los ungulados y su relación con las personas debe abordarse desde una perspectiva socio-ecológica.

Esta tesis se centra en las relaciones entre las personas y los ungulados silvestres, tanto en las interacciones positivas como negativas, y las herramientas de gestión empleadas para la mitigación de los conflictos. Concretamente esta tesis pretende

evaluar: i) el estado del arte de la investigación sobre las interacciones humano-ungulados (Capítulo 1); ii) los beneficios y perjuicios que proveen los ungulados silvestres para dos agentes implicados: la comunidad científica y los pastores (Capítulo 2); iii) el solapamiento de nicho entre la cabra montesa (*Capra pyrenaica*), especie nativa, y el arrui (*Ammotragus lervia*), especie exótica en la península ibérica, como ejemplo de un conflicto de conservación (Capítulo 3); iv) los efectos de los aportes suplementarios como herramienta de gestión sobre la especie objeto de la gestión (el arrui), otras especies no objetivo y las alteraciones en las propiedades edáficas (Capítulos 4 y 5). En el Capítulo 6 discutimos los resultados obtenidos en los capítulos anteriores.

Para establecer el estado del arte con respecto a las interacciones que se dan entre los humanos y los ungulados silvestres, revisamos las publicaciones científicas sobre este tema. Este capítulo mostró que los artículos científicos abordan los estudios, principalmente, desde la perspectiva de los conflictos, teniendo en poca consideración los servicios ecosistémicos. En general, la mayoría de las publicaciones tienen en consideración a agentes implicados, siendo los principales actores sociales relacionados con los ungulados silvestres los gestores ambientales y los cazadores. Además, las herramientas de gestión empleadas para la mitigación de los conflictos no suelen ser evaluadas, aun siendo recomendadas algunas de ellas como el control letal y el uso de barreras y elementos disuasorios.

En el Capítulo 2 abordamos las interacciones entre humanos y ungulados silvestres desde la perspectiva del nuevo término “Contribuciones de la Naturaleza para las Personas” (NCP por sus siglas en inglés) de dos de los agentes implicados menos considerados en las publicaciones científicas, es decir, los propios investigadores y los pastores. En este trabajo examinamos y comparamos las prioridades científicas a partir de los estudios publicados y las percepciones de los pastores respecto a los NCP proporcionados por los ungulados silvestres. Revisamos artículos científicos sobre los NCP proporcionados por los ungulados en España y realizamos entrevistas en profundidad a pastores en sistemas ganaderos extensivos donde los ungulados domésticos coexisten con los silvestres. Después comparamos si las prioridades científicas coinciden con lo percibido por los pastores. Ambos agentes implicados destacaron más los NCP negativos que los positivos, aunque éstos no coincidían en importancia. Respecto a los NCP negativos, los pastores no mencionaron la alteración del suelo, los daños a la silvicultura, a la salud humana, las colisiones de tráfico y los conflictos entre colectivos humanos. Consideraron como principales aspectos negativos de los ungulados los daños a la vegetación, la competencia por el pasto, los daños a otros animales de interés económico, los daños agrícolas y la transmisión de enfermedades. Por otro lado, mientras que en las publicaciones la caza deportiva adquiría gran importancia como NCP positivo, los pastores ni siquiera la tuvieron en cuenta, siendo para éstos agentes implicados la regulación de otros organismos el beneficio más importante. Estos resultados pueden tener dos implicaciones. Un mayor énfasis en los NCP negativos puede reforzar la idea de que los ungulados pueden suponer una amenaza para las personas en lugar de contribuir positivamente al bienestar social. El hecho de que las investigaciones no coincidan con los intereses de los pastores puede afectar a la tolerancia social hacia estas especies ya que los daños experimentados o percibidos no son evaluados. Nuestros resultados muestran la relevancia que supone considerar el conocimiento local, en este caso de los pastores, que es uno de los aspectos destacados por el enfoque que hemos tomado, es decir, desde los NCP.

Con respecto al Capítulo 3, evaluamos la competencia potencial entre la cabra montés nativa y el arrui exótico estableciendo el solapamiento del nicho en condiciones de coexistencia en la península ibérica. Para ello comparamos el nicho trófico midiendo el contenido de isótopos estables de δ15N y δ13C en pelo, así como el nicho ambiental a partir de modelos de nicho basados en datos de presencia a escala fina. Después evaluamos si ambas especies coocurren espacialmente, o existe segregación espacial como mecanismo de facilitación de coexistencia. Nuestros resultados apuntaron a que ambas especies comparten un nicho trófico y un nicho ambiental similares. Encontramos una asociación espacial negativa entre la cabra montesa y el arrui. Por tanto, las especies son ecológicamente similares y es posible que la segregación espacial detectada favorezca la coexistencia entre ambas en las sierras mediterráneas que cohabitan.

Para conocer los efectos de los aportes suplementarios para evitar daños agrícolas, en el Capítulo 4 evaluamos sus efectos en el comportamiento espacial del arrui, así como el uso de los comederos por parte de especies no objetivo de esos aportes. Para ello marcamos nueve arruis con collares GPS/GSM para establecer sus áreas de campeo sin aportes y con aportes, y lo mismo para el número de visitas a los comederos. Después comparamos ese área de campeo estimada y el número de visitas entre periodos para comprobar si hubo variaciones debidas a los aportes. Además, monitoreamos con cámaras de fototrampeo ocho los comederos para identificar que otras especies podían estar haciendo uso de los comederos. Obtuvimos que las áreas de campeo cambiaron para algunos individuos marcados, aunque no todos acudieron a los comederos durante los aportes. El número de visitas a los comederos se incrementó durante los aportes suplementarios. Identificamos a quince especies no objetivo que acudían a los comederos, especialmente el jabalí. Los arruis y los jabalíes mostraron una segregación temporal en cuanto al uso de los comederos. Nuestros resultados sugieren que la efectividad de los aportes suplementarios es limitada en cuanto al comportamiento espacial del arrui, por lo que la reducción de daños agrícolas es limitada.

Continuando con los aportes suplementarios como herramienta de gestión evaluada, en el Capítulo 5, evaluamos los efectos de esta herramienta sobre el suelo de un área montañosa de clima mediterráneo. Evaluamos este aspecto porque las propiedades fisicoquímicas y biológicas del suelo pueden verse alteradas debido a la concentración de la fauna silvestre donde se deposita la comida suplementaria. Para ello tomamos muestras de suelo de tres comederos y comparamos las características del suelo entre tres áreas: suelo de los comederos, suelo de alrededor de los comederos, y un suelo de referencia no alterado por los comederos. Nuestros resultados sugirieron que las propiedades físicas del suelo no se veían afectadas en los comederos. Sin embargo, la conductividad eléctrica, la concentración de nutrientes, la actividad microbiana y las comunidades microbianas en los comederos sí se alteraron debido a los aportes y la concentración de fauna, siendo los efectos alrededor de los comederos más débiles. La dinámica edáfica pudo verse modificada debido a estas alteraciones detectadas y contribuir al cambio global.

Finalmente, en el Capítulo 6 discutimos los resultados obtenidos en los capítulos previos, abordando también las limitaciones de cada uno, las implicaciones para la conservación de la biodiversidad y las perspectivas futuras sobre la relación entre los ungulados silvestres y los humanos.

Summary of materials and methods

Resumen global de los materiales y métodos

SUMMARY OF MATERIALS AND METHODS

In the general introduction of this thesis (Chapter 1), we searched in the Scopus database scientific articles published in English between 2000 and 2016 on human-ungulate relations and we systematically reviewed them. We used different terms related to 'conflict', 'ecosystem service', 'human-herbivore relation' and 'ungulate'. We exclude book chapters, conferences papers, reviews and theoretical papers. These papers analyzed either human-ungulates conflicts or ecosystem services provided by wild ungulates. We extracted of each publication its general information, category of conflicts and ecosystem services, stakeholders, and management tools suggested or mentioned by authors.

In Chapter 2, we addressed human-ungulate relations in Spain from the perspective of two stakeholders: scientists and shepherds. First, we reviewed scientific articles of human-ungulates relations, both positive and negative. For this we used terms such as 'conflict', 'ecosystem service', 'human-herbivore relation' and 'ungulate' in the Scopus database. We selected scientific articles published between 2000 and 2018, and we extracted negative and positive "Nature Contributions to People" (NCP) mentioned. Second, to assess the perceptions of the shepherds, we conducted 184 face-to-face questionnaires to them in extensive livestock farming systems in Spain. We extracted shepherds' perception of NCP provided by wild ungulates. Moreover, we built the variable NCP Provider index, which indicates the average shepherd perceptions of wild ungulates as providers of positive NCP for each species using a scale from very harmful to very beneficial. We carried out non-parametric tests to determine differences in the NCP Provider index between different species and to explore differences due to ecological factors as such as the diet, the origin and the presence of large predators. Finally, we compared with a correlation test whether the scientific priorities matched with the shepherds' perceptions.

In Chapter 3 we compared the niche overlap of the native Iberian ibex and the exotic aoudad to evaluate potential competition between them at three levels: trophic niche, environmental niche and spatial segregation. First, we compared the diet by the degree of isotopic niche overlap between species analysing the δ15N and δ13C values of hair samples from individuals of both species in the Region of Murcia. Second, we generated environmental niche models for each species in the mountains where they coexist. Third, we compared the similarity of the environmental niche models. Finally, we checked if they co-occurred spatially on 200 x 200m grid fine-scale.

In the Chapter 4, we evaluated the effect of diversionary feeding to avoid crop damage in the spatial behaviour of the exotic aoudad in the Sierra Espuña regional park in southeast Spain. Moreover, we also evaluated if other non-target species used this food contributions and co-occurred with the aoudad. We tracked nine aoudads with GPS/GSM collars during a period without diversionary feeding inputs and other period with inputs. This allowed us to estimate the home range and the number of visits to the diversionary feeding stations (DFS) of the tracked aoudads for both periods. We used non-parametric test to compare home ranges between periods, and we fitted a model to evaluate if animals increased the visits to the DFS between periods. To assess if non-target species used the DFS we monitored with automatic cameras eight of them during the period with food inputs. We calculated if ungulate species using the DFS co-occurred both temporally and spatially.

In the Chapter 5, we evaluated the physical, chemical and biological effects on soil due to the use of diversionary feeding in the Sierra Espuña regional park in southeast Spain. We took soil samples from the centre of three feeding stations (FS), its contour (C) and from another area outside of the DFS influence as a reference soil (RS). We determined in the lab the main physical, chemical, biochemical and biological properties of soil samples. Then we fitted a model to test whether soil properties differed among the sampled areas (FS, C and RS).

Summary of results

Resumen global de los resultados

SUMMARY OF RESULTS

In the general introduction we found that the largest proportion of publications about conflicts and ecosystem services related with wild ungulates were in Europe and North America. Papers were focused mainly on conflicts related with production damage as crops or livestock. Among ecosystem services highlighted the recreational hunting. Regarding stakeholders, the most considered in articles about human-ungulate relations were environmental managers, hunters and farmers. The most management tools considered and recommended in scientific publications were lethal control of ungulates and the use of deterrents and barriers to avoid problems with human activities.

In Chapter 2 we found that research on NCP provided by ungulates in Spain is linearly increasing, mainly focused on conflicts. Species that received higher scientific attention were several deer species and the wild boar. Negative NCP that received higher attention were vegetation, crop and silvicultural damage. The positive NCP that received the highest scientific attention belonged to the category of non-material contributions (e.g. hunting). Regarding the shepherds, they perceived ungulates as harmful. Main negative NCP identified by shepherds were grazing competence, disease transmission to livestock and crop damage. Among positive NCP, shepherds mostly mentioned the aesthetic value and the scavenging service provided by the wild boar. The average shepherds' perception of wild ungulates as providers of NCP (NCPP index) varied according to the diet and to the presence of large carnivores in the study area. Scientific priorities and shepherds' perceptions were not correlated.

In Chapter 3, we determined the isotopic values of the Iberian ibex and the aoudad and they did not differ. The environmental niche overlap between the species was 0.71, from a range from 0 to 1. We found that our study species were more similar than expected regarding the occupied habitat. The spatial co-occurrence analysis showed a negative association between the Iberian ibex and the aoudad at fine scale.

In Chapter 4 we found that five out of the nine tracked individuals used DFS during diversionary feeding inputs. We did not find differences in the home range size between periods. The model we did showed that the frequency of use of the DFS increased during the period with diversionary feeding. Regarding the use of DFS by wildlife, we detected fifteen non-target species, among which the wild boar highlighted. The temporal co-occurrence analysis showed a negative significant association between the aoudad and the wild boar.

In Chapter 5 we found no differences for the soil physical properties among FS, C and RS areas. However, for the chemical and biochemical properties the results showed that varied between areas, but not for all properties. Biological variables also showed differences between areas. Fungi, Bacteria and Actinobacteria biomass varied among sampled areas.

Chapter 1

General Introduction

BACKGROUND

Ecosystem functioning includes all cycling materials and energy, the interactions among organisms and the abiotic system (Simpson and Christensen 2012). All these biogeochemical and ecological processes interact with each other and they regulate the ecosystems. An important compartment in the functioning of the ecosystems is biodiversity, which encompasses from intra-specific genetic variation to biome distribution on the planet (see Hooper et al. 2005). Biodiversity can buffer process rates in response to environmental variation and it contributes to the stability and the functioning of ecosystem processes (Bardgett and van der Putten 2014; Díaz and Cabido 2001). Therefore, biodiversity is known to be closely linked to ecosystem function (Schwartz et al. 2000) and its alteration could have important ecological consequences (see Loreau et al. 2001). Human activities (e.g. habitat transformation or species introduction) have largely altered biodiversity (Mooney et al. 2009) and therefore modified the natural functioning of the ecosystems at the global and local scales (MEA 2005). Biodiversity alteration entails the modification of the biotic structure and composition of ecological communities due to the introduction of exotic species, or the decline or even extinction of native species. In fact, it has been recognized a global biodiversity crisis caused by anthropogenic impacts especially during the second half of the twentieth century, which could be a threat to human wellbeing (Johnson et al. 2017).

Human wellbeing has been related to biodiversity and its role in ecosystem functioning (Balvanera et al. 2006), as societies may benefit from biodiversity. For example, carrion consumption by scavenger communities benefits extensive farmers because they efficiently remove carcasses from the field (Morales-Reyes et al. 2017). All those benefits that people obtain from ecosystems are called ecosystem services, hereafter ES (Díaz et al. 2015). There are three types of ES: provisioning, cultural and regulating services. For example, people have benefited from biodiversity to survive throughout history, especially from vertebrate animals (Alves 2012).

Ungulate taxa stand out as species traditionally important for humans since they provide with three types of ecosystem services described above. Wild ungulates provide people with food and materials, such as bushmeat and leather, and some species are linked with cultural aspects of several societies (see Alves 2012). Moreover, ungulates are key species on many ecosystems, for example by conditioning nutrient cycles and influencing forest dynamics (Danell et al. 2006). They are globally distributed throughout Africa, America, Asia and Europe (without considering those introduced species in other continents such as Australia). Moreover, they are a diverse group of mammals typically herbivorous and they inhabit a wide range of different habitats, including forests, steppes, mountains and even rivers. Perissodactyla (odd-toed) and Artiodactyla (even-toed; Photo 1) orders are the classic groups considered as true ungulates. Currently, the ungulate term also includes other mammalian orders, which present hooves, or at least it was present in their ancestors (i.e. Tubulidentata (aardvark), Hyracoidea (hyraxes), Proboscidea (elephants), Pholidota (pangolins) and Sirenia (manatees; Wilson and Mittermeier 2011; Wilson and Mittermeier 2014)).

The Perissodactyla order includes three families (equidae, rhinocerotidae and tapiridae) with a total of 16 species: The Artiodactyla order is represented by ten families (camelidae, suidae, tayassuidae, hippopotamidae, tragulidae, moschidae, cervidae, bovidae, antilocapridae and giraffidae) and it includes 380 different species (Fennessy et al. 2016; Wilson and Mittermeier 2011; Table 1).

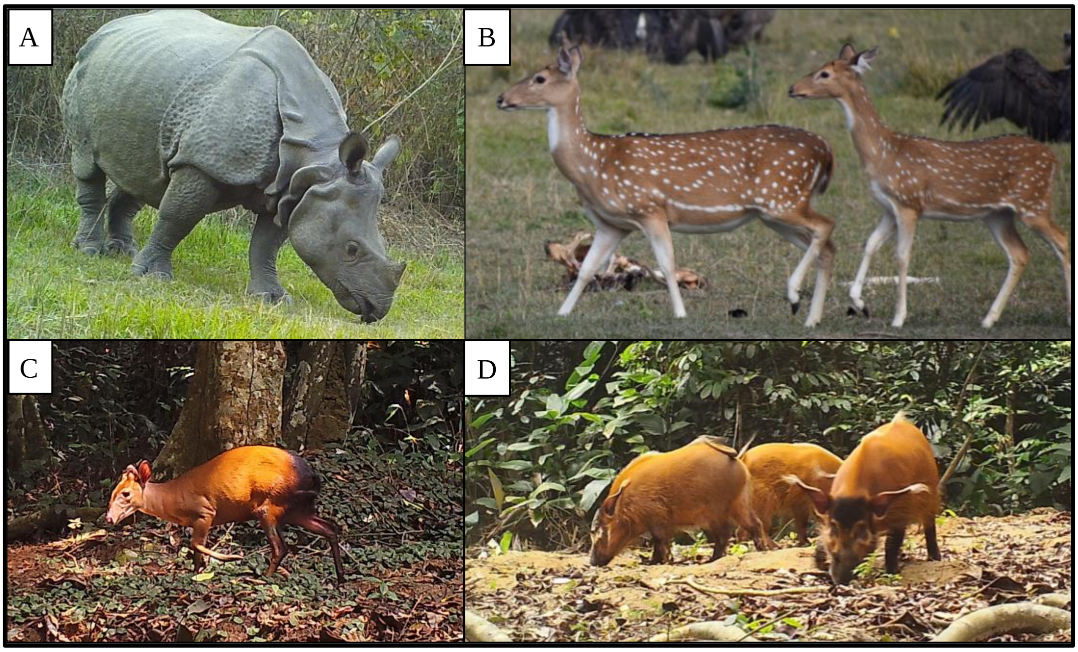

Photo 1. Examples species of Perissodactyla (A; rhino *Rhinoceros unicornis*) and Artiodactyla (B; chital *Axis axis*; C; Peters' duiker *Cephalophus callipygus*; D; red river hog *Potamochoerus porcus*) orders. A and B facilitated by Aishwarya Bhattacharjee, done during her fieldwork in Nepal. C and D facilitated by Lara Naves, done during her fieldwork in Republic of the Congo with ARC-SPAC organization.

Table 1. Families, number of species and global distribution of Perissodactyla and Artiodactyla orders. According to Fennessy et al. 2016, and Wilson and Mittermeier 2011.

Order	Family	Number of species	Distribution
Perissodactyla	*Equidae*	7	Africa; Asia
	Rhinocerotidae	5	Africa; Asia
	Tapiridae	4	America; Asia
Artiodactyla	*Camelidae*	3	America; Asia
	Suidae	17	Africa; Asia; Europe
	Tayassuidae	3	America
	Hippopotamidae	2	Africa
	Tragulidae	10	Africa; Asia
	Moschidae	7	Asia
	Cervidae	53	Africa; America; Asia; Europe
	Bovidae	279	Africa; America; Asia; Europe
	Antilocapridae	1	America
	Giraffidae	5	Africa

Modern interactions of humans with wild ungulates vary throughout the world depending on the species and the human societies. In many countries of Africa and Asia, wild ungulate populations are declining because of changes in land use and direct persecution, to the point that conservation measures are needed (Havemann et al. 2016; Ghoddousi et al. 2017). For example, the Sahara´s region (the largest hot desert located in North Africa) has experienced a great loss of megafauna since the second half of the twentieth century (Durant et al. 2014), favoured by the arrival of modern firearms and motorized vehicles (Valverde 2004). Nowadays, the exploitation of natural resources and poaching continues to be problem for the biodiversity and conservation of Sahara's wildlife (Duncan et al. 2014).

Paradoxically, in developed countries of Europe and North America, the trend of ungulate populations is the opposite, as they have increased in abundance and distribution during the last decades. This rewilding process (passive management of ecological succession) has benefited from the removal of predators, the introduction of exotic ungulate species, and the reduction of rural activities such as farming or hunting, increasing available habitat for wild ungulates (Apollonio et al. 2010; Navarro and Pereira 2015). Moreover, rewilding in developed countries has increased the amount of impacts (i.e. direct negative interactions between humans and other species; Redpath et al. 2013) between wild ungulates and human activities, as for example damage to agriculture and forestry (Dunkley and Cattet 2003; Gundersen et al. 2004).

Different management tools have been used to avoid or mitigate these emerging conflicts with wild ungulates, particularly in developed countries. For example, increasing hunting pressure, fencing or supplementary feeding (Photo 2) are popular management tools designed to alleviate conflicts related to wild ungulates. However, these management tools often do not help to solve the problems associated with wild ungulates because their populations continue to grow and affect human activities (Apollonio et al 2010). These strategies could present negative effects on wild populations, such as changes in population and community dynamics, disease transmission, alteration of natural behaviour or even condition their evolutionary potential (Dunkley and Cattet 2003; Geisser and Reyer 2004; Hayward and Kerley 2009).

Therefore, it exists a link between people and ungulates. Due to this, several authors have suggested decision-making processes, the establishment of management tools, conservation strategies and research about these species from a social-ecological perspective (e.g. Dressel et al. 2018; Lischka et al. 2018).

Photo 2. Aoudads (*Ammotragus lervia*) on a diversionary feeding station to mitigate damage in the surrounding crops.

STATE OF THE ART: A REVIEW OF HUMAN-UNGULATE RELATIONS

Applying social-ecological approaches in the research on human-ungulate relations would allow to identify current knowledge gaps regarding conflicts and ES perceived by stakeholders. Besides, it contributes to progress in the use and the efficiency of management tools. Moreover, it would provide relevant information for the future research agenda. In order to summarize and appraise the existing publications on human-ungulate relations in the scientific literature, we have reviewed related papers.

We systematically reviewed articles published between 2000 and 2016. We followed the guidelines of systematic reviews (Pullin and Knight 2009), which is a strict protocol to guarantee transparency and minimize the sources of bias. We searched in the Scopus database by using different terms related to ‘conflict’, ‘ecosystem service’, ‘human-herbivore relation’ and ‘ungulate’ (see Appendix S1.1 for the full search string). The search was made to title, abstract and keywords. We found 400 articles (excluding book chapters, reviews, theoretical papers and conferences papers; see appendix S.1.2) published in English and they analyzed either human-ungulates impacts and conflicts or ES provided by wild ungulates.

We coded each publication according to its general description (i.e., year of publication, journal and the ungulate species); category of conflicts; category of ES; stakeholders; and type of management strategy suggested or mentioned by authors (modified from Inskip and Zimmerman, 2009). The classification of conflicts was adapted from Peterson et al. (2010), but we included new conflicts that were derived from the literature review (Table 2). ES were categorized according to MEA (2005) and Haines-Young and Potschin (2018) classification, including regulating, provision and cultural ecosystem services (Table 3). Stakeholders and management tools identified can be found in Table S.1.1 and S.1.2, respectively.

Table 2. Conflicts related with wild ungulates extracted from the literature review. Adapted from Peterson et al. (2010).

Conflicts		Description
Damage to biodiversity	*Vegetation damage*	Negative effects on vegetation, including rooting (i.e., foraging activity within surface layers of soil)
	Animal biodiversity damage	Negative effects on wild animal species without direct economic interest, such as livestock or game species
Damage to production	*Grazing competence*	Wild ungulates consume pasture and other natural resources that could be used by livestock. For example, the European bison (*Bison bonasus*) competes directly with livestock (Kuemmerle *et al.* 2011)
	Disease	Risk of illness transmission from wild ungulates to livestock
	Physical damage to livestock	Direct physical damage caused by ungulates to livestock.
	Silvicultural damage	Impairment of natural forests or plantations intended for forestry
	Crop damage	Direct physical impairment of croplands and orchards
	Physical damage game species	Direct physical damage caused by ungulates to game species. For example, the wild boar as main nest predator of the common pheasant (*Phasianus colchicus*) (Senserini and Santilli 2016)
Damage to human	*Attacks*	Ungulates causing physical injuries to humans (Peterson *et al.* 2010)
	Damage to human health	Ungulates transmitting infections agents to humans (Peterson *et al.* 2010)
Material damage	*Property damage*	Ungulates damaging human properties, particularly buildings and / or physical structures, such as fences (Peterson *et al.* 2010)
	Traffic collisions	Ungulates damaging vehicles by ungulate-vehicle collision and / or causing traffic accidents (Peterson *et al.* 2010)
Human-human conflict		Conflict related to human disagreements over management decisions of wild ungulates or derived from different opinions and interests by different stakeholders (adapted from Peterson *et al.* 2010)

Table 3. ES provided by wild ungulates extracted from the literature review. Classification adapted from MEA (2005) and Haines-Young and Potschin (2018).

Ecosystem services		Description
Regulating	*Habitat maintenance*	Ungulates contribute to maintenance of habitats or positive for species important to humans. For example, grazing can contribute to maintain semi-open habitats (Vera 2000).
	Seed dispersion	Facilitation by ungulates of seed dispersion of species important to humans. For example, grass or small herbs species via the coat, hoof or feces (Gill and Beardall 2001)
	Maintenance of soils	Maintenance of soil structure (e.g. aeration; Swanepoel et al. 2016).
	Regulation of organisms	Removal of animal carcasses by wild boars, i.e., acting as a scavenger (Morales-Reyes et al. 2017) and / or reduction of attacks on livestock due to the presence of alternative prey (Sidorovich et al. 2003).
Provisioning	*Food resource*	Food production from wild ungulates, such as meat from red deer (Milner et al. 2006)
	Materials	Material production derived from wild ungulates, clothing or ornamental purposes (e.g. skin, horns, antlers).
	Medicinal resources	Materials derived from ungulates used for medicinal, veterinary or pharmacological purposes.
Cultural	*Educational and inspiration*	Opportunities for the development of the capabilities that allow humans to prosper through education, acquisition of knowledge and development of skills for well-being, information, and inspiration for art and technological design.
	Maintenance of options	Ungulates with capacity to keep human options open in order to support a later good quality of life.
	Existence value	Satisfaction for the existence of a particular ungulate species (e.g. García-Llorente et al. 2012).
	Recreation	Experiences provided by wild ungulates for human related with leisure, such as recreational hunting (Gamborg and Jensen 2017), or enjoy the aesthetic value derived from ungulate species (de Pinho et al. 2014)

Temporal and geographical distribution

Number of published studies were increasing since 2000 (Figure 1A). The largest proportion of research was performed in Europe (39.3%) and North America (34.3%). By contrast, Asia (14.8%), Africa (6.8%), Central and South America (3.5%) and Oceania (1.5%) received less scientific attention than the aforementioned regions (Figure 1B). It is striking the fact that just 6.8% of the publications were in African study areas, the continent with the highest number of ungulate species (n=204 according to Wilson and Mittermeier 2011). However, North America and Europe, with 12 and 14 different ungulates species, respectively, represented the 73.6% of publications about conflicts and ES related with ungulates.

Furthermore, just 8% of publications addressed some exotic species, despite the fact that the introduction of species is the second cause of biodiversity loss (Wilcove et al. 1998) and other alterations of ecosystem processes (Raizada et al. 2008). The study species of these publications belong to the most studied families of ungulates, such as the red deer, the cheetah deer (*Axis axis*), the wild boar, or the aoudad (*Ammotragus lervia*) introduced in different parts of the world out of their native range.

Conflicts and ES related with wild ungulates

Research publications were mainly focused only on conflicts (55.8%) and those dealing with both conflicts and ES (40.7%). Articles that only mentioned ES represented 3.5% of publications (Figure 2).

Regarding conflicts mentioned by scientific publications (n=386), 65.0% of articles referred to production damage, such as crop damage, silvicultural damage and diseases transmission to domestic animals; 36.3% mentioned biodiversity damage conflicts, mainly about vegetation biodiversity damage; 18.9% referred to material damage, such as traffic collisions and property damage. The rest of the conflicts (i.e. damage to humans, human-human conflicts and others) were cited in less than 10% of the publications.

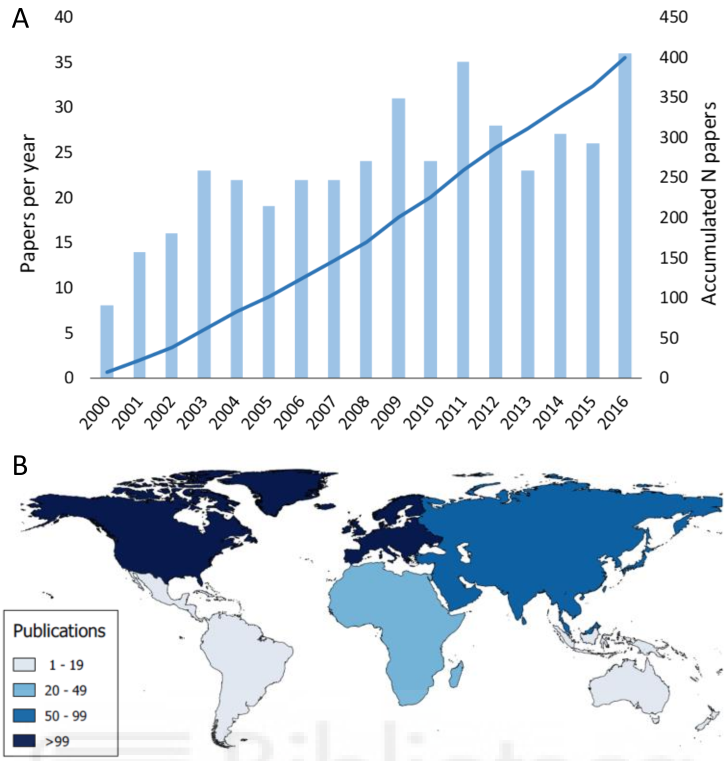

Figure 1. (A) Number of publications per year and accumulated number of publications. (B) World map showing the number of publications about human-ungulate relations per country between 2000 and 2016 (total n=400).

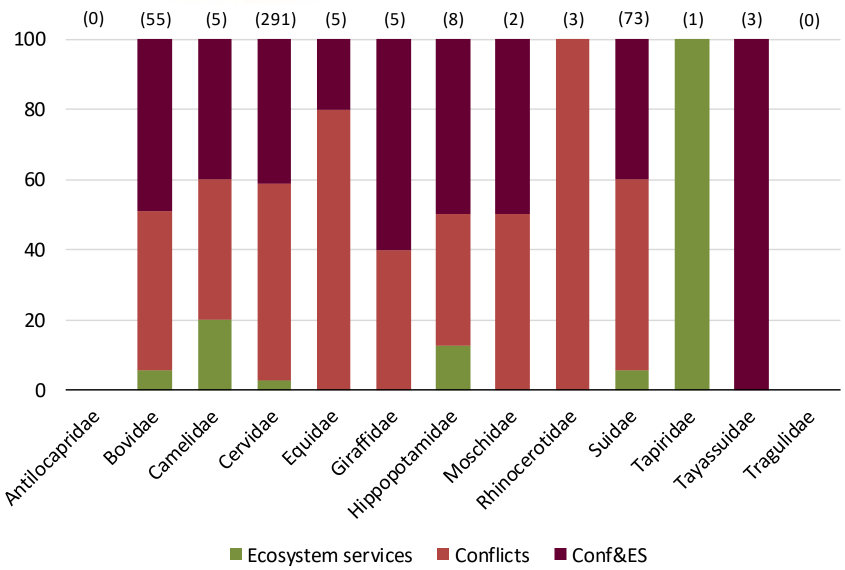

Figure 2. Global descriptive analysis of reviewed publications (%) according to their content in terms of ES and conflicts per family. Numbers in brackets indicate the number of publications of each family.

Amongst publications that mentioned ES (n=177), 80.2% referred to cultural ES, such as physical extractive experiences (e.g., recreational hunting); followed by provisioning ES (23.2%), such as food resource, and regulating ES (20.3%), such as habitat creation and maintenance (Table S.1.3).

Stakeholders

Most of the published articles about human-ungulate relations considered stakeholders in the studies (67.3%). The most frequent social actors considered were environmental managers (40.2% of publications that mentioned stakeholders), followed by hunters (38.7%) and farmers (37.2%), other stakeholders (e.g. authorities, researchers or drivers; 27.1%), foresters (22.3%), rural (12.6%) and urban residents (10.0%). Others social actors involved were cited in less than 10% of publications, as shepherds, general public, conservationist agencies, indigenous communities and tourists (Table 4). It is also remarkable that 62.8% of publications that mentioned stakeholders did it considering more than just one stakeholders.

Table 4. Scientific publications where stakeholders were mentioned or participated in the study. Percentage in brackets (%).

Stakeholder mentioned	Publications
Environmental managers	108 (40.1)
Hunters	104 (38.7)
Farmers	100 (37.2)
Others	73 (27.1)
Foresters	60 (22.3)
Rural residents	34 (12.6)
Urban residents	27 (10.0)
Shepherds/herders	24 (8.9)
General public	24 (8.9)
NGO/conservationists	19 (7.1)
Indigenous com.	12 (4.5)
Tourists	7 (2.6)

Management actions

We found that in the 61.5% of scientific publications mentioned some management strategy, and 59.5% of articles recommended at least one of them but only in 21.8% some were evaluated.

Among management tools considered in the scientific publications (n=246) the most mentioned were lethal control (43.1% of publications) and deterrents and barriers (e.g. fencing; 37.0%), followed by regulate local hunting (22.0%), others (e.g. measures on roads, predators; 17.9%) and economic compensations (11.4%; Table 5). Among others, supplementary feeding, zoning, aversive conditioning, co-management, education and awareness raising, translocation of animals, or livestock/crops guarding were mentioned in less than 10%.

Regarding management tools recommended in the scientific literature (n=238) to face and mitigate human-ungulate conflicts they are referred to lethal control (28.2% of publications), deterrents and barriers (25.6%), habitat management strategies (22.3%), others (20.0%), regulate local hunting (16.0%), co-management (13.4%), education and awareness raising (12.6%) and zoning (10.1%; Table 5). Other recommended tools such as supplementary feeding, economic compensation or aversive conditioning, among others, received less scientific attention (less than 10%).

Altogether, this review on human-ungulate relations allowed us to identify current knowledge gaps in this issue. First at all, conflicts predominate over ES in the scientific literature about human-ungulate relations, which is according with previous studies about human-wildlife relations (Kansky and Knight 2014). However, this contrasts with the fact that the scientific literature on ES has increased in the last years (Díaz et al. 2015).

Table 5. Management tools mentioned and recommended in the publications reviewed. Percentage in brackets (%).

Management tools	Mentioned publications	Recommended publications
Lethal control	106 (43.1)	67 (28.2)
Deterrents and barriers	91 (37.0)	61 (25.6)
Regulate local hunting	54 (22.0)	38 (16.0)
Others	44 (17.9)	49 (20.6)
Economic compensation	28 (11.4)	13 (5.5)
Supplementary feeding	24 (9.8)	14 (5.9)
Habitat management	23 (9.3)	53 (22.3)
Zoning	22 (8.9)	24 (10.1)
Aversive conditioning	19 (7.7)	12 (5.0)
Co-management	15 (6.1)	32 (13.4)
Education and awareness raising	14 (5.7)	30 (12.6)
Translocation	14 (5.7)	7 (2.9)
Livestock/crops guarding	13 (5.3)	8 (3.4)
Payment for ES	5 (2.0)	4 (1.7)
Tourism	5 (2.0)	6 (2.5)

The concept of ES already appeared in studies published in the 80s and 90s (e.g. Pearsall 1984; Cairns 1993), but in 1997 the term is widely implemented and applied mainly by researchers and politicians (see Constanza et al. 2017). Since they appeared, ES have suffered reclassifications from different perspectives. For example, Millennium Ecosystem Assessment (MEA 2005) project gave an ecological perspective, whereas the Economics of Ecosystems and Biodiversity (TEEB 2010) project focused on economic aspects of ES.

Given the constant scientific progress, from the concept of ES, it has been developed the new term Nature Contribution to People (NCP). NCP encompasses all the positive and negative aspects from the functioning of ecosystems to human well-being (Díaz et al. 2018). Moreover, NCP approach recognizes the role of culture in the links between people and nature, and it takes into account indigenous and local knowledge. This new approach has caused discrepancies among scientists related with ecosystem services, and some researchers do not support to apply the new term and its meanings (see Braat 2018; Maes et al. 2018). However, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) have approved and recognised the importance of NCP (IPBES 2017).

Regarding social actors related with human-ungulate relations, the most frequently considered in the published studies were environmental managers, hunters and farmers. The last two are related with the most common conflicts mentioned, thus, farmers are related with damage to production activities (e.g. crops and livestock), and hunters with recreational hunting as cultural ES. Environmental managers are stakeholders that need to find efficient tools and optimal strategies, in our case, for the best ungulate management aimed at mitigation conflicts and potentiation of ES.

The scientific community has recognized that the implication of stakeholders in decision-making process and strategies to manage wildlife is an important factor in driving human-wildlife conflicts (e.g. Dickman 2010; Redpath et al. 2013). Wildlife management requires the application of efficient strategies and tools addressed to species conservation and mitigation of conflicts with human activities. Related with wild ungulates, the most mentioned and recommended management tools were lethal control of ungulate populations and the use of deterrent and barriers (e.g. fences, electric fences or light and loud noises). These management tools have the greatest impact on the environment and in the wild ungulate populations, whereas others, such as education awareness raising or supplementary feeding, appeared in fewer publications. The former tool, however, is increasingly present in studies on the management and conservation of species (see Watkins et al. 2019; Liu and Sharp 2018). Supplementary feeding is also a management tool little mentioned and hardly recommended on scientific publications in our field of study. However, it is a strategy widely employed around the world, mainly by managers, hunters and tourist for recreation and it involves the entry of tons of food into ecosystems (Murray et al. 2016).

AIMS AND STRUCTURE OF THIS THESIS

The general aim of this thesis is to assess human-ungulate relations through conflicts and ES, their management and conservation. To achieve this general objective, these specific aims were proposed:

I. To review the human-ungulate relations in the framework of ecosystem services and conflicts at the global scale.

II. To analyse scientific research and the perception of stakeholders (shepherds) with respect conflicts and ES associated with wild ungulate populations in Spain.

III. To assess conservation conflicts associated with wild ungulate expansion, specifically between native and exotic species.

IV. To evaluate management tools, particularly the use of supplementary feeding, used for conflict mitigation.

This PhD dissertation is structured in five chapters (Table 6) and a General Discussion. We analysed conflicts and ES related with wild ungulates at the global scale (Chapter 1) and at the Spanish national scale (Chapter 2). In these chapters, we used literature review and social methods (surveys) to implicate stakeholders on the research. Chapter 1 (General Introduction) allowed to explore the state of the art in the research about conflicts and ES related with wild ungulates. In the Chapter 2, we compared the most important detriments and benefits considered by two stakeholders (scientific community and shepherds) from the perspective of NCP. The structure of these chapters follow the common sections of a scientific article: abstract, key words, introduction, material and methods, results and discussion. Moreover, it has been included an abstract in Spanish (*Resumen*).

Table 6. Features of each chapter of this PhD dissertation.

Chapter	Objectives addressed	Topics addressed	Methodology	Scale	Location
1	I	Conflicts and ES	Bibliographic review	Global	-
2	I and II	Conflicts and ES	Bibliographic review and surveys	National	Spain
3	III	Conflicts	Empirical	Regional	Murcia (SE Spain)
4	III and IV	Conflicts and Management	Empirical	Local	Sierra Espuña (SE Spain)
5	IV	Management	Empirical	Local	Sierra Espuña (SE Spain)

The other three chapters aim to provide insights on a long-term conservation conflict derived from the introduction of an exotic species in SE Spain (Box 1). We evaluated the potential competition between two ungulates (Chapter 3), one native (Iberian ibex) and other exotic (Aoudad). Then we evaluated the effects of supplementary feeding to avoid crop damage (i.e. diversionary feeding) on the spatial behaviour of the aoudad and the interactions with other non-target species (Chapter 4). We also analysed the effects of diversionary feeding on soil properties (Chapter 5). The structure of these chapters also follow the common sections of a scientific article, as has been describe previously, including each chapter an abstract in Spanish..

In the General Discussion we widely discuss the main results of this PhD dissertation. Finally, we present the conclusions of this research. Additional information can be found at the end of this dissertation in the Appendices section.

Box 1. The paradigmatic case of the aoudad

J.A. Valverde (1926-2003; Photo 3A), was a renowned Spanish biologist that noticed the decline of Saharan biodiversity. He managed to create during the 1960's the Saharan Fauna Rescue Park (currently called Experimental Station of Arid Zones; EEZA by its initials in Spanish http://www.eeza.csic.es) to prevent the extinction of ungulates such as the dama gazelle (*Nanger dama*), the dorcas gazelle (*Gazella dorcas*), the Cuvier`s gazelle (*Gazella cuvieri*), and the Saharan aoudad (*Ammotragus lervia sahariensis*). In the EEZA, these species are bred in captivity for later reintroduction programs. Moreover, another aoudad subspecies (*A. lervia lervia*; Photo 3B) was released in the Mediterranean mountains of SE Spain in 1970's also by Valverde recommendation. The Aoudad introduction in peninsular Spain could be understood as an attempt to save the species out of its African native range (besides the hunting interest; Cassinello 1998, Valverde 2004). It can also be considered as a pioneering project of "assisted colonisation", i.e. the introduction of species out of its natural distribution for conservation purpose (Seddon 2010) driving a paradigmatic conservation conflict.

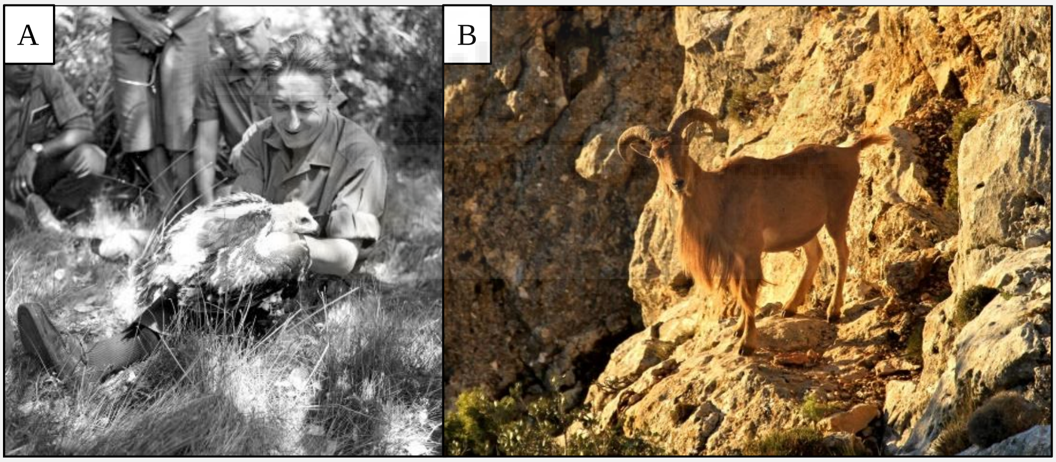

Photo 3. (A) José Antonio Valverde. (B) Aoudad (*A. lervia lervia*) in Sierra Espuña. By Sergio Eguía.

REFERENCES

Alves, R.R.N. 2012. Relationships between fauna and people and the role of ethnozoology in animal conservation. Ethnobiology and Conservation 1: 2.

Apollonio, M., Andersen, R., Putman, R. (Eds.). 2010. European ungulates and their management in the 21st century. Cambridge Univ. Press, Cambridge.

Bardgett, R.D.. van der Putten, W.H. 2014. Belowground biodiversity and ecosystem functioning. Nature 515: 505-511.

Braat, L.C. 2018. Five reasons why the Science publication “Assessing nature’s contributions to people” (Diaz et al. 2018) would not have been accepted in Ecosystem Services. Ecosystem Services 30: A1-A2.

Cassinello, J. 1998. *Ammotragus lervia*: a review on systematics, biology, ecology and distribution. Annales Zoologici Fennici 35: 149-162.

Danell, K., Bergström, R., Duncan, P., & Pastor, J. (Eds.). 2006. Large Herbivore Ecology, Ecosystem Dynamics and Conservation (Conservation Biology). Cambridge: Cambridge University Press.

de Pinho, J.R., Grilo, C., Boone, R.B., Galvin, K.A., Snodgrass, J.G. 2014. Influence of aesthetic appreciation of wildlife species on attitudes towards their conservation in Kenyan agropastoralist communities. PloS ONE 9: e88842.

Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J.R., Arico, S., Báldi, A., Bartuska, A., Baste, I.A., Bilgin, A., Brondizio, Chan, K.M.A., Figueroa, V.E., Duraiappah, A., Fischer, M., Hill, R., Koetz, T., Leadley, P., Lyver, P., Mace, G.M., Martín-López, B., Okumura, M., Pacheco, D., Pascual, U., Pérez, E.S., Reyers, B., Roth, E., Saito, O., Scholes, R.J., Sharma, N., Tallis, H., Thaman, R., Watson, R., Yahara, T., Hamid, Z.A., Akosim, C., Al-Hafedh, Y., Allahverdiyev, R., Amankwah, E., Asah, S.T., Asfaw, Z., Bartus, G., Brooks, A., Caillaux, J., Dalle, G., Darnaedi, D., Driver, A., Erpul, G., Escobar-Eyzaguirre, P., Failler, P., Fouda, A.M.M., Fu, B., Gundimeda, H., Hashimoto, S., Homer, F., Lavorel, S., Lichtenstein, G., Mala, W.A., Mandivenyi, W., Matczak, P., Mbizvo, C., Mehrdadi, M., Metzger, J.P., Mikissa, J.B., Moller, H., Mooney, H.A., Mumby, P., Nagendra, H., Nesshover, C., Oteng-Yeboa, A.A., Pataki, G., Roué, M., Rubis, J., Schultz, M., Smith, P., Sumaila, R., Takeuchi, K., Thomas, S., Verma, M., Yeo-Chang, Y., Zlatanova, D. 2015. The IPBES conceptual framework - connecting nature and people. Current Opinion in Environmental Sustainability 14: 1-16.

Díaz, S., Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16: 646-655.

Dickman, A.J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. Animal Conservation 13: 458-466.

Dressel, S., Ericsson, G., Sandström, C. 2018. Mapping social-ecological systems to understand the challenges underlying wildlife management. Environmental Science and Policy 84: 105-112.

Duncan, C., Kretz, D., Wegmann, M., Rabeil, T., Pettorelli, N. 2014. Oil in the Sahara: mapping anthropogenic threats to Saharan biodiversity from space. Philosophical Transactions of the Royal Society B: Biological Sciences 369: 20130191.

Dunkley, L., Cattet, M.R.L. 2003. A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Canadian Cooperative Wildlife Health Centre: Newsletters and Publications 21: 1-68.

Durant, S.M., Wacher, T., Bashir, S., Woodroffe, R., Ornellas, P., Ransom, C., Newby, J., Abáigar, T., Abdelgadir, M., El Alqamy, H., Baillie, J., Beddiaf, M., Belbachir, F., Belbachir-Bazi, A., Berbash, A. A. Bemadjim, N.E., Beudels-Jamar, R., Boitani, L., Breitenmoser, C., Cano, M., Chardonnet, P., Collen, B., Cornforth, W.A., Cuzin, F., Gerngross, P., Haddane, B., Hadjeloum, M., Jacobson, A., Jebali, A., Lamarque, F., Mallon, D., Minkowski, K., Monfort, S., Ndoassal, B., Niagate, B., Purchase, G., Samaïla, S., Samna, A.K., Sillero-Zubiri, C., Soultan, A.E., Stanley Price, M.R., Pettorelli, N. 2014, Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Diversity & Distributions 20: 114-122.

Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M.A., Vamberger, M., Fritz, U., Janke, A. 2016. Multi-locus analyses reveal four giraffe species instead of one. Current Biology 26: 2543-2549.

Gamborg, C., Jensen, F.S. 2017. Attitudes towards recreational hunting: A quantitative survey of the general public in Denmark. Journal of Outdoor Recreation and Tourism 17: 20-28.

García-Llorente, M., Martín-López, B., Iniesta-Arandia, I., López-Santiago, C.A., Aguilera, P.A., Montes, C. 2012. The role of multi-functionality in social preferences toward semi-arid rural landscapes: an ecosystem service approach. Environmental Science & Policy 19: 136-146.

Geisser, H., Reyer, H.U. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. Journal of Wildlife Management 68: 939-946.

Ghoddousi, A., Soofi, M., Kamidi, A.K., Ashayeri, S., Egli, L., Ghoddousi, S., Speicher, J., Khorozyan, I., Kiabi, B.H., Waltert, M. 2017. The decline of ungulate populations in Iranian protected areas calls for urgent action against poaching. Oryx 1-8.

Gill, R.M.A., Beardall, V. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74: 209-218.

Gundersen, H., Andreassen, H.P., Storaas, T. 2004. Supplemental feeding of migratory moose Alces alces: forest damage at two spatial scales. Wildlife Biology 10: 213-223.

Haines-Young, R., Potschin, M.B. 2018. Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure. Available from www.cices.eu.

Havemann, C.P., Retief, T.A., Tosh, C.A., de Bruyn, P.J.N. 2016. Roan antelope Hippotragus equinus in Africa: a review of abundance, threats and ecology. Mammal Review 46: 144-158.

Hayward, M.W., Kerley, G.I.H. 2009, Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? Biological Conservation 142: 1-13.

Hooper, D.U., Chapin, F.S., Ewell, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75: 3-35.

Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43: 18-34.

IPBES. 2017. Plenary 2 Decision2/4: page 39: https://e IPBES Plenary 5 Decision IPBES-5/1: Implementation of the first work programme of the Platform, page 23: <https://www.ipbes.net/event/ipbes-5-plenary>

Johnson, C.N., Balmform, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356: 270-275.

Kuemmerle, T., Radeloff, V. C., Perzanowski, K., Kozlo, P., Sipko, T., Khoyetskyy, P., Bashta, A-T., Chikurova, E., Parnikoza, I., Baskin, L., Angelstam, P., Waller, D.M. 2011. Predicting potential European bison habitat across its former range. Ecological Applications 21: 830-843.

Lischka, S.A., Teel, T.L., Johnson, H.E., Reed, S.E., Breck, S., Carlos, A.D., Crooks, K.R. 2018. A conceptual model for the integration of social and ecological information to understand human-wildlife interactions. Biological Conservation 225: 80-87.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804-808.

Maes, J., Burkhard, B., Geneletti, D. 2018. Ecosystem services are inclusive and deliver multiple values. A comment on the concept of nature's contributions to people. One Ecosystem 3: e24720.

Millennium Ecosystem Assessment. 2005. Ecosystem and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC.

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csányi, S., Stenseth, N.C. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. Journal of Applied Ecology 43: 721-734.

Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., Mace, G.M., Palmer, M., Scholes, R., Yahara, T. 2009. Biodiversity, climate change, and ecosystem services. Current Opinion in Environmental Sustainability 1: 46-54.

Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F., Margalida, A., Donázar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A. 2017. Farmer perceptions of the ecosystem services provided by scavengers: what, who and to whom. Conservation Letters 11: e12392.

Murray, M.H., Becker, D.J., Hall, R.J., Hernandez, S.M. 2016. Wildlife health and supplemental feeding: A review and management recommendations. Biological Conservation 204: 163-174.

Navarro L., Pereira H. (Eds.) 2015 Rewilding European Landscapes. Springer, Cham.

Peterson, M.N., Birckhead, J.L., Leong, K., Peterson, M.J., Peterson, T.R. 2010. Rearticulating the myth of human-wildlife conflict. Conservation Letters 3: 74-82.

Pullin, A.S., Knight, T.M. 2009. Data credibility: A perspective from systematic reviews in environmental management. In M. Birnbaum & P. Mickwitz (Eds.), Environmental program and policy evaluation: Addressing methodological challenges. New Directions for Evaluation pp 122: 65-74.

Raizada, P. Raghubanshi, A.S., Singh, J.S. 2008. Impact of invasive alien plant species on soil processes: a review. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 78: 288–298.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linell, J.D.C., Watt, A., Gutiérrez, R.J. 2013. Understanding and managing conservation conflicts. Trends in Ecology & Evolution 28: 100-109.

Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H., van Mantgem, P.J. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122: 297-305.

Seddon, P.J. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology 18: 796-802.

Senserini, D., Santilli, F. 2016. Potential impact of wild boar (*Sus scrofa*) on pheasant (Phasianus colchicus) nesting success. Wildlife Biology in Practice 12: 15-20.

Sidorovich, V.E., Tikhomirova, L.L., Jędrzejewska, B. 2003. Wolf Canis lupus numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. Wildlife Biology 9: 103-112.

Simpson, R.D., Christensen, N.L.Jr. (Eds). 2012. Ecosystem function and human activities. Springer Science & Business Media.

Swanepoel, M., Leslie, A.J., Hoffman, L.C. 2016. Farmers' perceptions of the extra-limital common warthog in the Northern Cape and free state provinces, South Africa. Wildlife Society Bulletin 40: 112-121.

Valverde, J.A., 2004. Memorias de un biólogo heterodoxo. V&V, Madrid.

Vera, F.W.M. 2000. Grazing ecology and forest history. CABI publishing.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Wilson, D.E., Mittermeier, R.A. (Eds.). 2011. Handbook of the Mammals of the World. Vol. 2. Hoofed Mammals. Lynx Edicions, Barcelona.

Wilson, D.E., Mittermeier, R.A. (Eds.). 2014. Handbook of the Mammals of the World. Vol. 4. Sea Mammals. Lynx Edicions, Barcelona.

Chapter 2

Scientific priorities and shepherds’ perceptions of ungulate’s contributions to people.

Roberto Pascual-Rico; Zebensui Morales-Reyes; Berta Martín-López; José Antonio Sánchez-Zapata

ABSTRACT

Nature´s contributions to people (NCP) are all the contributions of living nature, both positive and negative, to the societies' life´s quality. Ungulates play this dual role of providers of beneficial and detrimental NCP, as they are responsible of the supply of ecosystem services (e.g. extractive experiences, habitat maintenance) and conflicts (e.g. crops damage, traffic collisions). We examined scientific priorities and shepherds' perceptions regarding the provision of NCP by wild ungulates. We reviewed scientific articles of NCP provided by ungulates in Spain and conducted questionnaires regarding NCP to shepherds in farming systems of Spain where domestic and wild ungulates cohabit. Then, we compared whether the scientific priorities match with those perceived by shepherds. Both stakeholders highlight more detrimental than beneficial NCP, although there are some mismatches between scientific priorities and shepherds' perceptions. Regarding detrimental NCP, soil alteration, human safety or traffic collision were studied but not mentioned by shepherds. Contrarywise, shepherds mainly considered vegetation damage, grazing competence, damage to animals, crop damage and disease transmission to livestock as important detrimental NCP. Concerning beneficial NCP, whilst hunting was prominent in the publications, shepherds did not conceived it as an important beneficial contribution and considered the regulation of organisms (carcasses elimination, alternative preys) and non-extractive experiences such as the aesthetic value. These results can have twofold implications. The emphasis on detrimental NCP can reinforce the idea that ungulates can threaten humans rather than contribute to societies' wellbeing. The fact that research does not address the interests of shepherds can affect the social tolerance towards ungulates as the damages experienced or perceived by shepherds are not studied. Our results show the relevance of considering local knowledge systems of shepherds, something highlighted by the NCP approach.

Key words: Bovidae; Cervidae; damage; human-ungulates relations; Suidae

RESUMEN

Todo aquello que la naturaleza aporta a las personas, tanto positivo como negativo, se denomina contribuciones de la naturaleza a las personas (NCP por sus sigals en inglés). Los ungulados desempeñan esta doble función de proveedores de NCP beneficiosos y perjudiciales, ya que proporcionan servicios ecosistémicos (como experiencias extractivas o mantenimiento del hábitat) y conflictos (por ejemplo, daños a cultivos o colisiones de tráfico). En este trabajo examinamos las prioridades científicas y las percepciones de los pastores con respecto a los NCP proporcionados por los ungulados silvestres en España. Revisamos aquellos artículos científicos sobre las relaciones entre ungulados y humanos en España, y por otro lado realizamos cuestionarios sobre los NCP percibidos a pastores de sistemas de ganadería extensiva donde los ungulados domésticos cohabitan con los silvestres. Después comparamos si las prioridades científicas coinciden con las percepciones de los pastores. Ambos agentes destacan los NCP negativos frente a los beneficiosos, aunque estos conflictos varían entre lo estudiado en las publicaciones científicas y lo percibido por los pastores. Con respecto a los NCP perjudiciales, los pastores no mencionaron la alteración del suelo, el daño a la salud humana o las colisiones de tráfico, auque la comunidad científica los contempla en los estudios. En cambio, los pastores consideraron principalmente el daño a la vegetación, la competencia por el pasto, el daño a otros animales, el daño a los cultivos y la transmisión de enfermedades al ganado como importantes NCP negativos. En lo que respecta a los NCP beneficiosos, la caza destacaba en las publicaciones, sin embargo, los pastores no lo consideraron, valorando más la regulación de otros organismos (eliminación de carroñas, presas alternativas) y las experiencias no extractivas como el valor estético. Este énfasis en los NCP negativos puede reforzar la idea de que los ungulados son una amenaza para los humanos en lugar de contribuir al bienestar de las sociedades. El hecho de que la investigación no aborde los intereses de los pastores puede afectar la tolerancia social hacia los ungulados, ya que los daños experimentados o percibidos por los pastores no se estudian. Nuestros resultados muestran la relevancia de considerar los sistemas locales de conocimiento de los pastores, algo destacado por el enfoque de los NCP.

Palabras clave: Bovidae; Cervidae; daño; relaciones humano-ungulado; Suidae

INTRODUCTION

In the last decades, it has been acknowledged that biodiversity and its conservation contribute to societies' wellbeing through the provision of multiple ecosystem services (Brooks et al. 2006; Hevia et al. 2017). Likewise, there is also growing recognition that biodiversity can also undermine human wellbeing by causing natural hazards and impairing damages in livelihoods (e.g., Lyytimäki 2015; Shackleton et al. 2016). The fact that biodiversity can both positively and negatively affect human wellbeing has been recently acknowledged by the Intergovernmental Platform of Biodiversity and Ecosystem Services (IPBES 2017) through the concept of nature´s contributions to people (NCP), i.e., all the contributions of nature, both positive and negative, to the societies' quality of life (Díaz et al. 2018). Frequently, the outcome of an ecological process, species or functional guild is conceived by society as a benefit or as a detriment depending on the environmental and cultural contexts (Saunders and Luck 2016; Rasmussen et al. 2017). For example, scavengers can be perceived by shepherds as beneficial because the consumption of carcasses and at the same time as harmful because some predators attack livestock (Morales-Reyes et al. 2018).

In NCP research, scientific attention about beneficial contributions of wildlife are scarcely garnered any (Lyytimäki 2015; Shackleton et al. 2016). However, there is a large body of literature about the damages caused by wildlife to human wellbeing under the framework of human-wildlife conflicts, i.e. negative NCP (Peterson et al. 2010). The framework of human-wildlife conflicts refers to wildlife damages to food production, human safety, human properties or more generally livelihoods (Nyhus 2016). Despite the development on both positive and negative NCP research, although under the terms of conflicts and ecosystem services given the novelty of the NCP, yet the dual role of wildlife as beneficial and detrimental to human wellbeing is underexplored.

In addition, the research on NCP is unevenly distributed among taxonomic groups. For example, whilst the role of vegetation for providing positive NCP has been broadly studied, the role of vertebrates remains understudied (Hevia et al. 2017). By contrast, research on negative NCP is biased towards carnivores (Peterson et al. 2010; Kansky et al. 2014). However, there are other taxonomic groups that are relevant as providers of beneficial and detrimental NCP, such as vultures (Morales-Reyes et al. 2018) or rodents (Rasmussen et al. 2017). Ungulates are also a group that plays this dual role of providers of beneficial and detrimental NCP. Ungulates play a critical role for regulating NCP, such as habitat maintenance (Owen-Smith 1988; Sandom et al. 2014), seed dispersion (Gill and Beardall 2001) and scavenging (Ripple et al. 2014). They also provide material benefits as they are still source of food in many societies (Ripple et al. 2015) as well as nonmaterial, being attraction for nature-based tourism and recreational hunting (Naidoo et al. 2016). Ungulates can also be the source of damages, such as crops damage (Dunkley and Cattet 2003), damage of forest plantations (Gundersen et al. 2004), collisions with vehicles (Snow et al. 2015) and competition with livestock for resources (Gortázar et al. 2007). Because this dual role of ungulates as providers of benefits and source of damages, in this paper, we use the concept of NCP that explicitly acknowledges both positive and negative contributions of biodiversity to the societies' wellbeing (Díaz et al. 2018). The current absence of knowledge about the beneficial and detrimental NCP provided by ungulates can entail a blind spot for wildlife management and biodiversity conservation.

In this research, we examine the scientific interests and shepherds' perceptions regarding the provision of NCP by wild ungulates. Particularly, we analyzed the detrimental and beneficial NCP provided by wild ungulates through examining the scientific priorities and the shepherds' perceptions in peninsular Spain. We selected the wild ungulates of the peninsular Spain because their populations are increasing favoured by changes in land use (Acevedo et al. 2011) that lead to competition for resources with extensive livestock farming. We specifically aimed to: (1) identify which negative and positive NCP provided by wild ungulates were studied in the scientific literature of Spain; (2) determine whether wild ungulates were perceived as source of negative NCP or providers of positive NCP by shepherds in extensive and semi-extensive livestock farming systems in mountainous areas of Spain; and (3) compare whether the scientific priorities regarding negative and positive NCP of wild ungulates matched with the priorities derived from shepherds' perceptions.

MATERIAL AND METHODS

Scientific priorities: systematic review of articles

We reviewed scientific articles of human-ungulates relations, either negative or positive interactions, in Spain. We searched in the Scopus database by using a search string comprised by words that combined different terms related to 'conflict', 'ecosystem service', 'human-herbivore relation' and 'ungulate' (see Appendix S1 for the full search string). The search was made to title, abstract and keywords from 2000 to 2018. We found 406 articles of potential relevance published in English. Of these, we only selected those articles of wild ungulates that are present in peninsular Spain (Table S.2.1), excluding feral domestic ungulates. We excluded those articles of feral domestic ungulates. Eight species comprise the community of wild ungulates in the peninsular Spain: aoudad (*Ammotragus lervia*), chamois (*Rupicapra pyrenaica*), fallow deer (*Dama dama*), Iberian ibex (*Capra pyrenaica*), mouflon (*Ovis orientalis*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*). We screened the articles to ensure that they reported on empirical studies (i.e., we excluded reviews or theoretical papers) and analyzed either negative or positive NCP provided by wild ungulates. This screening returned a final set of 82 articles (See appendix S.2.3)

We coded each publication according to: (1) its general description (i.e., year of publication, journal and the ungulate species), (2) category of negative NCP and (3) category of positives NCP, both if they mentioned or evaluated the identified NCP. The classification of negative NCP was adapted from Peterson et al. (2010), but we included new negative NCP that were derived from the literature review (Table 1). We classified positive NCP according to Díaz et al. 2018 (Table 2).

To test whether there was any level of association between the species of wild ungulates in the peninsular Spain and the NCP studied in the scientific literature, we conducted Chi-square contingency tables and Fisher's exact test.

Shepherd perceptions

Study areas

We examined shepherds' perceptions in five mountains in Spain (Figure 1): Cantabrian Mountains, Pyrenees, Sierra Morena, Sierras de Cazorla, Segura y Las Villas Natural Park (hereafter, Cazorla) and Northwest of Murcia (hereafter, Murcia). These areas represent the main traditional and large extensive and semi-extensive livestock farming systems (i.e., pasture-based farming) in Spanish mountains. These areas host an important number of livestock heads (Table S.2.2) that cohabit with wild ungulates.

Eight species comprising the community of wild ungulates in the peninsular Spain, and only the red deer and the wild boar are present in the five areas. The aoudad is a non-native species introduced into Spain in the 1970s and inhabits mountains of Cazorla and Murcia. The roe deer is present in the Cantabrian Mountains, Pyrenees and Sierra Morena. The Iberian ibex is present in Sierra Morena, Cazorla and Murcia. The chamois is only present in the Cantabrian Mountains and Pyrenees. The fallow deer, another non-native species in the peninsular Spain, inhabits Cantabrian Mountains, Sierra Morena and Cazorla. The mouflon, also a non-native species introduced in the 1950s, occupies Pyrenees, Sierra Morena, Cazorla and Murcia (see Table S.2.1). Of the five study areas, stable populations of large carnivores, such as the brown bear (Ursus arctos) and the Iberian wolf (Canis lupus signatus), are only present in the Cantabrian Mountains.

Table 1. Categories of negative NCP related to with wild ungulates in peninsular Spain extracted from the literature review and their consideration by the surveyed shepherds. The classification of negative NCP was adapted from Peterson *et al.* (2010).

Categories of negative NCP		**Examples from scientific literature**	**Examples from shepherds**
Damage to biodiversity	*Vegetation damage*	Negative effects on vegetation, including rooting (i.e., foraging activity within surface layers of soil)	Yes. “They root meadows”, “They destroy the ground”
	Animal biodiversity damage	Negative effects on wild animal species without direct economic interest, such as lagomorphs (Carpio *et al.* 2014) or insects and arachnids (see Bernes *et al.* 2018).	Yes. “They displace other wild ungulates”
	Non-native	Exotic species introduction is related with biodiversity loss (Wilcove *et al.* 1998) and alteration of ecosystem processes and community structure (Hejda *et al.* 2009; Raizada *et al.* 2008).	Yes. “It is not native”
	Soil alteration	For instance, negative effects of wild ungulates on soil properties (Pascual-Rico *et al.* 2018).	No mentioned.
Damage to production	*Grazing competence*	Wild ungulates consume pasture and other natural resources that could be used by livestock. For example, the European bison (Bison bonasus) competes directly with livestock (Kuemmerle *et al.* 2011)	Yes. “They eat the livestock pastures”, “They eat the pastures that we pay””
	Diseases to livestock	Risk of illness transmission from wild ungulates to livestock	Yes. “They transmit diseases to livestock: mange, tuberculosis, ticks...”
	Silvicultural damage	Impairment of natural forests or plantations intended for forestry	No mentioned.
	Crop damage	Direct physical impairment of croplands and orchards	Yes. “Damage to agriculture”, “Destroy the crops”
	Damage to animals	Direct physical damage caused by ungulates to livestock and big and small game species. For example, the wild boar as main nest predator of the common pheasant (Phasianus colchicus) (Senserini and Santilli 2016).	Yes. “It feeds on game species”, “It destroys red-legged partridges nests”, “It attacks the cattle”, “It kills lambs”
Damage to human safety		Ungulates causing injuries, frightening and/or transmitting infections agents to humans (Peterson *et al.* 2010).	No mentioned.
Property damage		Ungulates damaging human properties, particularly buildings and / or physical structures, such as fences (Peterson *et al.* 2010)	Yes. “They damage the fences”, “They shoot down walls and fences”
Traffic collisions		Ungulates damaging vehicles by ungulate-vehicle collision and / or causing traffic accidents (Peterson *et al.* 2010)	No mentioned.
Human-human conflict		Conflict related to human disagreements over management decisions of wild ungulates or derived from different opinions and interests by different stakeholders (adapted from Peterson *et al.* 2010)	No mentioned.

Table 2. Categories of positive NCP provided by wild ungulates in peninsular Spain extracted from the literature review and their consideration as ecosystem services by the surveyed shepherds. Classification of NCP based on Díaz et al. (2018).

Categories of positive NCP		Examples from scientific literature	Examples from shepherds
Regulating	*Habitat maintenance*	The formation and continued production, by ungulates, of ecological conditions necessary or favourable for organisms important to humans (Díaz *et al.* 2018). E.g. to contribute to maintain semi-open habitats (Vera 2000) and nutrient cycling (Danell *et al.* 2006).	Yes, as grazing: "Cleans the forest", "Generates pasture biodiversity in inaccessible areas for livestock ".
	Dispersal of seeds	Facilitation by ungulates of seed dispersion of species important to humans. For example, grass or small herbs species via the coat, hoof or feces (Gill and Beardall 2001).	No mentioned.
	Maintenance of soils	E.g. contributing nutrients to the soil (Asner *et al.* 2004) and favour soil communities (Bueno and Jiménez 2014).	Yes. "Wild boars aerate the soil by opening up holes"
	Regulation of hazards and extreme events	E.g. herbivory can contribute to fire prevention (Velamazán *et al.* 2018).	No mentioned.
	Regulation of organisms	Removal of animal carcasses by wild boars, i.e., acting as a scavenger (Morales-Reyes *et al.* 2018), reduction of attacks on livestock due to the presence of alternative prey (Sidorovich *et al.* 2003) and wild ungulate carcasses as important food resource for vertebrate scavengers (Mateo-Tomás *et al.* 2015).	Yes, provision of both positive NCP, the wild board as scavenger and ungulates as alternative preys and carcasses "They are wolves food and they [wolves] do not come for livestock"
Material	*Food*	Production of food from wild ungulates, such as meat from red deer (Milner *et al.* 2006).	Yes, "Wild boar cold meat in autumn"
	Materials and assistance	Materials obtained directly from ungulates as fur (see MacMillan and Philips 2008)	No mentioned.
Non-material	*Supporting identities*	Source of satisfaction derived from knowing that a particular ungulate exists in the present (adapted from Díaz *et al.* 2018).	Yes. "It's so majestic that you have to protect it", "If they exist it's because of something", "They play their role"
	Physical and psychological experiences	Extractive experiences: Provision by ungulates of opportunities for physically beneficial leisure activities that entail extraction from nature, such as recreational hunting (Gamborg *et al.* 2018).	No mentioned.
		Non-extractive experiences: Provision by ungulates of beneficial opportunities related with being in close contact with nature, such as the aesthetic value derived from species (de Pinho *et al.* 2014).	Yes. "I like to see them", "Beautiful: the most pretty and wild"
	Maintenance of options	Conservation of species associated with future situations as extinction of other populations (Fernández-Olalla *et al.* 2016).	No mentioned.

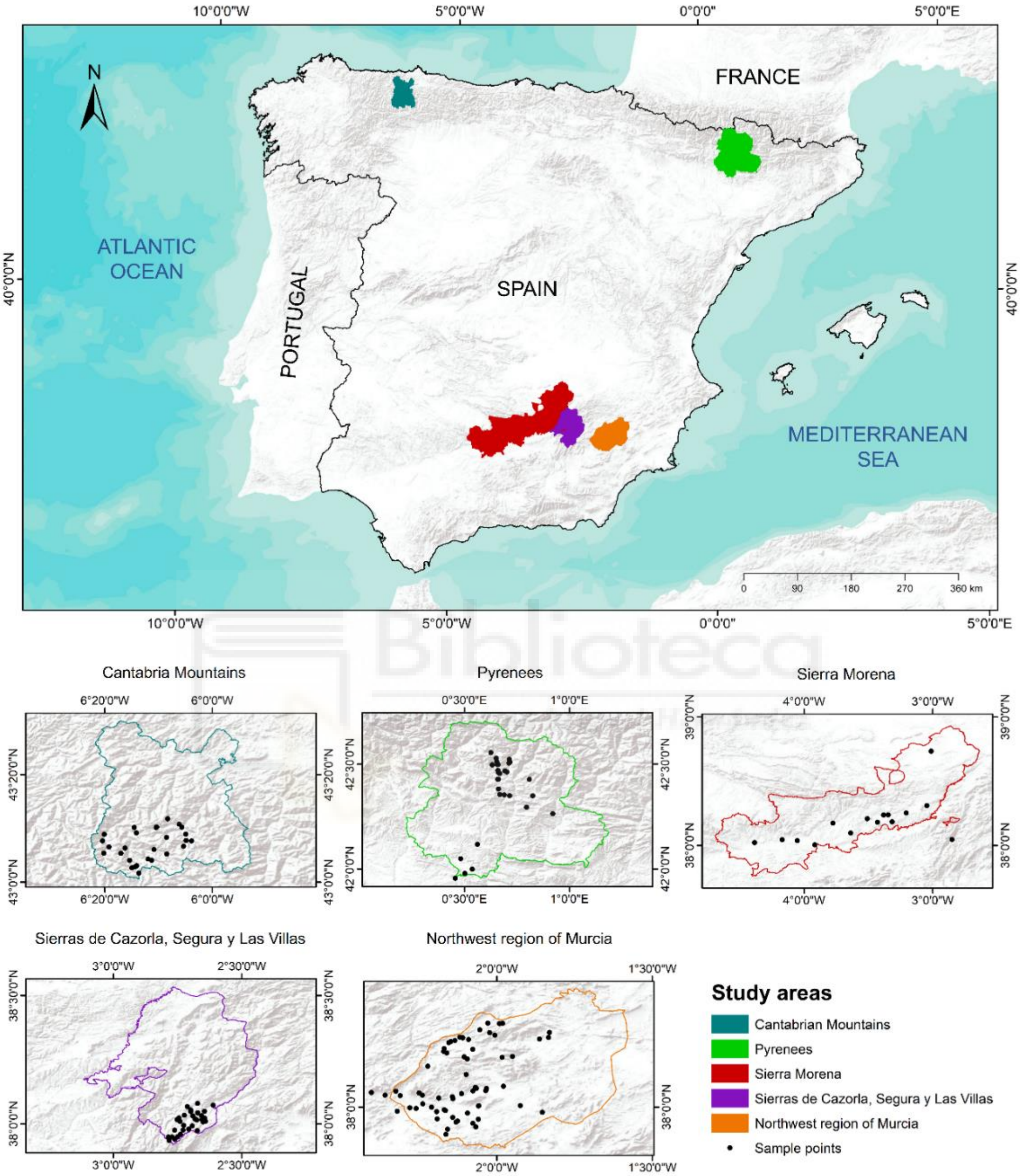

Figure 1. Map of peninsular Spain showing the five study areas, where questionnaires were conducted. Study areas are indicated with colored lines. Sampling points are indicated with black circles. Ungulate species present in each study area are shown in Table S.2.1.

Data collection and analyses

We conducted face-to-face questionnaires to shepherds from 2012 to 2016, collecting 184 questionnaires (see Table S.2.2 for the sample size in each study area). We structured the questionnaire in three main sections: (1) wild ungulate species that were known and seen by shepherds in the study area; (2) perception of NCP provided by wild ungulates in the study area; and (3) socio-demographic and farming characteristics of shepherds. We only asked questions concerning section two when respondents have known and seen the ungulate species existing in the study area (see Appendix S.2.2 and Figure S.2.1 for details about the species known and seen by shepherds in each farming system).

We conducted Chi-square contingency tables and Fisher's exact test to determine whether some wild ungulates were particularly perceived by shepherds as a source of a specific NCP. Based on the NCP derived from the perceptions of shepherds, we built the variable Nature Contributions to People Provider (*NCPP*) *index*, which indicates the average shepherd perceptions of wild ungulates as providers of NCP for each species using a five-point scale from very harmful (*NCPP index* = 1) to very beneficial (*NCPP index* = 5). Based on this, species with an assigned *NCPP index* ranged from 1 to 2 were considered harmful and, thus, as source of negative NCP; whilst species with *NCPP index* ranged from 4 to 5 were considered beneficial and, thus, as providers of positive NCP. We carried out Kruskal-Wallis test and Tukey post-hoc test to determine differences in the *NCPP index* perceived by shepherds between different species. We also performed Mann-Whitney U test to explore differences in the *NCPP index* due to different ecological factors: (1) the diet of ungulates (herbivore or omnivore), (2) their origin (native or non-native) and (3) the presence of large predators in the farming system.

Comparison between scientific priorities and shepherds' perceptions

To compare whether the scientific priorities given to both, negative and positive NCP, match with the priorities perceived by shepherds in extensive livestock farming systems, we performed two Spearman's correlation tests: one for negative and another for positive NCP. The variables included in the correlation test were the percentage of publications that mentioned each NCP, representing scientific priorities, and the percentage of shepherds indicating that wild ungulates were responsible of causing each NCP, representing shepherds' perceptions.

RESULTS

Scientific publications on NCP provided by wild ungulates

Research on NCP provided by ungulates in Spain has irregularly increased since 2000 (Figure S.2.2). A great number of publications addressed both kinds of NCP (45.1% of publications). Of the remaining publications, most articles addressed only negative NCP (36.6%), whilst 18.3% of publications focused only on ecosystem services. Species that received higher scientific attention were wild boars (61.0%), red deer (48.8%), roe deer (24.4%), Iberian ibex (22.0%), fallow deer (14.6%) and aoudad (12.2%). Other species studied in less than 10% of publications were the mouflon (7.3%), and the chamois (7.3%; Figure 2).

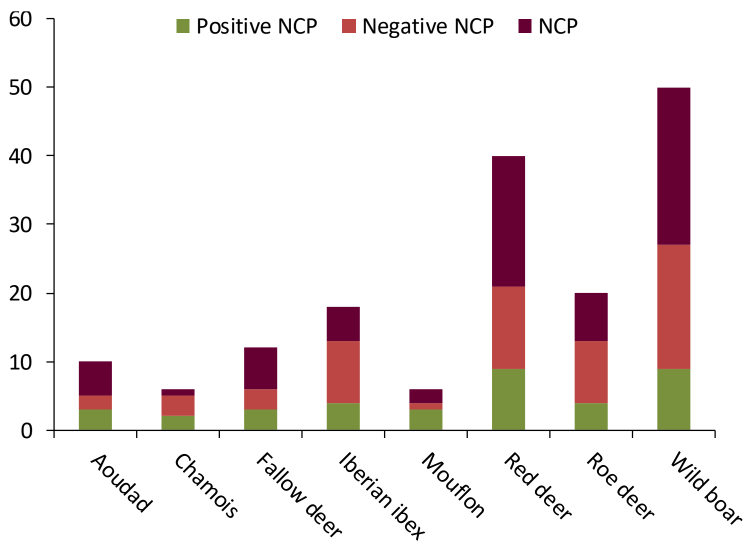

Figure 2. Number of publications for each species. Bars indicate total number of papers focused on each NCP type.

Negative NCP that received higher attention were damage to biodiversity (61.0% of publications), particularly vegetation damage (54.9%), animal biodiversity damage (20.7%), non-native species (11.0%) and soil alteration (11.0%); damage to production (37.8%), especially diseases to livestock (18.3%); damage to human (15.9%; including diseases transmission (15.9%) and direct attacks (2.4%)), and traffic collisions (14.6%). The remaining negative NCP were studied in less than 5% of publications (Figure 3A).

There was an association between some negative NCP and several species ($\chi2 = 156.6$, df = 84, $p < 0.001$). Particularly, we found significant positive association ($p < 0.05$) between vegetation damage and the Iberian ibex (and wild boars ($\chi2 = 3.2$), non-native species and both the aoudad ($\chi2 = 44.4$) and the fallow deer ($\chi2 = 14.6$), crop damage and the wild boar ($\chi2 = 5.8$). Some of the negative NCP less addressed by scientific literature acquired importance with some species, such as the association between grazing competence and both Iberian ibex ($\chi2 = 5.7$) and the wild boar ($\chi2 = 0.1$), silvicultural damage and the red deer ($\chi2 = 0.2$), and property damage and both the red deer ($\chi2 = 0.01$) and the wild boars ($\chi2 = 0.1$). Damage to animal biodiversity, soil alteration, diseases transmission to livestock, and damage to animals and to humans, as well as traffic collisions and human-human conflicts were not associated to any species (Figure 3B).

The positive NCP that received the highest scientific attention belonged to the category of non-material contributions (48.8% of publications), particularly physical and psychological experiences, where 48.8% of publications mentioned hunting (i.e., extractive experience). However, only 4.9% of publications mentioned the aesthetic value of wild ungulates (i.e., non-extractive experiences) and just 1.2% the cultural heritage (i.e., supporting identities) and 1.2% the maintenance of options for the future. Regulating contributions were mentioned in 22.0% of publications: regulation of organisms (8.5%; including scavenged carcasses (6.1%), scavenging by the wild boar (3.7%) and alternative prey (2.4%)), habitat maintenance (11.0%), dispersal of seeds (3.7%), maintenance of soils (2.4) and regulation of hazards and extreme

(1.2%). Material contributions were only mentioned in 4.9% of publications, being ungulates conceived as a source of food (4.9%) and materials and assistance resource (2.4%; Figure 4A). We did not find any association between the species studied and ecosystem services ($\chi 2 = 64.1$, df = 70, $p = 0.68$) (Figure 4B).

The positive NCP that received the highest scientific attention belonged to the category of non-material contributions (48.8% of publications), particularly physical and psychological experiences, where 48.8% of publications mentioned hunting (i.e., extractive experience). However, only 4.9% of publications mentioned the aesthetic value of wild ungulates (i.e., non-extractive experiences) and just 1.2% the cultural heritage (i.e., supporting identities) and 1.2% the maintenance of options for the future. Regulating contributions were mentioned in 22.0% of publications: regulation of organisms (8.5%; including scavenged carcasses (6.1%), scavenging by the wild boar (3.7%) and alternative prey (2.4%)), habitat maintenance (11.0%), dispersal of seeds (3.7%), maintenance of soils (2.4) and regulation of hazards and extreme (1.2%). Material contributions were only mentioned in 4.9% of publications, being ungulates conceived as a source of food (4.9%) and materials and assistance resource (2.4%; Figure 4A). We did not find any association between the species studied and ecosystem services ($\chi 2 = 64.1$, df = 70, $p = 0.68$) (Figure 4B).

Shepherds' perceptions of NCP provided by wild ungulates

A higher percentage of shepherds perceived wild ungulates as harmful (55.0%) than beneficial (20.1%). The way shepherds identified and described the NCP provided by wild ungulates is presented in Table 1. Among the negative NCP identified by shepherds, damage to production was the most mentioned (79.9% of shepherds), particularly grazing competence (37.5%), damage to animals (37.0%; which includes damage to game species (19.0%) to livestock (17.9%)), crop damage (32.1%) and diseases transmission to livestock (25.5%). The damage to animals was related to the role of wild boar as a predator and it included direct physical damage to livestock (19.0%), game species and their hatchlings and eggs (4.3%), and non-specified species (13.6%). Also highlight damage to biodiversity (40.2%), especially vegetation damage (41.3%); and property damage (7.6%; Figure 5A). Other negative NCP were no perceived by shepherd, as damage to human safety, traffic collisions or human-human conflicts. We found positive associations between several species and the negative NCP perceived by shepherds ($\chi2 = 401.8$, df = 49, $p < 0.001$). We found associations ($p < 0.05$) between: rooting behaviour (vegetation damage) and the wild boar ($\chi2 = 39.7$); grazing competence with livestock and the fallow deer ($\chi2 = 7.6$), the mouflon ($\chi2 = 6.2$) and the red deer ($\chi2 = 5.1$); disease transmission to livestock and both the fallow deer ($\chi2 = 3.9$) and the Iberian ibex ($\chi2 = 3.7$); crop damage with the wild boar ($\chi2 = 11.7$); and damage to animals and the wild boar ($\chi2 = 65.2$). Some of the less mentioned negative NCP acquired relevance for some particular species, such as animal biodiversity damage and the fallow deer ($\chi2 = 2.1$); non-native trait and the red deer ($\chi2 = 9.0$); property damage and both the chamois ($\chi2 = 17.7$) and the roe deer ($\chi2 = 22.5$; Figure 5B).

Among positive NCP, shepherds mostly mentioned regulating contributions (9.2%), as regulation of organisms (7.6%; including scavenging by the wild boar (6.0%) and alternative prey (1.6%)), habitat maintenance (2.2%) and maintenance of soils (0.5%). Non-material NCP were mentioned by 6.5% of shepherds, particularly non-extractive experiences (aesthetic value of wild ungulates; 4.3%) and supporting identities (2.2%). Material NCP were mentioned by 0.5% of shepherds (Figure 6A). We did not find significant positive associations between particular species and the positive NCP perceived by shepherds ($\chi2 = 33.8$, df = 35, $p < 0.53$; Figure 6B).

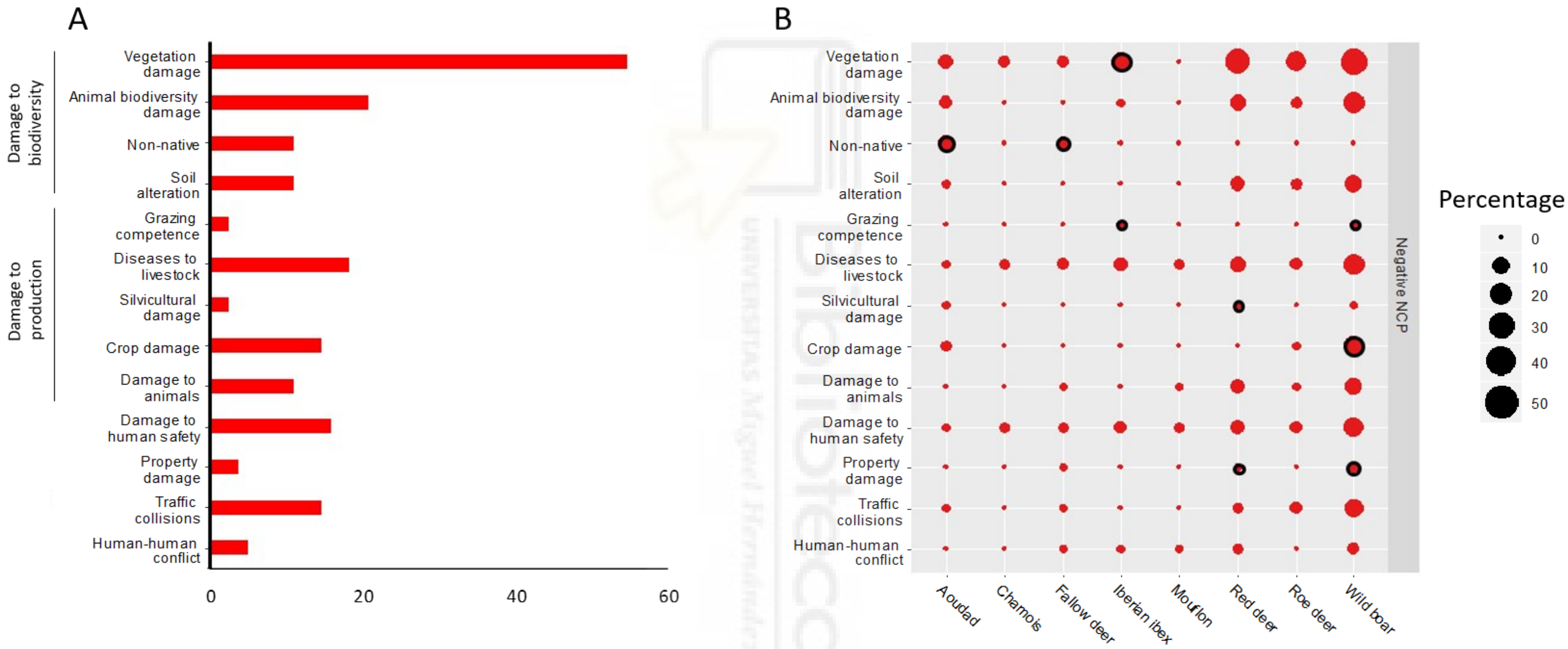

Figure 3. A) Percentage of publications that mentioned each negative NCP. B) Percentages of publications that mentioned each negative NCP by species (n = 82). Circles with black shape line indicate that differences among species were higher than expected (α = 0.05).

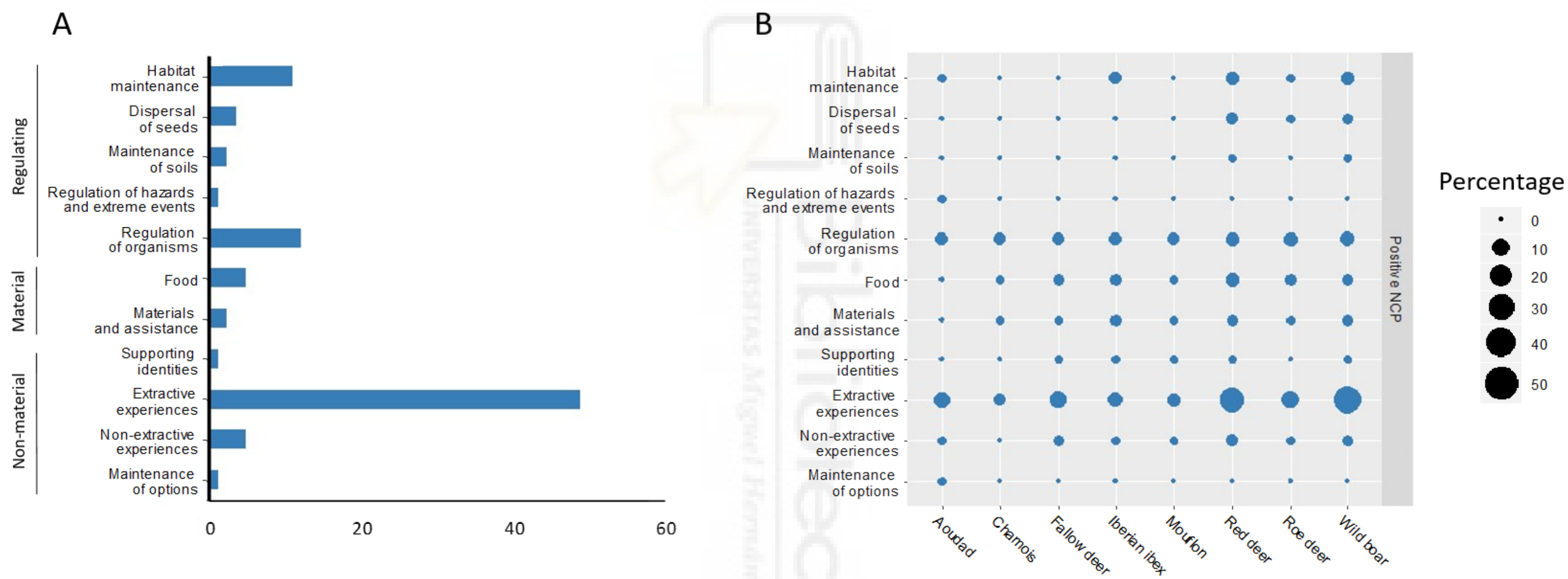

Figure 4. A) Percentage of publications that mentioned each positive NCP. B) Percentages of publications that mentioned positive NCP by species (n = 82). Circles with black shape line indicate that differences among species were higher than expected (α = 0.05).

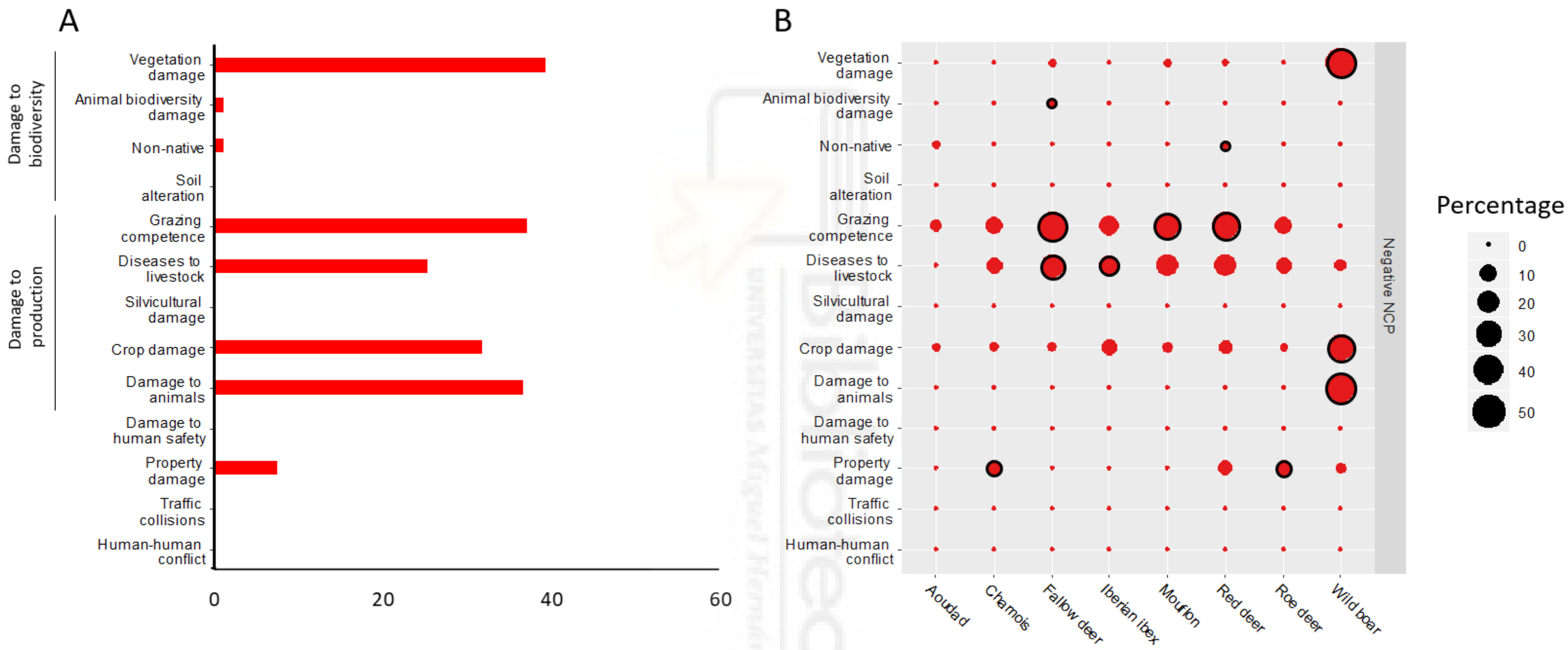

Figure 5. A) Percentage of shepherds that mentioned each negative NCP. B) Percentages of shepherds that mentioned negative NCP by species. Circles with black shape line indicate that differences among species were higher than expected (α = 0.05).

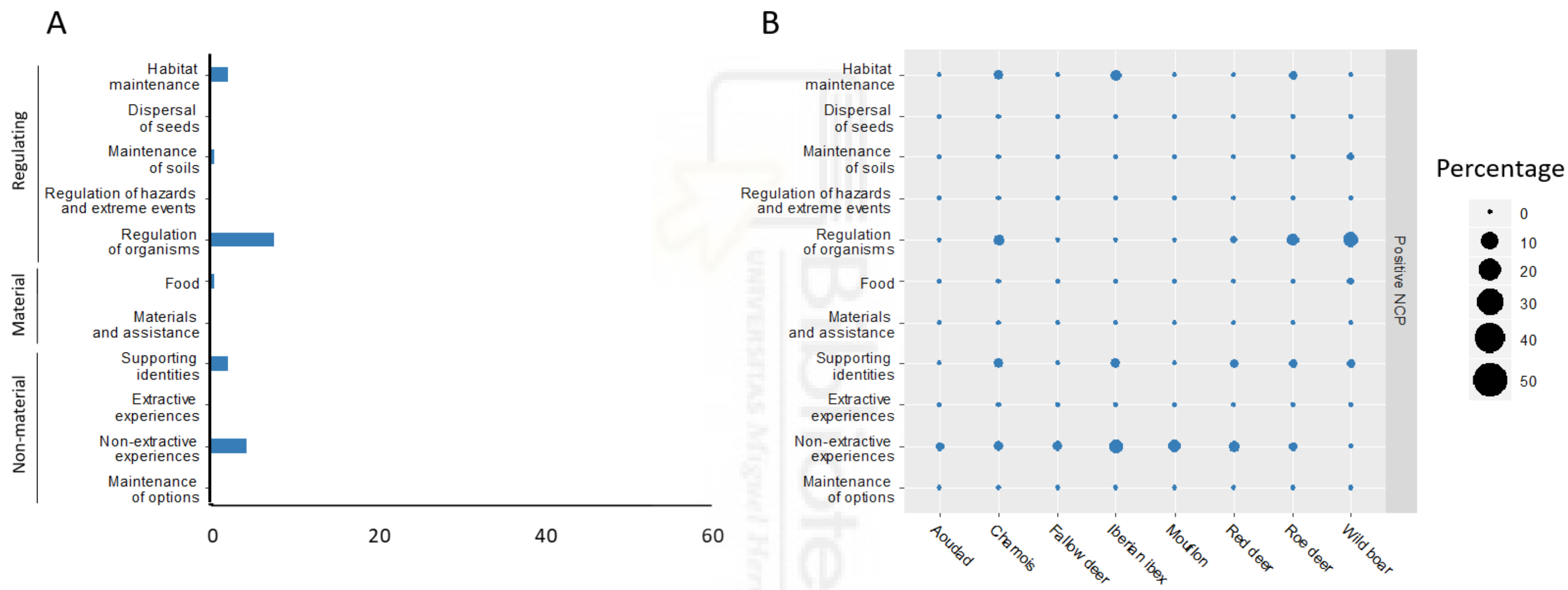

Figure 6. A) Percentage of shepherds that mentioned each positive NCP. B) Percentages of shepherds that mentioned each positive NCP by species. Circles with black shape line indicate that differences among species were higher than expected (α = 0.05).

The average shepherds' perception of wild ungulates as providers of NCP (*NCPP index*) varied among species ($\chi2$ = 215.93, df = 7, p < 0.001). Whilst the wild boar was assessed by shepherds with the lowest score (*NCPP index* = 1.42), indicating that this species was mostly considered as harmful; the chamois, the roe deer and the Iberian ibex were assessed with the highest scores (*NCPP index* ≥ 3.44), indicating that they were mostly perceived as providers of NCP (Table 3).

Table 3. Shepherds' perception of wild ungulates' capacity to provide NCP. It shows *NCPP index*, standard deviation (SD), and posthoc Tukey test grouping species according their *NCPP index*.

Species	*NCPP index*	SD	Tukey posthoc test
Chamois	3.53	1.16	a, b
Roe deer	3.51	1.24	a, b
Iberian ibex	3.44	1.44	a, b
Aoudad	3.00	1.65	a
Red deer	2.49	1.32	a, c
Mouflon	2.28	1.24	a, c
Fallow deer	2.17	1.13	a, c
Wild boar	1.42	0.98	d

NCPP index varied according to the diet of the wild ungulate species, since strict herbivores were significantly perceived by shepherds as providers of more positive NCP than omnivore species, i.e., wild boars (Mann-Whitney U test, p < 0.001). Moreover, *NCPP index* also varied according to the presence of large carnivores in the study area. We found that wild ungulates in areas with large carnivores were perceived by shepherds as more beneficial than in areas without large carnivores (Mann-Whitney U test, p < 0.001). We did not find differences in *NCPP index* between native and non-native species of wild ungulates (Mann-Whitney U test, p = 0.35).

Comparison between scientific priorities and shepherds' perceptions

Scientific priorities about negative NCP and shepherds' perceptions of negative NCP were not correlated (Spearman´s rho = 0.18, p = 0.56). In fact, some negative NCP such as soil alteration, silvicultural damage, damage to human safety, traffic collisions and human-human conflicts were only mentioned in the scientific literature, but were not perceived by shepherds (Figure S.2.3a). Likewise, we found no correlation between scientific priorities and shepherds' perceptions of positive NCP (Spearman´s rho = 0.34, p = 0.31). Dispersal of seeds, regulation of hazards and extreme events, materials and assistance, extractive experiences and maintenance of options were not perceived as positive NCP by shepherds, and were only mentioned in the scientific literature (Figure S.2.3b).

DISCUSSION

Despite the increasing attention to positive NCP in the last years (Díaz et al. 2015), most of the scientific attention regarding ungulates evaluated detrimental NCP (96% of articles). This result is consistent with former research on human-wildlife relations that show that publications are biased toward negative aspects (Kansky and Knight, 2014). It is also remarkable that the few scientific articles addressing beneficial NCP focussed on hunting (48.8% of reviewed articles) (e.g. Milner et al. 2006; Schley et al. 2008). The emphasis in the scientific literature on hunting as a beneficial NCP can have twofold explanations. On the one hand, hunting has been suggested as a management action to limit the populations of particular species that cause damage (i.e. negative NCP). For example, recreational hunting of wild boar has been identified among other measures to control its population across Europe (e.g., Massei et al. 2014). This control tool was also applied to the management of the red, fallow and roe deer (e.g., Ramos et al. 2006; Sobalak 2008). In this sense, hunting goes beyond the recreational experience (i.e. nonmaterial NCP) and it turns into a management recommendation. On the other hand, the focus on hunting can be also explained by the historical bias towards economic valuation in ecosystem service research (e.g. Gómez-Baggethun et al. 2010; Nieto-Romero et al. 2014). In fact, several studies on ungulates assess the economic value of hunting (Martínez-Jauregui et al. 2014; Popa et al. 2013).

Similar than the scientific literature, shepherds also mentioned more detrimental than beneficial NCP. Different factors determine shepherds' perception of wild ungulates as providers of positive or negative NCP, such as diet and the presence of large carnivores in the system. Regarding diet, we found that the only omnivorous species (i.e. the wild boar) was worse valued than strict herbivores because their feeding behaviour may provoke that shepherds perceive them as harmful. For instance, shepherds in other countries considered the wild boar as the main predator of their herds despite there was no evidence of such predation (but scavenging) on livestock (Herrero and Fernández de Luco 2003). Concerning the presence of large carnivores (i.e., wolves and brown bears), we found that in places where large carnivores are present, shepherds perceived some wild ungulate species as an alternative prey source and their presence is therefore considered beneficial because it can reduce carnivore attacks on livestock. This phenomenon has been detected also in other European countries. For example, Sidorovich et al. (2003) and Vos (2000) in Belarus and Portugal, respectively, demonstrated that wolf attacks on livestock increase when wild preys are scarce.

Despite that scientific priorities and shepherds' perceptions highlight more detrimental than beneficial NCP, there are some mismatches. For example, whilst soil alteration, damage to human safety or traffic collisions were considered in more than 10% of publications, they were not mentioned by shepherds. Contrarywise, shepherds mainly considered vegetation damage, grazing competence, damage to animals, crop damage and disease transmission to livestock as important detrimental NCP. The last four negative NCP perceived by shepherds are related with damage to production. As shepherds' livelihoods strongly depend on their livestock any potential threat is considered as relevant. In fact, a meta-analysis developed by Kansky et al. (2014)

concludes that the potential of experience damages can underpin negative perceptions toward wildlife.

Regarding beneficial NCP, whilst the ecosystem service of hunting was prominent in the scientific literature, shepherds did not conceived it as an important beneficial contribution. However, they considered most important positive NCP the regulation of other organisms (i.e. the capacity of the wild boar to remove carcasses and the role of other species as alternative prey for predators and carcasses for scavengers), followed by non-extractive experience such as the aesthetic value. These results are consistent with previous research that found that scavenging is positively valued by shepherds in Spain as it contributes to remove the carcasses of livestock (Morales-Reyes et al. 2018); and that ungulates are amongst the most valued organisms because their beauty (Frynta et al. 2013). The fact that shepherds do not conceived hunting as a beneficial NCP may be because they cannot access to big game hunting, although they considered that some ungulates could affect species of big and small game.

These results do not only demonstrate that scientific interests regarding biodiversity and positive NCP differ from shepherds interests, needs and perceptions (e.g. Martín-López et al. 2007; Iniesta-Arandia et al. 2014), but also that this mismatch can be determined by the absence of experiencing particular NCP. Furthermore, our results also show the relevance of consider shepherds' local knowledge as their understandings might be different than the scientific knowledge, which is something highlighted by the NCP approach (Díaz et al. 2018).

In addition, we found that even when scientific priorities and shepherds' perception match in terms of detrimental and beneficial NCP, the species responsible were different. For instance, shepherds did not consider the wild boar as a competitor for graze (grazing competition), whereas they perceived wild boars as harmful through rooting behavior and damage vegetation and crops. Further, whilst disease transmission to livestock was related mainly with the wild boar by scientific priorities (but not significant association), shepherds did not considered this potential risk as relevant. Instead, shepherds emphasized their scavenger behaviour and thus they might consider that wildboars reduce the risk of disease transmission via scavenging. Nevertheless, shepherds perceive some ungulates as potential transmissors of diseases -i.e. Iberian ibex and fallow deer-. Although there were not significant association among other species such as the mouflon and the red deer with diseases tranmission, they were considered as potential diseases transmitters by a high percentage of shepherds. It has been demonstrated that taxonomically related species are more susceptible to infection by the same parasite species (Freeland 1983). This factor could be crucial in the wildlife-livestock pathogen interaction as happened with sheep and bighorn (*O. canadensis*) (Wehausen et al. 2011) or between cattle (*Bos taurus*) and American bison (*Bison bison*) (Kilpatrick et al. 2009). So, shepherds' perception might be influenced by the taxonomic relation which is reflected in the physical similarity, particularly between Iberian ibex and domestic goat (*C. hircus*), both belonging Capra genus, and also with mouflon and sheep (*O. aries*) both belonging to the Ovis genus.

Former research has found that shepherds' perceptions regarding specific negative NCP do not correspond with the actual ecological processes (e.g., Herrero and Fernández de Luco 2003). For example, Ranglack et al. (2015) quantified the relative grazing impacts of bison, cattle and lagomorphs in an area where ranchers perceived the bison as the main competitor of cattle, but they found that lagomorphs were the largest consumers of biomass. Nevertheless, there is evidence about the correspondance between local knowledge and scientific knowledge of ecological processes, in particular with scavengers (Morales-Reyes et al. 2018). Former research has also highlighted the usefullnes of local knowledge to complement assessments of habitat use by mammals (Prado et al. 2014), or to obtain information on species abundance and population trends in terrestrial ecosystems (Anadón et al. 2009), whose results are aplicable to conservation policies and sustainable management measures.

CONCLUSIONS

The emphasis on detrimental NCP rather than beneficial NCP made by scientists and shepherds can reinforce the idea that wildlife, and in particular ungulates, can threaten humans, instead that contribute to our quality of life (Peterson et al. 2010). This could affect directly the conservation of these wildlife species through management policies, especially when stakeholder are involve in the development and implementation of management plans as its recommended (Young et al. 2013). Yet, some discrepancies were found between scientific priorities and shepherds' perceptions regarding the beneficial and detrimental NCP provided by ungulates. For example, those detrimental NCP mostly stated by shepherds (i.e. grazing competence and damage to animals) were little considered by the scientific literature. The fact that scientific research does not address the interests of shepherds can affect the social tolerance towards wildlife as the damages experienced or perceived by shepherds are not assessed. Therefore, future research on human-ungulate relations should focus on two key aspects: the beneficial NCP provided by ungulates and the existing damages experienced by shepherds. This research agenda will contribute to drift current perceptions about ungulates as sources of negative NCP to providers of positive NCP and to provide insights for managing the damages caused by ungulates.

ACKNOLEDGEMENTS

We thank to A. Margalida and J.A. Donázar for coordination tasks. M. Valverde, F. Botella, E. Arrondo, J. García-Fernández, A. Trujillano, P. Mateo-Tomás helped during the fieldwork. Thanks to F. Botella for his constructive criticism and for their comments on an earlier version of the manuscript. I. Pérez helped during the questionnaire design. We appreciate the generousity of the shepherds to share their knowledge and time. R.P.R. and Z.M.R. were supported by a pre-doctoral grant from the Spanish Ministry of Education (FPU13/05460 and FPU12/00823, respectively). The study was partially supported by MINECO and ERDF (project CGL2015-66966-C2-1-R).

REFERENCES

Acevedo, P., Farfán, M.A., Márquez, A.L., Delibes-Mateos, M., Real, R., Vargas, J.M. 2011. Past, present and future of wild ungulates in relation to changes in land use. Landscape Ecology 26: 19-31.

Anadón, J.D., Giménez, A., Ballestar, R., Pérez, I. 2009. Evaluation of local ecological knowledge as a method for collecting extensive data on animal abundance. Conservation Biology 23: 617-625.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T. 2004 Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources 29: 261–299.

Bernes, C., Macura, B., Jonsson, B.G., Junnien, K., Müller, J., Sandström, J., Lõhmus, A., Macdonald, E. 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates. A systematic review. Environmental Evidence 7: 13.

Brooks, T.M., Mittermeier, R.A., da Fonseca. G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L. 2006. Global biodiversity conservation priorities. Science 313: 58-61.

Bueno, C.G., Jiménez, J.J. 2014. Livestock grazing activities and wild boar rooting affect alpine earthworm communities in the Central Pyrenees (Spain). Applied Soil Ecology 83: 71-78

Carpio, A.J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F.S. 2014. The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit? Wildlife Biology 20: 161-166.

Danell, K., Bergström, R., Duncan, P., Pastor, J. (Eds.). 2006. Large Herbivore Ecology, Ecosystem Dynamics and Conservation (Conservation Biology). Cambridge University Press, Cambridge.

de Pinho, JR, Grilo C, Boone RB, Galvin KA, Snodgrass JG. 2014. Influence of aesthetic appreciation of wildlife species on attitudes towards their conservation in Kenyan agropastoralist Communities. PLoS ONE 9: e88842.

Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J.R., Arico, S., Báldi, A., Bartuska, A., Baste, I.A., Bilgin, A., Brondizio, Chan, K.M.A., Figueroa, V.E., Duraiappah, A., Fischer, M., Hill, R., Koetz, T., Leadley, P., Lyver, P., Mace, G.M., Martín-López, B., Okumura, M., Pacheco, D., Pascual, U., Pérez, E.S., Reyers, B., Roth, E., Saito, O., Scholes, R.J., Sharma, N., Tallis, H., Thaman, R., Watson, R., Yahara, T., Hamid, Z.A., Akosim, C., Al-Hafedh, Y., Allahverdiyev, R., Amankwah, E., Asah, S.T., Asfaw, Z., Bartus, G., Brooks, A., Caillaux, J., Dalle, G., Darnaedi, D., Driver, A., Erpul, G., Escobar-Eyzaguirre, P., Failler, P., Fouda, A.M.M., Fu, B., Gundimeda, H., Hashimoto, S., Homer, F., Lavorel, S., Lichtenstein, G., Mala, W.A., Mandivenyi, W., Matczak, P., Mbizvo, C., Mehrdadi, M., Metzger, J.P., Mikissa, J.B., Moller, H., Mooney, H.A., Mumby, P., Nagendra, H., Nesshover, C., Oteng-Yeboa, A.A., Pataki, G., Roué, M., Rubis, J., Schultz, M., Smith, P., Sumaila, R., Takeuchi, K., Thomas, S., Verma, M., Yeo-Chang, Y., Zlatanova, D. 2015. The IPBES conceptual framework - connecting nature and people. Current Opinion in Environmental Sustainability 14: 1-16.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Bauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y. 2018. Assessing nature's contributions to people. Science 359: 270-272.

Dunkley, L., Cattet, M.R.L. 2003. A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Canadian Cooperative Wildlife Health Centre: Newsletters and Publications 21: 1-68.

Fernández-Olalla, M., Martínez-Jauregui, M., Perea, R., Velamazán, M., San Miguel, A., 2016. Threat or opportunity? Browsing preferences and potential impact of *Ammotragus lervia* on woody plants of a Mediterranean protected area. Journal of Arid Environments 129: 9-15

Freeland, W.J. 1983. Parasites and the coexistence of animal host species. American Naturalist 121: 223-236.

Frynta, D., Šimková, O., Lišková, S., Landová, E. 2013. Mammalian Collection on Noah's Ark: The Effects of Beauty, Brain and Body Size. PLoS ONE 8: e63110.

Gamborg, C., Jensen, F.S., Sandøe, P. 2017. Killing animals for recreation? A quantitative study of hunters' motives and their perceived moral relevance. Society & Natural Resources 31: 489-502.

Gill, R.M.A., Beardall, V. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74: 209-218.

Gómez-Baggethun, E., de Groot, R., Lomas, P.L., Montes, C. 2010. The history of ecosystem services in economic theory and practice: from early notions to markets and payment schemes. Ecological Economics 69: 1209-1218.

Gortázar, C., Ferroglio, E., Höfle, U., Frölich, K., Vicente, J. 2007. Diseases shared between wildlife and livestock: A European perspective. European Journal of Wildlife Research 53: 241-256.

Gundersen, H., Andreassen, H.P., Storaas, T. 2004. Supplemental feeding of migratory moose Alces alces: forest damage at two spatial scales. Wildlife Biology 10: 213-223.

Hejda, M., Pysek, P., Jarosik, V. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97: 393-403.

Herrero, J., Fernández de Luco, D. 2003. Wild boars (*Sus scrofa* L.) in Uruguay: scavengers or predators? Mammalia 67: 485-491.

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., González, J.A. 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. Ecology & Evolution 7: 831-844.

Iniesta-Arandia, I., García-Llorente, M., Aguilera, P.A., Montes, C., Martín-López, B. 2014. Socio-cultural valuation of ecosystem services: uncovering the links between values, drivers of change, and human well-being. Ecological Economics 108: 36-48.

IPBES. 2017. Plenary 2 Decision2/4: page 39: https://e IPBES Plenary 5 Decision IPBES-5/1: Implementation of the first work programme of the Platform, page 23: <https://www.ipbes.net/event/ipbes-5-plenary>

Kansky, R., Kidd, M., Knight, A.T. 2014. Meta-Analysis of Attitudes toward Damage-Causing Mammalian Wildlife. Conservation Biology 28: 924-938.

Kansky, R., Knight, A.T. 2014. Key factors driving attitudes towards large mammals in conflict with humans. Biological Conservation 179: 93-105.

Kilpatrick, A.M., Gillin, C.M., Daszak, P. 2009. Wildlife-livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. Journal of Applied Ecology 46: 476-485.

Kuemmerle, T., Radeloff, V.C., Perzanowski, K., Kozlo, P., Sipko, T., Khoyetskyy, P., Bashta, A.T., Chikurova, E., Parkinoza, I., Baskin, L., Angelstam, P., Waller, D.M. 2011. Predicting potential European bison habitat across its former range. Ecological Applications 21: 830-843.

Lyytimäki, J. 2015. Ecosystem disservices: Embrace the catchword. Ecosystem Services 12: 136.

MacMillan, D.C., Phillip, S. 2008. Consumptive and non-consumptive values of wild mammals in Britain. Mammal Review 38: 189–204.

Martínez-Jauregui, M., Pardos, M., Balogh, P., Chauvin, C., Klopcic, M., Wilhelmsson, E., Herruzo, A.C. 2014. Hunting in European mountain systems: an economic assessment of game gross margins in nine case study areas. European Journal of Wildlife Research 60: 933-936.

Martín-López, B., Iniesta-Arandia, I., García-Llorente, M., Palomo, I., Casado-Arzuaga, I., García Del Amo, D., Gómez-Baggethun, E., Oteros-Rozas, E., Palacios-Agundez, I., Willaarts, B., González, J.A., Santos-Martín, F., Onaindia, M., López-Santiago, C., Montes, C. 2012. Uncovering ecosystem service bundles through social preferences. PLoS ONE 7: e38970.

Martín-López, B., Montes, C., Benayas, J. 2007. The non-economic motives behind the willingness to pay for biodiversity conservation. Biological Conservation 137: 67-82.

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Bauet, E., Hohmann, U., Monaco, A., Ozolins, J., Cellina, S., Podgórski, T., Fonseca, C., Markov, N., Pokorny, B., Rosell, C., Náhlik, A. 2014. Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. Pest Management Science 71: 492-500.

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sáncehz-Zapata, J.A.2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity & Distributions 21:913–924.

Milner, J.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Cdányi, S., Stenseth, N.C. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. Journal of Applied Ecology 43: 721-734.

Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F., Margalida, A., Donázar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A. 2018. Farmer perceptions of the ecosystem services provided by scavengers: what, who and to whom. Conservation Letters 11: e12392

Naidoo, R., Weaver, L.C., Diggle, R.W., Matongo, G., Stuart-Hill, G., Thouless, C. 2016. Complementary benefits of tourism and hunting to communal conservancies in Namibia. Conservation Biology 30: 628-638.

Nieto-Romero, M., Oteros-Rozas, E., González, J.A., Martín-López, B. 2014. Exploring the knowledge landscapes of ecosystem services assessments in Mediterranean agroecosystems: insights for future research. Environmental Science and Policy 37: 121-133.

Nyhus, P.J. 2016. Human-wildlife conflict and coexistence. Annual Review of Environment and Resources 41: 143-171.

Owen-Smith, N. 1988. Megaherbivores: The Influence of very large body size on ecology. In Barnes, R.S.K., Birks, H.J.B., Connor, E.F., Paine, R.T. editors. 1st paperback edition. Cambridge University Press, Cambridge.

Pascual-Rico, R., Morugán-Coronado, A., Botella, F., García-Orenes, F., Sánchez-Zapata, J.A. 2018. Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain. Applied Soil Ecology 127: 136-143.

Pechanec, V., Machar, I., Sterbova, L., Prokopova, M., Kilinova, H., Chobot, H., Cudlin, P. 2017. Monetary valuation of natural forest habitats in protected areas. Forests 8: 427.

Peterson, M.N., Birckhead, J.L., Leong, K., Peterson, M.J., Peterson, T.R. 2010. Rearticulating the myth of human-wildlife conflict. Conservation Letters 3: 74-82.

Popa, B., Pascu, M., Nită, D.M., Borz, S.A., Codreanu, C. 2013. The value of forest ecosystem services in Romanian protected areas – a comparative analysis of management scenarios. Bulletin of the Transilvania University of Brasov 6: 53-62.

Prado, H.M., Murrieta, R.S.S., Adams, C., Brondizio, E.S. 2014. Local and scientific knowledge for assessing the use of fallows and mature forest by large mammals in SE Brazil: Identifying singularities in folkecology. Journal of Ethnobiology and Ethnomedicine 10: 7

Raizada, P., Raghubanshi, A.S., Singh, J.S. 2008. Impact of invasive alien plant species on soil processes: a review. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 78: 288–298.

Ramos, J.A., Bugalho, M.N., Cortez, P., Iason, G.R. 2006. Selection of trees rubbing by red and roe deer in forest plantations. Forest Ecology and Management 222: 39-45.

Ranglack, D.H., Durham, S., du Toit, J.T. 2015. Competition on the range: science vs. perception in a bison-cattle conflict in the western USA. Journal of Applied Ecology 52: 467-474.

Rasmussen, L.V., Christensen, A.E., Danielsen, F., Dawson, N., Martin, A., Mertz, O., Sikor, T., Thongmanivong, S., Xaydongvanh, P. 2017. From food to pest: Conversion factors determine switches between ecosystem services and disservices. Ambio 46: 173.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J. 2014. Status and ecological effects of the world's largest carnivores. Science 343: 151-162.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M.W., Kerley, G.I.H., Levi, T., Lindsey, P.A., MacDonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., van Valkenburgh, B. 2015. Collapse of the world´s largest herbivores. Science Advances 1: 1-12.

Sandom, C.J., Ejrnaes, R., Hansen, M.D.D., Svenning, J.C. 2014 High herbivore density associated with vegetation diversity in interglacial ecosystems. Proceedings of the National Academy of Sciences 111: 4162-4167.

Saunders, M.E., Luck, G.W. 2016. Limitations of the ecosystem services versus disservices dichotomy. Conservation Biology 30: 1363-1365.

Schley, L., Dufrêne, M., Krier, A., Frantz, A.C. 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. European Journal of Wildlife Research 54: 589-599.

Senserini, D., Santilli, F. 2016. Potential impact of wild boar (*Sus scrofa*) on pheasant (Phasianus colchicus) nesting success. Wildlife Biology in Practice 12: 15-20.

Shackleton CM, Ruwanza S, Sanni GKS, Bennett S, de Lacy P, Modipa R, Mtati N, Sachikonye M, Thondhlana G (2016) Unpacking pandora's box: understanding and categorising ecosystem disservices for environmental management and human wellbeing. Ecosystems 19: 587.

Sidorovich, V.E., Tikhomirova, L.L., Je-drzejewska, B. 2003. Wolf Canis lupus numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. Wildlife Biology 9: 103-111.

Snow, N.P., Porter, W.F., Williams, D.M. 2015 Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. Biological Conservation 181: 44-53.

Sobalak, T.M. 2008. Analysis of game management in the Game Breeding Centres of the Poznan RDSF between 1995 and 2004. Folia Forestalia Polonica 50: 81-95.

Velamazán, M., San Miguel, A., Escribano, R., Perea, R. 2018. Use of firebreaks and artificial supply points by wild ungulates: Effects on fuel load and woody vegetation along a distance gradient. Forest Ecology and Management 427: 114-123

Vera, F.W.M. 2000. Grazing Ecology and Forest History [Electronic Resource]. CABI

Vos, J. 2000. Food habits and livestock depredation of two Iberian wolf packs (Canis lupus signatus) in the north of Portugal. Journal of Zoology 251: 457-462.

Wehausen, J.D., Kelley, S.T., Ramey, R.R. 2011 Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. California Fish and Game 97: 7-24.

Wilcove, D.S., Rothstein, D., Dubow, J, Phillips, A., Losos, E. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Young, J.C., Jordan, A., Searke, K.R., Butler, A., Chapman, D.S., Simmons, P., Watt, A.D. 2013 Does stakeholder involvement really benefit biodiversity conservation? Biological Conservation 158: 359-370.

Chapter 3

Ecological niche overlap between co-occurring native and exotic ungulates: insights for a paradigmatic conflict.

Roberto Pascual-Rico, José Antonio Sánchez-Zapata, Joan Navarro, Sergio Eguía, José Daniel Anadón, Francisco Botella

ABSTRACT

Exploitative competition implies an indirect interaction in which a resource exploited by one species is not available for another; e.g., when species share diet or habitat. It plays a key role in the community structure and dynamics. Here we evaluated the niche overlap under cohabit conditions between the exotic aoudad (*Ammotragus lervia*) and the native Iberian ibex (*Capra pyrenaica*) in the Iberian Peninsula, along two main dimensions, the trophic niche and the environmental niche. Then we assessed the spatial segregation of the species. We expected that if a niche overlap was high, competition could drive to spatial segregation to allow co-existence. We analyzed their trophic niche overlap by using the content of stable isotopes δ15N and δ13C in the hair of both species. To establish environmental niche competition, we compared the similarity in their habitat, estimated by environmental niche models based on the fine-scale presence records of each species obtained from field surveys. To test if spatial segregation occurred, we analyzed both species' co-occurrence. Our results indicated that both species shared a similar trophic niche measured by stable isotopes, both species showed a similar distribution of suitable areas, and that both species' environmental niches were more similar than expected. Finally, a negative spatial association was found between the aoudad and Iberian ibex. These results reveal that both species are ecologically similar and suggest that fine-scale spatial segregation might have favoured their co-existence in semiarid Mediterranean mountains. Our results show that integrating information on trophic and environmental niche overlap with fine scale spatial distribution might improve the study of competitive interactions among wild ungulates.

Key words: *Ammotragus*; Assisted colonization; *Capra*; Environmental model; Diet; Stable isotopes

RESUMEN

La competencia por explotación implica una interacción indirecta entre dos o más especies en la que un recurso consumido deja de estar disponible para el resto, por ejemplo, cuando dos especies comparten dieta o hábitat. Este proceso juega un papel importante en la dinámica de las comunidades y su estructura. En este trabajo evaluamos el solapamiento de nicho del arrui (*Ammotragus lervia*), especie exótica, y la cabra montesa (*Capra pyrenaica*), especie nativa, en las sierras en que coexisten de la península ibérica, comparando sus nichos tróficos y ambientales. Después analizamos la segregación espacial de estas especies, que esperábamos encontrar, en el caso de que el solapamiento de nicho fuese elevado, como mecanismo para permitir la coexistencia. Para establecer el solapamiento de nicho trófico medimos el contenido de isótopos estables de δ15N y δ13C contenido en el pelo de ambas especies. Para establecer el solapamiento de nicho, creamos modelos ambientales basados en la presencia de la especie a una escala fina y los comparamos. Realizamos un análisis de coocurrencia para testar si existía segregación espacial entre el arrui y la cabra montesa. Los resultados indicaron que ambas especies comparten un nicho trófico similar establecido a partir de isótopos estables, y una distribución similar por los hábitats disponibles, siendo su nicho ambiental más similar de lo esperado. Encontramos también una asociación espacial negativa entre las especies. Todo ello apunta a que las especies de estudio son ecológicamente similares y que a escala espacial fina la segregación espacial podría favorecer su coexistencia en los sistemas montañosos mediterráneos. Nuestros resultados muestran que integrando información sobre los nichos tróficos y ambientales a escala fina podría mejorarse el estudio sobre las interacciones de competencia entre los ungulados silvestres.

Palabras clave: *Ammotragus*; Colonización asistida; *Capra*; Modelo ambiental; Dieta; Isótopos estables

INTRODUCTION

Interspecific interactions such as competition play a key role in the ecosystem structure and dynamics (Barbosa and Castellanos, 2005; Tilman, 1987). For the competition process to happen, the following conditions must be met: 1) different species must share resources; 2) resources must be limited; 3) the joint exploitation of these resources must negatively affect both species' performance (Milne, 1961; Prins, 2000). Competition can be based on interference or exploitation among sympatric species (Begon et al. 2006). Interference competition happens when both species directly interact, preventing another species from exploiting resources (Begon et al. 2006; Linnell and Strand, 2000). Exploitative competition implies indirect interactions in which a resource consumed by one species is not available for another (Lang and Benbow, 2013; de Boer and Prins, 1990).

Studies that focus on competition between species that exploit the same resources (i.e. intraguild competition) usually encompass ecological processes with species that have co-evolved (Ballejo et al. 2018; Grassel et al. 2015; Wright 2002). Co-evolved competing species can co-exist because they differ in the realized niche; i.e. resources and conditions that a species exploits as a result of interactions with other species (Giller 1984). According to Hutchinson (1957), the niche concept is defined as an n-hyperdimensional volume, where n is the number of dimensions that compose the niche. Therefore, niche differentiation can occur along different dimensions, such as food or habitat. Among the mechanisms that facilitate co-existence and alleviate competition, predation (Chesson 2000) or spatial segregation on fine scales to exploit shared resources are highlighted processes (e.g. Barrio and Hik, 2013).

Novel intraguild competition processes may appear when exotic species are introduced beyond their natural range and interact with the native species they share resources with (Mooney and Cleland 2001). These new interactions can reduce the abundance and richness of native species (Blackburn et al. 2004; Gaertner et al. 2009). Introduced species are considered the second cause of biodiversity loss (Wilcove et al. 1998) and they are associated with alterations of ecosystem processes (Raizada et al. 2008) and the community structure (Hejda et al. 2009). It has also been detected that exotic species may affect the genetic diversity and the evolutionary pathway of native species (Mooney and Cleland 2001). This phenomenon has been evaluated in different areas of the world; e.g., introduced carnivores into Australia (Doherty et al. 2017) or Europe (Bonesi et al. 2004; Harrington et al. 2009), or between exotic and native deer in North America (Faas and Weckerly 2010).

In the case of wild ungulates, introductions usually respond to sport hunting interests (Spear and Chown 2009). Different studies on the competition between exotic and native ungulates have concluded that non native species impair native species (Stewart et al. 2002; Dolman and Wäber 2008; Odadi et al. 2011). Other works have also shown positive effects, such as facilitation processes by non native to native ungulates (Butt and Turner 2012), which reveals that different situations may occur in similar systems.

Besides translocations, wild ungulates are currently in a process of recolonization in developed countries (Apollonio et al. 2010). This rewilding process leads to an increased spatial overlap among ungulates. Considering that current ecosystems are subject to intense human influence which includes the elimination of predators, the presence of livestock and the introduction of exotic species (Latham 1999) novel competition interactions may arise.

Both natural rewilding and introductions are commonplace in Europe, including Mediterranean ecosystems (Apollonio et al. 2010). The Iberian ibex (*Capra pyrenaica*), an endemic ungulate to the Iberian Peninsula, had disappeared in most of its range. Nevertheless, since the mid-twentieth century, its populations have increased and large areas from which it had disappeared have been recolonised (Acevedo and Cassinello 2009).

The aoudad (*Ammotragus lervia*) is an ungulate native from North Africa, whose populations are decreasing in its native range due to habitat loss or degradation and human persecution (Durant et al. 2014). Currently the species is catalogued as vulnerable by IUCN in its native range (Cassinello et al. 2008). However, it has been introduced into several countries of Europe and America in the twentieth century. In southeastern Spain the aoudad was introduced for hunting (Cassinello 1998) and conservation purpose (Valverde 2004) in the 1970s. Dr J.A. Valverde was a renowned biologist that worried about the extinction of Sahara`s megafauna. Thus, Valverde and colleagues brought individuals from the Sahara (Spanish protectorate by that time) of several threaten ungulates (dama gazelle Nanger dama, dorcas gazelle Gazella dorcas, Cuvier`s gazelle Gazella cuvieri, and aoudad) as well as to a captivity breeding center (currently called Experimental Station of Arid Zones, EEZA by its initials in Spanish; http: http://www.eeza.csic.es). The aoudad was the only species to be released in a free range in the SE of the Iberian Peninsula in 1970 (Cassinello 1998). The fact of the introduction of an exotic species outside of its native range for conservation purpose is currently known as "assisted colonization" (Seddon 2010). Thus, the introduction of the aoudad in the Iberian peninsula for conservation purpose might be considered a pioneering example of an assisted colonization before devise that concept.

Since the 1990s, both the aoudad and Iberian ibex have co-existed in some mountains of the Region of Murcia (SE Spain), and the expansion of both species has been apparently influenced by habitat connectivity and interspecific competition (Anadón et al. 2018). Previous studies indicate that the introduced aoudad could compete with native ungulates, particularly with the Iberian ibex (Acevedo et al. 2007; but see Cassinello 2018). Besides the aoudad has been described as a potential hazard to threatened vegetation due to high population densities (Velamazán et al. 2017). Furthermore, crop damage has been also pointed out as another emergent issue leading to the application of management tools such as diversionary feeding to mitigate these impacts (Pascual-Rico et al. 2018). Due to these problems associated with the exotic species, the aoudad was first included in the Spanish catalogue of invasive species in 2013 (Real Decreto 630/2013, Spanish Government) although the population in Murcia Region introduced legally before 2007 was excluded. However, in a sentence by the Spanish Supreme Court (sentence 637/2016) following a demand by conservationist, the aoudad was included as an invasive exotic in all its range within the Spanish territory, which spurred a heated debate among the main stakeholders (i.e. wildlife managers, hunters, ecologist, farmers and conservationists). The potential competition between the aoudad and the Iberian Ibex was one of the main arguments to consider the exotic aoudad as an invasive species. Nevertheless, after national elections the new the Government approved a law (Law 7/2018) to return to the situation in which aoudad populations introduced legally before 2007 are not considered as invasive species. Given the changing legislative situation of a current conservation conflict among the stakeholders abovementioned, it is necessary to assess with scientific criteria the potential competition between the aoudad and the Iberian ibex.

Our main objective with the present study was to evaluate the potential competition between the Iberian ibex (native species) and the aoudad (exotic species) in the mountain ranges where they live in sympatry. Specifically, we evaluated the ecological niche overlap along two main dimensions, the environmental niche and the trophic niche, because they are the commonest partitioned dimensions (Schoener 1983; Toft 1985). Then we assessed the spatial co-occurrence of both species on the fine scale. We expected that if a niche overlap was high, competition could drive to spatial segregation to allow co-existence.

MATERIAL AND METHODS

Study area

The study was conducted in different areas in the Region of Murcia (SE Iberian Peninsula; see Figure 1 and Table S.3.1) where both the Iberian ibex and aoudad (Artiodactyla order) co-exist. This region forms part of the Iberian ibex’s historical range, which drastically declined in the first half of the twentieth century, followed by recovery over the last five decades (Anadón et al. 2018).

The aoudad was introduced into the region in the 1970s for hunting purposes, specifically in the Sierra Espuña Regional Park (37°47′–37°56′N, 1°27′–1°40′W). Since then, this exotic species has spread to other mountains in the region (see Appendices S.3.1 for more biological information about study species). Data on each mountain range in the study area is found in Table S.3.1.

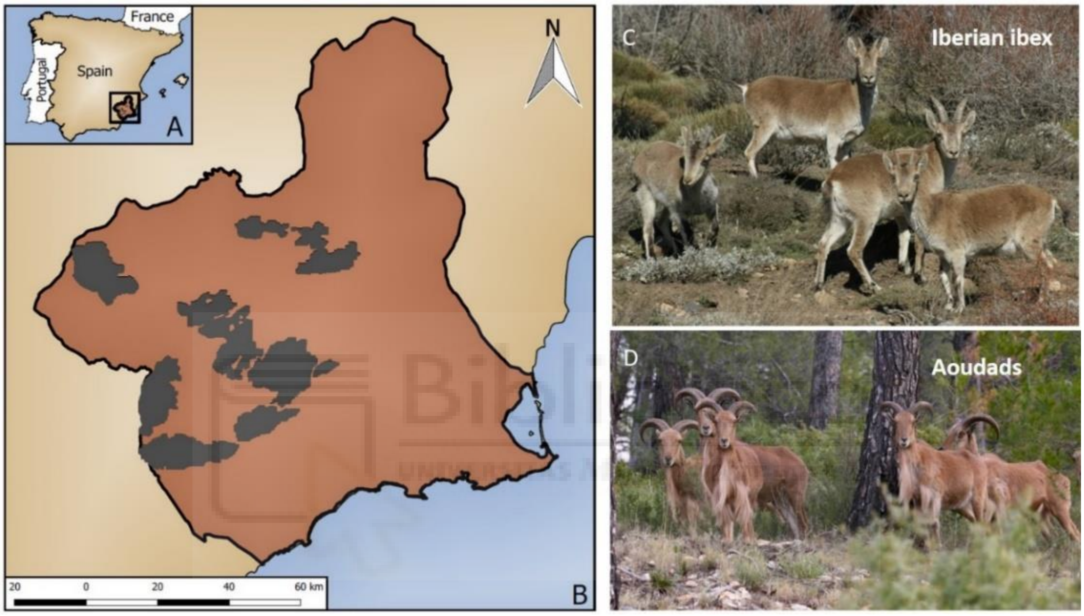

Figure 1. (A) Position of the study area in the Iberian Peninsula. (B) Map of the study area (mountains in the Region of Murcia, SE Spain). Black areas indicate the mountains where the Iberian ibex and the aoudad co-exist. (C-D) pictures of the study species by Sergio Eguía.

Trophic niche overlap

Veterinarians, in collaboration with local hunters, collected hair samples of both ungulates (Iberian ibex n=25; aoudad n=26) during different hunting seasons in 2013 and 2014 in the Region of Murcia (Figure 1). In all cases, the frontal dorsal hair nearest the skin was collected and cut by stainless steel surgical scissors. All hair samples were immediately stored in a plastic tube until their isotopic analyses were conducted. Hair samples were cleaned and powdered. Next 0.3-0.4 mg of each sample was packed into tin capsules. The isotopic analyses were performed at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana (www.ebd.csic.es/lie/index.html). Samples were combusted at 1020ºC using a continuous flow isotope-ratio mass spectrometry system (Thermo Electron) by means of a Flash HT Plus elemental analyzer interfaced with a Delta V Advantage mass spectrometer. The stable isotope ratios were expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite (δ13C) and atmospheric N2 (δ15N). Based on laboratory standards, the measurement error was ± 0.1 and ± 0.2 for δ13C and δ15N, respectively.

The trophic niche overlap was measured by comparing the degree of isotopic overlap between species (Jackson et al. 2011). To calculate the isotopic niche overlap between species, we used the framework proposed by Broennimann et al. (2012), which applies kernel smoothers to species occurrence in a two-dimensional gridded space. This space was defined for the respective overlap analysis by the δ15N and δ13C values of all the individuals (Navarro et al. 2015).

The overlap was calculated using the D-metric, which ranges from 0 (no overlap) to 1 (complete overlap). We applied a permutation-based approach (100 permutations) to evaluate whether the overlap values were higher than expected at random according to the available isotopic space (similarity test, Warren et al. 2008). These analyses were conducted using the 'ecospat' library in R software. Interspecific differences in the δ15N and δ13C values were tested by using Student's t-tests. The significance level for all the tests was set at $p < 0.05$.

Environmental niche overlap

We developed an environmental niche model (ENM) for both species in the mountains that they share. Then we compared the similarity of the resulting models. We used the Maximum Entropy Software, Maxent 3.3.3 k (Phillips and Dudik 2008), to develop an ENM of the two species independently using presence-only data. We compiled presence records of each species using the observations obtained from the autumn censuses of target species made in 2012, 2014, 2015 and 2016 in the mountains where both species were present (Iberian ibex n=174; aoudad n=429). We assigned the presence records to a grid cell matrix of 200 x 200 m of the study area. We used the area under the curve (AUC) that derived from the test data as a yardstick to evaluate the model's efficacy. We considered test AUC values > 0.75 with sufficient discriminatory capacity (Elith 2000).

To predict the habitat suitability of both the Iberian ibex and the aoudad, we used land cover and topography variables as environmental predictors (Table 1). We did not include climate variables because climate is not likely to be a key driving factor in both species' habitat suitability in our study area. Land cover variables represented the percentage cover of the habitat in the study area in a 200 x 200 m grid cell. Topography variables were obtained from a 5-meter resolution digital elevation model, from which the elevation and slope variables were developed.

We employed ENMToolsv.1.4.4 (Warren et al. 2010) to measure the similarity of the ENMs generated with MaxEnt. With this software, we calculated Schoener's (1968) D index to quantify niche similarity, which was estimated by comparing habitat suitability for each grid cell of the study area using ENMs.

To test whether ENMs were more similar than expected by chance, we ran a background test. To do so, the test generates a null distribution for the ENM difference expected between one species and the occurrence points placed at random within the range of the other species. The niche similarity hypothesis among species is rejected if Schoener's D is significantly higher or lower than those expected from the null distribution (Warren et al. 2010). In our case, significantly higher or lower values implies that D is over the 0.975 percentile or below the 0.025 percentile (the equivalent to p = 0.025) of the null distribution values (two-tailed comparison), respectively.

Table 1. Predictor variables used to assess habitat. All the variables were continuous.

Variable		Source
Land cover	Forest	CLC 2012 CC-BY 4.0 ign.es
	Shrubland	
	Grassland	
	Rocky	
	Croplands	
	Artificial areas	
Topography	Elevation	MDT5 2009 CC-BY 4.0 ign.es
	Slope	Derived from MDT5 2009 CC-BY 4.0 ign.es

Spatial segregation

We tested if our study species more or less co-occurred spatially than expected by random on the 200 x 200m grid scale. To calculate the number of cells occupied by at least one species, we used QGIS (2017; http://qgis.osgeo.org). The obtained dataset consisted in a presence–absence matrix with rows taken as species (n=2) and columns as occupied cells (n=465). We used the "co-occur" package in R (Griffith et al. 2016), which applies the probabilistic model of species' co-occurrence (Veech 2013) to assess if species co-occur positively or negatively.

RESULTS

Trophic niche overlap

The δ15N and δ13C values did not differ statistically between species (δ15N, Iberian ibex = 3.68 ± 1.05 ‰, aoudad = 3.38 ± 095 ‰, T = -1.08, p = 0.28; δ13C, Iberian ibex = -23.85 ± 0.66 ‰, aoudad = -23.94 ± 0.87‰, T = -0.42, p = 0.67). Similarly to the isotopic values, the isotopic niche overlap was high between both species (D-index = 0.59, p = 0.23), the trophic niche of the aoudad overlapped 84.4% the trophic niche of the Iberian ibex, and conversely, the trophic niche of the Iberian ibex overlapped 77.6% the trophic niche of the aoudad (Figure 2).

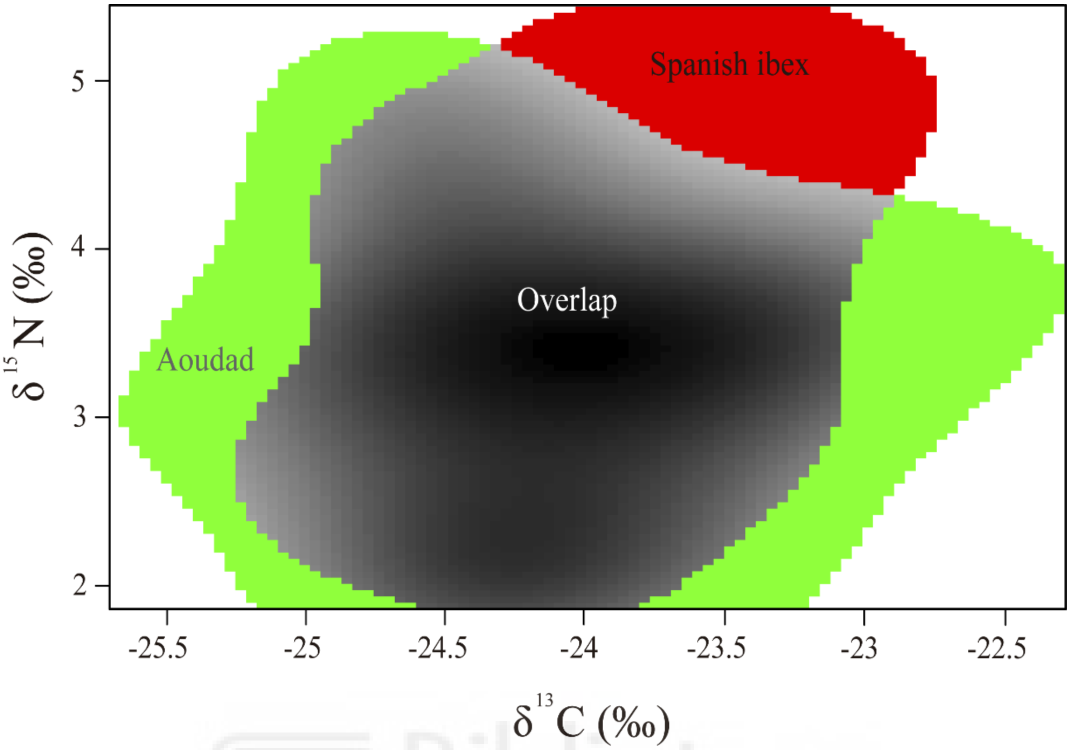

Figure 2. Isotopic niche of both the Iberian ibex and the aoudad, and the overlap niche between them.

Environmental niche overlap

The AUC of the MaxEnt model for the Iberian ibex was 0.88, and the AUC for the aoudad was of 0.82. Both species showed a very similar distribution of suitable areas (Figure 3). For the Iberian ibex, the model showed that this species correlated mainly with elevation and slope, and negatively with croplands. The other variables contributed less than 5% to the model. With the aoudad, croplands contributed the most and negatively to the model, as did slope, elevation and grassland (Figure 4).

The environmental niche overlap between the studied species was quantified using Schoener's D index, which was 0.71. The background test indicated that our study species were more similar than expected by chance (Schoener's D > 97.5% of the null distribution values; Figure 5).

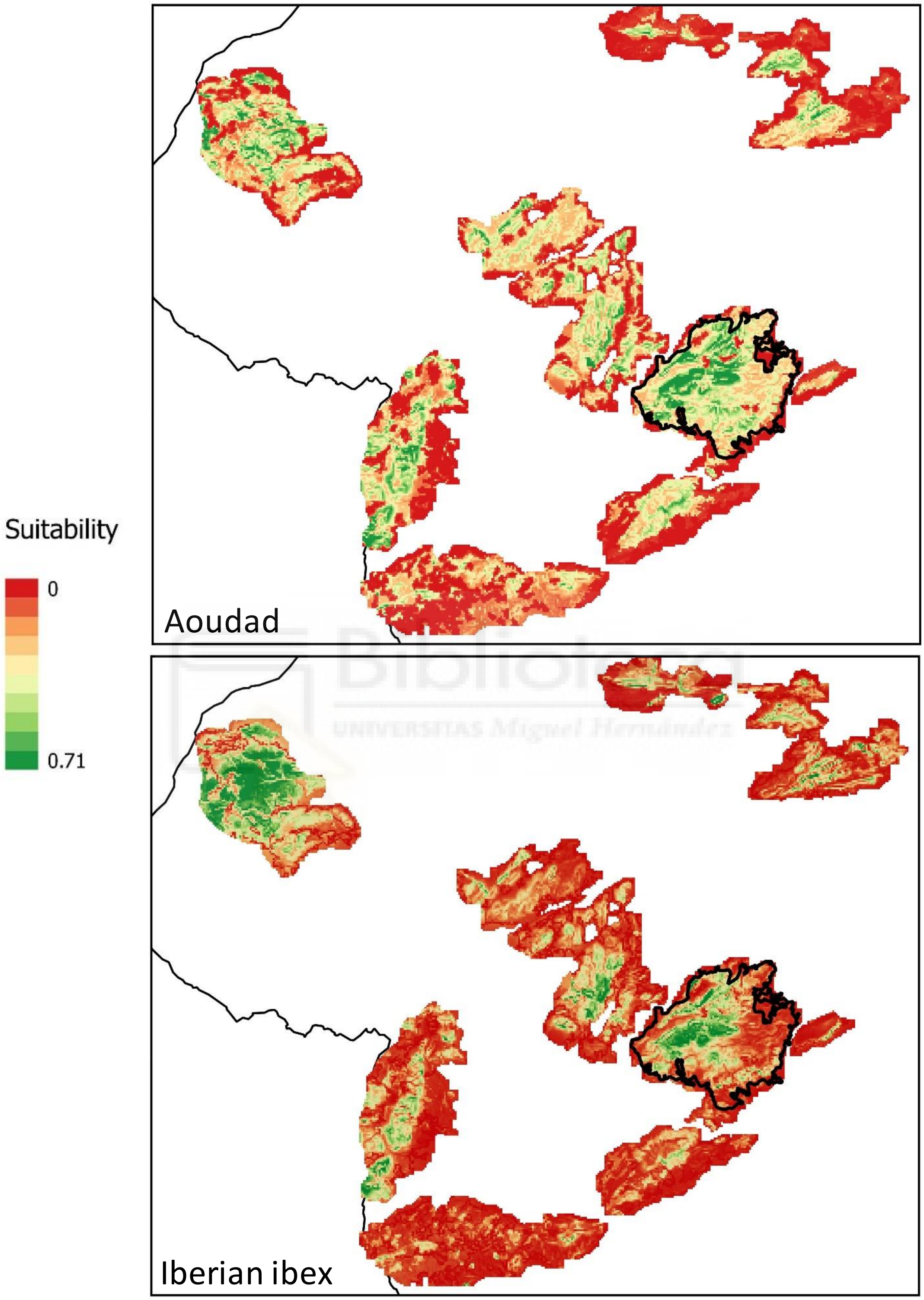

Figure 3. Habitat suitability models for both the aoudad and Iberian ibex as assessed from MaxEnt. The province and the Sierra Espuña Regional Park limits (black lines) are shown for spatial reference.

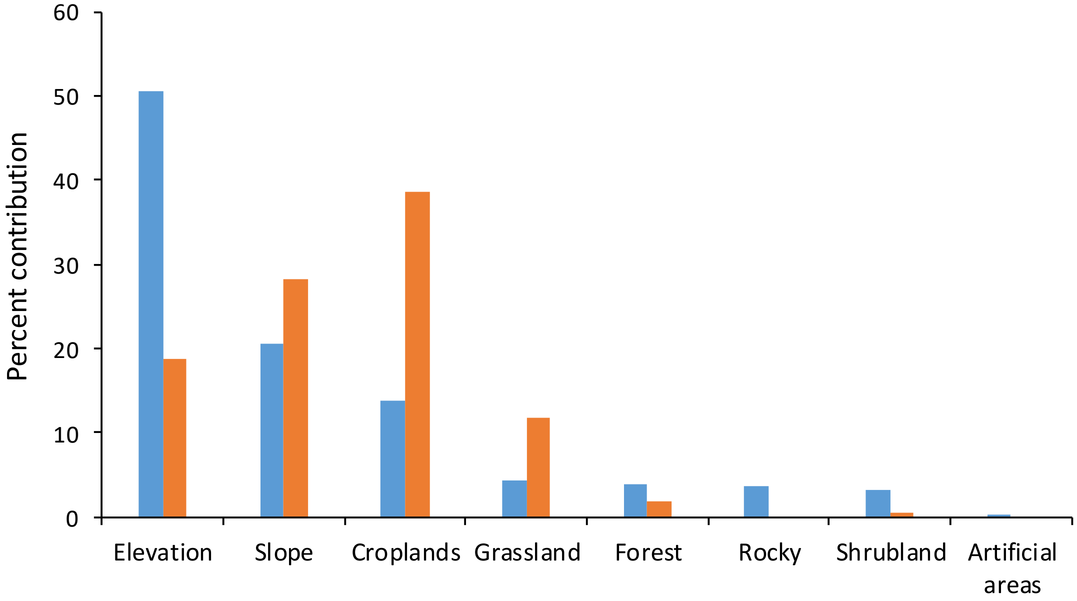

Figure 4. Contribution of the environmental variables to construct the MaxEnt environmental niche models for both the Iberian ibex (blue bars) and aoudad (orange bars).

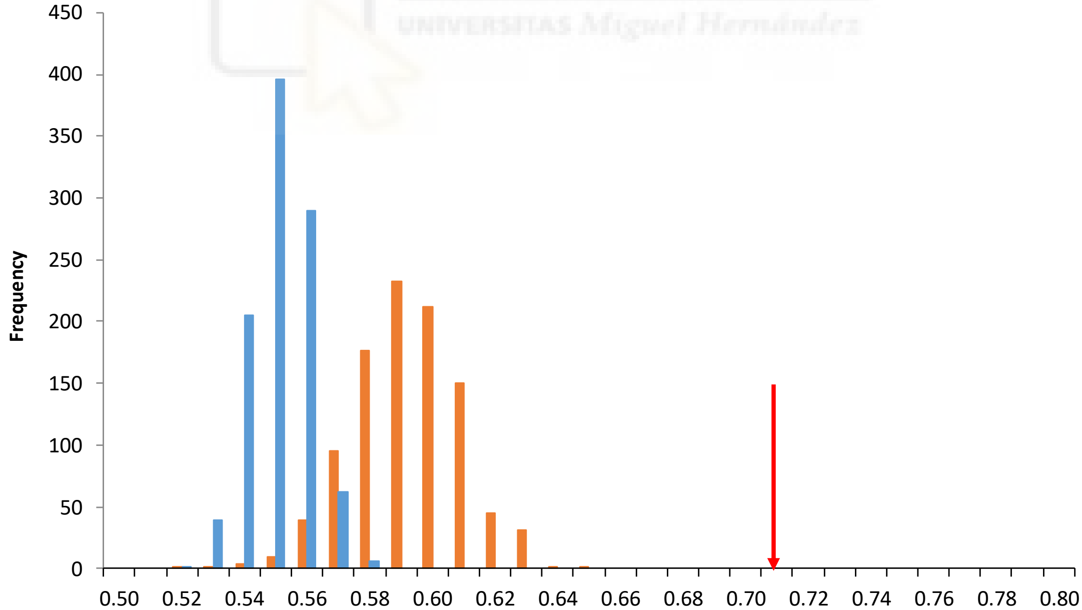

Figure 5. Background test histograms for the Iberian ibex (blue bars) and the aoudad (orange bars). Schoener's D index (red arrow) was higher for the null distributions generated of both the aoudad and Iberian ibex. This indicates that the two species are more similar than expected based on available habitat.

Spatial segregation

In the spatial segregation analysis on the fine scale, of the 465 cells of 200 x 200m occupied by at least one of the two species, we found that only six were both co-occurred species. The spatial co-occurrence analysis showed a negative significant association between the Iberian ibex and the aoudad ($p < 0.001$).

DISCUSSION

Our study case provides us with the opportunity to evaluate, in several ways, the differences in the ecological niche between exotic and native species of the same ecological guild. According to the stable isotope analysis results, the Iberian ibex and the aoudad showed high trophic niche similarity. Regarding habitat selection based on environmental niche models, the study species showed a large overlap in habitat use, but with slight differences on the fine scale. In the co-occurrence test, as the studied species showed a negative association, they avoided co-occurring on the fine scale. These results indicate that both species potentially compete in the trophic and environmental niche dimensions, and that spatial segregation might be a key mechanism to allow for long-term co-existence.

Trophic niche overlap

Among its many uses, the stable isotope analysis is a useful tool employed for reconstructing diets (Kelly 2000, Layman et al. 2012). δ15N is a proxy of a species' trophic level (Peterson and Fry 1987) and, although herbivores can consume vegetation with different δ15N levels (Pacyna et al. 2018), no differences were found in our study species. Nevertheless, similar δ13C values indicate that species feed on the same kind of vegetation, in our case C3 plants; i.e. they were mainly browsers in our study area. However, it must be considered that the feeding patterns of ungulates do not remain constant over time and some species show high feeding plasticity (Acevedo and Cassinello 2009; Lehmann et al. 2011). Studies about the Iberian ibex have demonstrated that browsing focuses on shrub or tree species. (Martínez 1989; Martínez 2002). The aoudad in the southeast of the Iberian Peninsula also showed preference for shrub species (Fernández-Olalla et al. 2016). Moreover, our study species also feed on grass and forb species (Martínez 1989; Martínez 2002; San Miguel et al. 2010). Therefore, the proportion of browse, grass and forb eaten by both the Iberian ibex and the aoudad might depend on vegetation availability, season and the weather conditions (Cassinello 1998; Wilson and Mittermeier 2011). For example in their natural distribution area, both species can habit from sea level up to about 3000 – 4000 m (Cassinello 1998; Granados et al. 2007), which indicates that they can occupy ecosystems with different plant communities. Moreover, the dietary plasticity of both ungulates allows them to feed on less palatable plants, such as Rhamnus lycioides bushes and Pinus halepensis trees (San Miguel et al. 2010). In our case, and according to the values established by Moreno-Gutiérrez et al. (2012) for δ13C of leaf cellulose for several plant species, S. tenacissima forbs and R. lycioides bushes may form an important part of the diet of both the Iberian ibex and the aoudad in our study area.

The aoudad showed a higher standard deviation of the δ13C levels than the Iberian ibex. Hence its trophic amplitude was wider. The trophic niche overlap of the aoudad on the Iberian ibex was higher than that of the Iberian ibex on the aoudad. These results may indicate that the aoudad feeds on a higher diversity of plants than the Iberian ibex, which could be interpreted as an advantage for the exotic species versus the native species. Nevertheless, native herbivores may have narrower trophic niches than sympatric exotic species because the diet of the former includes fewer items, but exploits better the resource by feeding on the most nutritious plants available (Jarman and Sinclair 1979; Reus et al. 2017).

Environmental niche overlap

The ecological niche models reveal that both the Iberian ibex and the aoudad similarly respond to habitat featuress, although the percentage contribution of each variable varied. The distribution of both species is positive linked to elevation and slope, and altered areas (i.e. croplands) appeared to be avoided. It is interesting that despite including only the mountain ranges where both species cohabit in this study, the ENMs slightly differed from one another. This means that the species in these restricted areas did not distribute in the same way. These results agree with previous studies conducted for both species (Acevedo et al. 2007; Anadón et al. 2018).

One of the ways to detect ecological niche differences is by comparing the ENMs developed by the MaxEnt software, which has been demonstrated as the most capable method for modelling distributions of mammals and other species (Hernandez et al. 2008; Phillips et al. 2006). According to de Boer and Prins (1990), a large overlap in habitat use could be a sign of non problematic co-existence between two species, while a small overlap might indicate segregation processes due to competition. The niche overlap found for our study species was large (Schoener's D index=0.71), and the background test showed that the environmental niches for both species were more similar than expected. This may be related to the fact that both species (included in the Caprini tribe) present morphological, biological and behavioural similarities.

Spatial segregation

If the niche overlap was large, we expected competition to possibly drive to spatial segregation. Our results showed that spatial segregation could already be acting as a mechanism to allow for co-existence, despite the interaction noted between our study species being a result of recent human intervention (with no common evolutionary history). Therefore, if we consider that our results indicate that both species are ecologically similar in terms of the evaluated niche dimensions and the detected spatial segregation, then both species could compete, especially when resources are limited; e.g., when environmental perturbations occur, such as drought periods. Competition between both the Iberian ibex and the aoudad could lead to one species' displacement, and even to one of them eliminating the other through the principle of competitive exclusion; i.e. one competing species eliminating or excluding another species (Hardin 1960). To determine the output (i.e. competitive exclusion or co-existence), it will be necessary to estimate the competition coefficient of each species and the carrying capacity of the environment in future research.

In summary, in the given conditions, the strong similarity in the trophic and environmental niche of both the Iberian ibex and the aoudad indicates potential competition between them. However, the spatial segregation on the fine scale seems to act as a mechanism to facilitate the co-existence between the native and exotic ungulate species.

Currently the aoudad has been eliminated of the Spanish Catalogue of Invasive Exotic Species for some areas where it was introduced. However, Carboneras et al. (2017) created a prioritised list of invasive alien species where the species are ranked according to their potential threat to biodiversity in Europe, and the aoudad is considered in a widespread phase invasion and major impact to biodiversity and ecosystems. This study sheds light on the research gap that exists on the interaction between the Iberian ibex and the exotic aoudad, which can be applied in the development of wildlife policies aimed at better management and conservation of the species.

The zoologist J.A. Valverde anticipated the future consequences of human activities on the Sahara's megafauna (see Durant et al. 2014; Brito et al. 2018) when he proposed the aoudad introduction in the Iberian Peninsula to conserve the species. However, this pioneering assisted colonization example, accomplished more than 40 years ago, failed to forecast the ongoing conflicts among different stakeholders and native species from a conservation perspective. Nowadays, assisted colonization is a controversial tool due to the possible consequences that may result (Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009), both short and long-term. Although it is rarely used (e.g. Kuussaari et al. 2011), there are several proposals for its application (e.g. https://theaustralianrhinoproject.org) that should be done with caution, if finally this tool is applied (Loss et al. 2011).

Ungulates (Artiodactyla order) are the mammals with the highest proportion of successful introductions around the world (Clout and Russell 2007). In their natural ranges, their abundance and distribution are increasing, which also occurs in new colonised areas for introduced species (Apollonio et al. 2010). The consequences of herbivore ungulate introduction, whatever the reason, can alter biodiversity interactions (Vázquez and Simberloff 2003), and tend to strongly impact the new ecosystems that they occupy (Duffy 2003). One of the new processes that may appear is competition between species. However, competition interaction are not easy to demonstrate in the field because manipulations to evaluate changes in carrying capacity and population dynamics in relation to the relative abundance of interacting species are difficult to perform in the wild (Hakkarainene and Korpimäki 1996). Nevertheless, our results show that integrating information on trophic and environmental niche overlap with fine scale spatial distribution might improve the study of competitive interactions among wild ungulates.

ACKNOWLEDGMENTS

We thank veterinaries M.J. Gens and F. Escribano and the Regional Ministry of Tourism, Culture and Environment of the Region of Murcia. Many thanks to P. Abellán for his help with the environmental niche analysis. RPR was supported by a pre-doctoral grant from the Spanish Ministry of Education (FPU13/05460). JN was funded by the Spanish National Program Ramón y Cajal (RYC-2015-17809).

REFERENCES

Acevedo, P., Cassinello, J. 2009. Biology, ecology and status of Iberian ibex *Capra pyrenaica*: a critical review and research prospectus. Mammal Review 39: 17-32.

Acevedo, P. Cassinello, J., Hortal, J., Gortázar, C. 2007. Invasive exotic aoudad (*Ammotragus lervia*) as a major threat to native Iberian ibex (*Capra pyrenaica*): a habitat suitability model approach. Diversity & Distributions 13: 587-597.

Anadón, J.D., Pérez-García, J.M., Pérez, I., Royo, J., Sánchez-Zapata, J.A. 2018. Disentangling the effects of habitat, connectivity and interspecific competition in the range expansion of exotic and native ungulates. Landscape Ecology 33: 597-608.

Apollonio, M., Andersen, R., Putman, R. 2010. European ungulates and their management in the 21st century. Cambridge Univ. Press, Cambridge.

Ballejo, F., Lambertucci, S.A., Trejo, A., de Santis, L.J.M. 2018. Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis. Bird Conservation International 28: 390-402.

Barbosa, P., Castellanos, I. 2005. Ecology of Predator-prey Interactions. Oxford University Press, New York.

Barrio, I.C., Hik, D.S. 2013. Good neighbours? Determinants of aggregation and segregation among alpine herbivores. Ecoscience 20: 276-282.

Begon, M., Townsend, C.R., Harper, J.L. 2006. Ecology: from individuals to ecosystems. Blackwell Publishing, Oxford.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J. 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305: 1955-1958.

Bonesi, L., Chanin, P., Macdonald, D.W. 2004. Competition between Eurasian otter Lutra lutra and American mink Mustela vison probed by niche shift. Oikos 106: 19-26.

Brito, J.C., Durant, S.M., Pettorelli, N., Newby, J., Canney, S., Algadafi, W., Rabeil, T., Crochet, P-A., Pleguezuelos, J.M., Wacher, T., de Smet, K., Vasconcelos, D.G., Ferreira da Silva, M.J., Martínez-Freiría, F., Abáigar, T., Campos, J.C., Comizzoli, P., Fahd, S., Fellous, A., Halilou, H., Garba, M., Hamidou, D., Harouna, A., Hatcha, M.H., Nagy, A., Silva, T.L., Sow, A. S., Vale; C.G., Boratyński, Z., Rebelo, H., Carvalho, S.B. 2018. Armed conflicts and wildlife decline: Challenges and recommendations for effective conservation policy in the Sahara-Sahel. Conservation Letters 11:e12446.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E., Graham, C.H., Guisan, A. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21: 481-497.

Butt, B., Turner, M.D. 2012. Clarifying competition: the case of wildlife and pastoral livestock in East Africa. Pastoralism 2: 1-15.

Carboneras, C., Genovesi, P., Vilà, M., Blackburn, T.M., Carrete, M., Clavero, M., D'hondt, B., Orueta, J.F., Gallardo, B., Geraldes, P., González-Moreno, P., Gregory, R.D., Nentwig, W., Paquet, J-Y., Pyšek, P., Rabitsch, W., Ramírez, I., Scalera, R., Tella, J.L., Walton, P., Wynde, R. 2018. A prioritised list of invasive alien species to assist the effective implementation of EU legislation. Journal of Applied Ecology. 55: 539-547.

Cassinello, J. 1998. *Ammotragus lervia*: a review on systematics, biology, ecology and distribution. Annales Zoologici Fennici 35: 149-162.

Cassinello, J. 2018. Misconception and mismanagement of invasive species: The paradoxical case of an alien ungulate in Spain. Conservation Letters 11:e12440

Cassinello, J., Cuzin, F., Jdeidi, T., Masseti, M., Nader, I., de Smet, K. 2008. *Ammotragus lervia*. The IUCN Red List of Threatened Species 2008: e.T1151A3288917.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution and Systematics 31: 343-366.

Clout, M., Russel, J.C. 2007. The invasion ecology of mammals: a global perspective. Wildlife Research 35: 180-184.

De Boer, W.F., Prins, H.H.T. 1990. Large herbivores that strive mightily but eat and drink as friends. Oecologia 82: 264-274.

Doherty, T.S., Dickman, C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G. 2017. Impacts and management of feral cats Felis catus in Australia. Mammal Review 47: 83-97.

Duffy, J.E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6: 680-687.

Durant, S.M., Wacher, T., Bashir, S., Woodroffe, R., Ornellas, P., Ransom, C., Newby, J., Abáigar, T., Abdelgadir, M., El Alqamy, H., Baillie, J., Beddiaf, M., Belbachir, F., Belbachir-Bazi, A., Berbash, A. A., Bemadjim, N.E., Beudels-Jamar, R., Boitani, L., Breitenmoser, C., Cano, M., Chardonnet, P., Collen, B., Cornforth, W.A., Cuzin, F., Gerngross, P., Haddane, B., Hadjeloum, M., Jacobson, A., Jebali, A., Lamarque, F., Mallon, D., Minkowski, K., Monfort, S., Ndoassal, B., Niagate, B., Purchase, G., Samaïla, S., Samna, A.K., Sillero-Zubiri, C., Soultan, A. E., Stanley Price, M.R., Pettorelli, N. 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Diversity & Distributions 20: 114-122.

Elith, J. 2000. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants, in: Ferson, S., Burgman, M. (Eds.), Quantitative methods for conservation biology. Springer, New York, pp. 39-58.

Faas, C.J., Weckerly, F.W. 2010. Habitat interference by axis deer on white-tailed deer. Journal of Wildlife Management 74: 698-706.

Fernández-Olalla, M., Martínez-Jauregui, M., Perea, R., Velamazán, M., San Miguel, A. 2016. Threat or opportunity? Browsing preferences and potential impact of *Ammotragus lervia* on woody plants of a Mediterranean protected area. Journal of Arid Environments 129: 9-15

Gaertner, M., Den Bree, A., Hui, C., Richardson, D.M. 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Progress in Physical Geography 33: 319-338.

Giller, P.S. 1984. Community structure and the niche. Chapman and Hall, London.

Granados, J.E., Soriguer, R.C., Pérez, J.M., Fandos, P., García-Santiago, J. 2007. *Capra pyrenaica*, Schinz 1838, in: Palomo, L.J., Gisbert, J., Blanco, J.C. (Eds.), Atlas y Libro Rojo de los Mamíferos terrestres de España. Direción General para la Biodiversidad-SECEM-SECEMU, Madrid, pp. 588.

Grassel, S.M., Rachlow, J.L., Williams, C.J. 2015. Spatial interactions between sympatric carnivores: asymetric avoidance of an intraguild predator. Ecology & Evolution 5: 2762-2773.

Griffith, D.M., Veech, J.A., Marsh, C.J. 2016. Cooccur: probabilistic species co-occurrence analysis in R. Journal of Statistical Software 69: 1-17.

Hakkarainen, H., Korpimaki, E. 1996. Competitive and Predatory Interactions among Raptors: An Observational and Experimental Study. Ecology 77: 1134-1142.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292-1297.

Harrington, L.A., Harrington, A.L., Yamaguchi, N., Thom, M.D., Ferreras, P., Windham, T.R., Macdonald, D.W. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90: 1207-1216.

Hejda, M., Pysek, P., Jarosik, V. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97: 393-403.

Hernandez, P.A., Franke, I., Herzog, S.K., Pacheco, V., Paniagua, L., Quintana, H.L., Soto, A., Swenson, J.J., Tovar, C., Valqui, T.H., Vargas, J., Young, B.E. 2008. Predicting species distributions in poorly-studied landscapes. Biodiversity & Conservation 17: 1353-1366.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H.P., Thomas, C.D. 2008. Assisted colonization and rapid climate change. Science 321: 345-346.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia 22:415-427.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80: 595-602.

Jarman, P.J., Sinclair, A.R.E. 1979. Feeding strategy and pattern of resource partitioning in ungulates, in: Sinclair, A.R.E., Norton-Griffiths, M. (Eds.), Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago, pp. 130-160.

Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78: 1-27.

Kuussaari, M., Heikkinen, R.K., Heliölä, J., Luoto, M., Mayer, M., Rytteri, S., von Bagh, P. 2015. Successful translocation of the threatened Clouded Apollo butterfly (*Parnassius mnemosyne*) and metapopulation establishment in southern Finland. Biological Conservation 190: 51-59.

Lang, J.M., Benbow, M.E. 2013. Species interactions and competition. Nature Education Knowledge 4:8.

Latham, J. 1999. Interspecific interactions of ungulates in European forests: an overview. Forest Ecology and Management 120: 13-21.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Review 87: 545-562.

Lehmann, D., Mfune, J.K.E., Gewers, E., Cloete, J., Brain, C., Woigt, C.C. 2011. Dietary plasticity of generalist and specialist ungulates in the Namibian desert: a stable isotopes approach. PloS ONE 8: e72190.

Linnell, J.D.C., Strand, O. 2000. Interferences interactions, co-existence and conservation of mammalian carnivores. Diversity & Distributions 6: 169-176.

Loss, S.R., Terwilliger, L.A., Peterson, A.C. 2011. Assited colonization: integrating conservation strategies in the face of climate change. Biological Conservation 144: 92-100.

Martínez, T. 1989. Recursos tróficos de la cabra montés (*Capra pyrenaica*, Schinz, 1938) en la sierra de Gredos, durante otoño e invierno. Ecología 3: 179-186.

Martínez, T. 2002. Summer feeding strategy of Spanish ibex *Capra pyrenaica* and domestic sheep Ovis aries in south-eastern Spain. Acta Theriologica 47: 479-490.

Milne, A. 1961. Definition of competition among animals. Cambridge University Press, Cambridge.

Mooney, H.A., Cleland, E.E. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences 98: 5446-5451.

Moreno-Gutiérrez, C., Dawson, T.E., Nicolás, E., Querejeta, J.I. 2012. Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem. New Phytologist 196: 489-496.

Navarro, J., Cardador, L., Brown, R., Phillips, R.A. 2015. Spatial distribution and ecological niches of non-breeding planktivorous petrels. Scientific Reports 5:12164.

Odadi, W.O., Karachi, M.K., Abdulrazak, S.A., Young, T.P. 2011. African wild ungulates compete with or facilitate cattle depending on season. Science 333: 1753-1755

Pacyna, A.N., Koziorowska, K., Chmiel, S., Mazerski, J., Polkowska, Z. 2018. Svalbard reindeer as an indicator of ecosystem changes in the Arctic terrestrial ecosystem. Chemosphere 203: 209-218.

Peterson, B.J., Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Review Ecology, Evolution and Systematics 18: 293-320.

Phillips, S.J. Anderson, R.P., Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231-259.

Phillips, S.J., Dudik, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161–175.

Prins, H.H.T. 2000. Competition between wildlife and livestock in Africa, in: Prins, H.H.T., Grootenhuis, J.G., Dolan, T.T. (Eds.), Wildlife conservation by sustainable use. Kluwer Academic Publishers, Boston, pp. 51–80.

Raizada, P., Raghubanshi, A.S., Singh, J.S. 2008. Impact of invasive alien plant species on soil processes: a review. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 78: 288–298.

Reus, M.L., de los Ríos, C., Peco, B., Giannoni, S.M., Campos, C.M. 2017. Relaciones tróficas entre mamíferos herbívoros nativos y exóticos del Parque Provincial Ischigualasto (San Juan, Argentina). Ecología Austral 27: 392-403.

Ricciardi, A., Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology and Evolution 24: 248-253.

San Miguel, A., Fernández-Olalla, M., Perea, R., Martínez-Jauregui, M., Rodríguez-Vidal, C. 2010. El arruí (*Ammotragus lervia* Pallas 1777) en Sierra Espuña (Murcia) ¿Amenaza u oportunidad? - Consejería de Presidencia, Dirección General de Medio Ambiente, Murcia.

Schoener, T.W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.

Schoener, T.W. 1983. Field experiments on interspecific competition. American Naturalist 122: 240-285.

Spear, D., Chown, S. L. 2009. Non-indigenous ungulates as a threat to biodiversity. Journal of Zoology 279: 1-17.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J., Johnson, B.K. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83: 229-244.

Tilman, D. 1987. The Importance of the Mechanisms of Interspecific Competition. American Naturalist 129: 769–774.

Toft, C.A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985: 1-21.

Valverde, J.A. 2004. Memorias de un biólogo heterodoxo. V&V, Madrid.

Vázquez, D.P., Simberloff, D. 2003. Changes in interaction biodiversity induced by an introduced ungulate. Ecology Letters 6: 1077-1083.

Veech, J.A. 2013. A probabilistic model for analysing species co-occurrence. Global Ecology and Biogeography 22: 252-260.

Velamazán, M., San Miguel, A., Escribano, R., Perea, R. 2017. Threatened woody flora as an ecological indicator of large herbivore introductions. Biodiversity & Conservation 26: 917-930.

Warren, D.L., Glor, R.E., Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62: 2868–2883.

Warren, D.L., Glor, R.E., Turelli, M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33: 607-611.

Wilcove, D.S., Rothstein, D., Dubow, J, Phillips, A., Losos, E. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.

Wilson, D.E., Mittermeier, R.A. 2011. Handbook of the Mammals of the World. Hoofed Mammals. Lynx Editions, Barcelona.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130: 1-14.

Chapter 4

Is diversionary feeding a useful tool to avoid human-ungulate conflicts? A case study with the aoudad.

Roberto Pascual-Rico, Juan Manuel Pérez-García, Esther Sebastián-González, Francisco Botella, Andrés Giménez, Sergio Eguía, José Antonio Sánchez-Zapata.

This chapter corresponds to the article:

Pascual-Rico, R., Pérez-García, J.M., Sebastián-González, E., Botella, F., Giménez, A., Eguía, S., Sánchez-Zapata, J.A. 2018. Is diversionary feeding a useful tool to avoid human-ungulate conflicts? A case study with the aoudad. European Journal of Wildlife Research 64: 67. DOI: 10.1007/s10344-018-1226-6.

ABSTRACT

Diversionary feeding (i.e. supplementary feeding used to mitigate damage to human activities) is a management tool widely employed to avoid human-wildlife conflicts, which could alter the spatial behaviour of target species, and it can affect other species present in the area, among other effects. We evaluated the effect of diversionary feeding in the spatial behaviour of the aoudad (*Ammotragus lervia*), an exotic ungulate associated with crop damage in the area, and we assessed the use of diversionary feeding stations (DFS) by non-target species. Nine aoudads were tracked with GPS/GSM collars. We compared their core home ranges and number of GPS locations in the DFS before and meanwhile food was available on them. Eight DFS were monitored with cameras to identify which species used the feeding sites. The home ranges changed for some individuals, but this variation was not related to supplementary feeding. Just five out of the nine tracked aoudads used DFS, and the number of GPS locations in the DFS by aoudad increased when food was available. DFS were used by fifteen non-target species of birds and mammals, and especially by the wild boar. Aoudads and wild boars segregated temporally but not spatially in their use of the DFS. Our study suggests that diversionary feeding had a limited effect on the spatial behaviour of the aoudad, suggesting that its effectiveness to reduce crop damage may be restricted.

Keywords: *Ammotragus lervia*; co-occurrence; wildlife management; home range; non-target species.

RESUMEN

La alimentación suplementaria empleada para mitigar el daño a las actividades humanas es una herramienta de gestión ampliamente utilizada para evitar conflictos entre seres humanos y la fauna silvestre. Esta herramienta podría alterar el comportamiento espacial de la especie a la que va dirigida, así como a otras especies presentes en el área. En este trabajo evaluamos el efecto de la alimentación suplementaria en el comportamiento espacial del arrui (*Ammotragus lervia*), un ungulado exótico asociado con daños a cultivos, y evaluamos el uso de las estaciones de alimentación por especies no objetivo. Se marcaron nueve arruis con collares GPS/GSM y comparamos las áreas de campeo y las visitas a los comederos antes y durante los aportes suplementarios. Ocho comederos fueron monitoreados con cámaras para identificar qué especies los usaban. Las áreas de campeo cambiaron para algunos de los individuos marcados, pero esta variación no se relacionó con la alimentación suplementaria. Solo cinco de los nueve arruis marcados usaban los comederos, y el número de visitas a los comederos aumentó cuando había comida disponible. Además, detectamos que quince especies de aves y mamíferos no objetivo de los aportes suplementarios usaban los comederos, y especialmente el jabalí. Arruis y jabalíes se segregaban temporalmente en los comederos, pero no espacialmente. Nuestro estudio apunta a que los aportes suplementarios tuvieron un efecto limitado en el comportamiento espacial del arrui, lo que sugiere que su efectividad para reducir el daño a cultivos puede ser limitada.

Palabras clave: *Ammotragus lervia*; coocurrencia; gestión de la fauna silvestre; área de campeo; especies no objetivo.

INTRODUCTION

Supplementary feeding is a usual practice as a wildlife management tool. For example, it can be used to help depleted populations of threatened species (Piper 2005; González et al. 2006; López-Bao et al. 2008; Krofel and Jerina 2016; Cortés-Avianza et al. 2016). Supplementary feeding is also used for human interests to facilitate wildlife observations such as touristic attractions (Orams 2002; Robb et al. 2008; Corcoran et al. 2013) or for hunting purposes to obtain good trophies for hunters and improve the quality of the game species (Putman and Staines 2004; Inslerman et al. 2006).

Supplementary feeding can also be used as a tool to mitigate human-wildlife conflicts and in this case it is known as diversionary feeding (Kubasiewicz et al. 2016). Forest damage (Gundersen et al. 2004; Sahlsten et al. 2010), crop damage (Dunkley and Cattet 2003), vehicle collisions (Snow et al. 2015) or predation of game species are some of the most relevant human-wildlife conflicts (Kubasiewicz et al. 2016). These conflicts are the result of increased interactions between humans and wildlife and they are characterized by having adverse effects from humans to wildlife and vice versa (Redpath et al. 2013).

Supplementary or diversionary feeding stations provide pulsed resources because large quantities of the resource become temporary available (Yang et al. 2008). Wildlife responds to these peaks in different ways depending on the species and on the individual behaviour of animals (Bergmüller and Taborsky 2010). Ungulate populations have a slow rate of population increase, so the short-term effects of diversionary feeding in these species are not reflected in population growth (Ostfeld and Keesing 2000). However, as observed for other species, diversionary feeding can affect ungulate spatial movements patterns, large-scale migrations or survival, which in a long-term could favour population growth (Robb et al. 2008; Blanco et al. 2011; Corcoran et al. 2013; Krofel and Jerina 2016; Cortés-Avianza et al. 2016). All these aspects make supplementary feeding a controversial management tool (Milner et al. 2014).

Besides the effects on the species to which diversionary feeding is intended, another non-target species can be affected by these inputs. For example, the abundance of some non-target species can vary due to habitat alteration in areas close to the feeding stations (Pedersen et al. 2014) and predation pressure on nests may increase due to animal concentration (Selva et al. 2014; Oja et al. 2015). Also, the use of feeding stations by different species could be a potential point for disease transmission because of their high-use (Bowman et al. 2015), producing a sanitary problem.

In 1970 an exotic ungulate, the aoudad (*Ammotragus lervia*) original from North Africa, was introduced in Sierra Espuña regional park (SE, Spain) because of hunting interests. The population rapidly increased during the following years, spreading in the region (Anadón et al. 2018). In the 1990's the population was drastically reduced because of sarcoptic mange outbreak (González-Candela 2002). To help the species recover from the outbreak, the managers of the regional park placed supplementary feeding stations. In 2009, the population had reached similar levels to those previous to the sarcoptic mange outbreak (Eguía et al. 2015). Population growth could have been favoured by the species' high birth rate, being twin births (~25% of total births) and multiple births per year relatively common (Cassinello 1998). This population increase resulted in the appearance of conflicts with farmers due to crop damage in areas around the regional park. As a response, the managers continued the supplementary feeding in order to avoid crop damage by reducing the home range and movements of the aoudad outside the regional park. Thus, supplementary feeding stations were transformed to diversionary feeding stations (DFS).

Our study aims to determine the effect of DFS on the spatial behaviour of the target species (i.e. the aoudad). We also aim to identify which other wildlife species may be affected by diversionary feeding. The specific objectives of our study are to assess 1) how the DFS affect the movement patterns of the aoudad; 2) which other non-target species are using the resources provided by the DFS; and 3) the spatio-temporal partitioning in the use of the DFS by different wildlife species, to identify possible interactions between the species. We predict that by providing food, the home range of the aoudad will be reduced around the DFS and that the number of encounters in the DFS of the species will increase. We also predict that other non-target species will use the food inputs, competing for the resources. This competition may be reflected in temporal and spatial segregation patterns among the competing species.

MATERIAL AND METHODS

Study area

The study was conducted in the Sierra Espuña regional park in southeast Spain (37°47′–37°56′N 1°27′–1°40′W). It occupies an area of 17,800 ha and includes habitats ranging thermo-, meso- and supra-Mediterranean from 300 to 1500 m.a.s.l. Pinus halepensis woods, scrublands and pasture dominate mountain range landscape. Rainfall ranges from 277 mm in the lower part of the mountains to 510 mm in the upper parts of the park. Average annual temperatures also follow an altitudinal gradient ranging from 12.8–18.4 °C.

During the previous year of the study (2014), five different municipalities of Murcia (Aledo, Alhama de Murcia, Mula, Pliego, Totana) registered crop damage close to Sierra Espuña Regional Park (< 5 km). A total of 71 cases were detected by the Regional Government. Mean distance from DFS to detected crop damage was 9.16 km, ranging from 1.11 km to 18.92 km.

Sixteen DFS (average size ± SD: 350.0 ± 129.6 m2) were located in the West and South of the regional park (Figure 1) in areas accessible to the entire aoudad population. DFS were active from mid-July to early October during 2015. The study was performed during summer, which coincide with the dry season with high temperatures. In the study year, the summer average temperature was higher than the average. Summer precipitations were overall normal, except for some months (July, August and September) that were considered wet (Table S.4.1; AEMET 2015). Weekly, 35 kg of fodder composed of a mixture of corn, barley, oats, pelleted sugar beet pulp and pelleted lucerne meal and about 10 kg of lucerne (*Medicago sativa*) were deposited on bare ground into each DFS for aoudads.

Aoudad home ranges and feeding stations use

The population of aoudads during the study period was estimated in 1286 individuals (CI: 755-2192) (Eguía et al. 2015). We tracked nine aoudads (4 males and 5 females) belonging to different social groups from this population. Animals were captured between April 14th and May 14th, and they were released in the same point where they were captured, with no transportation. Mean distance from aoudad released points to DFS was 6.2 km, ranging from 0.2 km to 12.8 km. Tracked aoudad ages ranged from 2 to 11 years and with a mean (± SD) weight of 39.44 ± 6.35 kg (Table 1). Aoudads were captured using a trap drawer and a stalking technique with an anaesthetic rifle. All capture proceedings were conducted following ethics statements (procedure authorized by the regional government, ref 201500036926). During captures, we were accompanied with at least one veterinary, public gamekeepers and rangers (see acknowledgements). Aoudads were tracked with GPS/GSM collars (Vertex Lite GSM made by Vectronic Aerospace GmbH) that registered positions every 2 hours. To reduce GPS error we used data Dilution of Precision (DOP) less than 10, which implies that the receiver uses at least five satellites to calculate the position. Lower levels of DOP indicate less error in the position (Langley, 1999).

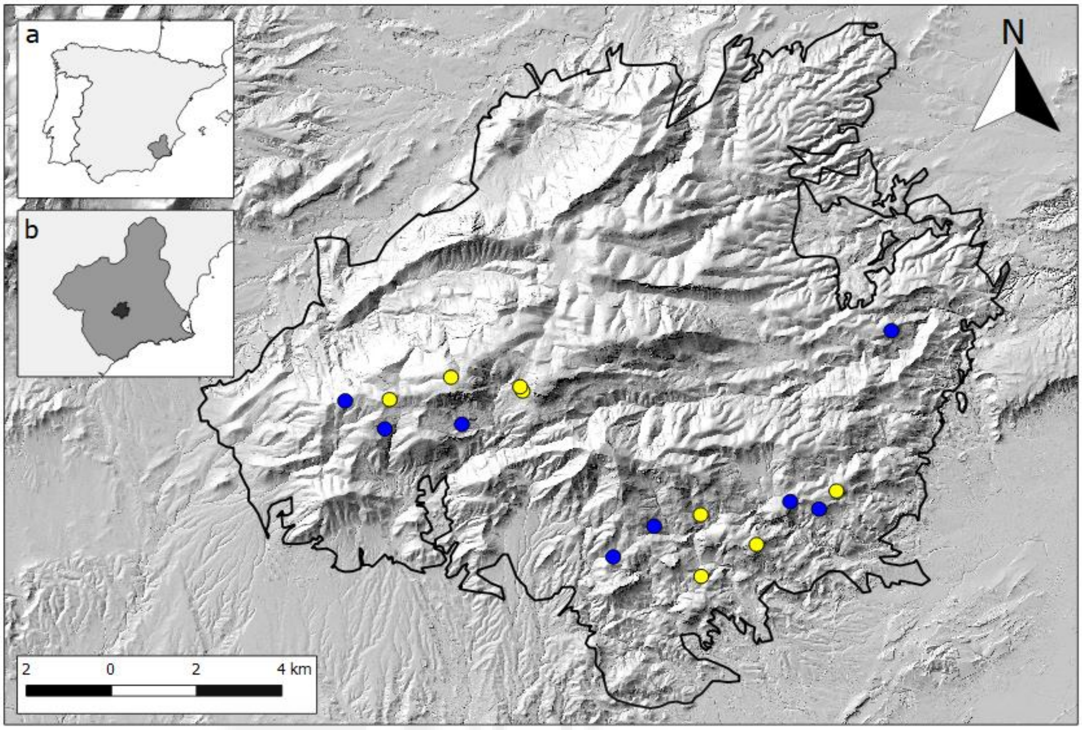

Figure 1. Sierra Espuña regional park. The 16 DFS are indicated with circles (yellow and blue). Blue circles represent DFS monitored with cameras traps. a) Region of Murcia in peninsular Spain. b) Sierra Espuña regional park in the Region of Murcia (dark grey).

Table 1. Tracked animals. Core home ranges (k50%) are in km2 during both studied periods. CHR before: core home range before diversionary feeding; CHR during: core home range during diversionary feeding. GPS locations in the DFS: percentage of days that tracked animals used DFS of the total tracked days for each study period, before and during diversionary feeding.

Animal	Sex	Age	CHR before	CHR during	GPS locations in the DFS before	GPS locations in the DFS during
B	♂	4	1.41	1.76	0.0	0.0
C	♀	11	3.67	1.23	3.1	52.3
D	♀	4	0.62	1.00	31.3	50.8
E	♀	8	0.99	0.58	9.4	0.0
F	♂	2	0.40	0.76	4.7	9.2
G	♀	2	0.94	0.65	0.0	0.0
H	♀	7	2.14	1.13	10.9	6.2
I	♂	3	3.28	0.31	29.2	40.0
J	♂	5	1.50	1.29	0.0	0.0

Home ranges were estimated using a fixed kernel (Worton, 1989) with the amount of smoothing determined by the reference smoothing parameter (Href). We considered only the core home range (isopleths of 50% probability) because this represents the main area used by the ungulates, often associated to important resources (Harris et al. 1990). Core home ranges were estimated for two periods, before diversionary feeding (from May 13th to July 15th, 63 days) and during diversionary feeding (from July 16th to September 18th, 64 days). These two periods did not reflect a seasonal change, but the date on which the use of supplementary feedings began. We calculated a fixed kernel for each period using R software (http://www.r-project.org/ R) and the "adehabitatHR" package (Calenge 2006).

We considered that an individual had used a DFS if the core home range overlapped with a buffer of 100 m radius around a DFS. We also assumed that an animal had used a DFS if at least one GPS location of one day was inside the 100 m buffer around a DFS (Margalida et al. 2017) during the whole study period. We pooled all positions from the same date of each tracked individual to assess if the individual had used the DFS (1/0, use or no use) each day.

We assessed whether additional inputs had an effect on the spatial behaviour of the aoudads using two approaches: 1) to test if diversionary feeding had an effect on the size of core home range (k50%), we compared this area before and during diversionary feeding using non-parametric Wilcoxon test. As some individuals never used DFS, we also compared the size of the core home range between periods just for individuals that used DFS at least once during the diversionary feeding period. And, 2) to evaluate if animals increased the number of days using the DFS between periods we fitted a binomial Generalized Linear Mixed Model (GLMM) with “GPS location in the DFS” (1/0, use or no use of the feeding points for each day) as the response variable, “individual ID” as random factor and “period” (before or during) as fixed factor. Additionally, to assess if the individuals had a differential use of the DFS, we performed a GLM with “GPS location at the DFS” (1/0, as in the previous analysis) as the response variable and Individual ID as a fixed term, and we performed an

ANOVA test comparing this model with a null model. The GLM including "individual ID" had a better performance than the null model ($p < 0.001$). Therefore, we included "individual ID" as random factor in the GLMM to assess the effect of supplementary feeding considering this variability and the repetitive nature of our data.

Statistical analyses were calculated using "Rcmdr" package (Fox and Bouchet-Valat 2017) and "lme4" package (Bates et al. 2015) in R software.

Use of DFS by wildlife

Eight randomly selected DFS were monitored with automatic cameras activated by movement (Bushnell HD) to assess their use by wildlife, especially by other ungulate species. Cameras were active from July 24th to October 6th 2015 (n = 73 days). Cameras were located in a nearby tree (around 3 m) from DFS. They were programmed to operate 24 h and to record one picture every 6 minutes after movement activated them. Pictures were downloaded weekly (except for 2 cameras, which were stolen between September 9th and 16th). For each picture we recorded date, time, photographed species and number of individuals of each species.

We finally calculated if ungulate species using the DFS co-occurred more or less than expected by random. We used the "coocur" package in R (Griffith et al. 2016), which uses the probabilistic model of species co-occurrence by Veech (2013). We studied the co-occurrence of the species both temporally (i.e. species occurring at the same time in the same DFS) and spatially (i.e. species occurring at the same DFS).

RESULTS

Aoudad home ranges and feeding stations use

We recorded a total of 8,541 GPS positions (Average ± SD: 949 ± 35 positions per individual; n = 9). Tracked individuals did not join the same group during the study period, staying in different social groups, although we found partial spatial overlap of core home ranges between some individuals (aoudad C with D, and E with H; Table 1). The average core home range during the total period was 1.65 ± 0.67 km2. Five out of the nine individuals used DFS during food supply. We did not find significant differences in the core home range size between periods, but the standard deviation of the areas "before" food inputs was 3 times larger than "during" (1.66 ± 1.20 km2 before vs 0.97 ± 0.40 km2 during; V = 33, $p = 0.25$; Table 1). We also did not detect differences in the core range size between periods when comparing only the individuals that used DFS during the diversionary feeding period (V = 12, $p = 0.31$).

The mean number of GPS locations in the DFS during the total period was 8.60 ± 11.70 (5.80 ± 7.00 before vs 11.40 ± 15.00 during), and an average of 11.9% of the days had GPS locations within a DFS (7.0% before vs 16.9% during). The GLMM showed that the frequency of use of the DFS increased during the period with supplementary food (z = 5.87; $p < 0.001$; Table 2).

Table 2. Binomial Generalized Linear Mixed Model, where the frequency of use (1/0, use or no use) is the response variable. "Individual ID" was included as a random factor in the model and "period" as a fixed factor.

	Estimate	**SE**	**z-value**	**p**
Intercept	-4.11	0.88	-4.65	< 0.001
Period	1.30	0.22	5.87	< 0.001

Use of DFS by wildlife

A total of 9,639 pictures were taken in all the DFS. Sixteen species were detected at the DFS (Table S.4.2), including two ungulates: the aoudad (70.7% of the pictures) and the wild boar (23.0%). Other species appeared with a frequency lower than 2%.

The temporal co-occurrence analysis showed a negative significant association between the aoudad and the wild boar (*Sus scrofa*; $p < 0.001$; Figure 2). However, spatial co-occurrence analysis did not show any significant association among these species ($p > 0.05$).

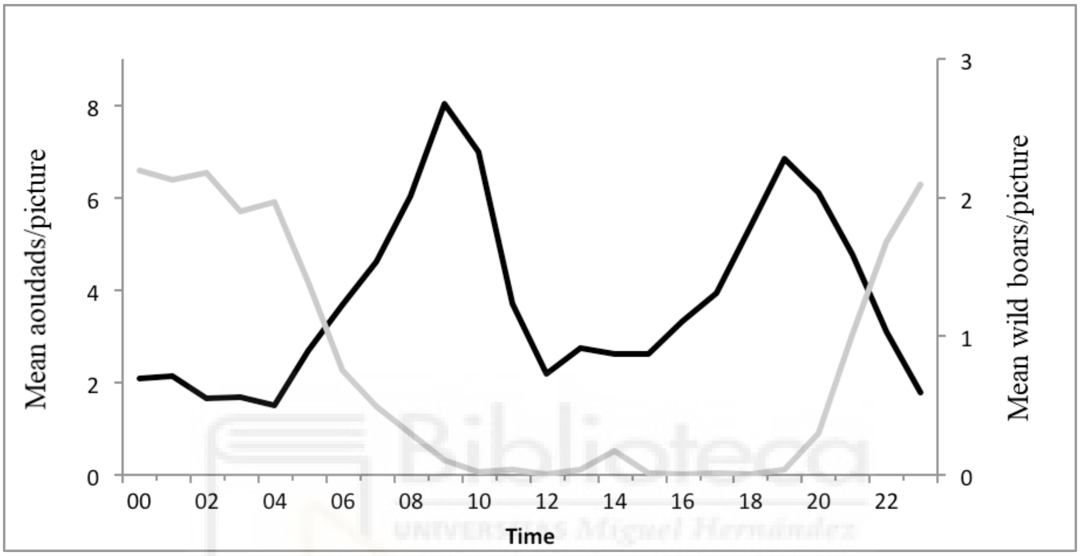

Figure 2. Average number of aoudad (black line) and wild boar (grey line) per picture along a day. Both ungulates use DFS at different times. When wild boar increases aoudad reduces its presence, and vice versa.

DISCUSSION

Contrary to our expectations, our results showed no change in the core home range of tracked aoudads due to food presence in the DFS and GPS tracking revealed that some individuals never used the DFS, even though the nine individuals had access to them. Our limited sample size (n = 9) may be insufficient to detect the effect of food supply in the core home ranges. However, we detected changes in the frequency of use of the DFS during the supplementary food period. Overall, just five out of the nine tracked aoudads reacted to the pulse resource that suppose supplementary feeding. So, the possible effects on the aoudad population did not seem to affect the entire population, However, as some individuals actively used the DFS when food was available, some conflicts associated with this species, such as crop damage, could be partially alleviated. Nevertheless, a comparative analysis about crop damage with and without diversionary feeding would be necessary to assess the effectiveness of DFS for reducing aoudad impact on crops (Geisser and Reyer 2004).

Despite only a part of the population used the DFS, fodder inputs may lead to high concentrations of animals in small areas, which might modify soil properties because of trampling and nutrient inputs (Dunkley and Cattet 2003, Pascual-Rico et al. 2018). Moreover, this animal concentration might also affect the surrounding vegetation due to herbivory pressure (Miranda et al. 2015). Although DFS can benefit fire-prone areas because of the reduction of fuel load by ungulates (Velamazán et al. 2018), this could be a problem for the conservation of threatened plant species (Velamazán et al. 2017, 2018). In addition, the high concentration of individuals of the same species in feeding sites could potentially increase the spread of diseases (Sorensen et al. 2014).

The variability showed by our tracked animals in the size of their core home ranges and in their GPS locations in the DFS could be related to animal behaviour. On the one hand, animal behaviour may be conditioned by the quality of the available forage and by the frequency and quantity of fodder inputs (Oja et al. 2015). The nutrient requirements of herbivores vary along the year and are affected by seasonal changes in vegetation (Langvatn et al. 1996; Miranda et al. 2012). Indeed, the study year was wetter than the average (AEMET 2016), and, specifically, the months in which supplementary feeding was employed (July, August and September) were classified as wet months. These precipitations could promote the growth of the local vegetation and favour a greater amount of resources available for the aoudad and, consequently, reduce the need to use DFS.

On the other hand, animal behaviour may also be conditioned by individual differences according to factors such as boldness or dominance (Bergvall et al. 2011). Boldness, expressed as low fearfulness behaviour, is linked to exploratory tendencies in novel situations (Bergvall et al. 2011), foraging (Wilson and Stevens 2005) and general activity (Wilson and McLaughlin 2007). Different responses detected to diversionary feeding may reflect these individual differences, as already described for other ungulate species (Sahlsten et al. 2010). Individual differences based on sex, age and position in the social group could also affect aoudad spatial behaviour. However, larger sample sizes are needed to address individual responses.

DFS were used by the target species but also by a wide community of generalist vertebrates, mainly herbivore and omnivore mammals and birds. This animal concentration at DFS may alter the environment, for example by increasing pressure on predation (Cortés-Avianza et al. 2016). Especially remarkable is the use of the DFS by wild boars (23% of the pictures at the DFS). Aoudad and wild boars showed a negative co-occurrence in time, mostly related to differences in the activity patterns among the species: the aoudad is crepuscular, while the wild boar is nocturnal. However, we did not detect a spatial segregation (i.e. preferential use of some DFS) between the two species. Altogether, these results indicate that wild boars are using DFS and they could benefit from this supplementary food (Diamond 1975).

This use of DFS by wild boars is not trivial. Several studies have shown that this species is widely related to human-wildlife conflicts, including the crop damage that was intended to avoid with this management strategy (Amici et al. 2012; Bleier et al. 2012; Colino-Rabanal et al. 2012). Diversionary feeding of wild boar has already been associated with an increase in nest predation (Selva et al. 2014; Oja et al. 2015) and spread of pathogens (Gortázar et al. 2006; Muñoz et al. 2010), but not to a reduction in crop damage by this species because of its large movement patterns (Geisser and Reyer 2004). Thus, the possible side effects of supplementary feeding on non-target species need to be accounted for when implementing this management action.

To conclude, our results show that diversionary feeding did not change the core home range of the target species, but increased the use frequency of DFS by several individuals. DFS were also used by other vertebrates, and particularly the wild boar, often considered a pest species subject to culling. Thus, diversionary feeding seems to have a limited effect to reduce human-wildlife conflicts (i.e. crop damage) in our study system. Future prospects predict an increase in conflicts associated with wild ungulates due to their increase in abundance and distribution (Apollonio et al. 2010). Thus, detailed evaluations of the possible management actions are needed to make the appropriate decisions and optimize the available resources.

ACKNOWLEDGEMENTS

We thank veterinary (F. Escribano), public gamekeepers (C. Esteban, J. J. Rodríguez, F. Yepes), rangers (Evaristo) and Ministry of Tourism, Culture and Environment of Murcia Region. RPR was supported by a pre-doctoral grant from the Spanish Ministry of Education (FPU13/05460) and the study was partially supported by MINECO and ERDF (projectCGL2015-66966-C2-1-R). JMPG and ESG were supported by a Juan de la Cierva research contract by the Ministry of Economy and Competitiveness (FJCI-2015-25632 and IJCI-2015-24947). GPS collars were partially supported by European Regional Development Fund (ERDF) of the European Union (P.O. 2007/2013).

REFERENCES

Agencia Estatal de Meteorología. 2016. Informe anual 2015. Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente. Madrid.

Agencia Estatal de Meteorología. 2015. Informe estacional climatológico verano 2015. Ministerio de Agricultura, Alimentación y Medio Ambiente. Madrid.

Amici, A., Serrani, F., Rossi, C.M., Primi, R. 2012. Increase in crop damage caused by wild boar (*Sus scrofa* L.): The “refuge effect”. Agronomy for Sustainable Development 32: 683-692.

Anadón, J.D., Pérez-García, J.M., Pérez, I., Royo, J., Sánchez-Zapata, J.A. 2018. Disentangling the effects of habitat, connectivity and interspecific competition in the range expansion of exotic and native ungulates. Landscape Ecology 33: 597-608.

Apollonio, M., Andersen, R., Putman, R. 2010. European ungulates and their management in the 21st century. Cambridge University Press, Cambridge.

Bates, D., Maechler, M., Bolker, B., Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1-48.

Bergmüller, R., Taborsky, M. 2010. Animal personality due to social niche specialisation. Trends in Ecology and Evolution 25: 504-511.

Bergvall, U.A., Schäpers, A., Kjellander, P., Weiss, A. 2011 Personality and foraging decisions in fallow deer, Dama dama. Animal Behaviour 81: 101-112.

Blanco, G., Lemus, J.A., García-Montijano, M. 2011 When conservation management becomes contraindicated: impact of food supplementation on health of endangered wildlife. Ecological Applications 21: 2469-2477.

Bleier, N., Lehoczki, R., Újváry, D., Szemethy, L., Csányi, S. 2012. Relationships between wild ungulates density and crop damage in Hungary. Acta Theriologica 57: 351-359.

Bowman, B., Belant, J.L., Beyer, Jr D.E., Martel, D. 2015. Characterizing non target species use at bait sites for white-tailed deer. Human Wildlife Interactions 9: 110-118.

Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516-519.

Cassinello, J. 1998. *Ammotragus lervia*: a review on systematics, biology, ecology and distribution. Annales Zoologici Fennici 35: 149-162.

Colino-Rabanal, V., Bosch, J., Muñoz, M.J., Peris, S.J. 2012. Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Animal Biodiversity Conservation 35: 247-252.

Corcoran, M.J., Wetherbee, B.M., Shivji, M.S., Potenski, M.D., Chapman, D.D., Harvey, G.M. 2013. Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the southern stingray, Dasyatis americana. PLoS ONE 8: e59235.

Cortés-Avianza, A., Blanco, G., DeVault, T.L., Markandya, A., Virani, M.Z., Brandt, J., Donázar, J.A. 2016. Supplementary feeding and endangered avian scavengers: benefits, caveats and controversies. Frontiers in Ecology and the Environment 14: 191-199.

Diamond, M. 1975. Assembly of species communities. In: Cody ML, Diamond JM (eds) Ecology and Evolution of Communities. Belknap Press, Cambridge, pp 342-444.

Duellman, W.E. 1978. The biology of an equatorial herpeto-fauna in Amazonian Ecuador. Trueb, l. (Eds.). Miscellaneous Publication Museum of Natural History. University of Kansas, Lawrence.

Dunkley, L., Cattet, M.R.L. 2003. A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Canadian Cooperative Wildlife Health Centre: Newsletters and Publications 21: 1-68.

Eguía, S., Botella, F., Giménez, A., Sánchez-Zapata, J.A,, Pascual, R., García-Martínez, E.J., Fuertes, F., Pérez-Morales, A., Morell, M. 2015. Elaboración del Plan de Gestión del Arruí en la Región de Murcia. Consejería de Agua, Agricultura y Medioambiente. Región de Murcia

Fox, J., Bouchet-Valat, M. 2017. Rcmdr: R Commander. R package version 2.3-2.

Geisser, H., Reyer, H.U. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. Journal of Wildlife Management 68: 939-946.

González, L.M., Margalida, A., Sánchez, R., Oria, J. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (Aquila adalberti). Biolical Conservation 129: 477–486.

González-Candela, M. 2002. Epidemiología de sarna sarcóptica (Sarcoptes scabiei) en la población de arruí (*Ammotragus lervia*) del Parque Regional de Sierra Espuña (Murcia). Doctoral Thesis. Universidad de Murcia.

Gortázar, C., Acevedo, P., Ruiz-Fons, F., Vicente, J. 2006 Disease risks and overabundance of game species. European Journal of Wildlife Research 52: 81-87

Griffith, D.M., Veech, J.A., Marsh, C.J. 2016. Cooccur: probabilistic species co-occurrence analysis in R. Journal of Statistical Software 69: 1-17.

Gundersen, H., Andreassen, H.P., Storaas, T. 2004. Supplemental feeding of migratory moose Alces alces: forest damage at two spatial scales. Wildlife Biology 10: 213-223.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T., Wray, S. 1990. Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20: 97-123.

Inslerman, R.A., Miller, J.E., Baker, D.L., Kennamer, J.E., Cumberland, R., Stinson, E.R., Doerr, P., Williamson, S.J. 2006. Baiting and supplemental feeding of game wildlife species. The Wildlife Society. Bethesda, Maryland.

Krofel, M., Jerina, K. 2016. Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biological Conservation 197: 40-46.

Kubasiewicz, L.M., Bunnefeld, N., Tulloch, A.I.T., Quine, C.P., Park, K.J. 2016. Diversionary feeding: an effective management strategy for conservation conflict? Biodiversity & Conservation 25: 1-22

Langley, R.B. 1999. Dilution of precision. GPS World 10: 52-59.

Langvatn, R., Albon, S.D., Burkey, T., Clutton-Brock, T.H. 1996.Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65: 653-670

López-Bao, J.V., Rodríguez, A., Palomares, F. 2008. Behavioural response of a trophic specialist, the Iberian lynx, to supplementary food: Patterns of food use and implications for conservation. Biological Conservation 141: 1857-1867.

Margalida, A., Pérez-García, J.M., Moreno-Opo, R. 2017. European policies on livestock carcasses management did not modify the foraging behavior of a threatened vulture. Ecological Indicators 80: 66-73.

Miranda, M., Cristóbal, I., Díaz, L., Sicilia, M., Molina-Alcaide, E., Bartolomé, J., Fierro, Y., Cassinello, J. 2015. Ecological effects of game management: Does supplemental feeding affect herbivory pressure on native vegetation? Wildlife Research 42: 353-361.

Muñoz, P.M., Boadella, M., Arnal, M., de Miguel, M.J., Revilla, M., Martínez, D., Vicente, J., Acevedo, P., Oleaga, A., Ruiz-Fons, F., Marín, C.M., Prieto, J.M., de la Fuente, J., Barral, M., Barberán, M., de Luco, D., Blasco, J.M., Gortázar, C. 2010. Spatial distribution and risk factors of Brucellosis in Iberian wild ungulates. BMC Infectious Diseases 10: 1-14.

Oja, R., Zilmer, K., Valdmann, H. 2015. Spatiotemporal Effects of Supplementary Feeding of Wild Boar (*Sus scrofa*) on Artificial Ground Nest Depredation. PLoSONE 10: e0135254.

Orams, M.A. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management 23: 281-293.

Ostfeld, R.S., Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15: 232-237.

Pascual-Rico, R., Morugán-Coronado, A., Botella, F., García-Orenes, F., Sánchez-Zapata, J.A. 2018. Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain. Applied Soil Ecology 127: 136-143.

Pedersen, S., Mathisen, K.M., Gorini, L., Andreassen, H.P., Røskaft, E., Skarpe, C. 2014. Small mammal responses to moose supplementary winter feeding. European Journal of Wildlife Research 60: 527-534.

Piper, S.E. 2005. Supplementary feeding programs: how necessary are they for the maintenance of numerous and healthy vultures populations? In: Houston DC, Piper SE (eds) Proceedings of the

international conference on conservation and management of vulture populations. Thessaloniki: Natural History Museum of Crete & WWF Greece. pp 41-50.
Putman, R.J., Staines, B.W. 2004. Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34: 285-306.
Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D.C., Watt, A., Gutiérrez, R.J. 2013. Understanding and managing conservation conflicts. Trends in Ecology and Evolution 28: 100-9.
Robb, G.N., McDonald, R.A., Chamberlain, D.E., Bearhop, S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6: 476-484.
Sahlsten, J., Bunnefeld, N., Månsson, J., Ericsson, G., Bergström, R., Dettki, H. 2010. Can supplementary feeding be used to redistribute moose Alces alces? Wildlife Biology 16: 85-92.
Selva, N., Berezowska-Cnota, T., Elguero-Claramunt, I. 2014. Unforeseen effects of supplementary feeding: ungulate baiting sites as hotspots for ground-nest predation. PLoSONE 9: e90740.
Snow, N.P., Porter, W.F., Williams, D.M. 2015. Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. Biological Conservation 181: 44-53.
Sorensen, A., van Beest, F.M., Brook, R.K. 2014. Impacts of wildlife baiting and supplemental feeding on infectious disease transmission risk: A synthesis of knowledge. Preventive Veterinary Medicine 113: 356-363.
Süld, K., Valdmann, H., Laurimaa, L., Soe, E., Davidson, J., Saarma, U. 2014. An invasive vector of zoonotic diseases sustained by anthropogenic resources: the racoon dogs in Northern Europe. Plos One 9:e96358.
Van Beest, F.M., Loe, L.E., Mysterud, A., Milner, J.M. 2010. Comparative space use and habitat selection of moose around feeding stations. Journal of Wildlife Management 74: 219-227.
Veech, J.A. 2013. A probabilistic model for analysing species co-occurrence. Global Ecology and Biogeography 22: 252-260.
Velamazán, M., San Miguel, A., Escribano, R., Perea, R. 2017. Threatened woody flora as an ecological indicator of large herbivore introductions. Biodiversity & Conservation 26: 917-930.
Velamazán, M., San Miguel, A., Escribano, R., Perea, R. 2018. Use of firebreaks and artificial supply points by wild ungulates: effects on fuel load and woody vegetation along a distance gradient. Forest Ecology Management 427: 114-123.
Wilson, A.D.M., McLaughlin, R.L. 2007. Behavioural syndromes in brook charr, Salvelinus fontinalis: prey-search in the field corresponds with space use in novel laboratory situations. Animal Behaviour 74: 689-698.
Wilson, A.D.M., Stevens, E.D. 2005. Consistency in context-specific measures of shyness and boldness in rainbow trout, Oncorhynchus mykiss. Ethology 111: 849-862.
Worton, B.J. 1989. Kernel methods for estimating the utilization in home-ranges studies. Ecology 70: 164-168.
Yang, L.H., Bastow, J.L., Spence, K.O., Wright, A.N. 2008. What can we learn from resource pulses? Ecology 89: 621-634.

Chapter 5

Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain.

Roberto Pascual-Rico, Alicia Morugán-Coronado, Francisco Botella, Fuensanta García-Orenes, José Antonio Sánchez-Zapata.

This chapter corresponds to the article:

Pascual-Rico, R., Morugán-Coronado, A., Botella, F., García-Orenes, F., Sánchez-Zapata, J.A. 2018. Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain. Applied Soil Ecology 127: 136-143. DOI: 10.1016/j.apsoil.2018.03.017.

ABSTRACT

Soil plays an important role in processes that maintain ecosystems function and support biodiversity. Physicochemical and biological soil properties can be altered by human activities, and through management tools that affect environment conditions. Diversionary feeding is a widely employed management tool to avoid human-wildlife conflicts. This practice could lead to concentrations of fauna in specific areas where food is deposited, which could affect physicochemical, biochemical and biological soil properties. We evaluated the effect of diversionary feeding on semiarid Mediterranean mountain soil in the Sierra Espuña Regional Park (SE Spain). The objective of diversionary feeding in this Regional Park is to mitigate crop damage caused by the aoudad (*Ammotragus lervia*), an exotic ungulate introduced for hunting interests in the 1970s. Three diversionary feeding stations were monitored with automatic cameras to verify their use by target and non-target species. We collected soil samples from the monitored feeding stations and compared soil characteristics from three areas: feeding stations soil, contour area soil (surrounding the feeding stations) and a reference soil (not influenced by feeding stations). Our results suggested no effects on soil physical properties. However, we found that diversionary feeding altered electrical conductivity, nutrient concentration, microbial activity and microbial communities at FS, but effects were weaker in the contour area. These alterations of soil dynamics contribute to change soil functionality and to reinforce global change. Not pouring food directly on soil is recommended to reduce these effects.

Keywords: *Ammotragus lervia*; PLFA; soil alteration; wildlife management.

RESUMEN

El suelo desempeña un papel importante en la función de los ecosistemas y la biodiversidad. Las propiedades fisicoquímicas y biológicas del suelo pueden alterarse debido a las actividades humanas, y mediante las herramientas de gestión que pueden afectar a las condiciones ambientales. Los aportes suplementarios son una herramienta de gestión empleada para evitar conflictos entre humanos y vida silvestre. Esta práctica podría llevar a concentraciones de fauna en las áreas donde se deposita el alimento, lo que podría afectar las propiedades fisicoquímicas, bioquímicas y biológicas del suelo. En este trabajo evaluamos el efecto de estos aportes en el suelo en el Parque Regional de Sierra Espuña (SE España). El objetivo los aportes suplementarios en este Parque Regional es mitigar los daños a los cultivos causados por el arrui (*Ammotragus lervia*), un ungulado exótico introducido por motivos cinegéticos en la década de 1970. Monitoreamos tres comederos con cámaras de fototrampeo para verificar su uso por parte del arrui y otras especies no objetivo. Tomamos muestras de suelo de los comederos monitoreados y comparamos las características del suelo de tres áreas: comederos, alrededor los comederos y un suelo de referencia (no influenciado por los comederos). Nuestros resultados sugieren que no hay efectos en las propiedades físicas del suelo. Sin embargo, encontramos que los aportes suplementarios modificaron la conductividad eléctrica, la concentración de nutrientes, la actividad microbiana y las comunidades microbianas en los comederos, pero los efectos fueron más débiles los alrededores. Estas alteraciones de la dinámica del suelo contribuyen a cambiar su funcionalidad y a reforzar el cambio global. No se recomienda verter alimentos directamente sobre el suelo para reducir estos efectos.

Palabras clave: *Ammotragus lervia*; PLFA; alteración del suelo; gestión de fauna silvestre.

INTRODUCTION

Many crucial processes to maintain terrestrial ecosystems take place in soils (Roger-Estrade et al. 2010). Soils support high biodiversity (Young and Crawford, 2004) which, together with their physicochemical properties, provide important ecosystem functions and services, such as decomposition (Coleman et al. 2004), nutrient cycling, soil productivity sustainability (Roger-Estrade et al. 2010), and resistance and resilience to abiotic disturbance and stress (Brussaard et al. 2007). Microbial soil communities are the most sensitive and rapid indicators of perturbations and land use changes (García-Orenes et al. 2013). Indeed, growing interest is being paid to quantitative description of microbial community structure and diversity as a potential soil quality evaluation tool (Zelles, 1999; Zornoza et al. 2009). Given its relationship with soil functionality, the influence of soil microorganisms and soil microbial population and activity have been proposed as useful indicators to evaluate soil's response to different management practices (García-Orenes et al. 2013). The microbial community's response can be assessed by changes in phospholipid fatty acid (PLFA) patterns (Zelles, 1999). PLFA use lipids of microbial membranes as biomarkers for specific groups of microorganisms (Bacteria, Fungi, G-Bacteria, G+ Bacteria and Actinobacteria), which allows a profile of the community structure to be created (DeGrood et al. 2005; Zornoza et al. 2009).

Soil management practices due to anthropogenic activities can alter physicochemical and biological soil properties (Jangid et al. 2008), and can also affect soil function. For example, nutrient income in ecosystems may alter ecological processes and influence global change (Oro et al. 2013). These nutrient incomes may significantly alter soil characteristics by influencing changes in biological, chemical and physical properties (Macci et al. 2013). One form of nutrient inputs in the environment that can alter soil properties is supplementary feeding (Dunkley and Cattet, 2003). This practise drives the concentration of animals in small areas, which might modify the structural and chemical properties of soil (Hiernaux et al. 1999; Martínez and Zinck, 2004; Savadogo et al. 2007), including organic matter turnover, nutrient capture and cycling (Van der Heijden et al. 2008), and the formation and stabilisation of soil aggregates (Chenu and Cosentino, 2011). Supplementary feeding is practised globally and as a wildlife management tool for several reasons. This practise is used to conserve threatened species (Cortés-Avianza et al. 2016; González et al. 2006; Krofel and Jerina, 2016; López-Bao et al. 2008; Piper, 2005), to facilitate wildlife observations as tourist attractions (Corcoran et al. 2013; Orams, 2002; Robb et al. 2008), and to promote human connectedness to nature (St Leger, 2003). One of the most widespread uses of supplementary feeding is to manage game species (Inslerman et al. 2006; Putman and Staines, 2004; Vicente et al. 2005), particularly to improve trophy quality, and to increase population density, productivity and survival, but also to mitigate conflicts.

Increasingly growing human activities, along with the expansion of ungulates, might cause interactions between them and lead to human-wildlife conflicts (Redpath et al. 2013). Conflicts, such as forest damage (Sahlsten et al. 2010), crop damage (Dunkley and Cattet, 2003) or vehicle collisions (Snow et al. 2015), are some relevant human-wildlife conflicts (Kubasiewicz et al. 2016). Supplementary feeding is often used as a tool to avoid these conflicts, in which case it is generally referred to as diversionary feeding (Kubasiewicz et al. 2016).

Publications about the effects of animal concentration on soil have focused mainly on livestock species (Betteridge et al. 1999; Castellano and Valone, 2007; Yong-Zhong et al. 2005). Several studies have also focused on wild boar (Cellina, 2008; Wirthner, 2011), especially in relation to rooting behaviour. Studies about effects of diversionary feeding stations (FS) on physicochemical and biological soil characteristics are scarce (Miranda et al. 2015; Oja et al. 2015; Selva et al. 2014). In this study, we evaluated the effect of FS on soil in the Sierra Espuña Regional Park, the Murcia Region, in SE Spain. There, the regional government uses diversionary feeding as a management tool for aoudad (*Ammotragus lervia*), an African ungulate introduced into SE Spain in the 1970s for hunting interests. FS were placed in the area in the 1990s after sarcoptic mange outbreak, which caused the aoudad population to drop by more than 90% (Eguía, et al. 2015). The aim of food inputs was to initially help species to recover from such outbreaks. However, the aoudad population recovered in 2000-2010, and the regional government continues to practice diversionary feeding to keep animals within the park's boundaries and to avoid damage to surrounding crops in summer. Our objective was to study how diversionary food inputs could alter soil characteristics in FS.

We hypothesised that the effects on soil would be: 1) compaction around feeding areas due to trampling; 2) higher nutrient concentrations at FS; 3) alterations of the soil microbial community structure because of food inputs and wildlife activity.

MATERIAL AND METHODS

Study area

The study was conducted in the Sierra Espuña Regional Park in SE Spain (37°47′–37°56′N 1°27′–1°40′W). It covers 17,800 ha and includes meso- and supra-Mediterranean habitats, which range from 500 to 1,500 m.a.s.l., with Pinus halepensis woods, scrublands and pasture dominating the mountain range landscape (Sánchez-Zapata and Calvo, 1999). Rainfall ranges from 277 mm in lower mountain areas to 510 mm in the park's upper parts. Average annual temperatures also follow an altitudinal gradient, which ranges from 12.8–18.4°C. The main soil found at the Sierra Espuña Regional Park is classified as Lithic Leptosol (WRB, 2014) with loam texture (37% sand, 50% silt and 13% clay). These soils are characterised by being shallow soil on rock (characteristic of many mountain soils) and they are rich in coarse fragments. They are only recognised at the subgroup level, which groups together all soils that are less than 50 cm thick to bedrock. The physicochemical and biochemical soil characteristics are described in Table 1 and microbiological measures in Table 2.

Experimental design

Feeding stations

Sixteen diversionary FS (average size 350.0 ± 129.6 m2) were located in the regional park (Figure 1). These FS consist in clear cut areas where forestry agents can access them by car to deposit supplementary feeding. In summer 2015, 35 kg of fodder and about 10 kg of lucerne were deposited weekly at each FS on bare ground, with no measures taken to prevent use by non-target species. This fodder was composed of a mixture of corn, barley, oats, pelleted lucerne meal and pelleted sugar beet pulp. The analytical fodder components included crude protein (10.4%), crude fats (2.8%), fibre (10.5%), ash (4.2%), sodium (0.05%) and phosphorus (0.28%).

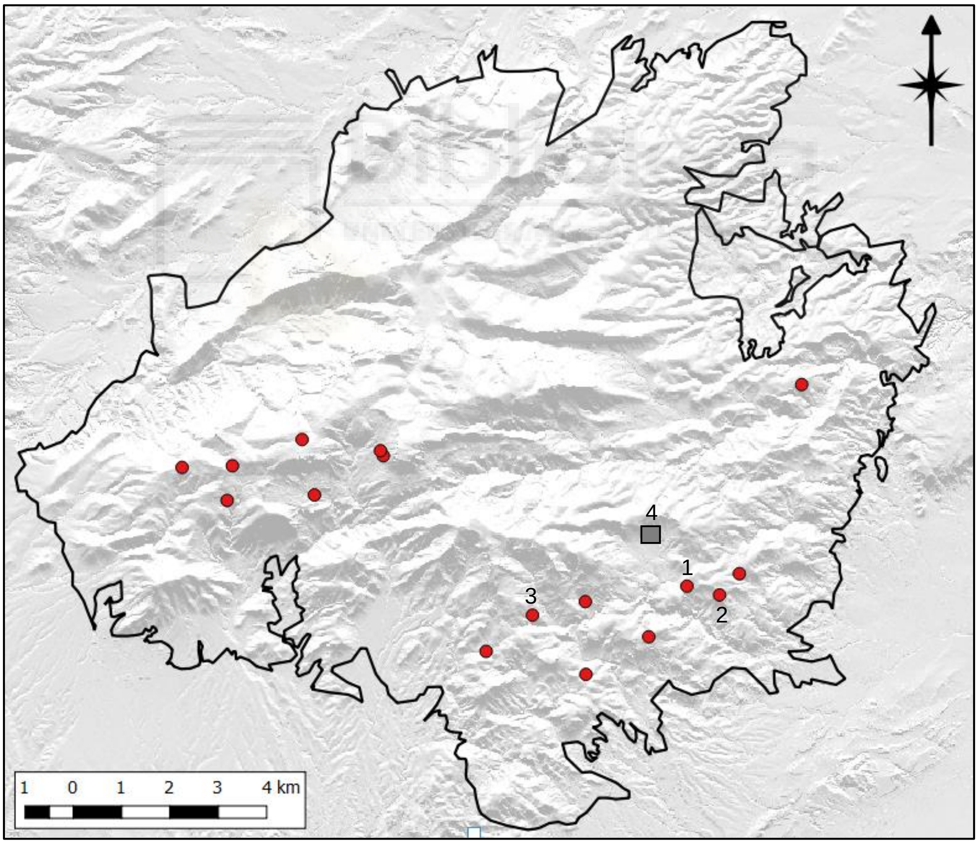

Figure 1. The Sierra Espuña Regional Park. The locations of 16 FS are indicated by red circles. Locations 1, 2 and 3 indicate the monitored FS and C where the soil samples were taken. A square indicates location 4, where the reference soil (RS) was collected, away from the influence of FS.

Table 1. Main characteristics of the reference soil (RS), feeding stations (FS) and contour (C) area of each sampled area (0-5 cm). Values are the mean ± standard deviation (n=6).

	RS	Sampled area 1		Sampled area 2		Sampled area 3	
		FS 1	**C 1**	**FS 2**	**C 2**	**FS 3**	**C 3**
AS (%)	58.58 ± 7.47	51.45 ± 8.75	64.06 ± 10.26	64.06 ± 14.32	68.17 ± 10.26	68.77 ± 2.11	65.59 ± 6.71
BD (g/cm3)	1.04 ± 0.13	1.27 ± 0.17	1.17 ± 0.21	0.99 ± 0.23	0.91 ± 0.21	0.91 ± 0.17	0.90 ± 0.13
pH (extract 1:5, w/v)	8.15 ± 0.36	8.12 ± 0.21	8.18 ± 0.24	7.72 ± 0.18	8.25 ± 0.24	7.22 ± 0.20	7.92 ± 0.15
EC(mS/cm)	0.17 ± 0.07	0.42 ± 0.13	0.33 ± 0.21	0.79 ± 0.24	0.17 ± 0.21	0.70 ± 0.28	0.51 ± 0.17
Corg (g/kg)	23.90 ± 13.69	38.22 ± 21.54	35.89 ± 17.99	41.65 ± 8.16	35.77 ± 17.99	38.92 ± 9.94	55.47 ± 6.44
N (g/kg)	2.31 ± 0.90	3.29 ± 1.71	3.67 ± 1.77	4.56 ± 0.89	3.39 ± 1.77	3.61 ± 1.18	4.53 ± 0.57
Na (mg/kg)	2.97 ± 1.90	8.49 ± 5.73	3.76 ± 2.56	12.26 ± 8.16	7.28 ± 2.56	5.48 ± 2.27	7.49 ± 2.86
K (mg/kg)	12.52 ± 1.87	18.89 ± 6.73	6.80 1.43	19.63 ± 4.02	9.81 ± 1.43	25.37 ± 7.42	13.45 ± 2.13
P (mg/kg)	4.76 ± 0.73	8.14 ± 4.90	4.69 ± 2.42	22.34 ± 13.01	4.19 ± 2.42	8.70 ± 4.63	4.03 ± 0.44
C/N	9.34 ± 3.29	11.37 ± 2.38	9.77 ± 1.29	9.13 ± 0.36	10.51 ± 1.29	11.05 ± 1.39	12.27 ± 0.74
Cmic (g/kg)	0.60 ± 0.35	0.91 ± 0.73	0.42 ± 0.13	0.22 ± 0.07	0.35 ± 0.13	0.46 ± 0.35	0.44 ± 0.14
BSR (C-CO2 (ug/h/g))	1.43 ± 0.76	6.59 ± 6.15	1.75 ± 0.71	3.53 ± 2.37	1.30 ± 0.71	3.81 ± 2.63	2.12 ± 0.65

AS: aggregate stability, BD: bulk density; BSR: basal soil respiration; EC: electrical conductivity; Corg: organic carbon; Cmic: microbial biomass carbon; C/N: carbon:nitrogen ratio; Mg: magnesium; Ca: calcium; K: potassium; N: nitrogen; Na: sodium; P: phosphorus.

Table 2. Microbiological characteristics of the reference soil (RS), feeding stations (FS) and contour of each sampled area (0-5 cm). Values are the mean ± standard deviation (n=6).

	RS	Sampled area 1		Sampled area 2		Sampled area 3	
		FS 1	**C 1**	**FS 2**	**C 2**	**FS 3**	**C 3**
Total PLFA	34.62 ± 30.68	8.68 ± 2.13	28.93 ± 20.76	14.86 ± 3.30	18.28 ± 20.76	13.42 ± 4.60	19.84 ± 26.21
Fungi	5.26 ± 4.59	0.86 ±0.76	3.15 ± 2.28	1.26 ± 0.90	1.04 ± 2.28	1.90 ± 1.24	2.31 ± 3.21
Bacteria	20.97 ± 19.05	5.41 ± 2.36	17.98 ± 13.87	8.95 ± 1.89	12.35 ± 13.87	7.49 ± 2.24	12.04 ± 16.71
B/F	3.88 ± 0.38	17.13 ± 15.74	5.58 ± 2.43	7.69 ± 4.31	12.68 ± 2.43	5.60 ± 3.91	5.76 ± 2.45
G+	9.29 ± 8.73	2.69 ± 1.26	7.95 ± 5.92	5.01 ± 1.29	5.81 ± 5.92	4.29 ± 1.48	6.45 ± 8.19
G-	3.68 ± 3.42	1.51 ± 0.32	3.32 ± 2.74	2.47 ± 0.71	2.18 ± 2.74	1.90 ± 0.73	2.42 ± 2.88
G-/G+	0.40 ± 0.04	0.65 ± 0.27	0.39 ± 0.05	0.49 ± 0.03	0.38 ± 0.05	0.44 ± 0.07	0.40 ±0.04
Actinobacteria	3.10 ± 2.85	0.74 ± 0.67	2.97 ± 2.36	1.08 ± 0.34	2.11 ± 2.36	0.97 ± 0.36	1.97 ± 2.74

Total PLFA, Fungi, Bacteria, G+, G- and Actinobacteria are expressed as µg/g of soil. B/F: Bacteria/Fungi ratio; G-/G+: Gram- bacteria/ Gram+ bacteria ratio.

We monitored three FS using automatic cameras, activated by movement (Bushnell HD), to assess their use by wildlife. Cameras were located in a nearby tree, about 3 m from the FS, and operated from 24 July 2015 to 6 October 2015 (75 days). They were programmed to record one picture every minute after detecting movement, and to operate 24 h/day. Pictures provided information about the species that fed at the FS, as well as the number of individuals, date and time. We downloaded the pictures taken by the automatic cameras weekly. The monitored FS enabled us to know the minimum number of target animals that visited each FS daily. We tested the differences between the maximum number of aoudad per day to verify that the three FS were used by the target species at the same intensity.

Soil sampling

We took soil samples from four locations. Three of them (locations 1, 2, and 3) included the monitored FS areas, and the contour FS areas (C) located between 10 m and 25 m around each FS, where vegetation was present (Figure 2). Location 4 was an area located further away from the other FS (>1 km), used to establish the soil characteristics not influenced by supplementary feeding, and was considered a reference soil (RS). Samples were taken from all locations in an area with a similar orientation and environmental conditions where the only apparent difference between areas was supplementary feeding. To evaluate the effects of diversionary feeding on soil, we compared the soil collected from the "sampled areas", FS, with the C and RS areas.

Six soil samples (100 cc cylinders) were collected at a depth of up to 5 cm within each FS 1 (37º50′N, 1º31′W), 2 (37º50′N, 1º30′W), and 3 (37º49′N, 1º33′W) (Figure 1) (n=18). The same procedure was applied to area C for each FS (n=18) and RS (n=6; 37º51´N 1º31´W). The field-moist soil samples were sieved at <2 mm and stored at environmental temperature for the physico-chemical analysis. An aliquot of each soil sample was kept cool (4°C) to analyse microbial properties, and also for the PLFA analysis. Portions of soil air-dried samples were sieved between 0.25-4 mm to determine aggregate stability. Soil texture was analysed and classified according to USDA (2004). Soil organic matter was removed by the H2O2 pre-treatment (6%). Size fractions (0.05-2 mm sand; 0.002-0.05 mm silt; 0.002 mm clay) were determined by the Bouyoucos method (Gee and Bauder, 1986). Aggregate stability (AS) was measured according to Roldán et al. (1994), based on Benito et al. (1986). Dry bulk density (BD) was determined in the cylinder soil samples dried at 105°C for 72 h and was then weighed (Blake and Hartge, 1986). Soil pH and electrical conductivity (EC) were measured with a 1:5 (w/v) aqueous solution. Soil organic carbon (Corg) was determined by the potassium dichromate oxidation method (Nelson and Sommers, 1982). Microbial biomass carbon (Cmic) was extracted by the chloroform fumigation and extraction procedure (Vance et al. 1987). Basal soil respiration (BSR) was measured in a multiple sensor respirometer (Micro-Oxymax, Columbus, OH, USA). Available phosphorus (P) was determined by the Burriel-Hernando method (Díez, 1982). Available sodium (Na) and potassium (K) were extracted with 1N ammonium acetate (Knudsen et al. 1982), measured by atomic absorption and emission spectrophotometry. Total nitrogen (N) was determined by the Kjeldahl method (Bremmer and Mulvaney 1982).

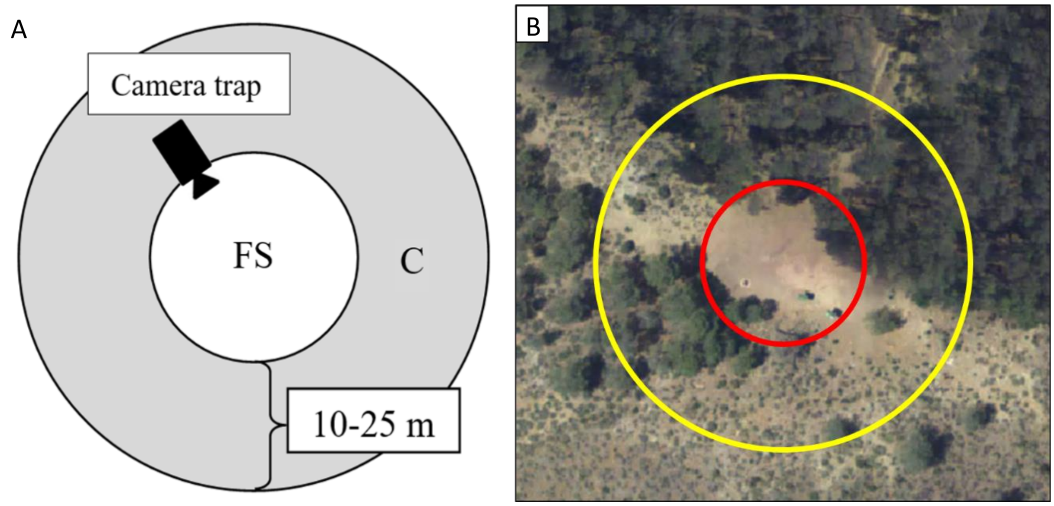

Figure 2. Diagram of the sampled location (A) and an orthoimage of location 1.A) includes feeding station (FS) and the contour area (C). Six samples were taken at each area (FS or C) of each location. B) shows the limits of FS area (red line) and C area (yellow line).

The PLFAs from soil samples were extracted and fractionated following the procedures by Bossio et al. (1998). Fatty acids were extracted from 10 g of the fresh soil (4ºC) samples using chloroform:methanol:phosphate buffer. After mild alkaline methanolysis, samples were analysed in a Hewlett Packard 6890 Gas Chromatograph with a 25 m Ultra 2 (5% phenyl)-methylpolysiloxane column (J and W Scientific, Folsom, CA, USA). Forty-eight fatty acids were identified. Microbial groups were assigned following Frostegärd et al. 2011, using the PLFAs groups: Fungi, Bacteria, Gram-negative bacteria (G−), Gram-positive bacteria (G+) and Actinobacteria (Ab) (Table S.5.1).

Statistical analysis

Soil properties were analysed by a principal component analysis (PCA). To reduce the number of variables included in the PCA a correlation analysis was run to test the relationship among the soil variables. The correlated variables, adjusted according to Holm's method, were EC and pH, Corg and N, Cmic and BSR, total PLFA and PLFA of each soil microbial group ($p < 0.001$). The variables finally included in PCA were physicochemical AS, BD, EC, N, Na, K, P, C/N, biochemical BSR and biological total PLFA. Samples with similar values of the physicochemical, biochemical and biological properties obtained similar scores and, therefore, grouped closer together when plotted. Significant PCA factors were selected according to Kaiser Criterion (eigenvalues >1).

To test whether our proposed measures of soil characteristics differed among the sampled areas (FS, C and RS), we fitted Generalized Linear Mixed Models (GLMM) using the soil physicochemical (AS, BD, EC, N, Na, K, P, C/N), biochemical (BSR) and biological (total PLFA, Fungi, Bacteria and Actinobacteria PLFA) variables measured as response variable. We included Fungi, Bacteria and Actinobacteria even though these variables were correlated with total PLFA because we needed to evaluate the changes in the soil microbial community structure (differences in the total PLFA merely indicates changes in the microbial biomass). We included "sampled area" as fixed factor and "location" as random term to control for pseudoreplication (Figure 1). We used Gaussian error distribution and "identity" as link function. The fit of the residuals of the models to a normal distribution was tested and so data was not transformed. We applied a Tukey post-hoc contrast of multiple comparisons of means.

All statistical analysis was performed with the Rstudio software (http://www.r-project.org/ R), "FactoMineR" (Le et al. 2008), "lmer4" (Bates et al. 2015) and "Rcmdr" packages (Fox and Bouchet-Valat, 2017).

RESULTS

Intensity of use and users species

The camera traps located at FS recorded 3,932 pictures during the 75-day period that they operated. Five bird and seven mammal species were detected, which were mostly consumers of diversionary food (Table 3). The aoudad was by far the most frequent species recorded at the three monitored FS (78.4% of all the pictures). The maximum number of recorded individuals was 40. No differences were detected in the intensity of the use of the sampled FS by aoudad ($\chi^2 = 3.85$, df = 2, $p = 0.15$).

Multivariate analysis

The PCA performed to group samples in relation to soil properties explained 61.8% of total variation, considering the first three axes. Figure 3 shows two axes. The soils sampled at FS (n=18) grouped mainly on the right with positive values for axis 1, and the RS samples (n=6) grouped on the left with negative values (Figure 3A). The C area samples were distributed along the component 1 axis with negative and positive values. Axis 1 (29.3% of explained variance) correlated positively with EC, N, K, P and BSR, and negatively with PLFA (Figure 3B). Axis 2 (17.5% of explained variance) correlated positively with AS and Na, and negatively with the C:N ratio and BSR. Axis 3 (14.9%) correlated with the physical variables, as positively and negatively with AS and BD, respectively.

Table 3. Photographed species at feeding stations. The percentage of pictures indicates the proportion of the total pictures (n=3932) in which the species appeared. Total sum is greater than 100% because some different species appeared in the same pictures. Mean±SD is the average of the individuals in the pictures; in brackets, the maximum number of individuals detected in a camera trap picture; – for the species with only one picture recorded.

	Species	Common name	% of pictures	Mean ± SD
Birds	*Aquila pennata*	Booted eagle	0.03	-(1)
	Caprimulgus sp	Nightjar	0.03	-(1)
	Corvux corax	Common raven	1.00	2.46 ± 1.61 (6)
	Columba palumbus	Common wood pigeon	2.90	2.13 ± 1.97 (16)
	Alectoris rufa	Red-legged partridge	0.30	4.82 ± 3.37 (8)
Mammals	*Ammotragus lervia*	Aoudad	78.40	4.13 ± 4.31 (40)
	Sus scrofa	Wild boar	23.45	0.72 ± 1.56 (9)
	Oryctolagus cuniculus	European rabbit	0.15	1.04 ± .021 (2)
	Meles meles	European badger	0.05	(1)
	Martes foina	Stone marten	0.03	-(1)
	Canis lupus familiaris	Domestic dog	0.05	1.13 ± 0.35 (2)
	Vulpes vulpes	European red fox	0.13	(1)

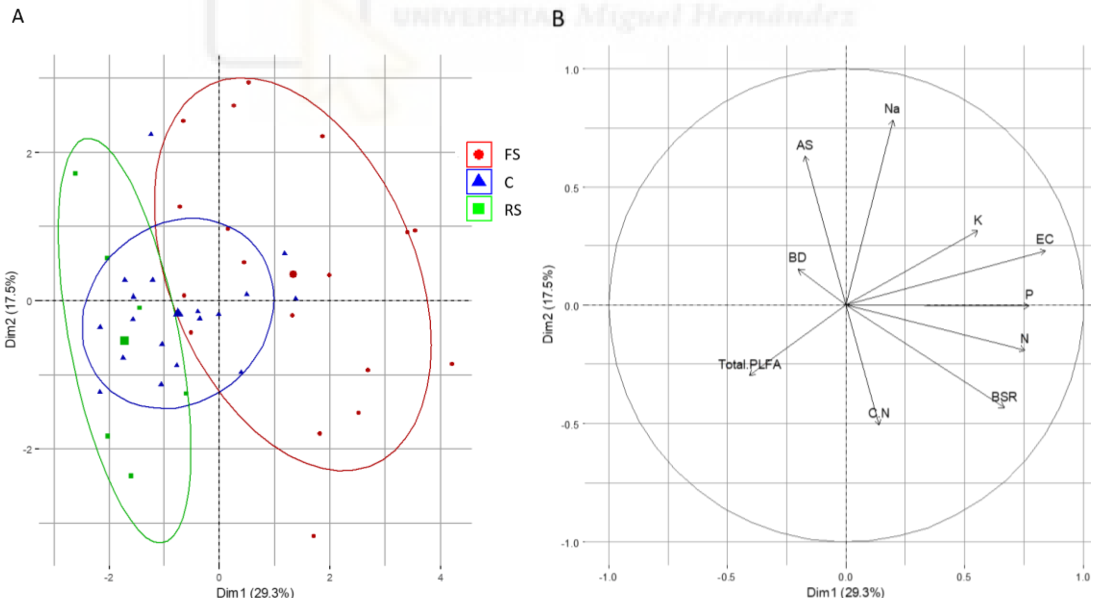

Figure 3. The scores (A) and loadings (B) plots from the PCA performed on the different parameters studied in the soil samples. A) Reference soil (green squares), Contour area (blue triangles) and feeding station (red circles). B) BD: bulk density; AS: aggregate stability; BSR: basal soil respiration; EC: electrical conductivity; Corg: organic carbon; C/N: carbon:nitrogen ratio; K: potassium; Na: sodium; P: phosphorus; Total.PLFA: total PLFA.

Soil physical, chemical and biochemical properties

We did not find any significant differences for the analysed physical properties AS and BD (GLMM, $p > 0.05$) among FS, C and RS areas (see Table 4). For the chemical properties, the results showed that EC values were higher at FS (GLMM, $p < 0.05$). N showed significant differences between RS and the other areas (GLMM, $p < 0.05$), while no differences were found for Na among areas (GLMM, $p > 0.05$). K showed marked differences between FS and C areas (t = -7.92, df = 37, $p < 0.05$), as did P (t = -4.12, df = 37, $p < 0.05$), but did not with RS (GLMM, $p > 0.05$). The C:N ratio did not show any differences among areas (GLMM, $p > 0.05$). Biochemical variable BSR was significantly higher at FS compared with C areas (t = -3.20, df = 37, $p < 0.05$), but was only marginally different with RS (t = -2.33, df = 6.12, $p < 0.10$).

Table 4. GLMMs fitted for testing the effects of supplementary feeding on physicochemical and biochemical soil properties. Similar letters mean no differences between areas.

Response variable	Predictor variable	t	df	*p*	Tukey´s post-hoc
AS	FS	18.43	3.12	0.00	a
	C	1.51	37.00	0.14	a
	RS	-0.43	3.12	0.70	a
BD	FS	10.38	2.34	0.01	a
	C	-1.07	37.00	0.29	a
	RS	-0.09	2.34	0.93	a
EC	FS	8.55	3.31	0.00	a
	C	-4.22	36.99	0.00	b
	RS	-3.16	3.31	0.04	b
N	FS	13.22	39.00	0.00	a
	C	0.11	39.00	0.91	a
	RS	-2.61	39.00	0.01	b
Na	FS	6.10	4.60	0.00	a
	C	-1.52	37.00	0.14	a
	RS	-2.01	4.60	0.11	a
K	FS	10.25	2.57	0.00	a
	C	-7.92	37.00	0.00	b
	RS	-2.11	2.57	0.14	a, b
P	FS	5.17	2.95	0.01	a
	C	-4.12	37.00	0.00	b
	RS	-1.64	2.95	0.20	a, b
C/N	FS	17.07	3.51	0.00	a
	C	0.55	37.00	0.59	a
	RS	-0.95	3.51	0.40	a
BSR	FS	6.73	6.12	0.00	a
	C	-3.20	37.00	0.00	b
	RS	-2.33	6.12	0.06	b

PLFA biomarkers

Total biomass was estimated as the sum of all the extracted PLFA (Total PLFA). Based on the GLMM test, the total PLFA showed significant differences between FS and RS (t = 2.73, df= 39, $p < 0.05$; Table 5) and marginal differences for FS and C (t = 1.74, df= 39, $p < 0.10$). A larger quantity of Fungi was found in RS (GLMM, $p < 0.05$). Significant differences were detected in Bacteria between FS and RS (t = 2.62, df= 39, $p < 0.05$). Actinobacteria showed significant differences between FS and the others areas (GLMM, $p < 0.05$).

Table 5. Results of the GLMMs fitted for testing the effects of supplementary feeding on PLFA biomarkers. Similar letters mean no differences between areas.

Response variable	Predictor variable	t	df	*p*	Tukey´s post-hoc
Total PLFA	FS	3.02	39.00	0.00	a
	C	1.74	39.00	0.09	a, b
	RS	2.73	39.00	0.01	b
Fungi	FS	2.41	39.00	0.02	a
	C	1.05	39.00	0.30	a
	RS	3.52	39.00	0.00	b
Bacteria	FS	2.80	39.00	0.01	a
	C	1.85	39.00	0.07	a, b
	RS	2.62	39.00	0.01	b
Actinobact	FS	2.23	39.00	0.03	a
	C	2.41	39.00	0.02	b
	RS	2.60	39.00	0.01	b

DISCUSSION

Our results showed that FS were used intensively by the target species (aoudad), but also by other non-target species. Aoudad were by far the most frequent, largest and abundant species to use this diversionary food, so aoudad could more strongly influence soil. The detection of non-target species, such as wild boar, is a common fact when this management tool is employed (Morris et al. 2010; Bowman et al. 2015). So, non-target species may also contribute to the effects on soil characteristics (Dunkley and Cattet, 2003), but to a lesser extent than aoudad.

The use of camtraps at FS allowed us to know the intensity of use throughout the study year. However, it was not a measure of cumulative long-term use by the target species. The aoudad population has been subject to variations in density over the years during which supplementary or diversionary feeding has been employed (Eguía, et al. 2015). However, no information is available about the use of these FS in previous years. In any case, we considered that, despite the intensity of use possibly varying interannually, it would be similar for the three FS on an intraanual basis.

Food, faeces and increased trampling in feeding areas could significantly affect structural and chemical soil properties, and could have a negative response on microbial activity (Dunkley and Cattet, 2003; Van der Heijden et al. 2008). Contrarily to our expectations, the physical soil properties evaluated by aggregate stability and bulk density showed no major variations among the compared areas. According to Herbin et al. (2011), soil damage due to trampling depends on the soil water condition, which very strongly influences physical soil properties. Wetting and drying cycles in soil can affect their structural stability (Morugán-Coronado et al. 2011). Rainfall was scarce in the study area during the diversionary feeding period (summer), which might explain why we did not detect any increase in the BD of FS soils despite wildlife trampling. Organic matter content has been positively related with AS (Arden-Clarke and Hodges 1988; Coleman et al. 2004; Kucza, 2007), so no differences in AS values among areas could result from fodder and excrements. Furthermore, rooting by wild boars can reduce bulk density (Wirthner, 2011), which would in turn reduce the effect of trampling. However, we were unable to confirm this effect because we did not record any rooting behaviour in the FS areas.

Regarding chemical properties, higher EC was found at FS. Incorporation of nutrients can increase conductivity, but the EC level reached at these sites was not adverse for soil (Morugán-Coronado et al. 2011). In other studies about leptosol soils, EC values ranged from 1.63 (Kizilkaya and Dengiz, 2010) to 2.37 mS/cm (Badía et al. 2013). In our study area, the EC values were lower than the leptosol soils reported in other studies despite anthropogenic management.

The highest concentration of N, K and P were found in FS and C areas. Regarding Na content, the values did not show differences among areas. The high concentration of some nutrients at FS could be due to food being poured directly on soil and to faecal pellets from wildlife (Eigenberg et al. 2002).

N is a limiting nutrient associated directly with microbial growth (Schimel and Weintraub, 2003). High N addition levels may alter the composition of soil microorganisms and have strong deleterious effects on forest ecosystems (Smith et al. 1999). Although N might be lost through trampling (Batey, 2009), trampling in our case did not contribute to reduce N levels, which reinforces its accumulation in areas used more by wildlife.

Na is a soluble cation that can be lost from soil through rainfall (Coleman et al. 2004). Despite rainfall being scarce in the area (semiarid region), it could have been enough to avoid Na from accumulating, despite its content in fodder (0.05%).

K and P are scarce in terrestrial ecosystems, and are limiting elements (van Breemen, 1993; Coleman et al. 2004). At FS, where natural vegetation cover is absent, K and P concentrations had higher levels than in the C area and RS. The absence of vegetation that assimilates these nutrients could imply their accumulation.

We detected no alterations in the C:N ratio among sites, unlike Gass and Binkley (2011) who found that intensive grazing correlated with nutrient loss. Goyal et al. (1999) found that inorganic fertilisers lowered the C:N ratio. In our case, fodder or faeces (organic origin) could have contributed to maintain the C:N ratio at values between 9 and 12, which indicates a fast relative decomposition rate (SSS, 2014). Other studies about unaltered leptosol soils showed the C/N ratio ranged from 13.30 (Bimüller et al. 2013) to 16.90 (Fernández-Delgado et al. 2015). These values may be related to insufficient nitrogen, as long as our soil samples had optimum conditions for decomposition.

Under natural conditions, low nutrients limit bacteria growth (Morita, 1997), but the application of organic matter and nutrients can promote greater activity for some opportunistic microorganisms (Emmerling et al. 2000; García-Orenes et al. 2010). This would lead to increased BSR (Chander andBrookes, 1993; Leita et al. 1995; Dilly, 1999), which is partially supported by our results.

To evaluate biological soil characteristics, BSR is a weak predictor for species richness (Nielsen et al. 2011), so we assessed the PLFA method as an indicator of the soil microbial community structure (Zelles, 1999). This method is a rapid inexpensive way to assay the biomass and composition of microbial communities in soils, and is suitable for detecting changes in soil community (Frostegård, et al. 2011). Based on the Total PLFA values, our results proved a different community structure of microbiota among areas. The distribution and abundance of soil microorganisms are usually patchy, which makes it difficult to determine their mean abundances without having to deal with a wide variance in their means (Coleman et al. 2004). In the C and RS areas, the microbial community may be closer to an equilibrium status because conditions could undergo fewer alterations than FS. Fungi, Bacteria and Actinobacteria were negatively affected in the FS areas possibly due to alterations to soil characteristics.

Evaluating the effects of animal concentration on soil has been limited to studies mostly on livestock management (Herbin et al. 2011; Ludvíkova et al. 2014). In contrast, there are very little evidences for the effects of wild ungulates management on soil properties. Considering the expansion of wild ungulates in developed countries (Apollonio et al. 2010), it is interesting to know how these animals can influence their habitats at different levels, including biodiversity and soil functioning (Jangid et al. 2008; Macci et al. 2013; García-Orenes et al. 2013). Our results showed that diversionary feeding targeted to wild ungulates might affect soil properties on the small scale (feeding stations) on semiarid Mediterranean mountains. The main detected effects by the diversionary feeding were on the concentration of particular nutrients (N, P, K) and on the soil microbial structure. We recommend metagenomics studies to better understand the microbial community that changes due to diversionary feeding. These effects should be considered to evaluate management strategies for wild ungulates and establish the appropriate measures to minimize the effects, for example not pouring food directly on soils.

ACKNOWLEDGEMENTS

We thank the Ministry of Tourism, Culture and the Environment of the Murcia Region. Pascual-Rico was supported by a pre-doctoral grant from the Spanish Ministry of Education, Education, Culture and Sport (FPU13/05460), and the study was partially supported by MINECO and ERDF (projectCGL2015-66966-C2-1-R). Thanks also go to Carlos Linares for his work in the laboratory.

REFERENCES

Apollonio, M., Andersen, R., Putman, R. 2010. European ungulates and their management in the 21st century. Cambridge University Press, Cambridge.

Arden-Clarke, C., Hodges, R.D. 1988. The environmental effects of conventional and organic/biological farming systems. II. Soil ecology, soil fertility and nutrient cycles. Biological Agriculture and Horticulture 5: 223-287.

Badía, D., Martí, C., Aznar, J.M., León, J. 2013. Influence of slope and parent rock on soil genesis and classification in semiarid mountainous environments. Geoderma 193-194: 13-21.

Bates, D., Maechler, M., Bolker, B., Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67: 1-48.

Batey, T. 2009. Soil compaction and soil management -a review. Soil Use and Management 25: 335-345.

Benito, E., Gómez-Ulla, A., Diaz-Fierros, F. 1986. Descripción de un simulador de lluvia para estudios de erodibilidad del suelo y estabilidad de los agregados al agua. Anales de Edafología y Agrobiología 45: 115-126.

Betteridge, K., Mackay A.D., Shepherd, T.G., Barker, D.J., Budding, P.J., Devantier, B.P., Costall, D.A. 1999. Effect of cattle and sheep treading on surface configuration of a sedimentary hill soil. Soil Research 37: 743-760.

Bimüller, C., Naumann, P.S., Buegger, F., Dannenmann, M., Zeller, B., von Lützow, M., Kögel-Knabner, I. 2013. Rapid transfer of 15N from labeled beech leaf litter to functional soil organic matter fractions in a Rendzic Leptosol. Soil Biology and Biochemistry 58: 323-331.

Blake, G.R., Hartge, K.H. 1986. Bulk density, in: Klute, A. (Ed.), Methods of Soil Analysis: Part 1, Physical and Mineralogical Methods. American Society of Agronomy, Madison, pp. 363-376.

Bossio, D.A., Scow, K.M., Gunapala, N., Graham, K.J. 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microbial Ecology 36: 1-12.

Bowman, B., Belant, J.L., Beyer Jr, D.E., Martel, D. 2015. Characterizing non-target species use at bait sites for white-tailed deer. Human–Wildlife Interactions 9: 110–118.

Bremmer, J.M., Mulvaney, C.S. 1982. Regular Kjeldahl method, in: Norman, A.G. (Ed.), Methods of Soil Analysis: Part 2, Physical and Mineralogical Methods. American Society of Agronomy, Madison, pp. 1162-1163.

Brussaard, L., de Ruiter, P.C., Brown, G.G. 2007. Soil biodiversity for agricultural sustainability. Agriculture, Ecosystems & Environment 121: 233-244.

Castellano, M.J., Valone, T.J. 2007. Livestock, soil compaction and water infiltration rate: Evaluating a potential desertification recovery mechanism. Journal of Arid Environment 71: 97-108.

Cellina, S. 2008. Effects of supplemental feeding on the body condition and reproductive state of wild boar *Sus scrofa* in Luxembourg. PhD thesis, University of Sussex, UK.

Chander, K., Brookes, P.C. 1993. Residual effects of zinc, copper and nickel in sewage sludge on microbial biomass in a sandy loam. Soil Biology and Biochemistry 25: 1231-1239.

Chenu, C., Cosentino, D. 2011. Microbial regulation of soil structural dynamics, in: Ritz, K., Yoing, I. (Eds.), The Architecture and Biology of Soils: Life in Inner Space. CABI, Cambridge, pp. 37-70.

Coleman, D.C., Crossley, D.A., Hendrix, P.F. 2004. Fundamentals of soil ecology, second edition. Academic press, San Diego.

Corcoran, M.J., Wetherbee, B.M., Shivji, M.S., Potenski, M.D., Chapman, D.D. 2013. Supplemental feeding for ecotourism reverses diel activity and alters movement patterns and spatial distribution of the southern stingray, Dasyatis americana. PLoS ONE 8: e59235.

Cortés-Avianza, A., Blanco, G., DeVault, T.L., Markandya, A., Virani, M.Z., Brandt, J., Donázar, J.A. 2016. Supplementary feeding and endangered avian scavengers: benefits, caveats and controversies. Frontiers in Ecology and Environment 14: 191-199.

DeGrood, S.H., Claassen, V.P., Scow, K.M. 2005. Microbial community composition on native and drastically disturbed serpentine soils. Soil Biology and Biochemistry 37: 1427-1435.

Díez, J.A. 1982. Consideraciones sobre la utilización de la técnica extractiva de Burriel y Hernando para la evaluación del P asimilable en suelos. Anales de Edafología y Agrobiología 41: 1345-1353.
Dilly, O. 1999. Nitrogen and phosphorus requirement of the microbiota in soils of the Bornhöved Lake district. Plant & Soil 212: 173-181.
Dunkley, L., Cattet, M.R.L. 2003. A comprehensive review of the ecological and human social effects of artificial feeding and baiting of wildlife. Canadian Cooperative Wildlife Health Centre: Newsletters and Publications 21: 1-68.
Eguía, S., Botella, F., Giménez, A., Sánchez-Zapata, J.A., Pascual, R., Martínez-Noguera, E.J., Fuertes, F., Pérez-Morales, A. y Morell, M. 2015. Elaboración del plan de gestión del arruí en la Región de Murcia. Consejería de Agua, Agricultura y Medio Ambiente. Región de Murcia.
Eigenberg, R.A., Doran, J.W., Nienaber, J.A., Ferguson, R.B., Woodbury, B.L. 2002. Electrical conductivity monitoring of soil condition and available N with animal manure and a cover crop. Agriculture, Ecosystem & Environment 88: 183-193.
Emmerling, C., Liebner, C., Haubold-rosar, M., Katzur, D., Schoder, D. 2000. Impact of application of organic waste materials on microbial and enzyme activities of mine soils in the Lusatian coal mining region. Plant & Soil 22: 129-138.
Fernández-Delgado, M., Gómez-Brandón, M., Knapp, A., Stöhr, D., Insam, H. 2015. Chemical and microbiological properties of alpine forest soils: Effects of pelletized ashes in a short-term trial. Forest Ecology & Management 357: 42-49.
Fox, J., Bouchet-Valat, M. 2017. Rcmdr: R Commander. R package version 2.3-2.
Frostegård, Å., Tunlid, A., Bååth, E. 2011. Use and misuse of PLFA measurements in soils. Soil Biology and Biochemistry 43: 1621-1625.
García-Orenes, F., Guerrero, C., Roldán, A., Mataix-Solera, J., Cerdà, A., Campoy, M., Zornoza, R., Bárcenas, G., Caravaca, F. 2010. Soil microbial biomass and activity under different agricultural management systems in a semiarid Mediterranean agroecosystem. Soil & Tillage Research 109: 110-115.
García-Orenes, F., Morugán-Coronado, A., Zornoza, R., Scow, K., Cerda, A. 2013. Changes in soil microbial community structure influenced by agricultural management practices in a Mediterranean agroecosystem. Plos ONE 8: e80522.
Gass, T.M., Binkley, D. 2011. Soil nutrient losses with ungulate grazing. Journal of Applied Ecology 48, 952-960.
Gee, G.W., Bauder, J.W. 1986. Particle size analysis, in: Klute, A. (Ed.), Methods of soil analysis. Part 1. Physical and Mineralogical Methods, second ed. American Society of Agronomy, Madison, pp 383-412.
González, L.M, Margalida, A., Sánchez, R., Oria, J. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (Aquila adalberti). Biological Conservation 129: 477-486.
Goyal, S., Chander, K., Mundra, M.C., Kapoor, K.K. 1999. Influence of inorganic fertilizers and organic amendments on soil organic matter and soil microbial properties under tropical conditions. Biology and Fertility of Soils 29: 196- 200.
Herbin, T., Hennessy, D., Richards, K.G., Piwowarczyk, A., Murphy, J.J., Holden, N.M. 2011. The effect of dairy cow weight on selected soil physical properties indicative of compaction. Soil Use and Management 27: 36-44.
Hiernaux, P., Bielders, C.L., Valentin, C., Bationo, A., Fernández-Rivera, S. 1999. Effects of livestock grazing on physical and chemical properties of sandy in Sahelian rangelands. Journal of Arid Environment 41: 231-245.
Inslerman, R.A., Miller, J.E., Baker, D.L., Kennamer, J.E., Cumberland, R., Stinson, E.R., Doerr, P., Williamson, S.J. 2006. Baiting and supplemental feeding of game wildlife species. The Wildlife Society. Bethesda, Maryland.
Jangid, K., Williams, M.A., Franzluebbers, A.J., Sanderlin, J.S., Reeves, J.H., Jenkins, M., Endale, D.M., Coleman, D.C., Whitman, W.B. 2008. Relative impacts of land-use, management intensity and fertilization upon soil microbial community structure in agricultural systems. Soil Biology and Biochemistry 40: 315-323.

Kızılkaya, R.I., Dengiz, O. 2010. Variation of land use and land cover effects on some soil physico-chemical characteristics and soil enzyme activity. Žemdirbystė-Agriculture 2: 15-24

Knudsen, D., Peterson, G.A., Pratt, P.F. 1982. Lithium, sodium and potassium, second ed. Page, Madison WI.

Krofel, M., Jerina, K. 2016. Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biological Conservation 197: 40-46.

Kubasiewicz, L.M., Bunnefeld, N., Tulloch, A.I., Quine, C.P., Park, K. 2016. Diversionary feeding: an effective management strategy for conservation conflict? Biodiversity & Conservation 25: 1-22.

Kucza, J. 2007. Wlasciwosci hydrologiczne materii organicznej gleb lesnych na przykladzie gleb pod swierczynami istebnianskimi. Zeszyty Naukowe Akademii Rolniczej w Krakowie 320: 1-176.

Le, S., Josse, J., Husson, F. 2008. FactoMineR: An R package for multivariate analysis. Journal of Statistical Software 25: 1-18.

Leger, L.S. 2003. Health and nature-new challenges for health promotion. Health Promotion International 18: 173-175.

Leita, L., DeNobili, M., Mondini, C., Muhlbachoura, G., Marchinol, L., Bragato, G., Contin, M. 1995. Influence of inorganic and organic fertilization on soil microbial biomass, metabolic quocient and heavy metal bioavailability. Biology and Fertility of Soils 28: 371-376.

López-Bao, J.V., Rodríguez, A., Palomares, F. 2008. Behavioural response of atrophic specialist, the Iberian lynx, to supplementary food: patterns of food use and implications for conservation. Biological Conservation 141: 1857-1867.

Ludvíková, V., Pavlü, V.V., Gaisler, J., Hejcman, M., Pavlü, L. 2014. Long term defoliation by cattlr grazing with and without trampling differently affects soil penetration resistance and plant species composition in Agrostis capillaris grassland. Agriculture, Ecosystems & Environment 197: 204-211.

Macci, C., Doni, S., Peruzzi, E., Bardella, S., Filippis, G., Ceccanti, B., Masciandaro, G. 2013. A real-scale soil phytoremediation. Biodegradation 24: 521-538.

Martínez, L.J., Zinck, J.A. 2004. Temporal variation of soil compaction and deterioration of soil quality in pasture areas of Colombian Amazonia. Soil & Tillage Research 75: 3-17.

Miranda, M., Cristóbal, I., Díaz, L., Sicilia, M., Molina-Alcaide, E., Bartolomé, J., Fierro, Y., Cassinello, J. 2015. Ecological effects of game management: does supplemental feeding affect herbivory pressure on native vegetation? Wildlife Research 42: 353-361.

Morita, R.Y. 1997. Bacteria in oligotrophic environments: starvation-survival lifestyle. Chapman and Hall, New York.

Morris, G.A.I.L., Conner, L.M., Oli, M.K. 2010. Use of supplemental northern bobwhite (Colinus virginianus) food by non-target species. Florida Field Naturalist 38: 99-105.

Morugán-Coronado, A., García-Orenes, F., Mataix-Solera, J., Arcenegui, V., Mataix-Beneyto, J. 2011. Short-term effects of treated wastewater irrigation on Mediterranean calcareous soil. Soil & Tillage Research 112: 18-26.

Nelson, D.W., Sommers, L. 1982. Total carbon, organic carbon, and organic matter, in: Norman, A.G. (Ed.), Methods of soil analysis: Part 2. Chemical and microbiological properties. American Society of Agronomy, Madison, pp. 539-579.

Nielsen, U.N., Ayres, E., Wall, D.H., Bardgett, R.D. 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. European Journal of Soil Science 62: 105-116.

Oja, R., Zilmer, K., Valdmann, H. 2015. Spatiotemporal effects of supplementary feeding of wild boar (*Sus scrofa*) on artificial ground nest depredation. PLoS ONE 10: e0135254.

Orams, M.A. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management 23: 281-293.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16: 1501-1514.

Piper, S.E. 2005. Supplementary feeding programs: how necessary are they for the maintenance of numerous and healthy vultures populations? In: Houston, D.C., Piper, S.E. (Eds.), Proceedings of

the International Conference on Conservation and Management of Vulture Populations. Thessaloniki: Natural History Museum of Crete and WWF Greece, pp. 41-50.
Putman, R.J., Staines, B.W. 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34: 285-306.
Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D.C., Watt, A., Gutiérrez, R.J. 2013. Understanding and managing conservation conflicts. Trends in Ecology and Evolution 28: 100-9.
Robb, G.N., McDonald, R.A., Chamberlain, D.E., Bearhop, S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6: 476-484.
Roger-Estrade, J., Anger, C., Bertrand, M., Richard, G. 2010. Tillage and soil ecology: Partners for sustainable agriculture. Soil & Tillage Research 111: 33-40.
Roldán, A., García-Orenes, F., Lax, A. 1994. An incubation experiment to determine factors involving aggregation changes in an arid soil receiving urban refuse. Soil Biology and Biochemistry 26: 1699-1707.
Sahlsten,J., Bunnefeld, N., Månsson, J., Ericsson, G., Bergström, R., Dettki, H. 2010. Can supplementary feeding be used to redistribute moose Alces alces? Wildlife Biology 16: 85-92.
Sánchez-Zapata, J.A., Calvo, J.F. 1999. Raptor distribution in relation to landscape composition in semi-arid Mediterranean habitats. Journal of Applied Ecology 36: 254-262.
Savadogo, P., Sawadogo, L., Tiveau, D. 2007. Effects of grazing intensity and prescribed fire on soil physical and hydrological properties and pasture yield in the savannah woodlands of Burkina Faso. Agriculture, Ecosystems & Environment 118: 80-92.
Schimel, J.P., Weintraub, M.N. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology and Biochemistry 35: 549-563.
Selva, N., Berezowska-Cnota, T., Elguero-Claramunt, I. 2014. Unforeseen effects of supplementary feeding: ungulate baiting sites as hotspots for ground-nest predation. PLoS ONE 9: e90740.
Smith, V.H., Tilman, G.D., Nekola, J.C. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution 100: 179-196.
Snow, N.P., Porter, W.F., Williams, D.M. 2015. Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. Biological Conservation 181: 44-53.
Soil Survey Staff, 2014. Keys to soil taxonomy, twelfth ed. USDA-Natural Resources Conservation Service, Washington DC.
van Breemen, N. 1993. Soils as biotic constructs favouring net primary productivity. Geoderma 57: 183–211.
Van der Heijden, M.G., Bardgett, R.D., Van Straalen, N.M. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11, 296-310.
Vance, E.D., Brookes, P.C., Jenkinson, D.S. 1987. An extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry 19: 703-707.
Vicente, J., Ruiz-Fons, F., Vidal, D., Höfle, U., Acevedo, P., Villanúa, D., Fernández-de-Mera, I.G., Martin, M.P., Gortázar, C. 2005. Serosurvey of Aujezky's disease virus infection in European wild boar in Spain. Veterinary Record 156: 408-412.
Wirthner, S. 2011. The role of wild boar (*Sus scrofa* L.) rooting in forest ecosystems in Switzerland. PhD Thesis, University of Bern, Switzerland.
World Reference Base for Soil Resources, 2014. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome. Journal of Environmental Quality 28: 1442-1447.
Yong-Zhong, S., Yu-Lin, L., Jian-Yuan, C., Wen-Zhi, Z. 2005. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. Catena 59: 267-278.
Young, I.M., Crawford, J.W. 2004. Interaction and self-organization on the soil-microbe complex. Science 304: 1634-1637.

Zelles, L. 1999. Fatty acid patterns of phospholipids and lipopolysaccharides in the characterization of microbial communities in soil: a review. Biology and Fertility of Soils 29: 111.

Zornoza, R., Guerrero, C., Mataix-Solera, J., Scow, K.M., Arcenegui, V., Mataix-Beneyto, J. 2009. Changes in soil microbial community structure following the abandonment of agricultural terraces in mountainous areas of Eastern Spain. Applied Soil Ecology 42: 315-323.

Chapter 6

General Discussion

TRENDS IN UNGULATE RESEARCH

The studies of ungulate ecology published during the second half of the 20th century generally addressed topics from a purely ecological perspective. These topics included regulation of vegetation and primary productivity (e.g. Hobbs 1996), competitive interactions (e.g. Lamprey 1963; Leuthold 1978), soil ecology (Ben-Shahar and Coe 1992). Many of these works pursued to understand the implications of ungulates in ecosystem functioning, where landscapes were usually pristine and with no human alteration. For example, in relation with wild ungulates McNaughton et al. (1988) highlight contrasting ecosystem functioning in landscapes with high and low abundance of wild ungulates because of their effects on habitat and energy flow regulation. Owen-Smith (1989) discussed about megaherbivores and their regulating effect on ecosystems. Most of these studies did not approach their work from a socioecological perspective, although they usually discuss about the role of human activities.

Currently, a great amount of scientific literature is published from a perspective where ecological systems interact positively or negatively with humans (e.g. human-ungulate relations; see Chapter 1). We recognise that our systematic review was focused on human-wildlife interactions and we did not consider works outside our search criteria, which could limit our framework. However, nowadays it is difficult to find non-altered areas where interactions between wildlife (or other ecosystem components) and human activities do not occur given the widespread human occupation over different environments (Goudie 2013).

As shown in the different chapters of the thesis, there is a great amount of scientific publications on human-ungulate relations from a conflict perspective, relegating ES. Nevertheless, studies considering an Ecosystem Services framework have increased in recent years. Thus, research on ungulate ecology has changed over the years incorporating new perspectives and approaches. Besides, human-ungulate relations identified at the global and national scales were not exactly the same since they were context dependent in time and space (Lengyel et al. 2014).

ES is one of the concepts that most influenced ecological research during the last two decades. This concept appeared at the beginning of this century and it allowed to link human welfare to ecosystem functioning (MEA 2005). Results from ES scientific studies have been considered into global and regional conservation policy decisions (see Constanza et al. 2017). Recently, the new term Nature's Contributions to People (NCP; Díaz et al. 2018) has also emerged. NCP supposes a new change in the socio-ecological research framework, integrating in a further way the people (e.g. through local knowledge incorporation) and the environment. In any case, the conceptual framework of ecosystem services (based on the categories of beneficial nature's contributions to people of Díaz et al., 2018) might be useful to override the mostly negative approaches that dominate the scientific literature in relation to ungulates and humans.

LESSONS FROM A PARADIGMATIC CASE: THE AOUDAD

Human activities have been intensified in different parts of the world and their impacts on the environment during the last century are obvious. Resource exploitation, habitat destruction, contamination and poaching have detrimental effects on wildlife, including ungulates and contribute to biodiversity loss (e.g. Duncan et al. 2014; Mishra and Fitzherbert 2004). Wars are extreme human-human conflicts that can also promote large scale damages to biodiversity and ecosystems (Atkins et al. 2019; Brito et al. 2017). One of this conflicts led the biologist Dr. J.A. Valverde, who witnessed the sharp decline of the Saharan megafauna, to create the Experimental Station of Arid Zones (EEZA by its initials in Spanish, http://www.eeza.csic.es) The EEZA established during the 1960's aimed to promote in situ conservation programs for endangered ungulates such as the dama and the dorcas gazelle. Such programs along with the creation of protected areas are among the most common and successful consevation strategies (Lindsey et al. 2017).

But the strategy was different for another Saharan ungulate. The aoudad (Photo 1), whose populations in their African native range are threatened, was released for conservation and hunting purposes in SE Spain since the 1970's. This could be considered a pioneering program of assisted colonization (Seddon et al. 2010); a controversial management tool because it is not possible to predict the consequences that may result of species introductions (Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009).

More than forty years since the aoudad introduction Peninsular Spain, different conflicts related with this species and its management have emerged (Pascual-Rico et al. 2017a), including competition with the native Iberian ibex (Photo 2), damage to the native flora, or crop damage. Because of these, the species was included in the Spanish Catalogue of Invasive Exotic Species (Real Decreto 630/2013, Spanish Government). After several legislative changes regarding the aoudad (and other exotic species present in Spain), the Government approved a law (Law 7/2018) to allow populations introduced legally before 2007 to be excluded of the Spanish Catalogue of Invasive Exotic Species.

Despite the controversy about the aoudad invasiveness in Peninsular Spain (see Cassinello 2018; Roll and Berger-Tal 2018), our results supported potential competition between the Iberian ibex and the aoudad (Chapter 3). The introduction of exotic ungulate species has been a common practice unrelated to conservationist reasons. Species such as the wild boar (*Sus scrofa*), the American mountain goat (*Oreamnos americanus*) or deer species were introduced in areas outside their natural range. These species have been related with negative effects on native ungulates because intraguild competition process and impacts on native forest (e.g. Dolman and Wäber 2008; Galetti et al. 2015; Gross 2001).

Photo 1. Saharan aoudad (*Ammotragus lervia sahariensis*) photographed in Morocco. Harmusch association.

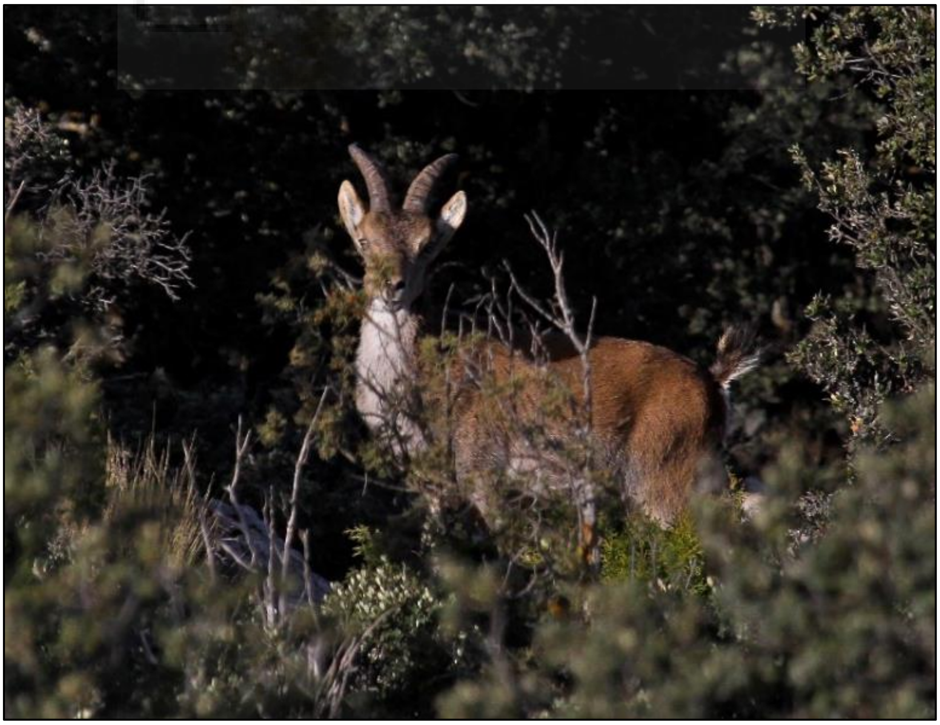

Photo 2. Iberian ibex (*Capra pyrenaica*) in Sierra Espuña. By Sergio Eguía.

Although exotic ungulates have been related with vegetation damage over threatened species because of their palatability (e.g. Velamazán et al. 2017), vegetation damage could be due to high densities, and not because of their exotic origin (Fernández-Olalla et al. 2016). According to Fernández-Olalla et al. (2016) and Velamazán et al. (2018), the aoudad could be considered in the introduced areas as a functional substitute of wild ungulates and livestock where they are absent and as consumer of woody fuel to prevent fire events. But the recolonization of this areas by the native Spanish ibex and the conflicts with different stakeholders reinforces its role as exotic invasive species.

Among the management tools applied to the aoudad in Peninsular Spain highlight the diversionary feeding in Sierra Espuña Regional Park. Diversionary feeding affected the species differentially. Although the aoudad can cause crop damage, Sierra Espuña tracked aoudads just include less of three percent of croplands in their home range (Pascual-Rico et al. 2017b). Some authors evaluated the efficiency of this management tool on target species (e.g. Putman and Staines 2004; Van Beest et al. 2010), but it remains controversial. Often it is recommended to employ this management tool in combination with other strategies (such as integrating stakeholders or lethal control) to improve their efficiency (see Huijser et al. 2009; Reimoser 2003).

Moreover, non-target species used diversionary feeding (Chapter 4). This is a common problem associated with diversionary feeding and it has appeared in different parts of the world (e.g. Selva et al. 2017; Fležar et al. 2019). Besides, food and wildlife concentration altered soil properties (Chapter 5). Soil alteration has been detected in previous studies but in relation to domestic ungulates (e.g. Castellano and Valone, 2007; Yong-Zhong et al. 2005). These unexpected effects must be addressed to improve management strategies.

Paradoxically, the aoudad introduction is an example of how a conservation measure (i.e. assisted colonisation) has turned into a long term conservation conflict demanding large management efforts decades after its introduction.

BIODIVERSITY CONSERVATION & FUTURE PERSPECTIVES

Ungulates are at the forefront of conservation and management strategies for contrasting reasons. On the one hand, wild ungulates are recolonizing large areas of developed countries in Europe and North America under a rewilding scenario (Apollonio et al. 2010). On the other hand, many ungulate species are decreasing and even facing extinction in many other regions of the world (e.g. Durant et al. 2014). Introduction of non-native species and the elimination of predator are of changes that greatly affects ecosystem functioning (e.g. Gass and Binkley 2011; Nuñez et al. 2010). Moreover, several anthropogenic activities such as forestry and agriculture are developed in some cases close to the habitat (or even constituting the own habitat) of some ungulate species (e.g. Boan et al. 2011; Hegel et al. 2009; Reimoser 2003). All these disturbing factors contribute to the promotion of conflicts between wild ungulates and human activities. In addition, strategies to mitigate conflicts which propose the recovery of natural ecosystem functioning are scarce (e.g. Beschta et al. 2013; Licht et al. 2010; Tanentzap et al. 2009), and other strategies with human intervention are often proposed (see Chapter 1).

In spite of the negative aspects related with wild ungulates, it has been increasingly demonstrated that these animals are also associated with positive aspects to humans and for the ecosystem functioning. Wild ungulates (and other species) are related with cultural and provisioning ES through tourism and sport hunting. These activities generate economic benefits and promote conservation (Naidoo et al. 2011; Naidoo et al. 2016). Besides, wild ungulates are key species as providers of regulating ES, such as forming part of the nutrient cycle or even conditioning the vegetation structure of terrestrial ecosystems (Danell et al. 2006). A recent study has showed that ungulates could modulate the vegetation responses to climate variability by reducing the amplitude of seasonal oscillation in vegetation greenness at the landscape-scale (Barbosa et al. in press).

The future management of wild large herbivores will require ecologists to co-operate with sociologists, economists, politicians and the public (Gordon et al. 2004) to apply the most appropriate measures that favour the conservation and natural functioning of ecosystems and the coexistence between humans and wildlife. Moreover, it is recommendable to develop more studies approaching the role of ungulates in the ecological functioning of the human dominated ecosystems in the Anthropocene.

REFERENCES

Apollonio, M., Andersen, R., Putman, R. (Eds.). 2010. European ungulates and their management in the 21st century. Cambridge Univ. Press, Cambridge.

Barbosa, J.M., Pascual-Rico, R., Eguía, S., Sánchez-Zapata, J.A. Ungulates attenuate the response of Mediterranean vegetation to climate oscillations. Ecosystems (MS# ECO-18-0438).

Ben-Shahar, R., Coe, M.J. 1992. The relationships between soil factors, grass nutrients and the foraging behaviour of wildebeest and zebra. Oecologia 90: 422–428.

Beschta, R.L., Donahue, D.L., DellaSala, D.A., Rhodes, J.J., Karr, J.R., O'Brien, M.H., Fleischner, T.L., Williams, C.D. 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. Environmental Management 51: 474-491.

Boan, J.J., McLaren, B.E., Malcolm, J.R. 2011. Influence of post-harvest silviculture on understory vegetation: implications for forage in a multi-ungulate system. Forest Ecology and Management 262: 1704-1712.

Brito, J.C., Durant, S.M., Pettorelli, N., Newby, J., Canney, S., Algadafi, W., Rabeil, T., Crochet, P-A., Pleguezuelos, J.M., Wacher, T., de Smet, K., Vasconcelos, D.G., Ferreira da Silva, M.J., Martínez-Freiría, F., Abáigar, T., Campos, J.C., Comizzoli, P., Fahd, S., Fellous, A., Halilou, H., Garba, M., Hamidou, D., Harouna, A., Hatcha, M.H., Nagy, A., Silva, T.L., Sow, A. S., Vale; C.G., Boratyński, Z., Rebelo, H., Carvalho, S.B., 2018. Armed conflicts and wildlife decline: Challenges and recommendations for effective conservation policy in the Sahara-Sahel. Conservation Letters. 11:e12446.

Cassinello, J. 2018. Misconception and mismanagement of invasive species: The paradoxical case of an alien ungulate in Spain. Conservation Letters 11: e12440.

Castellano, M.J., Valone, T.J. 2007. Livestock, soil compaction and water infiltration rate: Evaluating a potential desertification recovery mechanism. Journal of Arid Environments 71: 97-108.

Constanza, R., de Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S., Grasso, M. 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosystem Services 28: 1-16.

Danell, K., Duncan, P., Bergström, R., Pastor, J. (Eds). 2006. Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Published by Cambridge University Press. Cambridge University Press.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Bauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y. 2018. Assessing nature's contributions to people. Science 359: 270-272.

Dolman, P.M., Wäber, K. 2008. Ecosystem and competition impacts of introduced deer. Wildlife Research 35: 202-214.

Duncan, C., Kretz, D., Wegmann, M., Rabeil, T., Pettorelli, N. 2014. Oil in the Sahara: mapping anthropogenic threats to Saharan biodiversity from space. Philosophical Transactions of the Royal Society B: Biological Sciences 369: 20130191.

Durant, S.M., Wacher, T., Bashir, S., Woodroffe, R., Ornellas, P., Ransom, C., Newby, J., Abáigar, T., Abdelgadir, M., El Alqamy, H., Baillie, J., Beddiaf, M., Belbachir, F., Belbachir-Bazi, A., Berbash, A. A. Bemadjim, N.E., Beudels-Jamar, R., Boitani, L., Breitenmoser, C., Cano, M., Chardonnet, P., Collen, B., Cornforth, W.A., Cuzin, F., Gerngross, P., Haddane, B., Hadjeloum, M., Jacobson, A., Jebali, A., Lamarque, F., Mallon, D., Minkowski, K., Monfort, S., Ndoassal, B., Niagate, B., Purchase, G., Samaïla, S., Samna, A.K., Sillero-Zubiri, C., Soultan, A.E., Stanley Price, M.R., Pettorelli, N. 2014, Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Diversity & Distributions 20: 114-122.

Fernández-Olalla, M., Martínez-Jauregui, M., Perea, R., Velamazán, M., San Miguel, A. 2016. Threat or opportunity? Browsing preferences and potential impact of *Ammotragus lervia* on woody plants of a Mediterranean protected area. Journal of Arid Environments 129: 9-15.

Fležar, U., Costa, B., Bordjan, D., Jerina, K., Krofel, M. 2019. Free food for everyone: artificial feeding of brown bears provides food for many non-target species. European Journal of Wildlife Research 65: 1.

Galetti, M., Camargo, H., Siqueira, T., Keuroghlian, A., Donatti, C.I., Jorge, M.L.S.P., Pedrosa, F., Kanda, C.Z., Ribeiro, M.C. 2015. Diet overlap and foraging activity between feral pigs and native peccaries in the pantanal. PloS ONE 10:e0141459.

Gass, T.M., Binkley, D. 2011. Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. Journal of Applied Ecology 48: 952–960.

Gordon, I.J., Hester, A.J., Festa-Bianchet, M. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41: 1021-1031.

Goudie, A.S. 2013. Human impact on the natural environment: past, present and future. Seventh Edition. John Wiley & Sons. Oxford.

Gross, J.E. 2001. Evaluating effects of an expanding mountain goat population on native bighorn sheep: a simulation model of competition and disease. Biological Conservation 101: 171-185.

Hegel, T.M., Gates, C.C., Eslinger, D. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90: 222-235.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60: 695-713.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H.P., Thomas, C.D. 2008. Assisted colonization and rapid climate change. Science 321: 345-346.

Huijser, M.P., Duffield, J.W., Clevenger, A.P., Ament, R.J., McGowen, P.T. 2009. Cost–benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: a decision support tool. Ecology and Society 14: 15.

Lamprey, H.F. 1936. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. African Journal of Ecology 1: 63-92.

Lengyel, S., Kosztyi, B., Ölvedi, T.B., Gunton, R.M., Kunin, W.E., Schmeller, D.S., Henle, K. 2014. Conservation strategies across spatial scales. Scaling in Ecology and Biodiversity Conservation 133-136.

Leuthold, W. 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35: 241.

Licht, D.S., Millspaugh, J.J., Kunkel, K.E., Kochanny, C.O., Peterson, R.O. 2010. Using small populations of wolves for ecosystem restoration and stewardship. Bioscience 60: 147-153.

Lindsey, P.A., Chapron, G., Petracca, L.S., Burnham, D., Hayward, M.W., Henschel, P., Hinks, A.E., Garnett, S.T., Macdonald, D.W., Macdonald, E.A., Ripple, W.J., Zander, K., Dickman, A. 2017. Relative efforts of countries to conserve world’s megafauna. Global Ecology and Conservation 10: 243-252.

McNaughton, S.J., Ruess, R.W., Seagle, S.W. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38: 794-800.

Millennium Ecosystem Assessment. 2005. Ecosystem and human well-being: biodiversity synthesis. World Resources Institute, Washington, DC.

Mishra, C., Fitzherbert, A. 2004. War and wildlife: a post-conflict assessment of Afghanistan’s Wakham Corridor. Oryx 38: 102-105.

Naidoo, R., Weaver, L.C., Diggle, R.W., Matongo, G., Stuart-Hill, G., Thouless, C. 2016. Complementary benefits of tourism and hunting to communal conservancies in Namibia. Conservation Biology, 30: 628-638.

Naidoo, R., Weaver, L.C., Stuart-Hill, G., Tagg, J. 2011. Effect of biodiversity on economic benefits from communal lands in Namibia. Journal of Applied Ecology 48: 310-316.

Nuñez, M.A., Bailey, J.K., Schweitzer, J.A. 2010. Population, community and ecosystem effects of exotic herbivores: A growing global concern. Biological Invasions 12: 297-301.

Owen-Smith, N. 1989. Megafaunal extinctions: the conservation message from 11,000 years B.P. Conservation Biology 3: 405-412.

Pascual-Rico, R., Botella, F., Giménez, A., Eguía, S., Sánchez-Zapata. 2017a. Percepción social de conflictos y servicios ecosistémicos del Arrui (*Ammotragus lervia*). Ballesteros, G.A., Belmonte F., Sánchez, J.M., Robledano F. (Eds.). Biodiversidad y procesos ecológicos en el Sureste Ibérico. Universidad de Murcia. Servicio de Publicaciones. Murcia, cap 23: 191-200.

Pascual-Rico, R., Pérez-García, J.M., Botella, F., Giménez, A., Eguía, S., Sánchez-Zapata, J.A. 2017b. "Área de campeo y uso del hábitat del arruí (*Ammotragus lervia*) en Sierra Espuña (Murcia)" en Gustavo A. Ballesteros Pelegrín, Francisco Belmonte Serrato, Jorge M. Sánchez Balibrea y Francisco Robledano Aymerich (Eds.). Biodiversidad y procesos ecológicos en el Sureste Ibérico. Universidad de Murcia. Servicio de Publicaciones, Murcia, cap 22: 184-190.

Putman, R.J., Staines, B.W. 2004. Supplementary feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34: 285-306.

Reimoser, F. 2003. Steering the impacts of ungulates on temperate forest. Journal of Nature Conservation 10: 243-252.

Ricciardi, A., Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology and Evolution 24: 248-253.

Roll, U., Berger-Tal, O. 2018. Gritty until proven irritant—What makes a species invasive? Comment on Cassinello (2018). Conservation Letters 11: e12597.

Seddon, P.J. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. Restoration Ecology 18: 796-802.

Selva, N., Teitelbaum, C.S., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Bojarska, K., Mueller, T. 2017. Supplementary ungulate feeding affects movement behavior of brown bears. Basic Applied Ecology 24: 68-76.

Tanentzap, A.J., Burrows, L.E., Lee, W.G., Nugent, G., Maxwell, J.M., Coomes, D.A. 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology 46: 1064-1072.

Van Beest, F.M., Loe, L.E., Mysterud, A., Milner, J.M. 2010. Comparative space use and habitat selection of moose around feeding stations. Journal of Wildlife Management 74: 219-227.

Velamazán, M., San Miguel, A., Escribano, R., Perea, R. 2017. Threatened Woody flora as an ecological indicator of large herbivore introductions. Biodiversity and Conservation 26: 917-930.

Velamazán, M., San Miguel, A., Escribano, R., Perea, R. 2018. Use of firebreaks and artificial supply points by wild ungulates: Effects on fuel load and woody vegetation along a distance gradient. Forest Ecology and Management 427: 114-123.

Yong-Zhong, S., Yu-Lin, L., Jian-Yuan, C., Wen-Zhi, Z. 2005. Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. Catena 59: 267-278.

Conclusions

CONCLUSIONS

1 At the global scale, human-ungulate relations are approached mostly from a negative perspective in which conflicts exceed benefits. However, positive interactions between humans and ungulates are also arising under the framework of ecosystem services. At other scales, such as the national scale, the dimension of human-ungulate relations differs between stakeholders suggesting that conflicts and services are context dependent.

2 The incorporation of stakeholder perceptions and local ecological knowledge in scientific research might improve decision-making processes, conservation measures and wildlife management strategies. Considering stakeholder interests in the scientific studies and their divulgation can affect positively the tolerance of society towards wildlife.

3 The introduction of exotic species could lead to the emergence of unpredictable impacts affecting the ecosystems and the conflicts with human activities. This may happen independently of the reason for the introduction (e.g. hunting purposes, aesthetic value, accidentally); even if it is done for conservation purposes (i.e. assisted colonisation). The results on the potential competition between the native Spanish and the Aoudad described by means of niche overlap might help to shed light on a long-term conservation conflict.

4 Diversionary feeding as a management tool had limited effect on the spatial behaviour of the target species and its efficiency may be restricted. Furthermore, if applied, it is advisable to avoid the use of the feeding stations by non-target species and the unintended effects on the soil.

5 Ungulate management in human dominated landscapes might benefit from proper scientific evaluation. It is necessary to check the effectiveness of the management tools implemented but also, and more importantly, to promote adaptive management oriented by ecological research in a scenario of rewilding.

Conclusiones

CONCLUSIONES

1 A escala global, las relaciones entre los humanos y los ungulados se abordan generalmente desde una perspectiva negativa en la cual los conflictos superan a los beneficios. Sin embargo, en los estudios científicos se consideran cada vez más las interacciones positivas en el marco de los servicios ecosistémicos entre los humanos y los ungulados. A otras escalas, como a escala nacional, las relaciones entre los humanos y los ungulados difieren entre los agentes implicados, lo que sugiere que los conflictos y los servicios ecosistémicos identificados dependen del contexto.

2 La incorporación en la investigación de las percepciones de los agentes implicados y del conocimiento ecológico local puede mejorar el proceso de toma de decisiones, las medidas de conservación y las estrategias de gestión de fauna silvestre. El hecho de considerar los intereses de los agentes implicados en la ciencia y la divulgación de los resultados científicos puede afectar positivamente la tolerancia social hacia la fauna silvestre. Los resultados de la competencia potencial entre la cabra montés autóctona y el arrui descritos por el solapamiento de nichos podrían ayudar a arrojar luz sobre un conflicto de conservación a largo plazo.

3 La introducción de especies exóticas puede causar impactos en los ecosistemas y provocar conflictos con las actividades humanas. Esto puede suceder independientemente del motivo de la introducción (por ejemplo, por intereses cinegéticos, valores estéticos o accidentalmente), incluso aunque sea por razones de conservación (es decir, colonización asistida).

4 Los aportes suplementarios tuvieron un efecto variable sobre el comportamiento espacial de la especie objetivo, por lo que su eficiencia debe ser limitada. Además, si se emplea, es recomendable evitar que especies no objetivo usen los comederos y los efectos sobre el suelo.

5 La gestión de los ungulados en los paisajes dominados por los humanos podría beneficiarse de una evaluación científica adecuada. Es necesario evaluar la efectividad de las herramientas de gestión empleadas pero también, y más importante, promover una gestión adaptativa orientada por la investigación en ecología en un escenario de recuperación de fauna (rewilding).

Appendices

Chapter 1

General Introduction

S.1.1. List of keywords used in the systematic review.

Ecosystem services

"*ecosystem service**" OR "*ecosystem good**" OR "*environmental service**" OR

Conflicts

"*conflict**" OR "*damage**" OR "*impair**" OR "*harm**" OR

Human-ungulate relation

"*human-wildlife*" OR "*human-ungulate**" OR "*human-hervibore**" AND

Ungulates

("hervibore"* AND *"mammal"* AND *"ungulate"*) OR (*"Antilocapra"* OR *"Addax"* OR *"Aepyceros"* OR *"Alcelaphus"* OR *"Ammodorcas"* OR *"Ammotragus"* OR *"Antidorcas"* OR *"Antilope"* OR *"Beatragus"* OR *"Bison"* OR *"Bos"* OR *"Boselaphus"* OR *"Bubalus"* OR *"Budorcas"* OR *"Capra"* OR *"Capricornis"* OR *"Cephalophus"* OR *"Connochaetes"* OR *"Damaliscus"* OR *"Dorcatragus"* OR *"Eudorcas"* OR *"Gazella"* OR *"Hemitragus"* OR *"Hippotragus"* OR *"Kobus"* OR *"Litocranius"* OR *"Madoqua"* OR *"Naemorhedus"* OR *"Nanger"* OR *"Neotragus"* OR *"Oreamnos"* OR *"Oreotragus"* OR *"Oryx"* OR *"Ourebia"* OR *"Ovibos"* OR *"Ovis"* OR *"Pantholops"* OR *"Pelea"* OR *"Philantomba"* OR *"Procapra"* OR *"Pseudois"* OR *"Pseudoryx"* OR *"Raphicerus"* OR *"Redunca"* OR *"Rupicapra"* OR *"Saiga"* OR *"Sylvicapra"* OR *"Syncerus"* OR *"Taurotragus"* OR *"Tetracerus"* OR *"Tragelaphus"* OR *"Sus"* OR *"Babyrousa"* OR *"Hylochoerus"* OR *"Phacochoerus"* OR *"Potamochoerus"* OR *"Catagonus"* OR *"Pecari"* OR *"Tayassu"* OR *"Moschus"* OR *"Hexaprotodon"* OR *"Hippopotamus"* OR *"Giraffa"* OR *"Okapia"* OR *"Camelus"* OR *"Lama"* OR *"Vicugna"* OR *"Alces"* OR *"Axis"* OR *"Blastocerus"* OR *"Capreolus"* OR *"Cervus"* OR *"Dama"* OR *"Elaphodus"* OR *"Elaphurus"* OR *"Hippocamelus"* OR *"Hydropotes"* OR *"Mazama"* OR *"Muntiacus"* OR *"Odocoileus"* OR *"Ozotoceros"* OR *"Przewalskium"* OR *"Pudu"* OR *"Rangifer"* OR *"Rucervus"* OR *"Rusa"* OR *"Equus"* OR *"Ceratotherium"* OR *"Dicerorhinus"* OR *"Diceros"* OR *"Rhinoceros"* OR *"Acrocodia"* OR *"Tapirella"* OR *"Tapirus"* OR *"Hyemoschus"* OR *"Moschiola"* OR *"Tragulus"*).

Appendix S.1.2. References selected in the search of articles

Akashi, N. 2006. Height growth of young larch (*Larix kaempferi*) in relation to the frequency of deer browsing damage in Hokkaido, Japan, Journal of Forest Research 11: 153-156.

Akashi, N., et al. 2011. Effects of deer abundance on broad-leaf tree seedling establishment in the understory of *Abies sachalinensis* plantations. Journal of Forest Research 16: 500-508.

Akashi, N., et al. 2015. Significance of woody browse preferences in evaluating the impact of sika deer browsing on tree seedlings. Journal of Forest Research 20: 396-402.

Akashi, N., Terazawa, K. 2005. Bark stripping damage to conifer plantations in relation to the abundance of sika deer in Hokkaido, Japan. Forest Ecology and Management 208: 77-83.

Albrycht, M. et al. 2016. The demographic pattern of wild boars (*Sus scrofa*) inhabiting fragmented forest in North-Eastern Poland. Baltic Forestry 22: 251-258.

Allred, B.W. et al. 2013. Conservation implications of native and introduced ungulates in a changing climate. Global Change Biology 19: 1875-1883.

Ameztegui, A., Coll, L. 2015. Herbivory and seedling establishment in Pyrenean forests: Influence of micro- and meso-habitat factors on browsing pressure, Forest Ecology and Management 342: 103-111.

Amici, A. et al. 2012. Increase in crop damage caused by wild boar (*Sus scrofa* L.): The “refuge effect”. Agronomy for Sustainable Development 32: 683-692.

Anderson, A. et al. 2016. Economic estimates of feral swine damage and control in 11 US states. Crop Protection 89: 89-94.

Ando, M. et al. 2006. Expansion of dwarf bamboo, *Sasa nipponica*, grassland under feeding pressure of sika deer, *Cervus nippon*, on subalpine coniferous forest in central Japan. Journal of Forest Research, 11: 51-55.

Ando, M., et al. 2003. Bark stripping preference of sika deer, *Cervus nippon*, in terms of bark chemical contents. Forest Ecology and Management 177: 323-331.

Atickem, A., Loe, L.E. 2014. Livestock-wildlife conflicts in the Ethiopian highlands: Assessing the dietary and spatial overlap between mountain nyala and cattle. African Journal of Ecology 52: 343-351.

Augustine, D J., Mcnaughton, S.J. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology 41: 45-58.

Austin, Z. et al. 2009. Mapping wildlife: integrating stakeholder knowledge with modelled patterns of deer abundance by using participatory GIS. Wildlife Research 36: 553.

Baasch, D.M. et al. 2010. Resource selection by elk in an agro-forested landscape of northwestern Nebraska. Environmental Management 46: 725-737..

Bagchi, S., et al. 2004. Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan mountains. Animal Conservation 7: 121-128.

Ball, J.P., Dahlgren, J. 2002. Browsing damage on pine (*Pinus sylvestris* and *P. contorta*) by a migrating moose (*Alces alces*) population in winter: Relation to habitat composition and road barriers. Scandinavian Journal of Forest Research 17: 427-435.

Ballari, S.A. et al. 2015. Invasive wild boar in Argentina: using protected areas as a research platform to determine distribution, impacts and management. Biological Invasions 17: 1595-1602.

Banko, P.C. et al. 2014. Evaluating the Long-Term Management of Introduced Ungulates to Protect the Palila, an Endangered Bird, and Its Critical Habitat in Subalpine Forest of Mauna Kea, Hawaii. Arctic, Antarctic, and Alpine Research 46: 871-889.

Bariyanga, J.D. et al. 2016. Effectiveness of Electro-Fencing for Restricting the Ranging Behaviour of Wildlife: A Case Study in the Degazetted Parts of Akagera National Park. African Zoology 51: 183-191.

Barrett, M.A., Stiling, P. 2007. Relationships among Key deer, insect herbivores, and plant quality. Ecological Research 22: 268-273.

Barrios-Garcia, M.N. et al. 2012. Patterns of use and damage by exotic deer on native plant communities in northwestern Patagonia. European Journal of Wildlife Research 58: 137-146.

Bates, B., Hersey, K. 2016. Lessons learned from bison restoration efforts in utah on western rangelands. Rangelands 38: 256-265.

Bee, J.N., et al. 2007. Resistance and resilience of New Zealand tree species to browsing. Journal of Ecology 95: 1014-1026.

Bennett, A.M.I., Coulson, G. 2011. The impacts of sambar *Cervus unicolor* on the threatened shiny Nematolepis Nematolepis wilsonii. Pacific Conservation Biology 16: 251-260.

Bergquist, J., et al. 2001) Effects of shelterwood and soil scarification on deer browsing on planted Norway spruce *Picea abies* L. (Karst) seedlings. Forestry 74: 359-367.

Bergquist, J., et al. 2003. Interactions among forestry regeneration treatments, plant vigour and browsing damage by deer. New Forests 25: 25-40.

Bergquist, J., et al. 2003. Responses of young Norway spruce (*Picea abies*) to winter browsing by roe deer (*Capreolus capreolus*): Effects on height growth and stem morphology. Scandinavian Journal of Forest Research 18: 368-376.

Bergqvist, G. et al. 2001. Patterns of stem damage by moose (*Alces alces*) in young *pinus sylvestris* stands in Sweden. Latitudes 3: 363-370.

Bergqvist, G., et al. 2003. Effects of moose (*Alces alces*) rebrowsing on damage development in young stands of Scots pine (*Pinus sylvestris*). Forest Ecology and Management 176: 397-403.

Bergqvist, G., et al. 2013. Summer browsing by moose on Scots pine, Scandinavian Journal of Forest Research 28: 110-116.

Bergqvist, G., et al. 2014. Recent browsing damage by moose on scots pine, birch and aspen in young commercial forests-effects of forage availability, moose population density and site productivity. Silva Fennica 48: 1-13.

Beringer, J., et al. 2003. Evaluation of an animal-activated scarecrow and a monofilament fence for reducing deer use of soybean fields. Wildlife Society Bulletin 31: 492-498.

Bhatnagar, Y.V. et al. 2009. Endangered markhor *Capra falconeri* in India: Through war and insurgency. Oryx 43: 407-411.

Bidwell, D. 2010. Bison, boundaries, and brucellosis: Risk perception and political ecology at Yellowstone. Society and Natural Resources 23: 14-30.

Biggs, J. et al. 2005. Animal-related vehicle accidents at the Los Alamos National Laboratory, New Mexico. The Southwestern Naturalist 49: 384-394.

Biondi, K.M. et al. 2011. White-tailed deer incidents with U.S. civil aircraft. Wildlife Society Bulletin 35: 303-309.

Birkett, A., Stevens-Wood, B. 2005. Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. African Journal of Ecology 43: 123-130.

Blackwell, B. F. and Seamans, T. W. 2009. Enhancing the perceived threat of vehicle approach to deer. Journal of Wildlife Management 73: 128-135.

Bleier, N. et al. 2012. Relationships between wild ungulates density and crop damage in Hungary. Acta Theriologica 57: 351-359.

Bobrowski, M., et al. 2015. Modelling browsing of deer on beech and birch in northern Germany. Forest Ecology and Management. 358: 212-221.

Borkowski, J., Obidziński, A. 2003. The composition of the autumn and winter diets in two Polish populations of fallow deer. Acta Theriologica 48: 539-546.

Borkowski, J., Ukalski, K. 2012. Bark stripping by red deer in a post-disturbance area: The importance of security cover. Forest Ecology and Management 263: 17-23.

Bosch, J. et al. 2014. A maximum entropy model for predicting wild boar distribution in Spain. Spanish Journal of Agricultural Research 12: 984-999.

Boulanger, J.R., Curtis, P.D. 2016. Efficacy of surgical sterilization for managing overabundant suburban white-tailed deer. Wildlife Society Bulletin 40: 727-735.

Bowman, J.L. 2012. The role, size, and effectiveness of safety zones for creating refuges for white-tailed deer. Human-Wildlife Interactions 6: 291-297.

Bradford, J.B., Hobbs, N.T. 2008. Regulating overabundant ungulate populations: An example for elk in Rocky Mountain National Park, Colorado. Journal of Environmental Management 86: 520-528.

Brown, G.S. et al. 2007. Predicting the impacts of forest management on woodland caribou habitat suitability in black spruce boreal forest. Forest Ecology and Management 245: 137-147.

Brugière, D. et al. 2006. Population abundance of the common hippopotamus *Hippopotamus amphibius* in the Haut Niger National Park, Republic of Guinea. Mammalia 70-2: 14-16.

Bueno, C.G. et al. 2011. Assessment of wild boar rooting on ecological and pastoral values of alpine pyrenean grasslands. Pirineos 166: 51-67.

Burgas, A., et al. 2015. Do attacks by jaguars *Panthera onca* and pumas *Puma concolor* (Carnivora: Felidae) on livestock correlate with species richness and relative abundance of wild prey? Revista de Biología Tropical 62: 1459.

Cahill, S. et al. 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. Animal Biodiversity and Conservation 2: 221-233.

Cai, J. et al. 2008. Factors affecting crop damage by wild boar and methods of mitigation in a giant panda reserve. European Journal of Wildlife Research 54: 723-728.

Calenge, C. et al. 2004. Efficiency of spreading maize in the garrigues to reduce wild boar (*Sus scrofa*) damage to Mediterranean vineyards. European Journal of Wildlife Research 50: 112-120.

Campos, C.M. et al. 2008. Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of Prosopis seeds. Seed Science Research 18: 91-100.

Carpio, A.J. et al. 2014. Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem. Animal Biodiversity and Conservation 37: 115-125.

Cavieres, L.A., Fajardo, A. 2005. Browsing by guanaco (*Lama guanicoe*) on *Nothofagus pumilio* forest gaps in Tierra del Fuego, Chile. Forest Ecology and Management 204: 237-248.

Cerkal, R., Muska, F. 2010. Damage caused by wild game animals to field crops in the Czech Republic - A historical summary from 1786 to the year 2005. Journal fur Kulturpflanzen 62.

Čermák, P. et al. 2009. Relationships between browsing damage and woody species dominance. Journal of Forest Science 55: 23-31.

Čermák, P. et al. 2018. Damage by deer barking and browsing and subsequent rots in Norway spruce stands of Forest Range MoP. Journal of Forest Science 50: 24-30.

Čermák, P., Mrkva, R. 2003. Browsing damage to broadleaves in some national nature reserves (Czech Republic) in 2000-2001. Ekologia Bratislava 22: 394-403.

Čermák, P., Mrkva, R. 2018. Effects of game on the condition and development of natural regeneration in the Vrapač National Nature Reserve. Journal of Forest Science 52: 329-336.

Čermák, P., Strejček, M. 2007. Stem decay by *Stereum sanguinolentum* after red deer damage in the Českomoravská vrchovina Highlands. Journal of Forest Science 53: 567-572.

Charco, J. et al. 2016. Impact of deer rubbing on pine forests: implications for conservation and management of *Pinus pinaster* populations. European Journal of Forest Research 135: 719-729.

Chigwenhese, L. et al. 2016. Monitoring African buffalo (*Syncerus caffer*) and cattle (*Bos taurus*) movement across a damaged veterinary control fence at a Southern African wildlife/livestock interface. African Journal of Ecology 54: 415-423.

Cipollini, K., et al. 2009. Amur honeysuckle (*Lonicera maackii*) management method impacts restoration of understory plants in the presence of white-tailed deer (*Odocoileus virginiana*). Invasive Plant Science and Management 21: 45-54.

Coe, P.K. et al. 2015. Identifying migration corridors of mule deer threatened by highway development. Wildlife Society Bulletin 39: 256-267.

Colligan, G.M. et al. 2011. Factors affecting white-tailed deer browsing rates on early growth stages of soybean crops. Human-Wildlife Interactions 5: 321-332.

Crimmins, S.M. et al. 2015. Responses of Female White-Tailed Deer Home-Ranges to Increased Resource Availability. Northeastern Naturalist 22: 403-412.

Curtis, P.D., Boulanger, J.R. 2010. Relative effectiveness of repellents for preventing deer damage to Japanese yews. HortTechnology 20: 730-734.

Cutini, A. et al. 2011. Roe deer (*Capreolus capreolus* L.) browsing effects and use of chestnut and Turkey oak coppiced areas. Annals of Forest Science 68: 667-674.

DAngelo, G.J., Grund, M.D. 2015. Evaluating competing preferences of hunters and landowners for management of deer populations. Human-Wildlife Interactions 9: 236-247.

Datiko, D. and Bekele, A. 2013. Conservation challenge: human-herbivore conflict in Chebera Churchura National Park, Ethiopia. Pakistan Journal of Biological Sciences 16: 1758-1764.

DeBano, S.J. et al. 2016. Diet Overlap of Mammalian Herbivores and Native Bees: Implications for Managing Co-occurring Grazers and Pollinators. Natural Areas Journal 36: 458-477.

Decker, S.E. et al. 2010. The return of the king or bringing snails to the garden? The human dimensions of a proposed restoration of european bison (*Bison bonasus*) in Germany. Restoration Ecology 18: 41-51.

Decker, S.E., Bath, A.J. 2010. Public versus expert opinions regarding public involvement processes used in resource and wildlife management. Conservation Letters 3: 425-434.

DeGroote, L.W. et al. 2011. Susceptibility of cultivated native wildflowers to deer damage. Southeastern Naturalist 10: 761-771.

Delger, J.A. et al. 2011. Preference of white-tailed deer for corn hybrids and agricultural husbandry practices during the growing season. Human-Wildlife Interactions 5: 32-46.

Delibes-Mateos, M., Delibes, A. 2014. Pets becoming established in the wild: free-living Vietnamese potbellied pigs in Spain. Animal Biodiversity and Conservation 36.2: 209-215.

den Herder, M., et al. 2009. The effects of timber harvest, forest fire, and herbivores on regeneration of deciduous trees in boreal pine-dominated forests. Canadian Journal of Forest Research 39: 712-722.

DeVore, R.M. et al. 2016. Elk resource selection patterns in a semiarid riparian corridor. Journal of Wildlife Management 80: 479-489.

Duncan, A.J. et al. 2001. Clonal variation in monoterpene concentrations in Sitka spruce (*Picea sitchensis*) saplings on their susceptibility to browsing damage by red deer (*Cervus elaphus*). Forest Ecology and Management 148: 259-269.

Dunham, K.M. et al. 2010. Human-wildlife conflict in Mozambique: A national perspective, with emphasis on wildlife attacks on humans. Oryx 44: 185-193.

Ebert, C. et al. 2012. Estimating wild boar *Sus scrofa* population size using faecal DNA and capture-recapture modelling. Wildlife Biology 18: 142-152.

Edenius, L. et al. 2014. Ungulate-adapted forest management: Effects of slash treatment at harvest on forage availability and use. European Journal of Forest Research 133: 191-198.

Edenius, L. et al. 2015. Browsing and damage inflicted by moose in young Scots pine stands subjected to high-stump precommercial thinning. Scandinavian Journal of Forest Research 30: 382-387.

Elmeros, M. et al. 2011. Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): A field test. European Journal of Wildlife Research 57: 1223-1226.

Engeman, R. et al. 2016. Photographic estimation of wild boar damage to alpine grazing pastures in the Carpathian Mountains of central Romania. Environmental Science and Pollution Research 23: 4949-4952.

Engeman, R.M. et al. 2003. Prevalence and economic value native habitat Florida state parks. Environmental Conservation 30: 319-324.

Engeman, R.M. et al. 2014. Benefits to rare plants and highway safety from annual population reductions of a “native invader,” white-tailed deer, in a Chicago-area woodland. Environmental Science and Pollution Research 21: 1592-1597.

Enoki, T., et al. 2016. Changes in spatial patterns of sika deer distribution and herbivory of planted seedlings: a comparison before and after deer population control by culling. Journal of Forest Research 21: 84-91.

Escós, J.M. et al. 2008. Estimating population trends using population viability analyses for the conservation of *Capra pyrenaica*. Acta Theriologica 53: 275-286.

Estes, R.D. et al. 2008. The impact of horning by wildebeest on woody vegetation of the Serengeti ecosystem. Journal of Wildlife Management 72: 1572.

Ezebilo, E.E.et al. 2012. Browsing damage by moose in Swedish forests: Assessments by hunters and foresters. Scandinavian Journal of Forest Research 27: 659-668.

Fellers, G., Osbourn, M. 2007. Abundance and impacts of fallow deer leks at point reyes national seashore California Fish and Game 93: 149-160.

Fernández-Olalla, M. et al. 2016. Threat or opportunity? Browsing preferences and potential impact of *Ammotragus lervia* on woody plants of a Mediterranean protected area. Journal of Arid Environments 129: 9-15.

Ficetola, G. et al. 2016. Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. Current Zoology 60: 170-179.

Fletcher, J.D. et al. 2001. Wildlife herbivory and rare plants: The effects of white-tailed deer, rodents, and insects on growth and survival of Turks cap lily. Biological Conservation 101: 229-238.

Flueck, W.T. 2001. Body reserves and pregnancy rates of introduced red deer in Patagonia (Argentina) after a period of drought. Ecologia Austral 11: 17-24.

Ford-Thompson, A.E.S. et al. 2015. Dimensions of local public attitudes towards invasive species management in protected areas. Wildlife Research 42: 60.

Foster, D.R. et al. 2002. Wildlife dynamics in the changing New England landscape. Journal of Biogeography 29: 1337-1357.

Fox, J.L., Dorji, T. 2009. Traditional hunting of tibetan antelope, its relation to antelope migration, and its rapid transformation in the Western Chang Tang Nature Reserve. Arctic, Antarctic, and Alpine Research 41: 204-211.

Frackowiak, W. et al. 2013. Factors affecting the level of damage by wild boar in farmland in north-eastern Poland. Pest Management Science 69: 362-366.

Fuentes-Allende, N. et al. 2016. Is human disturbance causing differential preference of agricultural landscapes by taruka and feral donkeys in high Andean deserts during the dry season? Journal of Arid Environments 135: 115-119.

Fuller, J.A. et al. 2007. Reproduction and survival of Yellowstone bison. Journal of Wildlife Management 71: 2365-2372.

Gadd, M.E. 2005. Conservation outside of parks: attitudes of local people in Laikipia, Kenya. Environmental Conservation 32: 50-63.

Gagnon, J.W. et al. 2015. Cost-effective approach to reducing collisions with elk by fencing between existing highway structures. Human-Wildlife Interactions 9: 248-264.

Gallagher, G.R., Prince, R.H. 2003. Negative operant conditioning fails to deter white-tailed deer foraging activity. Crop Protection 22: 893-895.

Gandiwa, E. 2011. Preliminary assessment of illegal hunting by communities adjacent to the northern Gonarezhou National Park, Zimbabwe. Tropical Conservation Science 4: 445-467.

Gaskamp, J.A. et al. 2016. Pseudorabies Virus and *Brucella abortus* from an Expanding Wild Pig (*Sus scrofa*) Population in Southern Oklahoma, USA. Journal of Wildlife Diseases 52: 383-386.

Geisser, H., Reyer, H.U. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. Journal of wildlife management 68: 939-946.

Geisser, H., Reyer, H.U. 2005. The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). Journal of Zoology 267: 89-96.

Geremia, C. et al. 2014. Integrating population- and individual-level information in a movement model of Yellowstone bison. Ecological Applications 24: 346-362.

Gerner, J. et al. 2011. Red deer at a crossroads-An analysis of communication strategies concerning wildlife management in the “Bayerischer Wald” National Park, Germany. Journal for Nature Conservation 19: 319-326.

Gilsdorf, J.M., et al. 2004. Evaluation of a deer-activated bio-acoustic frightening device for reducing deer damage in cornfields. Wildlife Society Bulletin 32: 515-523.

Gilsdorf, J.M., et al. 2004. Propane exploders and Electronic Guards were ineffective at reducing deer damage in cornfields. Wildlife Society Bulletin 32: 524-531.

Gionfriddo, J.P. et al. 2011. Health effects of GnRH immunocontraception of wild white-tailed deer in New Jersey. Wildlife Society Bulletin 35: 149-160.

Godvik, I.M.R., et al. 2009. Temporal scales, trade-offs, and functional responses in red deer habitat selection. Ecology 90: 699-710.

Gomes, V.G.N., et al. 2016. Vertebrate florivory on the short-columnar cactus *Echinopsis rhodotricha* K. Schum. in the Brazilian Chaco. Plant Ecology 217: 1481-1487.

Gorham, D.A., Porter, W.F. 2011. Examining the potential of community design to limit human conflict with white-tailed deer. Wildlife Society Bulletin 35: 201-208.

Goulding, M.J. 2002. Press responses to the presence of free-living Wild Boar (*Sus scrofa*) in southern England 32: 272-282.

Grund, M.D. 2011. Survival analysis and computer simulations of lethal and contraceptive management strategies for urban deer. Human-Wildlife Interactions 5: 23-31.

Gülci, S., Akay, A.E. 2015. Assessment of ecological passages along road networks within the Mediterranean forest using GIS-based multicriteria evaluation approach. Environmental Monitoring and Assessment 187: 1-13.

Gulsby, W.D. et al. 2011. Movements and home ranges of white-tailed deer in response to roadside fences. Wildlife Society Bulletin 35: 282-290.

Gundersen, H., et al. 2018. Supplemental feeding of migratory moose *Alces alces*: forest damage at two spatial scales. Wildlife Biology 10: 213-223.

Gurung, B., et al. 2009. Impact of grazing restrictions on livestock composition and husbandry practices in Madi Valley, Chitwan National Park, Nepal. Environmental Conservation 36: 338-347.

Haaverstad, O., et al. 2014. Wild boar rooting in a northern coniferous forest - minor silviculture impact. Scandinavian Journal of Forest Research 29: 90-95.

Halley, D. J., et al. 2007. Variation in stable isotope ratios of carbon and nitrogen in Hokkaido sika deer *Cervus nippon* during 1990-2000: possible causes and implications for management. Wildlife Biology 12: 211-217.

Haney, M.J., Conover, M.R. 2013. Ungulate damage to safflower in Utah. Journal of Wildlife Management 77: 282-289.

Harden, C.D., et al. 2006. Influence of exurban development on hunting opportunity, hunter distribution, and harvest efficiency of white-tailed deer. Wildlife Society Bulletin 33: 233-242.

Harding, L.E. et al. 2007. Reintroduction of the Arabian oryx *Oryx leucoryx* in Jordan: War and redemption. Oryx 41: 478-487.

Härkönen, S., et al. 2008. Effect of cleaning methods in mixed pine-deciduous stands on moose damage to Scots pines in southern Finland. Scandinavian Journal of Forest Research 23: 491-500.

Härkönen, S., Heikkilä, R. 2009. The use of birch tar in the prevention of moose damage in young Scots pine stands. Estonian Journal of Ecology 58: 53-59.

Harper, E.E. et al. 2016. Stakeholder attitudes and beliefs toward wild pigs in Georgia and Illinois. Wildlife Society Bulletin 40: 269-273.

Haule, K.S., et al. 2002. Striving for sustainable wildlife management: The case of Kilombero Game Controlled Area, Tanzania. Journal of Environmental Management 66: 31-42.

Hearn, R., et al. 2014. The cultural and land use implications of the reappearance of the wild boar in North West Italy: A case study of the Val di Vara. Journal of Rural Studies 36: 52-63.

Hegel, T.M., et al. 2009. The geography of conflict between elk and agricultural values in the Cypress Hills, Canada. Journal of Environmental Management 90: 222-235.

Heilmann, L.C. et al. 2006. Will tree euphorbias (*Euphorbia tetragona* and *Euphorbia triangularis*) survive under the impact of black rhinoceros (*Bicornis diceros minor*) browsing in the Great Fish River Reserve, South Africa? African Journal of Ecology 44: 87-94.

Heinze, E. et al. 2011. Habitat use of large ungulates in northeastern Germany in relation to forest management. Forest Ecology and Management 261: 288-296.

Hell, P. et al. 2005. Losses of mammals (Mammalia) and birds (Aves) on roads in the Slovak part of the Danube Basin. European Journal of Wildlife Research 51: 35-40.

Henderson, D.W. et al. 2000. Human perceptions before and after a 50% reduction in an urban deer herds density. Wildlife Society Bulletin 28: 911-918.

Henderson, D.W. et al. 2000. Responses of urban deer to a 50% reduction in local herd density. Wildlife Society Bulletin 28: 902-910.

Herfindal, I. et al. 2015. Associational relationships at multiple spatial scales affect forest damage by moose. Forest Ecology and Management 348: 97-107.

Heroldová, M., et al. 2003. Breakage of rowan caused by red deer: An important factor for *Sorbeto-Piceetum* stand regeneration? Forest Ecology and Management 181: 131-138.

Herrero, A. et al. 2016. From the individual to the landscape and back: Time-varying effects of climate and herbivory on tree sapling growth at distribution limits. Journal of Ecology 104: 430-442.

Herrero, J. et al. 2005. Fruits and roots: Wild boar foods during the cold season in the southwestern pyrenees. Italian Journal of Zoology 72: 49-52.

Herrero, J. et al. 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. European Journal of Wildlife Research 52: 245-250.

Herrero, J., Fernández De Luco, D. 2003. Wild boars (*Sus scrofa* L.) in Uruguay: Scavengers or predators? Mammalia 67: 485-491.

Hildreth, A.M. et al. 2012. Use of partially fenced fields to reduce deer damage to corn. Wildlife Society Bulletin 36: 199-203.

Hobbs, N.T. et al. 2012. Native predators reduce harvest of reindeer by Sámi pastoralists. Ecological Applications 22: 1640-1654.

Hofman-Kamińska, E., Kowalczyk, R. 2012. Farm crops depredation by european bison (*Bison bonasus*) in the vicinity of forest habitats in Northeastern Poland. Environmental Management 50: 530-541.

Holmes, S.A., et al. 2008. White-tailed deer (*Odocoileus Virginianus*) alter herbaceous species richness in The Hiawatha National Forest, Michigan, USA. The American Midland Naturalist 159: 83-97.

Homolka, M., et al. 2008. White-tailed deer winter feeding strategy in area shared with other deer species. Folia Zoologica 57: 283-293.

Honda, T. 2009. Environmental factors affecting the distribution of the wild boar, sika deer, asiatic black bear and Japanese macaque in central Japan, with Implications for Human-Wildlife Conflict. Mammal Study 34: 107-116.

Honda, T. et al. 2009. Effectiveness of newly-designed electric fences in reducing crop damage by medium and large mammals. Mammal Study 34: 13-17.

Honda, T. et al. 2010. possibility of agronomical techniques for reducing crop damage by sika deer. Mammal Study 35: 119-124.

Honda, T., et al. 2008. Risk factors affecting the probability of damage by sika deer in plantation forests in Yamanashi Prefecture, Japan. Landscape and Ecological Engineering 4: 97-102.

Honda, T., Kawauchi, N. 2011. Methods for constructing a wild boar relative-density map to resolve human-wild boar conflicts. Mammal Study 36: 79-85.

Hörnberg, S. 2001. Changes in population density of moose (*Alces alces*) and damage to forests in Sweden. Forest Ecology and Management 149: 141-151.

Hothorn, T., Müller, J. 2010. Large-scale reduction of ungulate browsing by managed sport hunting. Forest Ecology and Management 260: 1416-1423.

Hu, H., Jiang, Z. 2002. Trial release of Père Davids deer *Elaphurus davidianus* in the Dafeng Reserve, China. *Oryx* 36: 196-199.

Hu, J. et al. 2010. Do local communities support the conservation of endangered Przewalskis gazelle? European Journal of Wildlife Research 56: 551-560.

Hua, X. et al. 2016. Wildlife damage and cultivated land abandonment: Findings from the mountainous areas of Chongqing, China. Crop Protection 84: 141-149.

Hubbard, R.D., Nielsen, C.K. 2011. Cost-benefit analysis of managed shotgun hunts for suburban white-tailed deer. Human-Wildlife Interactions 5: 13-22.

Humber, J.M., Hermanutz, L. 2011. Impacts of non-native plant and animal invaders on gap regeneration in a protected boreal forest. Biological Invasions 13: 2361-2377.

Hygnstrom, S.E. et al. 2018. White-tailed deer browsing and rubbing preferences for trees and shrubs that produce nontimber forest products. HortTechnology 19: 204-211.

Ickes, K., et al. 2003. Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. Journal of Ecology 91: 222-233.

Ickes, K., et al. 2010. Impacts of Nest Construction by Native Pigs (*Sus scrofa*) on Lowland Malaysian Rain Forest Saplings. Ecological Society of America 86: 1540-1547.

Jalkanen, A. 2001. The probability of moose damage at the stand level in Southern Finland. Silva Fennica 35: 159-168.

Jarnemo, A. et al. 2014. Managing landscapes for multiple objectives: Alternative forage can reduce the conflict between deer and forestry. Ecosphere 5: 97.

Jenkins, R.K.B. et al. 2002. Management implications of antelope habitat use in the Kilombero Valley, Tanzania. *Oryx* 36: 161-169.

Jennings, B., et al. 2014. A spatially explicit model of the white-tailed deer population in Delaware. Human-Wildlife Interactions 8: 195-209.

Johansson, A. 2014. Effect of roe buck removal on marking intensity. Acta Theriologica 45: 123-128.

Johnson, H.E. et al. 2014. Evaluation of techniques to reduce deer and elk damage to agricultural crops. Wildlife Society Bulletin 38: 358-365.

Jordan, R.A., Schulze, T.L. 2009. Deer browsing and the distribution of *Ixodes scapularis* (Acari: Ixodidae) in Central New Jersey Forests. Environmental Entomology 34: 801-806.

Kaji, K. 2012. Population Parameters Spatial sika deer distribution Hokkaido Island, Japan. Wildlife Society Bulletin 28: 699-707.

Kalén, C. 2006. Deer Browsing and Impact on Forest Development. Journal of Sustainable Forestry 21:53-64.

Kalén, C., Bergquist, J. 2004. Forage availability for moose of young silver birch and Scots pine. Forest Ecology and Management 187: 149-158.

Kaltenborn, B.P., et al. 2014. The role of wild reindeer as a flagship species in new management models in Norway. Norsk Geografisk Tidsskrift 68: 168-177.

Kamler, J. et al. 2009. Evaluation of potential deer browsing impact on sunflower (*Helianthus annus*). European Journal of Wildlife Research 55: 583-588.

Kanga, E.M. et al. 2012. Human-hippo conflicts in Kenya during 1997-2008: Vulnerability of a megaherbivore to anthropogenic land use changes. Journal of Land Use Science 7: 395-406.

Kathryn Mceachern, A., et al. 2009. Climate alters response of an endemic island plant to removal of invasive herbivores. Ecological Applications 19: 1574-1584.

Kauffman, M.E., et al. 2012. Unintended consequences of bovine brucellosis management on demand for elk hunting in northwestern Wyoming. Human-Wildlife Interactions 6: 12-29.

Kelly, D.L. 2002. The regeneration of *Quercus petraea* (sessile oak) in southwest Ireland: A 25-year experimental study. Forest Ecology and Management 166: 207-226.

Kendall, C.J. 2011. The spatial and agricultural basis of crop raiding by the Vulnerable common hippopotamus *Hippopotamus amphibius* around Ruaha National Park, Tanzania. *Oryx*, 45: 28-34.

Keyser, P.D. et al. 2016. Density-dependent recruitment patterns in white-tailed deer. Wildlife Society Bulletin 33: 222-232.

Kiffner, C. et al. 2008. Probability of recent bark stripping damage by red deer (*Cervus elaphus*) on Norway spruce (*Picea abies*) in a low mountain range in Germany: A preliminary analysis. Silva Fennica 42: 125-134.

Kilpatrick, A.M., et al. 2009. Wildlife-livestock conflict: The risk of pathogen transmission from bison to cattle outside Yellowstone National Park. Journal of Applied Ecology 46: 476-485.

Kilpatrick, H., Spohr, S. 2000. Spatial and temporal use of a suburban landscape by female white-tailed deer. Wildlife Society Bulletin 28: 1023-1029.

Kilpatrick, H.J., et al. 2007. Acceptance of Deer Management Strategies by Suburban Homeowners and Bowhunters. Journal of Wildlife Management 71: 2095-2101..

Kilpatrick, H.J., et al. 2011. Effects of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79: 949-954.

Kimball, B.A., et al. 2005. Hydrolyzed casein reduces browsing of trees and shrubs by white-tailed deer. HortScience 40: 1810-1814.

Kimball, B.A., Nolte, D.L. 2006. Development of a new deer repellent for the protection of forest resources. Western Journal of Applied Forestry 21: 108-111.

Kondoh, H., et al. 2013. A geostatistical approach to spatial density distributions of sika deer (*Cervus nippon*). Journal of Forest Research 18: 93-100.

Kopij, G. and Panek, M. 2016. Effect of winter temperature and maize food abundance on long-term population dynamics of the wild boar *Sus Scrofa.* Polish Journal of Ecology 64: 436-441.

Kraft, L.S. et al. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. Forest Ecology and Management 199: 219-230.

Krueger, L.M., Peterson, C.J. 2006. Effects of white-tailed deer on *Tsuga canadensis* regeneration: evidence of microsites as refugia from browsing. The American Midland Naturalist 1562: 353-362.

Kuemmerle, T. et al. 2011. Predicting potential European bison habitat across its former range. Ecological Applications 213: 830-843.

Kuijper, D.P.J. et al. 2009. Do ungulates preferentially feed in forest gaps in European temperate forest? Forest Ecology and Management 258: 1528-1535.

Kullberg, Y., Bergström, R. 2001. Winter browsing by large herbivores on planted deciduous seedlings in southern Sweden. Scandinavian Journal of Forest Research 16: 371-378.

Kumara, H.N. et al. 2004. Diversity and management of wild mammals in tea gardens in the rainforest regions of the Western Ghats, India: A case study from a tea estate in the Anaimalai Hills. Current Science 87: 1282-1287.

Kupferschmid, A.D., Bugmann, H. 2005. Effect of microsites, logs and ungulate browsing on *Picea abies* regeneration in a mountain forest. Forest Ecology and Management 205: 251-265.

Kupferschmid, A.D., Bugmann, H. 2008. Ungulate browsing in winter reduces the growth of Fraxinus and Acer saplings in subsequent unbrowsed years. Plant Ecology 198: 121-134.

Laarmann, D. et al. 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. Forest Ecology and Management 258S: S187-S195.

Lafferty, D.J.R. et al. 2016. Moose (*Alces alces*) hunters subsidize the scavenger community in Alaska. Polar Biology 39: 639-647.

Lauber, T.B. et al. 2007. The role of ethical judgments related to wildlife fertility control. Society and Natural Resources 20: 119-133.

Lavelle, M.J. et al. 2010. Response of deer to containment by a poly-mesh fence for mitigating disease outbreaks. Journal of Wildlife Management 74: 1620-1625.

Laznik, Ž., Trdan, S. 2014. Evaluation of different soil parameters and wild boar (*Sus scrofa* [L.]) grassland damage. Italian Journal of Animal Science 13: 759-765.

Leblond, M. et al. 2007. management of roadside salt pools to reduce moose-vehicle collisions. Journal of Wildlife Management 71: 2304-2310.

Lee, M.E., Miller, R. 2003. Managing elk in the wildland-urban interface: attitudes of Flagstaff, Arizona residents. Wildlife Society Bulletin 31: 185-191.

Lent, P.C. et al. 2009. Continued decline in tree euphorbias (*Euphorbia tetragona* and *E. triangularis*) on the Great Fish River Reserve , Eastern Cape , South Africa. African Journal of Ecology 48: 923-929.

Leong, K.M. 2010. The tragedy of becoming common: Landscape change and perceptions of wildlife. Society and Natural Resources 23: 111-127.

Leroy, R. et al. 2009. The last African white giraffes live in farmers fields. Biodiversity and Conservation 18: 2663-2677.

Li, L. et al. 2013. Factors influencing wild boar damage in Taohongling National Nature Reserve in China: A model approach. European Journal of Wildlife Research 59: 179-184.

Linkie, M. et al. 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Animal Conservation 10: 127-135.

Loeb, R.E. et al. 2011. Arboreal composition changes following white-tailed deer restoration to urban park forests without off-trail park visitor trampling. Urban Forestry and Urban Greening 10: 305-310.

López-Sánchez, A. et al. 2016. Livestock vs. wild ungulate management in the conservation of Mediterranean dehesas: Implications for oak regeneration. Forest Ecology and Management 362: 99-106.

Lovari, S. et al. 2014. Unexpected consequences of reintroductions: Competition between reintroduced red deer and Apennine chamois. Animal Conservation 17: 359-370.

Lovely, K.R. et al. 2013. Land parcelization and deer population densities in a rural county of Virginia. Wildlife Society Bulletin 37: 360-367.

Lubow, B.C. et al. 2016. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. Journal of Wildlife Management 66: 757-775.

Lunde, E. T. et al. 2016. Assessing the effect of roads on impala (*Aepyceros melampus*) stress levels using faecal glucocorticoid metabolites. African Journal of Ecology 54: 434-441.

Månsson, J. et al. 2007. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. Scandinavian Journal of Forest Research 22: 407-414.

Månsson, J., et al. 2009. Fertilization-Effects on deciduous tree growth and browsing by moose. Forest Ecology and Management 258: 2450-2455.

Månsson, J., Jarnemo, A. 2013. Bark-stripping on Norway spruce by red deer in Sweden: level of damage and relation to tree characteristics. Scandinavian Journal of Forest Research 28: 117-125.

Marchiori, E., et al. 2012. Wild red deer (*Cervus elaphus* L.) grazing may seriously reduce forage production in mountain meadows. Italian Journal of Animal Science 11: 47-53.

Martínez Pastur, G. et al. 2016. Effectiveness of fencing and hunting to control *Lama guanicoe* browsing damage: Implications for *Nothofagus pumilio* regeneration in harvested forests. Journal of Environmental Management 168: 165-174.

Masuko, T. et al. 2011. Effects of the feeding of wild Yeso sika deer (*Cervus nippon yesoensis*) on the prevention of damage due to bark stripping and the use of feeding sites. Animal Science Journal 82: 580-586.

Mathisen, K.M. et al. 2014. Long-term effects of supplementary feeding of moose on browsing impact at a landscape scale. Forest Ecology and Management 314: 104-111.

McCance, E.C. et al. 2015. Spatial and temporal analysis of factors associated with urban deer-vehicle collisions. Human-Wildlife Interactions 9: 119-131.

McCoy, J.E., et al. 2005. Dispersal by yearling male white-tailed deer and implications for management. Journal of Wildlife Management 69: 366-376.

McLaren, B.E. et al. 2000. Spatial and temporal patterns of use by moose of pre-commercially thinned, naturally-regenerating stands of balsam fir in central Newfoundland. Forest Ecology and Management 133: 179-196.

Melin, M. et al. 2015. Detecting moose (*Alces alces*) browsing damage in young boreal forests from airborne laser scanning data. Canadian Journal of Forest Research 46: 10-19.

Meriggi, A. et al. 2015. Short-term responses of Wolf feeding habits to changes of wild and domestic ungulate abundance in Northern Italy. Ethology Ecology and Evolution 27: 389-411.

Metslaid, M., et al. 2013. The condition of scots pine stands in Lahemaa national park, Estonia 25 years after browsing by moose (*Alces alces*). Boreal Environment Research 18: 25-34.

Metslaid, M., et al. 2013. The effect of simulated bark stripping by moose on scots pine height growth: An experimental treatment. Baltic Forestry 19: 61-66.

Milner, J.M. et al. 2006. Temporal and spatial development of red deer harvesting in Europe: Biological and cultural factors. Journal of Applied Ecology 43: 721-734.

Milner, J.M., et al. 2013. Boom and bust of a moose population: A call for integrated forest management. European Journal of Forest Research 132: 959-967.

Mishra, C., et al, A. 2006. Mammals of the high altitudes of western Arunachal Pradesh, eastern Himalaya: An assessment of threats and conservation needs. Oryx 40: 29-35.

Mishra, C., Fitzherbert, A. 2004. War and wildlife: A post-conflict assessment of Afghanistans Wakhan Corridor. Oryx 38: 102-105.

Monzón, A., et al. 2012. Integrating the deer (*Cervus elaphus*) in the Portuguese forests: Impacts and new challenges for forest certification. Forest Ecology and Management 267: 1-6.

Moore, E.K. et al. 2015. Landscape-scale vegetation patterns influence small-scale grazing impacts. Biological Conservation 192: 218-225.

Moore, N.P. et al. 2000. Browsing by fallow deer (*Dama dama*) in young broadleaved plantations: Seasonality, and the effects of previous browsing and bud eruption. Forestry 73: 437-445.

Moraga, C.A. et al. 2015. Effects of livestock on guanaco *Lama guanicoe* density, movements and habitat selection in a forest-grassland mosaic in Tierra del Fuego, Chile. Oryx 49: 30-41.

Morelle, K., Lejeune, P. 2015. Seasonal variations of wild boar *Sus scrofa* distribution in agricultural landscapes: a species distribution modelling approach. European Journal of Wildlife Research 61: 45-56.

Morgan, D.G., et al. 2008. A real options approach to forest-management decision making to protect Caribou under the threat of extinction. Ecology and Society 13.

Mounet, C. 2010. Attitudes of the farming community towards the wolf, the wild boar and those in favour of their presence: a conflict of use and representation. Revue de Géographie Alpine 94: 99-109.

Mrtka, J., Borkovcová, M. 2013. Estimated mortality of mammals and the costs associated with animal-vehicle collisions on the roads in the Czech Republic. Transportation Research Part D: Transport and Environment 18: 51-54.

Nagaike, T., Hayashi, A. 2003. Bark-stripping by Sika deer (*Cervus nippon*) in *Larix kaempferi* plantations in central Japan. Forest Ecology and Management 175: 563-572.

Náhlik, A. et al. 2009. Space use and activity patterns of red deer in a highly forested and in a patchy forest-agricultural habitat. Acta Silvatica & Lignaria Hungarica 5: 109-118.

Nelson, J.L., et al. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. Ecosystems 11: 156-171.

Nentwig, W., et al. 2010. A generic impact-scoring system applied to alien mammals in Europe: Contributed paper. Conservation Biology 24: 302-311.

Neumann, W. et al. 2012. Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. Biological Conservation 145: 70-78.

Nevalainen, S. et al. 2016. Moose damage in national forest inventories (1986- 2008) in Finland. Silva Fennica 50.

Nevřelová, M., Ružičková, J. 2015. Woody plants affected by ungulates in winter period, impacts and bark renewal. Ekologia Bratislava 34: 235-248.

Ng, J.W.,et al. 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban enviroment. Human-Wildlife Conflicts 2: 34-47.

Nichols, R.V., Spong, G., et al. 2014. Ungulate browsing on conifers during summer as revealed by DNA. Scandinavian Journal of Forest Research 29: 650-652.

Nikula, A. et al. 2008. Modelling the factors predisposing Scots pine to moose damage in artificially regenerated sapling stands in Finnish Lapland. Silva Fennica, 42: 587-603.

Nilsen, E. B. et al. 2009. The role of ecological and economic factors in the management of a spatially structured moose *Alces alces* population. Wildlife Biology 15: 10-23.

Novosel, H. et al. 2012. The game damages on agricultural crops in Croatia, Journal of Central European Agriculture. Journal of Central European Agriculture 13: 631-642.

O'Farrill, G. et al. 2012. Effective dispersal of large seeds by Bairds tapir: A large-scale field experiment. Journal of Tropical Ecology 28: 119-122.

Ohashi, H. et al. 2013. Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. European Journal of Wildlife Research 59: 167-177.

Olaussen, J.O., Mysterud, A. 2012. Red deer hunting-commercializing versus availability. European Journal of Wildlife Research 58: 597-607.

Olson, D.D. et al. 2015. How does variation in winter weather affect deer-vehicle collision rates? Wildlife Biology 21: 80-87.

Olson, K.A. et al. 2011. Death by a thousand huts? Effects of household presence on density and distribution of Mongolian gazelles. Conservation Letters 4: 304-312.

Orihashi, K. et al. 2002. Development of a method for forest cafeteria tests for evaluating chemical deterrents against bark stripping by sika deer (*Cervus nippon yesoensis*). Journal of Forest Research 7: 35-40.

Palmer, S.C.F., Truscott, AM.. 2003. Seasonal habitat use and browsing by deer in Caledonian pinewoods. Forest Ecology and Management 174: 149-166.

Pandey, P., et al. 2016. The wild boar as a driver of human-wildlife conflict in the protected park lands of Nepal. European Journal of Wildlife Research 62: 103-108.

Pedersen. et al. 2012. Apparent prevalence of swine brucellosis in feral swine in the United States. Human-Wildlife Interactions 6: 38-47.

Pellerin, M. et al. 2010. Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. Forest Ecology and Management 260: 429-437.

Pépin, D. et al. 2006. Relative impact of browsing by red deer on mixed coniferous and broad-leaved seedlings: An enclosure-based experiment. Forest Ecology and Management 222: 302-313.

Perea, R. et al. 2015. The reintroduction of a flagship ungulate *Capra pyrenaica*: Assessing sustainability by surveying woody vegetation. Biological Conservation 181: 9-17.

Perea, R., Gil, L. 2014. Tree regeneration under high levels of wild ungulates: The use of chemically vs. physically-defended shrubs. Forest Ecology and Management 312: 47-54.

Pérez, E., Pacheco, L.F. 2006. Damage by large mammals to subsistence crops within a protected area in a montane forest of Bolivia. Crop Protection 25: 933-939.

Peterson, C.C., Messmer, T.A. 2010. Can public meetings accurately reflect public attitudes toward wildlife management? Journal of Wildlife Management 74: 1588-1594.

Peterson, M.N. et al. 2005. A tale of two species: habitat conservation plans as bounded conflict. Journal of Wildlife Management 68: 743-761.

Pierson, T.G., De Calesta, D.S. 2015. Methodology for estimating deer browsing impact. Human-Wildlife Interactions 9: 67-77.

Potts, J.M. et al. 2014. Predicting the future range and abundance of fallow deer in Tasmania, Australia. Wildlife Research 41: 633-640.

Proffitt, K.M. et al. 2016. Hunter access affects elk resource selection in the Missouri breaks, Montana. Journal of Wildlife Management 80: 1167-1176.

Rajský, M. et al. 2008. Influence supplementary feeding on bark browsing by red deer (*Cervus elaphus*) under experimental conditions. European Journal of Wildlife Research. 544: 701-708.

Ramos, J.A. et al. 2006. Selection of trees for rubbing by red and roe deer in forest plantations. Forest Ecology and Management 222: 39-45.

Ranglack, D.H., Du Toit, J.T. 2015. Habitat Selection by Free-Ranging Bison in a Mixed Grazing System on Public Land. Rangeland Ecology and Management 68: 349-353.

Ranglack, D.H., Du Toit, J.T. 2016. Bison with benefits: Towards integrating wildlife and ranching sectors on a public rangeland in the western USA. Oryx 50: 549-554.

Ranglack, D.H., et al. 2015. Competition on the range: Science vs. perception in a bison-cattle conflict in the western USA. Journal of Applied Ecology 52: 467-474.

Rao, K.S. et al. 2002. Crop damage and livestock depredation by wildlife: A case study from Nanda Devi Biosphere Reserve, India. Journal of Environmental Management 66: 317-327.

Rea, R.V. 2011. Impacts of Moose (*Alces alces*) browsing phology and potential timber quality. Silva Fennica 45: 227-236.

Reimoser, S. et al. 2009. Roe-deer habitat suitability and predisposition of forest to browsing damage in its dependence on forest growth-Model sensitivity in an alpine forest region. Ecological Modelling, 220: 2231-2243.

Renaud, P.C., et al. 2003. Damage to saplings by red deer (*Cervus elaphus*): Effect of foliage height and structure. Forest Ecology and Management 181: 31-37.

Retzer, V., et al. 2006. Variation of precipitation and its effect on phytomass production and consumption by livestock and large wild herbivores along an altitudinal gradient during a drought, South Gobi, Mongolia. Journal of Arid Environments 66: 135-150.

Rhoads, C.L., et al. 2010. Home Range and Movement Rates of Female Exurban White-Tailed Deer. Journal of Wildlife Management 74: 987-994.

Rhoads, C.L., et al. 2013. Movements of female exurban white-tailed deer in response to controlled hunts. Wildlife Society Bulletin 37: 631-638.

Richer, M.C. et al. 2006. Impacts of white-tailed deer grazing in hay fields of southern Québec. Wildlife Society Bulletin 33: 1274-1281.

Riginos, C., Young, T.P. 2007. Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. Oecologia 153: 985-995.

Rogerson, J.E. et al. 2014. The impacts of white-tailed deer browsing and distance from the forest edge on soybean yield. Wildlife Society Bulletin 38: 473-479.

Rosatte, R. et al. 2007. The Restoration of Elk (*Cervus elaphus*) in Ontario, Canada: 1998-2005. Restoration Ecology 15: 34-43.

Ross, T., Wikeem, B. 2002. What can long-term areas tell us? Rangelands 24: 21-27.

Roturier, S., Roué, M. 2009. Of forest, snow and lichen: Sámi reindeer herders knowledge of winter pastures in northern Sweden. Forest Ecology and Management 258: 1960-1967.

Rutberg, A.T. et al. 2004. Effects of immunocontraception on a suburban population of white-tailed deer *Odocoileus virginianus*. Biological Conservation 116: 243-250.

Rutherford, A.C., Schmitz, O.J. 2010. Regional-Scale assessment of deer impacts on vegetation within western Connecticut, USA. Journal of Wildlife Management 74: 1257-1263.

Ruuhola, T. et al. 2016. Effects of bedrock and surficial deposit composition on moose damage in young forest stands in Finnish Lapland. Silva Fennica, 50: 1-20.

Saalfeld, S.T., Ditchkoff, S.S. 2007. Survival of Neonatal White-Tailed Deer in an Exurban Population. Journal of Wildlife Management 71: 940-944.

Sahlsten, J. et al. 2010. Can supplementary feeding be used to redistribute moose *Alces alces*? Wildlife Biology 16: 85-92.

Saint-Andrieux, C. et al. 2009. Factors affecting beech *Fagus sylvatica* bark stripping by red deer *Cervus elaphus* in a mixed forest. Wildlife Biology 15: 187-196.

Saito, M. et al. 2012. Predicting the risk of wild boar damage to rice paddies using presence-only data in chiba prefecture, Japan. International Journal of Pest Management 58: 65-71.

Saito, M., et al. 2011. Both environmental factors and countermeasures affect wild boar damage to rice paddies in Boso Peninsula, Japan. Crop Protection. 30: 1048-1054.

Sakai, S. et al. 2016. Social and ecological factors associated with the use of non-timber forest products by people in rural Borneo. Biological Conservation 204: 340-349.

Sandström, C., et al. 2013. Conflict resolution through ecosystem-based management: The case of Swedish moose management. International Journal of the Commons 7: 549-570.

Saniga, M. 2018. Quantitative and qualitative damage caused by mammals and birds to the planting and natural seeding. Journal of Forest Science 49: 37-43.

Santilli, F., et al. 2004. Evaluation of three repellents for the prevention of damage to olive seedlings by deer. European Journal of Wildlife Research 50: 85-89.

Schlageter, A., Haag-Wackernagel, D. 2011. Effectiveness of solar blinkers as a means of crop protection from wild boar damage. Crop Protection 30: 1216-1222.

Schlageter, A., Haag-Wackernagel, D. 2012. Evaluation of an odor repellent for protecting crops from wild boar damage. Journal of Pest Science 85: 209-215.

Schley, L. et al. 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. European Journal of Wildlife Research 54: 589-599.

Schlichting, P.E. et al. 2016. Determinants of variation in home range of wild pigs. Wildlife Society Bulletin 40: 487-493.

Schwenk, W.S., Strong, A.M. 2011. Contrasting patterns and combined effects of moose and insect herbivory on striped maple (*Acer pensylvanicum*). Basic and Applied Ecology 12: 64-71.

Seamans, T.W., et al. 2002. Coyote hair as an area repellent for white-tailed deer. International Journal of Pest Management 48: 301-306.

Seamans, T.W., Helon, D.A. 2008. Evaluation of an electrified mat as a white-tailed deer (*Odocoileus virginianus*) barrier. International Journal of Pest Management 54: 89-94.

Semiadi, G., Meijaard, E. 2006. Declining populations of the Javan warty pig *Sus verrucosus* Oryx 40: 50-56.

Senserini, D., Santilli, F. 2016. Potential impact of wild boar (*Sus scrofa*) on pheasant (*Phasianus colchicus*) nesting success. Wildlife Biology in Practice 12: 15-20.

Sheppard, D.J. et al. 2010. Ten years of adaptive community-governed conservation: Evaluating biodiversity protection and poverty alleviation in a West African hippopotamus reserve. Environmental Conservation 37: 270-282.

Shibata, E., Torazawa, Y. 2008. Effects of bark stripping by sika deer, *Cervus nippon*, on wind damage to coniferous trees in subalpine forest of central Japan. Journal of Forest Research 13: 296-301.

Shimazaki, A., Miyashita, T. 2002. Deer browsing reduces leaf damage by herbivorous insects through an induced response of the host plant. Ecological Research 17: 527-533.

Sidorovich, V.E., et al. 2018. Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990-2000. Wildlife Biology 9: 103-111.

Siipilehto, J., Heikkilä, R. 2005. The effect of moose browsing on the height structure of Scots pine saplings in a mixed stand. Forest Ecology and Management 205: 117-126.

Simon, J., Kolář, C. 2001. Economic evaluation of bark stripping by red deer on the basis of analysis on a time growth series of spruce stands in the Hrubý Jeseník Mts. Journal of Forest Science 47: 402-409.

Singer, J.W. et al. 2004. Predicting yield loss in indeterminate soybean from pod density using simulated damage studies. Agronomy Journal 96: 584-589.

Singer, J.W., Meek, D.W. 2004. Repeated biomass removal affects soybean resource utilization and yield. Agronomy Journal 96: 1382-1389.

Skonhoft, A. 2005. The costs and benefits of a migratory species under different management schemes. Journal of Environmental Management 76: 167-175.

Skonhoft, A. et al. 2013. Balancing income and cost in red deer management. Journal of Environmental Management 115: 179-188.

Smith, R.K. et al. 2011. Resolving management conflicts: Could agricultural land provide the answer for an endangered species in a habitat classified as a World Heritage Site? Environmental Conservation 38: 325-333.

Smith, R.W. et al. 2012. Effects of wildlife grazing on the production, ground cover and plant species composition of an established perennial pasture in the Midlands region, Tasmania. Wildlife Research 39: 123.

Snow, N.P., et al. 2015. Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. Biological Conservation 181: 44-53.

Sobalak, T.M. 2007. Analysis of game management in the Game Breeding Centres of the Poznan RDSF between 1995 and 2004. Folia Forestalia Polonica, Series A 49-50: 81-95.

Soga, A. et al. 2015. Relationship between spatial distribution of sika deer-train collisions and sika deer movement in Japan. Human-Wildlife Interactions 9: 196-210.

Speed, J.D.M. et al. 2014. General and specific responses of understory vegetation to cervid herbivory across a range of boreal forests. Oikos 123: 1270-1280.

Springer, M.T., et al. 2013. The effect of white-tailed deer browsing on wheat quality and yields in Delaware. Wildlife Society Bulletin 37: 155-161.

Stedman, R.C. et al. 2008. Deer hunting on Pennsylvania's public and private lands: A two-tiered system of hunters? Human Dimensions of Wildlife 13: 222-233.

Stevens, K. et al. 2011. Large mammals surviving conflict in the eastern forests of Afghanistan. Oryx 45: 265-271.

Stewart, C.M. 2011. Attitudes of urban and suburban residents in Indiana on deer management. Wildlife Society Bulletin 35: 316-322.

Stewart, C.M., et al. 2007. The Impact of White-Tailed Deer on Agricultural Landscapes in 3 National Historical Parks in Maryland. Journal of Wildlife Management 71: 1525-1530.

Storm, D.J. et al. 2007. Space use and survival of white-tailed deer in an exurban landscape. Landscape Journal of Wildlife Management 71: 1170-1176.

Stronen, A.V. et al. 2007. Farmer attitudes toward wolves: Implications for the role of predators in managing disease. Biological Conservation 135: 1-10.

Stull, D.W. et al. 2011. Comparison of fencing designs for excluding deer from roadways. Human-Wildlife Interactions 5: 47-57.

Suchant, R., et al. 2003. Wildlife habitat analysis-a multidimensional habitat management model. Journal for Nature Conservation 10: 253-268.

Sullivan, T.L., Messmer, T.A. 2012. Perceptions of deer-vehicle collision management by state wildlife agency and department of transportation administrators, Wildlife Society Bulletin 31: 163-173.

Suraud, J.P. et al. 2012. Higher than expected growth rate of the Endangered West African giraffe *Giraffa camelopardalis peralta*: A successful human-wildlife cohabitation. Oryx 46: 577-583.

Swanepoel, M., et al. 2016. Farmers perceptions of the extra-limital common warthog in the Northern Cape and free state provinces, South Africa. Wildlife Society Bulletin 40: 112-121.

Szemethy, L. et al. 2003. Seasonal home range shift of red deer in a forest-agriculture area in southern Hungary. Acta Theriologica 48: 547-556.

Tadesse, S.A., Kotler, B.P. 2016. Attitudes of local people towards the mountain nyala (*Tragelaphus buxtoni*) in Munessa, Ethiopia. African Journal of Ecology 54: 488-499.

Takeuchi, T., et al.. 2011. Altitudinal differences in bark stripping by sika deer in the subalpine coniferous forest of Mt. Fuji. Forest Ecology and Management 261: 2089-2095.

Tamura, A. 2016. Potential of soil seed banks in the ecological restoration of overgrazed floor vegetation in a cool-temperate old-growth damp forest in eastern Japan. Journal of Forest Research 21: 43-56.

Tanentzap, A.J. et al. 2011. Seeing the forest for the deer: Do reductions in deer-disturbance lead to forest recovery? Biological Conservation 144: 376-382.

Taylor, B.D. et al. 2013. Consumption of whole cottonseed by white-tailed deer and nontarget species. Human-Wildlife Interactions 7: 99-106.

Telesco, R.L. et al. 2007. Identifying sites for elk restoration in Arkansas. Journal of Wildlife Management 71: 1393-1403.

Terry, E.L. et al. 2013. Winter habitat ecology of mountain caribou in relation to forest management. Journal of Applied Ecology 37: 589-602.

Thurfjell, H. et al. 2009. Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): Agricultural fields and edges. European Journal of Wildlife Research 55: 517-523.

Trdan, S., Vidrih, M. 2008. Quantifying the damage of red deer (*Cervus elaphus*) grazing on grassland production in southeastern Slovenia. European Journal of Wildlife Research 54: 138-141.

Tsukada, H. et al. 2009. Effect of distance from farm periphery on the risk of forage damage by sika deer (*Cervus nippon*). Grassland Science 55: 193-199.

Tsukada, H. et al. 2013. Simple quantitative method for estimation of herbage damage caused by sika deer (*Cervus nippon*). Grassland Science 59: 146-155.

Tsukada, H., et al. 2012. Damage to round bale silage caused by sika deer (*Cervus nippon*) in central Japan. Grassland Science 58: 179-187.

Turek, K., et al. 2016. The impact of thinning type on bark stripping damage intensity caused by red deer (*Cervus elaphus* L.). Baltic Forestry 22: 246-250.

Twehryo, M., et al. 2010. Feeding patterns of sitatunga (*Tragelaphus speki*) in the Rushebeya-Kanyabaha wetland, south western Uganda. African Journal of Ecology 48: 1045-1052.

Tzilkowski, W. M., et al. 2007. Wildlife damage to corn in Pennsylvania: farmer and on-the-ground estimates. The Journal of Wildlife Management 66: 678-682.

Ueda, H., et al. 2003. Seasonal change in browsing by sika deer on hinoki cypress trees on Mount Takahara, central Japan. Ecological Research 18: 355-364.

Uno, H. et al. 2006. Evaluation of relative density indices for sika deer in eastern Hokkaido, Japan. Ecological Research 21: 624-632.

Urbanek, R.E. et al. 2012. Acceptability and Conflict Regarding Suburban Deer Management Methods, Human Dimensions of Wildlife, 17: 389-403.

Urbanek, R.E. et al. 2013. Determinants of public perceptions of suburban deer density. Human Dimensions of Wildlife 18: 82-96.

Urbanek, R.E., et al. 2011. Urban and suburban deer management by state wildlife-conservation agencies. Wildlife Society Bulletin 35: 310-315.

Vahter, T., Kaimre, P. 2009. Method for evaluation of moose damage in cultivated pine forests of estonia. Baltic Forestry 15: 262-267.

van Beest, F.M. et al. 2010. Comparative Space Use and Habitat Selection of Moose Around Feeding Stations. Journal of Wildlife Management 74: 219-227.

van Doormaal, N. et al. 2015. Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in Central Japan. European Journal of Wildlife Research 61: 517-527.

Vázquez, D.P., et al. 2010. Introduced deer and the pollination and reproduction of an animal-pollinated herb. Botany 88: 110-118.

Vercauteren, K.C. et al. 2007. Health inspection service a fence design for excluding elk without impeding other wildlife part of the environmental sciences commons. Rangeland Ecology and Management 60: 529-532.

VerCauteren, K.C., et al. 2006. Efficacy of an animal-activated frightening device on urban elk and mule deer. Wildlife Society Bulletin 33: 1282-1287.

Viherä-Aarnio, A., Heikkilä, R. 2006. Effect of the latitude of seed origin on moose (*Alces alces*) browsing on silver birch (*Betula pendula*). Forest Ecology and Management 229: 325-332.

Vila, B. et al. 2004. Assessing spatial variation in browsing history by means of fraying scars. Journal of Biogeography 31: 987-995.

Vospernik, S. 2006. Probability of bark stripping damage by red deer (*Cervus elaphus*) in Austria. Silva Fennica 40: 589-601.

Wagner, M. W. et al. 2007. Collective action and social capital of wildlife management associations. Journal of Wildlife Management 71: 1729-1738.

Wallgren, M. et al. 2013. Spatial distribution of browsing and tree damage by moose in young pine forests, with implications for the forest industry. Forest Ecology and Management 305: 229-238.

Walter, W.D. et al. 2009. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. Landscape Ecology 24: 1405-1420.

Ward, A.I. 2005. Expanding ranges of wild and feral deer in Great Britain. Mammal Review 35: 165-173.

Ward, A.I. et al. 2004. Modelling the cost of roe deer browsing damage to forestry. Forest Ecology and Management 191: 301-310.

Ward, A.I. et al. 2008. Conifer leader browsing by roe deer in English upland forests: Effects of deer density and understorey vegetation. Forest Ecology and Management 256: 1333-1338.

Ware, I.M., et al. 2014. Conflicting management objectives on the Colorado Plateau: Understanding the effects of bison and cattle grazing on plant community composition. Journal for Nature Conservation 22: 293-301.

Webber, B.L., et al. 2010. Disturbance affects spatial patterning and stand structure of a tropical rainforest tree. Austral Ecology 35: 423-434.

Węgorek, P. et al. 2016. Influence of *Capreolus capreolus* L. and *Cervus elaphus* L. feeding simulation on disease incidence rate and maize yielding. Fresenius Environmental Bulletin 25: 4269-4276.

Weisberg, P.J. et al. 2002. An ecosystem approach to population management of ungulates. Journal of Environmental Management 65: 181-197.

Weladji, R.B., Tchamba, M.N. 2003. Conflict between people and protected areas within the Bénoué Wildlife Conservation Area, North Cameroon. Oryx 37: 72-79.

West, B.C., Parkhurst, J.A. 2002. Interactions between deer damage, deer density, and stakeholder attitudes in Virginia. Wildlife Society Bulletin 30: 139-147.

White, M.A. 2012. Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest. Forest Ecology and Management 269: 222-228.

Whittaker, D. et al. 2001. Understanding beliefs and attitudes about an urban wildlife hunt near Anchorage, Alaska. Wildlife Society Bulletin 29: 1114-1124.

Widmer, O. et al. 2004. The effects of hurricane Lothar on habitat use of roe deer. Forest Ecology and Management 195: 237-242.

Williams, S., Ward, J. 2006. Exotic seed dispersal by white-tailed deer in Southern Connecticut. Natural Areas Journal 26: 383-390.

Williams, S.C. et al. 2013. Evaluation of organized hunting as a management technique for overabundant white-tailed deer in suburban landscapes. Wildlife Society Bulletin 37: 137-145.

Williams, S.C., et al. 2008. Endozoochory by white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface. Forest Ecology and Management 255: 940-947.

Wilson, C.J. 2004. Rooting damage to farmland in Dorset, southern England, caused by feral wild boar *Sus scrofa*. Mammal Review 34: 331-335.

Wilson, C.J., et al. 2009. An assessment of agricultural damage caused by red deer (*Cervus Elaphus* L.) and fallow deer (*Dama Dama* L.) in Southwest England. Wildlife Biology in Practice 5: 104-114.

Xie, J., et al. 2001. DeerKBS: A knowledge-based system for white-tailed deer management. Ecological Modelling 140: 177-192.

Yamamura, K. et al. 2008. Harvest-based Bayesian estimation of sika deer populations using state-space models. Population Ecology 50: 131-144.

Yen, S.C. et al. 2015. Residents attitudes toward reintroduced sika deer in Kenting National Park, Taiwan. Wildlife Biology 21: 220-226.

Yokoyama, S. et al. 2001. Impact of bark stripping by sika deer, *Cervus nippon*, on subalpine coniferous forests in central Japan. Forest Ecology and Management 140: 93-99.

Zamora, R. et al. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: Consequences for forest regeneration. Forest Ecology and Management 144: 33-42.

Table S.1.1. Categories of stakeholders identified in the reviewed publications.

Stakeholders identified	Urban residents	People that live in non-rural areas
	Foresters	Those skilled in forestry or in charge of a forest
	Farmers	Producers of crop and animal products (livestock owners) who produce for subsistence or for commercial purposes
	Shepherds/herders	Producers of animal products (sheep owners) who produce for subsistence or for commercial purposes
	Hunters	Those who hunts game animals for food or in sport
	Indigenous communities	Native group of people of a given area
	Rural residents	Country people
	Environmental managers	Responsible for implementing and monitoring environmental strategies.
	NGO/conservationists	Non-Governmental Organizations with the objective of promote conservation
	Tourists	People who visit a given area
	General public	Those people non related with any stakeholder
	Others	E.g. administrations, researchers, students…

Table S.1.2. Different management tools (mentioned or recommended) in the reviewed publications.

Management tools	Payment for ES	Payments for ecosystem services, hunting business
	Economic compensation	Compensation, insurance, economic development or incentive schemes
	Tourism	e.g. ecotourism
	Livestock/crops guarding	People or dogs (either livestock herding or guarding dogs) protecting livestock or crops
	Education and awareness raising	Community outreach and education initiatives; provision of grants for community development in exchange for communitywide agreements to safeguard livestock and protect wildlife
	Co-management	Community-based management based on cooperation, collaboration processes and deliberation
	Deterrents and barriers	Scarecrows; lights and loud noises; pyrotechnics; face masks; specialized electric fencing; fences preventing cattle entering forests; wire mesh, wooden pole or nylon netting barriers around villages
	Translocation	Translocation of problem animals to protected areas; areas a distance from human habitation
	Aversive conditioning	Electrified human dummies or stuffed animals
	Lethal control	Selective removal or regulated harvest of ungulates
	Zoning	Harvest management units; separating livestock grazing from ungulates habitat
	Regulate local hunting	e.g. communal rights
	Supplementary feeding	Artificial food contributions to maintain ungulates in a specific area to avoid conflicts
	Habitat management	Actions in the environment to avoid or mitigate conflicts (e.g. maintenance of connectivity, adequate silvicultural practices)
	Others	e.g. contraceptive techniques to reduce ungulate populations, reducing speed limits (for traffic), monitoring damage and social attitudes by researchers.

Table S.1.3. Number of publications where conflicts and ecosystem services were mentioned.

Conflicts		Publications
Damage to biodiversity	Vegetation damage	145
	Animal biodiversity damage	27
Damage to production	Grazing competence	30
	Disease	44
	Physical damage to livestock	12
	Silvicultural damage	120
	Crop damage	147
	Physical damage game species	4
Damage to human	Attacks	14
	Damage to human health	25
Material damage	Property damage	37
	Traffic collisions	67
Human-human conflict		31
Other conflicts		13

Ecosystem services		Publications
Regulating	Habitat maintenance	24
	Seed dispersion	14
	Maintenance of soils	1
	Regulation of organisms	6
Provisioning	Food	40
	Materials	9
	Medicinal resources	1
Cultural	Educational and inspiration	4
	Maintenance of options	2
	Existence value	19
	Recreation	148

Chapter 2

Scientific priorities and shepherds' perceptions of ungulate's contributions to people.

Appendix S.2.1. Full search string for the systematic review.

(TITLE-ABS-KEY (("_ecosystem service_*" OR "_ecosystem good_*" OR "_environmental service_*" OR "_benefit_*" OR "_pros_" OR "_upside_*" OR "_advantage_*" OR "_conflict_*" OR "_damage_*" OR "_impair_*" OR "_harm_*" OR "_cons_" OR "_downside_*" OR "_drawback_*" OR "_threat_*" OR "_disturbance_*" OR "_perturbation_*" OR "_negativ* affect_*" OR "_positiv* affect_*" OR "_negativ* effect_*" OR "_positiv* effect_*")) AND TITLE-ABS-KEY (("_Ammotragus lervia_" OR "_aoudad_*" OR "_barbary sheep_" OR "_Capra pyrenaica_" OR "_Iberian ibex_*" OR "_Spanish ibex_*" OR "_Wild goat_" OR "_Capreolus capreolus_" OR "_Cervus elaphus_" OR "_Dama dama_" OR "_deer_" OR "_Ovis musimon_" OR "_Ovis orientalis_" OR "_Ovis gmelini_" OR "_mouflon_" OR "_Rupicapra rupicapra_" OR "_chamois_" OR "_Sus scrofa_" OR "_wild boar_" OR "_ungulat_*" OR "_big game_" OR "_game species_")) AND TITLE-ABS-KEY (_spain_ OR "_Iberian peninsular_" OR "_Mediterranean_" OR "_temperate_")) AND PUBYEAR > 1999 AND PUBYEAR < 2019 AND (LIMIT-TO (DOCTYPE ,"ar") OR LIMIT-TO (DOCTYPE, "ip")) AND (LIMIT-TO (LANGUAGE , "English"))

Appendix S.2.2. Known and seen index of shepherds in each farming system.

Overall, Knowledge index is significantly higher than Seen index (V = 5050, $p < 0.0001$). We did not detect differences in Knowledge index between species (χ2 = 8.24, df = 7, $p = 0.31$), and marginal differences in Seen index between species (χ2 = 12.10, df = 7, $p < 0.10$). The general trend for each species and area is that high percentage of shepherds known the wild ungulates species present, being the percentage of those who have seen each species smaller. For example, aoudad and mouflon in North Murcia, roe deer and Iberian ibex in Sierra Morena, or fallow deer in Pyrenees, in which the percentage of shepherds who have seen each species is less than 25 %.

Appendix S.2.3. References selected in the search of articles

Acevedo, P., et al. 2007. The Iberian ibex is under an expansion trend but displaced to suboptimal habitats by the presence of extensive goat livestock in central Spain. Biodiversity and Conservation 16: 3361–3376.

Acevedo, P., et al. 2007. Invasive exotic aoudad (*Ammotragus lervia*) as a major threat to native Iberian ibex (*Capra pyrenaica*): A habitat suitability model approach. Diversity and Distributions 13: 587–597.

Acevedo, P., et al. 2014. Spatial distribution of wild boar population abundance: Basic information for spatial epidemiology and wildlife management. Ecological Indicators 36: 594–600.

Ameztegui, A., Coll, L. 2015. Herbivory and seedling establishment in Pyrenean forests: Influence of micro- and meso-habitat factors on browsing pressure. Forest Ecology and Management 342: 103–111.

Aranaz, A., et al. 2004. Bovine tuberculosis (*Mycobacterium bovis*) in wildlife in Spain. Journal of Clinical Microbiology 42: 2602–2608.

Azorit, C., et al. 2005. Influence of age and environment on antler traits in Spanish red deer (*Cervus elaphus hispanicus*). Zeitschrift Für Jagdwissenschaft 48: 137–144.

Barja, I. 2009. Prey and Prey-Age Preference by the Iberian Wolf Canis Lupus Signatus in a Multiple-Prey Ecosystem. Wildlife Biology 15: 147–154.

Bosch, J., et al. 2014. A maximum entropy model for predicting wild boar distribution in Spain. Spanish Journal of Agricultural Research 12: 984–999.

Bueno, C.G., Jiménez, J.J. 2014. Livestock grazing activities and wild boar rooting affect alpine earthworm communities in the Central Pyrenees (Spain). Applied Soil Ecology 83: 71–78.

Cahill, S., et al. 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. Animal Biodiversity and Conservation 2: 221–233.

Carpio, A.J., et al. 2016. Factors Affecting Red-Legged Partridge *Alectoris rufa* Abundance on Big-Game Hunting Estates: Implications for Management and Conservation . Ardeola 62: 283–297.

Carpio, A.J., et al. 2014. Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem. Animal Biodiversity and Conservation 37: 115–125.

Carpio, A.J., et al. 2014. The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit? Wildlife Biology 20: 161–166.

Carpio, A.J., et al. 2014. Predation of simulated red-legged partridge nests in big game estates from South Central Spain. European Journal of Wildlife Research 60: 391–394.

Carpio, A.J., et al. 2015. Effects of the overabundance of wild ungulates on natural grassland in Southern Spain. Agroforestry Systems 89: 637–644.

Cassinello, J., Acevedo, P. 2006. Prospects for population expansion of the exotic aoudad. Diversity and Distributions 666–678.

Castro, J., et al. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: A 4-year study. Restoration Ecology 123: 352–358.

Charco, J., et al. 2016. Impact of deer rubbing on pine forests: implications for conservation and management of *Pinus pinaster* populations. European Journal of Forest Research 135: 719–729.

Colino-Rabanal, V.J., et al. 2018. Ungulate: vehicle collision rates are associated with the phase of the moon. Biodiversity and Conservation 27: 681–694.

Colino-Rabanal, V.J. et al. 2012. Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Animal Biodiversity and Conservation 35: 247–252.

Cowie, C.E., et al. 2016. Interactions between four species in a complex wildlife: livestock disease community: implications for *Mycobacterium bovis* maintenance and transmission. European Journal of Wildlife Research 62: 51–64.

D’Amico, M., et al. 2016. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. Journal of Applied Ecology 53: 181–190.

Duarte, J., et al. 2015. Deer populations inhabiting urban areas in the south of Spain: habitat and conflicts. European Journal of Wildlife Research 61: 365–377.

Fedriani, J.M., Delibes, M. 2009. Seed dispersal in the Iberian pear, Pyrus bourgaeana : A role for infrequent mutualists. Ecoscience 16: 311–321.

Fernández-Llario, P., Mateos-Quesada, P. 2005. Udder preference in wild boar piglets. Acta Ethologica 8: 51–55.

Fernández-Olalla, M., et al. 2016. Threat or opportunity? Browsing preferences and potential impact of Ammotragus lervia on woody plants of a Mediterranean protected area. Journal of Arid Environments 129: 9–15.

Fernández, J.D., Gómez, J.M. 2012. Advantages and drawbacks of living in protected areas: The case of the threatened *Erysimum popovii* (Brassicaceae) in SE Iberian Peninsula. Biodiversity and Conservation 21: 2539–2554.

Garcá, D., Obeso, J.R. 2003. Facilitation by herbivore-mediated nurse plants in a threatened tree, Taxus baccata: local effects and landscape level consistency. Ecography 739–750.

García-Bocanegra, I., et al. 2016. Spatio-temporal trends and risk factors affecting West Nile virus and related flavivirus exposure in Spanish wild ruminants. BMC Veterinary Research 12: 1–9.

Gassó, D., et al, E. 2016. Oxidative stress in wild boars naturally and experimentally infected with *Mycobacterium bovis*. PLoS ONE 11: 1–17.

Giménez-Anaya, A., et al. 2016. Wild boar battues reduce crop damages in a protected area. Folia Zoologica, 65: 214–220.

Giménez-Anaya, A., et al. 2008. Foo habits of wild boar (*Sus scrofa*) in a Mediterranean coastal wetland. Wetlands 28: 197–203.

Gómez-Aparicio, L., et al. 2008. Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores? Journal of Vegetation Science 19: 161–172.

Gómez, J.M., Zamora, R. 2000. Differential impact of vertebrate and invertebrate herbivores on the reproductive output of *Hormathophylla spinosa*. Ecoscience 7: 299–306.

Gómez, J.M. 2003. Herbivory Reduces the Strength of Pollinator-Mediated Selection in the Mediterranean Herb *Erysimum mediohispanicum*: Consequences for Plant Specialization . The American Naturalist 162: 242–256.

Gómez, J.M. 2005. Long-term effects of ungulates on performance, abundance, and spatial distribution of two montane herbs. Ecological Monographs 75: 231–258.

Gómez, J.M., Hódar, J.A. 2008. Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*). Forest Ecology and Management 256: 1384–1389.

Gómez, J.M., et al. 2002. Ungulate damage on Scots pines in Mediterranean environments: effects of association with shrubs. Canadian Journal of Botany 79: 739–746.

Gonçalves, P., et al. 2016. A new method for ageing wild boar using dental measures. Ecological Indicators 62: 328–332.

González-Crespo, C., et al. 2018. Stochastic assessment of management strategies for a Mediterranean peri-urban wild boar population. PLoS ONE 13: 1–19.

Herrero, A., et al.2012. Limits of pine forest distribution at the treeline: Herbivory matters. Plant Ecology 213: 459–469.

Iglesias-Merchan, C., et al. 2018. A new large-scale index (AcED) for assessing traffic noise disturbance on wildlife: stress response in a roe deer (Capreolus capreolus) population. Environmental Monitoring and Assessment 190.

Laskurain, N.A., et al. 2013. Intensification of domestic ungulate grazing delays secondary forest succession: Evidence from exclosure plots. Journal of Vegetation Science 24: 320–331.

López-Montoya, A.J., et al. 2017. Drivers of population growth variations for two Mediterranean sympatric Deer. Ecological Research 32: 703–712.

Lopez-Saez, J.A., et al. 2014. Peatlands in the Toledo Mountains (central Spain): characterisation and conservation status. Mires and Peat 15: 23.

López-Sánchez, A., et al. 016. Livestock vs. wild ungulate management in the conservation of Mediterranean dehesas: Implications for oak regeneration. Forest Ecology and Management 362: 99–106.

López-Sánchez, A., et al. 2016. Scattered trees and livestock grazing as keystones organisms for sustainable use and conservation of Mediterranean dehesas. Journal for Nature Conservation 33: 58–67.

Lozano, J., et al. 2007. Increase of large game species in Mediterranean areas: Is the European wildcat (*Felis silvestris*) facing a new threat? Biological Conservation 138: 321–329.

Mangas, J.G., Rodríguez-Estival, J. 2010. Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. Forest Ecology and Management 260: 1274–1281.

Martín-Hernando, et al. 2007. Lesions associated with *Mycobacterium tuberculosis* complex infection in the European wild boar. Tuberculosis 87: 360–367.

Martinez-Jauregui, et al. 2015. What does hunting market price reflect? The role of species, landscape and management. Wildlife Research 42: 280.

Mata, C., et al. 2008. Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. Journal of Environmental Management 88: 407–415.

Mateo-Tomás, P., Olea, P.P. 2010. When hunting benefits raptors: A case study of game species and vultures. European Journal of Wildlife Research 56: 519–528.

Mateo-Tomás, P., et al. 2017. Both rare and common species support ecosystem services in scavenger communities. Global Ecology and Biogeography 26: 1459–1470.

Mateo-Tomás, P., et al. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions 21: 913–924.

Mateos, M.D., Delibes, A. 2014. Pets becoming established in the wild: free–living Vietnamese potbellied pigs in Spain. Animal Biodiversity and Conservation 2: 209–215.

Muñoz, A., et al. 2009. Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. Basic and Applied Ecology 10: 151–160.

Muñoz, P.M., et al. 2009. Spatial distribution and risk factors of Brucellosis in Iberian wild ungulates. BMC Infectious Diseases 10.

Naranjo, V., et al. 2008. Influence of methylmalonyl-CoA mutase alleles on resistance to bovine tuberculosis in the European wild boar (*Sus scrofa*). Animal Genetics 39: 316–320.

Navarro-Castilla, Á., et al. 2018. Does ungulate disturbance mediate behavioural and physiological stress responses in Algerian mice (*Mus spretus*)? A wild exclosure experiment. Hystrix, the Italian Journal of Mammalogy 29: 87–94.

Obeso, J.R. 2004. Growth, nutrient content, fruit production and herbivory in bilberry. Forestry 77: 213–223.

Pascual-Rico, R., et al. 2018. Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain. Applied Soil Ecology 127: 136–143.

Pato, J., et al. 2016. Experimental evidence from Cantabrian mountain heathlands suggests new recommendations for management of *Vaccinium myrtillus* L. Plant Ecology and Diversity 9: 199–206.

Paula, S., Ojeda, F. 2011. Response to recurrent disturbance in two co-occurring resprouter heath species: The ecological consequences of withstanding herbivores. Plant Ecology 212: 2035–2045.

Perea, R., Gil, L. 2014a. Shrubs facilitating seedling performance in ungulate-dominated systems: Biotic versus abiotic mechanisms of plant facilitation. European Journal of Forest Research 133: 525–534.

Perea, R., Gil, L. 2014b. Tree regeneration under high levels of wild ungulates: The use of chemically vs. physically-defended shrubs. Forest Ecology and Management 312: 47–54.

Perea, R., et al. 2014. Big game or big loss? High deer densities are threatening woody plant diversity and vegetation dynamics. Biodiversity and Conservation 23: 1303–1318.

Peredo, A., et al. 2013. Mammalian seed dispersal in Cantabrian woodland pastures: Network structure and response to forest loss. Basic and Applied Ecology 14: 378–386.

Pérez-González, J., Carranza, J. 2009. Female-biased dispersal under conditions of low male mating competition in a polygynous mammal. Molecular Ecology 18: 4617–4630.

Porrero, M.C., et al. 2013. Methicillin resistant Staphylococcus aureus (MRSA) carriage in different free-living wild animal species in Spain. Veterinary Journal 198: 127–130.

Puerta-Piñero, C., et al. 2012. Direct and indirect landscape effects on Quercus ilex regeneration in heterogeneous environments. Oecologia 170: 1009–1020.

Quirós-Fernández, F., et al. 2017. Hunters serving the ecosystem: the contribution of recreational hunting to wild boar population control. European Journal of Wildlife Research 63: 4–9.

Risco, D., et al. 2018. Vaccination Against Porcine Circovirus-2 Reduces Severity of Tuberculosis in Wild Boar. EcoHealth 15: 388–395.

Santos, J.P.V., et al. 2018. The importance of intrinsic traits, environment and human activities in modulating stress levels in a wild ungulate. Ecological Indicators 89: 706–715.

Segura, A., et al. 2014. Biotic and abiotic factors modulating wild boar relative abundance in Atlantic Spain. European Journal of Wildlife Research 60: 469–476.

Suárez-Esteban, A., et al. 2014. Unpaved roads disrupt the effect of herbivores and pollinators on the reproduction of a dominant shrub. Basic and Applied Ecology 15: 524–533.

Taylor, P., et al. 2010. Unexpected role of ungulate carcasses in the diet of Golden Eagles Aquila chrysaetos in Mediterranean mountains. Bird Study 57: 352–360.

Torres-Porras, J., et al. 2014. The tragedy of the commons: Unsustainable population structure of Iberian red deer in hunting estates. European Journal of Wildlife Research 60: 351–357.

Torres-Porras, J., et al. 2015. Conifer plantations negatively affect density of wild boars in a mediterranean ecosystem. Folia Zoologica 64: 25–31.

Velamazán, M., et al. 2018a. Compatibility of regeneration silviculture and wild ungulates in a Mediterranean pine forest: implications for tree recruitment and woody plant diversity. Annals of Forest Science 75.

Velamazán, M., et al. 2018b. Use of firebreaks and artificial supply points by wild ungulates: Effects on fuel load and woody vegetation along a distance gradient. Forest Ecology and Management 427: 114–123.

Vicente, J., et al. 2004. Long-term epidemiology, effect on body condition and interspecific interactions of concomitant infection by nasopharyngeal bot fly larvae (*Cephenemyia auribarbis* and *Pharyngomyia picta* , Oestridae) in a population of Iberian red deer (*Cervus elaphus*). Parasitology 129: 349–361.

Zamora, R., et al. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a mediterranean environment: Consequences for forest regeneration. Forest Ecology and Management 144: 33–42.

Zuberogoitia, I., et al. 2014. Ungulate vehicle collisions in a peri-urban environment: Consequences of transportation infrastructures planned assuming the absence of ungulates. PLoS ONE 9.

Table S.2.1. Species included in the questionnaires (i.e., offered species) in each study area. See Mateo-Tomás et al. (2015) and Sebastián-González et al. (2016) for a more detailed description of the study areas.

Common name	Scientific name	Cantabrian Mountains	Pyrenees	Sierra Morena	Cazorla	Murcia
Aoudad	*Ammotragus lervia*	No	No	No	Yes	Yes
Chamois	*Rupicapra pyrenaica*	Yes	Yes	No	No	No
Fallow deer	*Dama dama*	Yes	No	Yes	Yes	No
Iberian ibex	*Capra pyrenaica*	No	No	Yes	Yes	Yes
Mouflon	*Ovis orientalis*	No	Yes	Yes	Yes	Yes
Red deer	*Cervus elaphus*	Yes	Yes	Yes	Yes	Yes
Roe deer	*Capreolus capreolus*	Yes	Yes	Yes	No	No
Wild boar	*Sus scrofa*	Yes	Yes	Yes	Yes	Yes

Table S.2.2. Total shepherd population (N), total number of questionnaires conducted (n), margin of error, and main socio-demographic and farming characteristics of the shepherds for the set of study areas and in each study area. Mean ± SD are shown. Total shepherd population (N) refers to farms with > 25 heads of sheep or goats, and > 10 head of cattle or horses.

Variable	Cantabrian Mountains	Pyrenees	Sierra Morena	Cazorla	Murcia	National
N	246	86	30	122	176	660
n	40	32	21	33	58	184
Margin of error (%)	14.2	13.8	11.9	14.6	10.6	6.1
Socio-demographic characteristics						
Average age of shepherds	50.4 ± 13.9	49.2 ± 11.3	45.3 ± 7.0	47.2 ± 6.9	53.4 ± 11.2	50.6 ± 11.4
Male (%)	77.5	84.4	100	100	98.3	90.8
Female (%)	22.5	15.6	0	0	1.7	9.2
Farming characteristics						
Total number of livestock	88.0 ± 74.7	527.1 ± 542.9	796.8 ± 371.7	695.2 ± 348.7	696.7 ± 503.3	507.9 ± 482.4
Number of sheep	2.6 ± 7.7	470.0 ± 562.2	751.9 ± 360.0	660.0 ± 337.9	635.7 ± 527.7	446.9 ± 499.9
Number of goats	18.1 ± 55.6	17.2 ± 36.2	39.9 ± 67.3	29.1 ± 55.7	58.8 ± 126.5	34.3 ± 86.3
Number of cattle	64.3 ± 66.0	39.5 ± 80.4	4.8 ± 21.8	5.8 ± 23.1	0.3 ± 2.1	24.8 ± 55.8
Number of horses	2.9 ± 6.2	0.9 ± 4.3	0.2 ± 0.6	0.4 ± 1.2	0	1.5 ± 4.7
Shepherds performing transhumance (%)	20.0	18.8	100	63.6	0	21.5

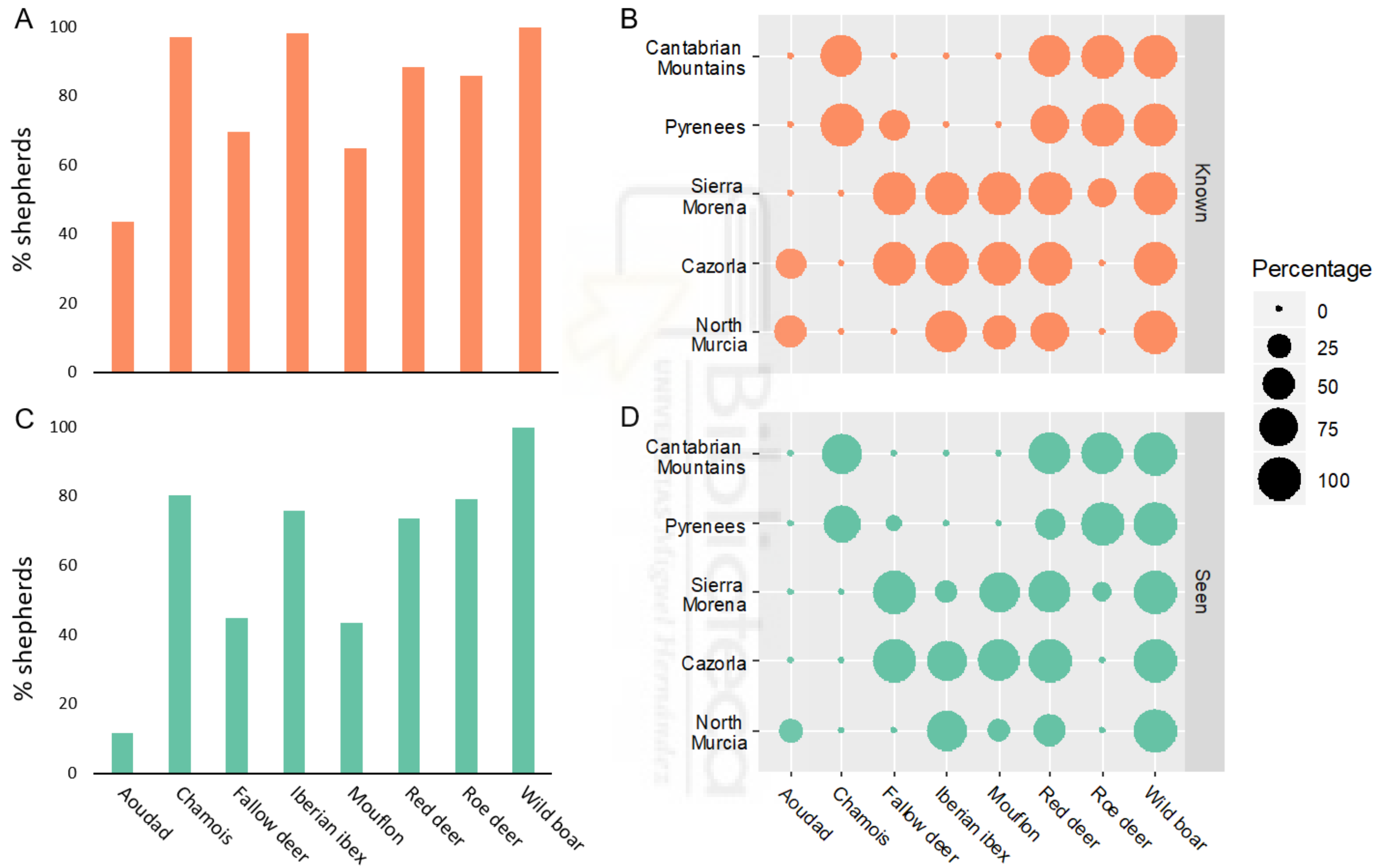

Figure S.2.1. (A) Percentage of the total shepherds who knew the species by which they were asked. (B) Percentage of the total shepherds at different study areas who knew the species by which they were asked. (C) Percentage of the total shepherds who had ever seen the species by which they were asked. (D) Percentage of shepherds who had ever seen the species by which they were asked.

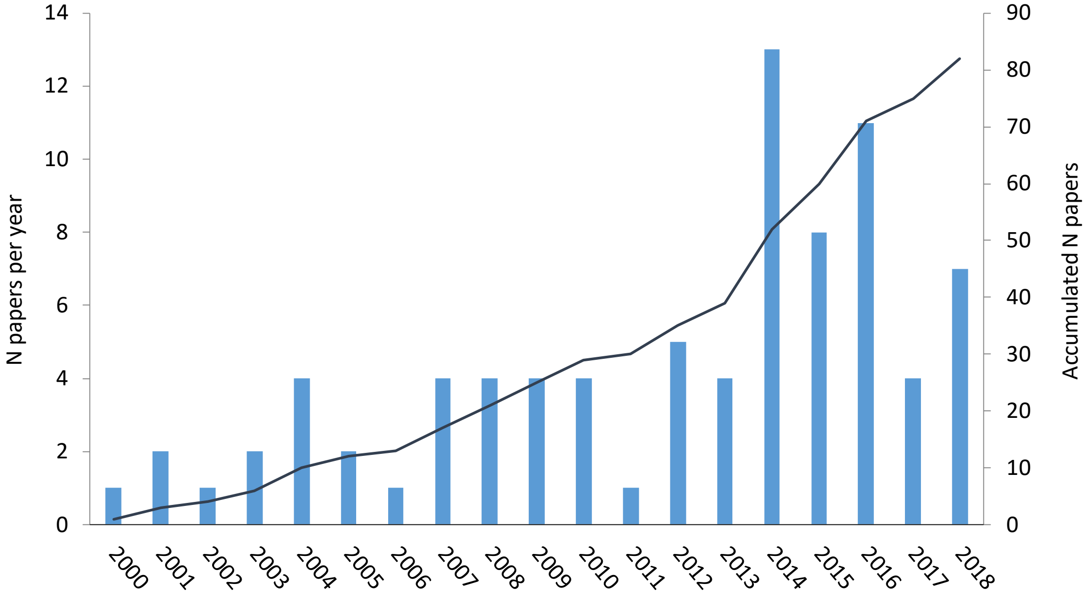

Figure S.2.2. Number of publications per year about human-ungulate relations in Spain (total n = 82).

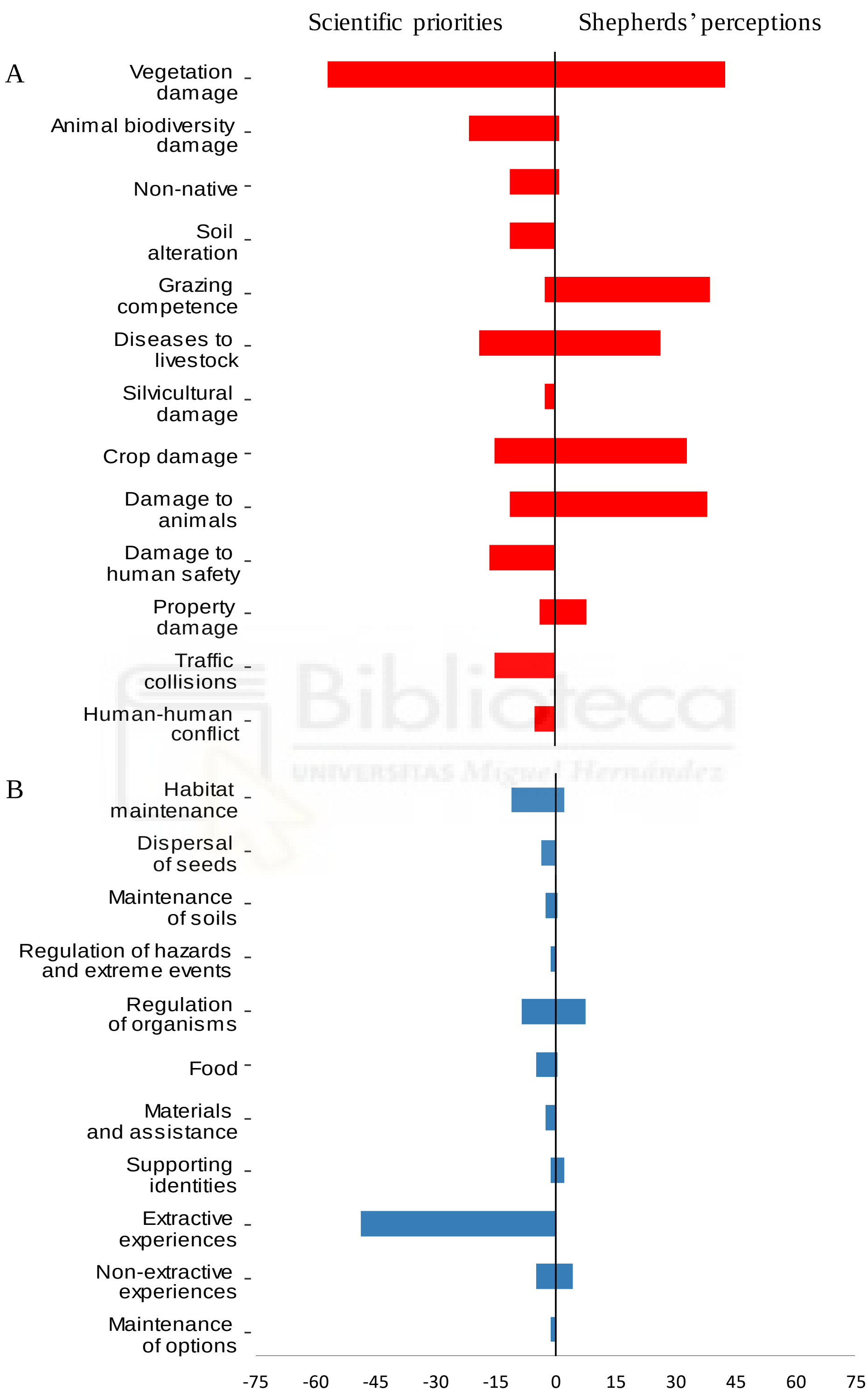

Figure S.2.3. (a) Percentages of publications that mentioned each conflict (left red bars) and ecosystem service (left blue bars) and (b) percentages of shepherds that perceived each conflict (right red bars) and ecosystem service (right blue bars).

References

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sáncehz-Zapata, J.A.2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity & Distributions 21:913–924.

Sebastián-González, E., Moleón, M., Gibert, J.P., Botella, F., Mateo-Tomás, P., Olea, P.P., Guimarães, P.R., Sánchez-Zapata, J.A. 2016. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. Ecology 97: 95-105.

Chapter 3

Ecological niche overlap between co-occurring native and exotic ungulates: insights for a paradigmatic conflict.

S.3.1. Biological characters of the study species, Iberian ibex and aoudad.

Iberian ibex (*Capra pyrenaica*) is a wild ungulate native of the Iberian Peninsula. Its weight ranges from 30 kg to 90 kg, the largest. Both genders have horns, but males show longer and wider horns than females. Iberian ibex is a gregarious species and it is grouped in herds of different size, which vary throughout the year. During the autumn occurs the rut season, and males and females constitute mixed herds. During the rest of the year it is possible to find herds of males and, separately, herds of females, young males, sub-adults and new offspring (births occur during the spring) (Granados et al. 2007, Wilson and Mittermeier 2011).

Aoudad (*Ammotragus lervia*) is an ungulate native from North Africa and it was introduced in several parts of the world, including the Iberian Peninsula. Its weight ranges from 12 kg to 130 kg in the case of the biggest. Males and females have horns, and they are bigger in males (Cassinello et al. 2007). A characteristic feature of the species is the mane that presents from the neck to the forelegs (Cassinello 1998). As in the case of the Iberian ibex, the aoudad is also a gregarious species and it shows similar behaviour regarding the changes of the herds throughout the year. However, the aoudad is more social than the Iberian ibex, usually forms large herds and their rut season begins earlier with respect to the Iberian ibex (Anadón et al. 2018).

Table S.3.1. Main characteristics of the mountain ranges of the study area.

Mountain range	***Area (ha)***	***Maximum altitude (m.a.s.l.)***
Burete	9869.1	1191
Cambrón	13996.6	1510
Espuña	23193.9	1576
Gigante-Pericay	17468.5	1481
Lavia	5263.8	1204
Molino	6535.3	1481
Muela	1296.7	623
Oro	3705.0	939
Ricote	7975.9	1106
Tercia	10917.5	983
Torrecilla	19902.6	1053
Villafuerte	19944.7	1728
Mean	11672.5 ± 7160.4	1239.6 ± 321.1

Supporting references

Anadón, J.D., Pérez-García, J.M., Pérez, I., Royo, J., Sánchez-Zapata, J.A. 2018. Disentangling the effects of habitat, connectivity and interspecific competition in the range expansion of exotic and native ungulates. Landscape Ecology 33: 597-608.

Cassinello, J. 1998. *Ammotragus lervia*: a review on systematics, biology, ecology and distribution. Annales Zoologici Fennici 35: 149-162.

Cassinello, J., Serrano, E., Calabuig, G., Acosta, P., Pérez, J.M. 2007. *Ammotragus lervia* Pallas, 1777, in: Palomo, L.J., Gisbert, J., Blanco, J.C. (Eds.), Atlas y Libro Rojo de los Mamíferos terrestres de España. Direción General para la Biodiversidad-SECEM-SECEMU, Madrid, pp. 374-377.

Granados, J.E., Soriguer, R.C., Pérez, J.M., Fandos, P., García-Santiago, J. 2007. *Capra pyrenaica*, Schinz 1838, in: Palomo, L.J., Gisbert, J., Blanco, J.C. (Eds.), Atlas y Libro Rojo de los Mamíferos terrestres de España. Direción General para la Biodiversidad-SECEM-SECEMU, Madrid, pp. 588.

Wilson, D.E., Mittermeier, R.A. 2011. Handbook of the Mammals of the World. Hoofed Mammals. Lynx Editions, Barcelona.

Chapter 4

Is diversionary feeding a useful tool to avoid human-ungulate conflicts? A case study with the aoudad.

Table S.4.1. Precipitation registered in the region of Murcia during the study period 2015 summer per month compared with the median precipitation in the region.

Month	Registered precipitation (mm)	Median
May	16.5	33.7
June	1.4	7.8
July	4.7	1.5
August	12.0	5.7
September	74.5	21.2

Table S.4.2. Photographed species at the monitored feeding stations from July 24th to October 6th 2015 (n = 73 days). We show the percentage of pictures (N = 9,639) in which animals were observed and the average (± SD) number of individuals detected in each picture. Maximum number of individuals detected in parentheses.

	Species	Common name	% of pictures	Mean ± SD (Max. individuals)
Mammals	*Ammotragus lervia*	Aoudad	70.7	4.13 ± 4.31 (40)
	Sus scrofa	Wild boar	23.0	0.72 ± 1.56 (13)
	Canis lupus familiaris	Domestic dog	< 0.1	1.13 ± 0.35 (2)
	Martes foina	Stone marten	< 0.1	1 (1)
	Meles meles	European badger	< 0.1	1 (1)
	Oryctolagus cuniculus	European rabbit	1.2	1.04 ± .021 (2)
	Vulpes vulpes	European red fox	0.1	1 (1)
Birds	*Alectoris rufa*	Red-legged partridge	0.8	4.82 ± 3.37 (14)
	Aquila pennata	Booted eagle	< 0.1	1 (1)
	Caprimulgus sp	Nightjar	< 0.1	1 (1)
	Columba palumbus	Common wood pigeon	1.8	2.13 ± 1.97 (16)
	Corvux corax	Common raven	0.4	2.46 ± 1.61 (6)
	Garrulus glandarius	Eurasian jay	1.2	1.37 ± 0.72 (4)
	Passer domesticus	Sparrow	< 0.1	1 (1)
	Pyrrhocorax pyrrhocorax	Red-billed chough	0.5	16.65 ± 14.02 (82)
	Streptopelia turtur	European turtle dove	< 0.1	1.20 ± 0.45 (2)

Chapter 5

Soil properties in relation to diversionary feeding stations for ungulates on a Mediterranean mountain.

Table S.5.1. The investigated biomarker indices.

Group designation	Biomarkers
Bacteria	i15:0, 15:0, a15:0, i16:0, 16:1ω7, i17:0, a17:0, cy17:0, 17:0, cy19:0
Fungi	18:2ω6
G- bacteria	cy17:0, cy19:0, 17:1ω9c, 16:1ω7c, 18:1ω9c
G+ bacteria	i14:0, i15:0, a15:0, i16:0, i17:0, a17:0
Actinobacteria	10Me17:0, 10Me18:0

Acknowledgements/

Agradecimientos

Como no tengo muy claro con quien empezar los agradecimientos, voy a empezar por quienes me han mantenido con fuerzas los últimos cinco años: a mi madre y sus tuppers llenos hasta el borde con caldo, amor y cariño. Por supuesto también al resto de mi familia (padre, hermanos, cuñados y sobrinos), para que sigamos reuniéndonos alrededor de la mesa muchos años más.

No hay manera de agradecer a Andrés, Paco y Toni (tutor y directores de tesis) lo que me ha supuesto haber realizado el doctorado junto a ellos. Con mucho esfuerzo y paciencia me han transmitido cómo "hacer ciencia", cómo hacerla bien y mejor aún. Tras cada reunión o charla, científica o no, algo había para mejor, ya fuese un trabajo científico o la manera de ver algún aspecto del mundo. Mil gracias a cada uno por la confianza y la entrega.

Pero el Área de Ecología la compone mucha más gente que han contribuido a que este periodo fuese insuperable, aportando consejos, ideas y apoyo. Gracias a todos mis compañeros y amigos: Eva, cuya defensa de tesis fue la primera que vi en mi vida (no puedo decir que no sabía dónde me metía…); JuanMa (saurio), Roberto (rtuga), Alicia y Zebensui. No me olvido de los compañeros postdocs: Viqui, Esther (egresada regresada), Jomar (nuestro toque internacional). Y también a las nuevas incorporaciones para que la ciencia no decaiga: Nati, MariCarmen y Lara (que me facilitó algunas de las fotos de su trabajo en Congo para esta tesis).

Otra parte del equipo ya indispensable y que llegó para ponernos a todos firmes fue Isa, técnico de laboratorio y comandante en jefe. Aún nos preguntamos cómo sobrevivíamos sin ti.

Merece especial mención (se la ha ganado a pulso con sus chistes malos) el navarrosevillano señor Eneko, con quien he pasado muy buenos ratos tanto de trabajo como de ocio (aunque no puedo diferenciarlos) y que será el siguiente…

Gracias a este equipazo, además de tener ayuda por parte de ellos con lo relacionado con esta tesis, he podido participar y colaborar en otros proyectos como jornadas tortugueras en el sureste y más al sur (en Marruecos), campañas carroñeras de fototrampeo en Navarra y Nepal, socioecología en Asturias, marcaje de buitres en Cádiz, marcaje y seguimiento de ungulados en Sierra Espuña y Cazorla, reuniones de trabajo en el campo (la mejor oficina), salidas porque sí, y los jueves de cañas.

Con todos reunidos podemos arreglar el mundo en lo relativo a las tortugas, los buitres, las aves acuáticas, los carnívoros, los ungulados, los servicios ecosistémicos, los conflictos, la etología, los modelos basados en el individuo, la genética, la teledetección y todas las relaciones entre estos campos (y los que me he dejado).

Mucho del trabajo de campo habría sido imposible sin la ayuda y experiencia de los celadores de caza Borrascas, Casimiro y Yepes, que me enseñaron mil rincones y barrancos de Sierra Espuña mientras salíamos a buscar la suerte (más bien a los arruis). También al equipo veterinario, María José y Fernando siempre presente y dispuesto. A Patricia, por la mano gigante echada con las entrevistas en Somiedo.

Por supuesto también a todos aquellos que desde las distintas administraciones nos permitieron y facilitaron el trabajo: Andrés, Matías, David, José Antonio.

En la ciencia no se puede ir por libre ni trabajar aislado, por lo que la colaboración entre investigadores es crucial. Gracias a Fuensanta, Alicia y Carlos con quienes tuve que echar unas cuantas horas de laboratorio y gabinete en el Departamento de Agroquímica.

Además, durante las estancias internacionales he podido colaborar con otros laboratorios y conocer magníficos investigadores. Gracias Jimi e Irene por la acogida en Nueva York durante aquellos dos meses. Y a todos los que estando allí en el Ánadon's Lab me ayudaron e hicieron esta estancia tan agradable, Olivia (del loud lab), Ash (del quiet lab, que también me ha prestado fotos de sus expediciones a Nepal), y muy en especial a Pedro Abellán y Narci, por sus scripts de R, tours turísticos y el pollo de Acción de Gracias.

La segunda estancia la hice en Lüneburg, Alemania. Fueron tres meses increíbles bajo la tutela de Berta, y Jorge como compañero de despacho. Mil gracias a los dos por las charretas y reuniones al aire libre que de las que tanto aprendí. También doy las gracias a Henrik. su buen rollo, las cenas en su casa y las partidas a juegos de mesa con otros muchos estudiantes de los que no recuerdo los nombres.

Entrar en una casa con desconocidos en países desconocidos es siempre un riesgo. Y yo tuve muchísima suerte con mis compañeros de piso. Gracias Corina, Eleonor, Martina y Helge por hacerme sentir como en casa.

Agradecer a todos mis amigos los buenos ratos y las muchas risas, tanto a la panda eldense como a la tribu que se mueve por Elche: Alfonso, Chuma, Jona, Ludi y su murcianico Gabri, La Roci, Marian (por enseñarme a tomar el coulant con gintonic), Pakito, Toño, Tuqui. Y a Gaëlle (guiño, guiño), que, aunque apareció hace poco, ha hecho mucho.

Y siguiendo con las amistades, Sergio (cuyas fotos también aparecen en este trabajo), Eugenio y Bea. El equipo islero-montañero del que solo puedo estar orgulloso y feliz de haber compartido y aprendido tanto con ellos en el campo, las historias y aventuras vividas, todos los censos de ungulados en los que he participado con ellos, los vermuts...

Mucha gente ha contribuido en esta tesis directa o indirectamente. Y espero no haberme olvidado de nadie. En cualquier caso, muchas gracias a todos. El resultado ha sido este trabajo tras cinco años de esfuerzo, y del que estoy tremendamente orgulloso. Y esto sería más o menos un poco todo.

Chim pum

Roberto Pascual Rico PhD Thesis