

UNIVERSIDAD AUTÓNOMA DE MADRID
FACULTAD DE CIENCIAS
Departamento de Ecología



**Ecología del guanaco (*Lama guanicoe*) en la Patagonia chilena:
el papel de las interacciones bióticas en su abundancia,
distribución y selección de hábitat.**

Memoria presentada por **Esperanza C. Iranzo Sanz** para optar al
Grado de Doctor en Ecología por la Universidad Autónoma de Madrid

Bajo la dirección de:

Juan E. Malo Arrázola
Profesor Titular
Departamento de Ecología
Universidad Autónoma de Madrid

Juan Traba Díaz
Profesor Titular
Departamento de Ecología
Universidad Autónoma de Madrid

TESIS DOCTORAL
Madrid, febrero de 2017

A mis padres

A mi tía Pilarín

Presentation

Humans play a key role in the loss of biodiversity that we are facing today. Human activity has a great impact on nature, causing species extinctions and threatening the survival of many species and ecosystems. Large herbivores are not an exception in this framework. Threats to them include poaching, habitat destruction and fragmentation, and the introduction of livestock which competes with wild herbivores and usually forces them to occupy suboptimal habitats.

Many conservation actions are carried out to deal with biodiversity loss, outstandingly the declaration of protected areas. When successful, species conservation programs may also lead to the growth and expansion of wild populations outside the protected areas, resulting in conflicts with the socio-economic development of the neighbouring areas.

Torres del Paine National Park (Chile) and its surroundings are a natural area where the socio-economic development and the conservation of wildlife converge. The main economic activity in the area is livestock farming, although in recent years tourism boosted by the National Park has become a complementary source of income. In parallel, the guanaco population growth within the protected area resulting from its protection in the last twenty years has caused its expansion towards surrounding private ranches. There, a conflict between wildlife conservation and economic activity has arisen.

In this context, this doctoral thesis takes advantage from the "natural experiment" provided by the protected area and its surroundings that differ basically in the presence of livestock along with wild species. This makes of Torres del Paine a perfect scenario to test diverse ecological hypotheses related with niche theory and the diffusion of populations, as much as to improve the present knowledge of guanaco ecology and behavior, which were the subject of study of this doctoral thesis.

The increase in the abundance and occupation area of guanaco could lead to resource competition with livestock outside the National Park. This thesis tries to (i) determine the existence (or not) of such potential for competition, (ii) study specific aspects of guanaco ecology, (iii) determine the state of its population and (iv) examine interspecific interactions at the community level between native and exotic herbivores.

Specifically, this thesis estimates the population size and density of guanacos in the area. It also describes the social and demographic structure of the population and its dispersion pattern, as well as the factors that influence their distribution and social structure (CHAPTER 2). To evaluate the possible consequences of guanacos expanding to private ranches and their potential for competition with livestock, CHAPTER 3 compares habitat selection of both species in sympatry and that of the guanaco in absence of sheep, both in winter and late spring- early summer.

Guanacos and sheep are part of a community of wild herbivores in which livestock has recently been introduced, so the processes of niche overlap and segregation due to competition can extend beyond the guanaco-sheep relationship. In order to address the community-level effects of livestock introduction, as well as to detect changes in niche dimensions due to intra- and interspecific competition, CHAPTER 4 analyses niche breadth and niche overlap between all species pairs of the herbivore assemblage. Once the effect of competition in the guanaco niche has been determined, CHAPTER 5 assesses the role of predation risk and habitat structure in the antipredator behaviour of guanaco. Finally, the main findings of this thesis are discussed in CHAPTER 6 and summarized in Conclusions section.

Agradecimientos

Escribir la única sección de la tesis que van a leer más de cinco personas, con el tiempo jugando en contra, y no dejarse a nadie por el camino es tarea harto complicada, así que vaya por delante un gran GRACIAS a todas las personas que han compartido conmigo estos años y que, de una manera u otra, han contribuido a que esta tesis llegue a buen puerto. No obstante, hay ciertas personas que me han acompañado en el desarrollo de la tesis a las que considero necesario mencionar detenidamente.

En primer lugar quiero dar las gracias a mis directores, los Juanes, por ofrecerme la oportunidad de realizar la tesis en un sitio tan privilegiado como es el Parque Nacional Torres del Paine, del que he quedado absolutamente prendada y a día de hoy, tras recorrer una pequeña parte del mundo, sigue siendo el lugar al que volvería una y mil veces. Gracias, además, por confiar en mí para llevar a cabo este proyecto, y por no dejarme por imposible a pesar de mi tozudez maña. Gracias, porque además de directores habéis sido compañeros de aventuras y amigos, y porque a pesar de vuestras muchas obligaciones siempre habéis encontrado un momento para dedicarme.

Por supuesto, a continuación les toca el turno al resto de compañeros de aventuras patagónicas, Cris, Pablo, Helios y la larga lista de chilenos con los que he tenido el privilegio de compartir largas horas de camioneta, sándwiches y algún que otro mate: Mari, Nico, Dani, Benito, Sandra, Ilenia, Romi, Cristián y todos los demás. Muchas gracias por los buenos ratos que hemos pasado, guardo un recuerdo muy especial de todos vosotros. Pablico, gracias por tus consejos siempre racionales y tu forma de ver las cosas, he aprendido mucho de ti. También me gustaría dar las gracias a Giorgio Castellaro y Heiko Wittmer por permitirme realizar sendas estancias en sus grupos. De las dos experiencias he aprendido muchísimo tanto a nivel personal como científico.

A partir de aquí se complica seguir un orden claro con los agradecimientos y muchas personas van a aparecer repetidas en distintos momentos, pero lo voy a intentar. Como todo becario he pasado miles, por no decir infinitas, horas en el departamento. De todo este tiempo me voy con buen sabor de boca gracias a los excelentes compañeros que he tenido. Gracias a Carlos, Roci, Cris, Paco, Violeta, Mariola, y algún visitante ocasional por los indispensables desayunos, durante mucho tiempo han sido una pequeña motivación para ir

a la uni los días de más pereza. Las comidas en la biblioteca también han dado mucho de sí y me llevo muy buenos recuerdos. Por allí ha pasado mucha gente en estos 5 años, algunos siguen, otro ya no, pero por suerte hay nuevas incorporaciones. Me resulta imposible nombraros a todos y si lo intento sé que me dejaré a alguien, así que los que coméis o habéis comido allí os podéis dar por aludidos: gracias por los chistes, los chismes, los postres y, en general, por tantas comidas en buena compañía.

A los demás compañeros de departamento de Ecología también os debo un gracias muy grande por haberme acogido tan bien entre vosotros. Bichis, Fátima, Eduardo, Pablico, Salva, Cris Mata, Javi, Paloma, Ángel, Julia, Adri, Anabel, Carmen, Pedro, Begoña, Manolo, Emilio, Juanes... no podía escribir unos agradecimientos sin nombraros específicamente. He pasado ratos fantásticos con vosotros, y creo que hemos tenido casi tantas conversaciones absurdas como serias. Tampoco me puedo olvidar de mis compañeros del despacho C-105, Irene, Aimara, Isra, Bea, Pablo, Ana, Mariola, peces y bichos palo (sí, también ellos), gracias por todas las conversaciones y ratos de desconexión entre análisis y análisis. Aunque no hemos compartido nunca despacho, puede que por suerte para las dos, no puedo evitar mencionar especialmente a Cris Rota, desde que llegaste al departamento has sido una gran amiga y un gran apoyo, tengo muchas cosas por las que darte las gracias, pero si tengo que elegir una, me quedo con las innumerables tardes de viernes hasta las mil en la uni... ¿hay mejor plan que ese?

En el tiempo que he estado en el departamento de Ecología han pasado por allí personas a las que les tengo un cariño especial, con las que también he compartido muy buenos momentos: Paula, Desi, Bea, Carmen, Violeta, Montse, Cris Ajolota, Nacho, Berta, y por supuesto mi maestra en el arte de combinar la tesis con las bolitas, Irene. Aunque nos veamos menos, sigue siendo un gusto reencontrarme con vosotros fuera de la UAM.

Pero mi vida en la uni no se reduce al departamento de Ecología, y durante estos años también he compartido muy buenos ratos y conversaciones de lo más interesantes con otras personas: Bea, Miguel, Isidro, Pablo, Lys, Ana, Raúl, pasar tiempo con vosotros siempre es genial y no dejo de aprender cosas nuevas, ¡gracias!, y aquí llega el momento de dar *gracias a la vida que me ha dado tanto* como diría Violeta Parra (aunque los agradecimientos vayan a tener varias páginas, dicho queda). Gracias a Jesús, Chiqui, Juan y Paco por llevar la cafetería con tanto arte y salero. Y gracias a los compañeros de montícola, especialmente a Cristian, Seoane, Adri, Mar, Moni, Bea y Juancho por todas las excursiones pajareras y por permitirme aprender de vosotros.

En estos años en Madrid también he conocido mucha gente valiosa fuera del entorno universitario. En particular quiero dar las gracias a mis compañeros de piso, que a pesar de no saber lo que es un guanaco y en ocasiones no ser capaces ni de pronunciar su nombre, siempre han conseguido arrancarme una sonrisa al llegar a casa por muy negra que fuera la nube que había sobre mi cabeza: Garazi, Laia, Aser, Marta, Antonio, Alazne, Eddy y Marwane, sin vosotros estos años no habrían sido lo mismo. Y por supuesto no me puedo olvidar de todos mis amigos y compañeros de swing (Jesús, Yen, Carles, Susana, Jero, Carlos, etc), con los que he compartido tantos bailes, risas y cervezas. El baile y vosotros sois una de las razones de que esta tesis haya durado más de lo esperado, pero ni me arrepiento ni hubiera podido encontrar mejor excusa para no terminarla antes, así que ¡gracias!

También me gustaría dar las gracias a Juan Zanón por motivarme (y ayudarme) a pedir lo que ha sido el desencadenante para que terminase la tesis, porque sin esa motivación estos agradecimientos hubieran tardado unos cuantos meses más en llegar. En estos últimos (apresurados) momentos de la tesis, hay varias personas que me han echado una mano (o un salvavidas, si se quiere). Gracias especialmente a Carlos y Roci por su ayuda con la maquetación y resolver mis dudas a horas intempestivas; gracias a Pau por su ayuda con el diseño de la portada; y gracias a Guille por ayudarme a revisar el documento final y estar dispuesto a pasar un rato juntos a pesar de mi conversación monotemática.

Teniendo padres aficionados a la naturaleza es difícil saber si mi pasión por la biología es propia o heredada. En todo caso, ellos son los principales responsables de que haya llegado a este punto, y aunque no vayan los primeros en los agradecimientos son, sin duda, las personas a las que más agradezco. Gracias por vuestro apoyo, amor y dedicación y, en general, gracias por todo. Jaime, tú has sido mi maestro en muchos aspectos científicos y personales, muchas gracias por ello. Como hermana pequeña que soy he seguido tus pasos dos años por detrás: primero biología en Pamplona, luego máster y tesis en Madrid, y ahora toca saltar el charco. Aunque nuestros destinos son distintos, espero que volvamos a coincidir en el futuro en la misma ciudad y poder volver a compartir visitas a museos, exposiciones, conciertos, comidas caseras y muchas, muchas excursiones. Al resto de mi familia, muchas gracias también por haber estado siempre ahí.

Hay mucha gente que ha pasado por mi vida compartiendo distintos momentos, unos han permanecido más y otros menos, pero algunas de estas personas han sido especialmente importantes en mi camino hacia la biología y la investigación. Supongo que puedo empezar por mi profesora de pre-

escolar, Ángela, que nos llenó la cabeza (y la clase) de pájaros y otros animales, lo que derivó en que alguno de ellos terminase en mi casa. Ya en la ESO, tuve un profesor de biología que consiguió que me gustase más, si cabía, gracias Jorge. Durante la carrera he tenido muy buenos profesores, algunos de ellos me ayudaron a dar mis primeros pasos en la investigación, por lo que les estoy especialmente agradecida: Enrique Baquero, Rafa Miranda y Arturo Ariño, gracias. Con vosotros comencé mi modesta carrera en la investigación, primero con artrópodos y luego con peces. Estos primeros pasos fueron seguidos por otros que me llevaron a descubrir el mundo de los reptiles y lo maravilloso y a la vez durísimo que es trabajar con animales en el campo. Los meses que pasé en Jaca, primero en prácticas y luego por amor al arte me convencieron para querer dedicarme a la investigación y me llevaron a donde estoy hoy. En ese periodo hubo una persona muy importante que me acompañó en las primeras etapas de la tesis, cuando la simple palabra tesis es más grande que el mundo y por mucho que abras los brazos no hay por dónde agarrarla. Sin ese apoyo, no habría llegado hasta aquí.

Por supuesto, un papel fundamental para no desistir en el intento de "hacer la tesis" lo han tenido mis amigos de Zaragoza, Pamplona y Madrid. Gracias Raquel, Ángela, Mapi, Alba, Goyo, Mikel, Jaime, Marta, Laia, Payito, Beas, Cris, Carmen y un largo etc. Muchas gracias por todos los buenos ratos y conversaciones que hemos compartido. Y gracias a todas las personas que me siguen llamando amiga a pesar de mis repetidas negativas para quedar por estar liada con la tesis (esa tesis que nunca he sido capaz de explicarles muy bien sobre qué iba), gracias por vuestra paciencia y por no darme por perdida. Por suerte, la tan nombrada tesis es una vez en la vida, y espero poder retomar vuestra amistad con dedicación plena a partir de ahora.

Por último, y aunque suene un poco raro, gracias a los guanacos, porque sin ellos esta tesis no sería posible, y porque son unos bichos apasionantes.

Índice general

Índice general	xi
Índice de figuras	xiii
Índice de tablas	xv
1 Introducción general	1
1.1 Selección de hábitat	2
1.2 Factores que modifican la selección de hábitat de una especie .	3
1.3 Vida en grupo	7
1.4 Efectos antrópicos sobre la biodiversidad y la conservación de la naturaleza	8
1.5 El guanaco como modelo de estudio	10
1.6 Zona de estudio: Parque Nacional Torres del Paine y su entorno	12
1.7 Objetivos y estructura de la presente tesis doctoral	17
2 Diffusive dispersal in a guanaco growing population: an exam- ple of ungulate expansion beyond the limits of protected areas	21
2.1 Introduction	23
2.2 Materials and methods	26
2.3 Results	33
2.4 Discussion	36
2.5 Acknowledgements	41
3 Niche segregation between wild and domestic herbivores in Chilean Patagonia	43
3.1 Introduction	45
3.2 Materials and methods	47
3.3 Results	52
3.4 Discussion	57
3.5 Acknowledgements	62
4 Realised niche changes in a native herbivore assemblage asso- ciated to the presence of livestock	63

4.1	Introduction	65
4.2	Materials and Methods	68
4.3	Results	73
4.4	Discussion	78
4.5	Acknowledgements	82
4.6	Supplementary Material	84
5	Effect of predator abundance and perceived predation risk on guanaco antipredator behavior: vigilance, group size and cohe- sion	93
5.1	Introduction	95
5.2	Materials and methods	97
5.3	Results	101
5.4	Discussion	103
5.5	Acknowledgements	106
5.6	Supplementary Material	108
6	Discusión general	109
	Conclusiones	119
	Bibliografía	123

Índice de figuras

Figura 1.1 Zona de estudio.	13
Figura 1.2 Formaciones vegetales.	16
Figure 2.1. Guanaco population in TPNP between 1996 and 2010.	24
Figure 2.2. Study area.	27
Figure 2.3. Factors influencing guanaco abundance.	35
Figure 3.1. Study area.	48
Figure 3.2. Spatial pattern of aggregation between guanaco and sheep.	53
Figure 3.3. Habitat selection and habitat availability in winter.	56
Figure 3.4. Habitats used by guanaco and sheep in preferred and marginal areas in winter.	57
Figure 3.5. Habitat selection and habitat availability in summer.	59
Figure 3.6. Habitats used by guanaco and sheep in preferred and marginal areas in summer.	60
Figure 4.1. Study area.	69
Figure 4.2. Niche overlap among native species.	76
Figure 4.3. Effects of intespecific abundance in guanaco and sheep niche breadth.	78
Figure C.1. Summary of the analytical process.	88
Figure G.1. Niche overlap among domestic species.	92
Figure 5.1. Study area.	98
Figure 5.2. Interpretation of the intensity of group vigilance.	100

Índice de tablas

Table 2.1. Raw values for the response and environmental variables per sector.	31
Table 2.2. GLM results for guanaco abundance.	33
Table 2.3. Factors affecting proportion of social guanaco groups.	37
Table 2.4. Total number of guanacos (and groups) recorded during surveys.	38
Table 2.5. Guanaco density and abundance estimated in winter and summer.	39
Table 3.1. Description of habitat types.	49
Table 3.2. Results of general discriminant analysis (GDA) per season.	54
Table 3.3. Matrix of structure coefficients for discriminant axes in each season.	55
Table 3.4. Seasonal habitat availability.	58
Table 4.1. Seasonal mean overlap between species.	75
Table 4.2. Niche overlap between species pairs.	77
Table A.1. Variables recorded to estimate habitat availability.	84
Table B.1. Description of the 15 sectors.	85
Table B.2. Mean habitat availability in winter.	86
Table B.3. Mean habitat availability in summer.	87
Table D.1. Total animals and groups count.	89
Table E.1. Results of general discriminant analysis (GDA) per season.	90
Table F.1. Matrix of structure coefficients for discriminant axes of GDAs.	91
Table 5.1. Model averaged for guanaco family group size.	102
Table 5.2. Model averaged for guanaco family group cohesion.	102
Table 5.3. Model averaged for guanaco family group vigilance.	103
Table S.1. Variables used for MaxEnt models.	108



CAPÍTULO 1

Introducción general

La presencia, abundancia y distribución espacial de las especies es un proceso multiescalar que se puede afrontar a distintas escalas de estudio (Wiens 1989, Soberón 2007). Así, en función de la escala toman relevancia distintos factores para explicar la presencia y abundancia de los organismos (Chase y Leibold 2003, Soberón 2007). A gran escala, los factores que restringen la distribución global de una especie son de tipo geográfico, climático e histórico (Ricklefs y Schluter 1993). A escala local, la distribución y abundancia de una especie, además de la forma en que se estructuran las comunidades en que se insertan, dependen de sus preferencias y tolerancias a las condiciones bióticas y abióticas del entorno, y de las interacciones intra e interespecíficas en que se ven involucradas (Fretwell y Lucas 1970, Chase y Leibold 2003). Es a esta escala de estudio a la que tiene lugar la presente tesis doctoral, por lo que los siguientes apartados se han desarrollado teniendo en cuenta esta consideración aunque no se manifieste de forma explícita.

La teoría de nicho propone que las comunidades animales se estructuran mediante un proceso de partición de recursos que regula las relaciones entre especies y entre individuos de la misma o distinta especie (MacArthur and Wilson 1967). Así, dentro de una comunidad evolutivamente estructurada, cada especie y cada individuo explotan un conjunto de recursos determinado y distinto del de otras especies o individuos, si bien puede existir cierto grado de solapamiento (May and MacArthur 1972, Codron et al. 2011).

Hutchinson (1957) propuso la definición moderna de nicho ecológico como el espacio n-dimensional que reúne las condiciones necesarias para que una especie o individuo sobreviva y se reproduzca. Este espacio o hipervolumen está constituido por una serie de dimensiones de nicho, o ejes, con significado biológico que típicamente responden a variables ambientales del

medio físico y abiótico. Además, Hutchinson (1957) diferenció entre nicho fundamental (el rango absoluto de condiciones abióticas que permiten idealmente la supervivencia de una especie o individuo) y nicho realizado, que incorpora al nicho potencial las interacciones interespecíficas, y que por tanto constituye un subespacio del nicho fundamental.

Posteriormente esta teoría fue desarrollada por otros autores (ver, p.e. Soberón 2007), y se fueron incluyendo nuevos aspectos que influyen en la estructuración de las comunidades y el nicho de las especies, como son el efecto de la disponibilidad y distribución de los recursos tróficos y espaciales, la depredación y las interacciones interespecíficas (Chase y Leibold 2003, Soberón y Peterson 2005, Soberón 2007). Construyendo así, el concepto actual de nicho ecológico (Chase y Leibold 2003).

1.1 Selección de hábitat

El hábitat es un determinante básico de la distribución y abundancia de los organismos. Un hábitat puede definirse como el subconjunto de factores ambientales físicos y bióticos que una especie requiere para su supervivencia y reproducción (Hall et al. 1997). Como tal, el hábitat está incluido dentro del concepto de nicho hutchinsoniano. Los hábitats pueden presentar heterogeneidad temporal y espacial (May 1974), es decir, la capacidad de un hábitat para proporcionar los recursos necesarios para que un individuo pueda sobrevivir y reproducirse, son desiguales en el tiempo y el espacio.

La forma en que una especie o animal utiliza los recursos de un hábitat se entiende como uso del hábitat. Este uso del hábitat está influenciado por las adaptaciones morfológicas y fisiológicas de una especie y sus respuestas de comportamiento innatas y aprendidas a estímulos externos e internos (Rosenzweig 1981). El uso desproporcionado de un hábitat, por encima de su disponibilidad se considera selección de hábitat, este es un proceso activo y multiescalar por el cual una especie escoge entre distintos recursos disponibles (Johnson 1980). Tanto el uso como la selección de hábitat pueden ser considerados en un sentido general, o atendiendo a aspectos o necesidades específicas como forrajeo, reproducción o refugio.

La selección de hábitat depende, además de la abundancia y distribución de recursos, de la densidad de la especie y de las densidades e interacciones con otras especies (competencia, facilitación y depredación). Siendo la selección diferencial de hábitat uno de los principales mecanismos que permiten la coexistencia de especies.

El estudio de la selección de hábitat comenzó considerando exclusivamente la elección óptima que debería ser hecha por un individuo (por ejemplo, MacArthur y Pianka 1966, Rosenzweig 1974), o permitió que esa elección fuera influida por la competencia intraespecífica (Fretwell y Lucas 1970). Posteriormente, Lawlor y Maynard Smith (1976) introdujeron la densidad poblacional en la selección óptima del hábitat. Hasta llegar a la actualidad en que los estudios de selección de hábitat incorporan otras variables bióticas como la competencia interespecífica o la depredación (Morris 2009, Delgado et al. 2013, Tarjuelo et al. 2016).

En teoría, un individuo siempre debería seleccionar aquellos hábitats que maximizan su fitness (Abramsky et al. 2002). Esta asunción se cumple bajo circunstancias concretas que permiten una selección de hábitat idealizada libre ("ideal-free distribution", sensu Fretwell y Lucas 1970), es decir, cuando los hábitats disponibles dentro del rango geográfico de una especie son de calidad similar, son igualmente susceptibles de ser seleccionados (Fretwell y Lucas 1970). En este escenario, al aumentar la densidad poblacional, la especie se expandirá hacia el uso de hábitats secundarios. Sin embargo, no es el único escenario posible. Así, el comportamiento territorial también influye en la idoneidad del hábitat al reducir la cantidad de hábitat adecuado disponible ("ideal-despotic distribution", sensu Fretwell 1972). La consecuencia última de la territorialidad es similar al aumento poblacional en el escenario anterior, acelerando la disminución del hábitat adecuado, y favoreciendo la selección de hábitats alternativos.

1.2 Factores que modifican la selección de hábitat de una especie

Distribución espacial y temporal de recursos

La distribución espacial y temporal de los recursos es uno de los principales determinantes del uso del hábitat de una especie (Wiens 1986). La abundancia y disponibilidad de estos recursos no es estable en el tiempo ni en el espacio, y esta variabilidad afecta al uso del hábitat de las especies e individuos (Southwood 1977) que adaptan y modifican sus patrones de uso de los recursos para lidiar con estos cambios.

Los cambios temporales (por ejemplo entre estaciones o entre años) están influidos en gran medida por la historia de vida y la disposición espacial de los recursos disponibles. Una misma especie frecuentemente requiere recursos específicos para diferentes momentos de su vida. Así, la distribución de los

1. INTRODUCCIÓN

recursos que necesita para cubrir sus necesidades energéticas, pueden diferir de la distribución de los recursos necesarios para reproducirse o protegerse. Por tanto, los individuos deben adaptar su uso y selección del hábitat de manera que les permita utilizar los recursos de manera efectiva.

La variabilidad espacial en la disponibilidad de recursos, especialmente los tróficos, tiene un claro reflejo en la distribución y comportamiento de las especies. Por ejemplo, en el caso de los ungulados, la distribución espacial del alimento establece el tamaño máximo de grupo (Jarman 1974). Si a dicha variabilidad se le añade la escala temporal, el resultado son movimientos de corta distancia o movimientos migratorios en busca de hábitats que ofrezcan mayor cantidad y/o calidad de recursos (Owen-Smith 2002). Cuando la variabilidad no implica ausencia total de recursos, las especies pueden adaptar su uso de estos de forma que presenten un comportamiento sedentario pero con diferente uso y/o preferencias en distintos momentos.

Por último, hay que tener en cuenta que la disponibilidad y abundancia de recursos no depende sólo de factores abióticos como el clima, sino que se puede ver afectada por factores bióticos como la densidad de coespecíficos, o la presencia de competidores o depredadores que reducen o limitan la disponibilidad y el uso de los recursos.

Competencia interespecífica

La competencia es un proceso de interacción intra o interespecífica por el cual los organismos involucrados comparten requerimientos (tróficos, espaciales, reproductivos), y estos son limitantes (Begon 1999). Además, los organismos involucrados ven disminuido su fitness como consecuencia de dicha interacción. Según la visión clásica del principio de exclusión competitiva (Gause 1934), dos especies con idénticos requerimientos (igual nicho) no pueden coexistir en un mismo momento y lugar, siendo la especie dominante en términos competitivos la que persistirá y desplazará a la especie subordinada hacia hábitats subóptimos (Codron et al. 2011, Zhang et al. 2015), pudiendo llegar a producir incluso su extinción local (Mishra et al. 2002).

No obstante, las especies coexistentes en tiempo evolutivo pueden experimentar procesos de compactación y segregación de nicho que facilita su coexistencia. Efectivamente, bajo la presión selectiva impuesta por la competencia, especies que coexisten pueden particionar los recursos espaciales, tróficos y/o temporales que comparten (Chase y Leibold 2003, Bolnick et al. 2010). Este reparto de recursos, que debe reflejarse en una contracción de los nichos realizados (sensu Soberón 2007), tiene como consecuencia una reducción del solapamiento y, por tanto, de la competencia entre las especies,

1.2. Factores que modifican la selección de hábitat de una especie

permitiendo una coexistencia estable a través de la segregación de sus nichos (Chesson 2000, Di Bitetti et al. 2009). En cualquier caso, es esperable que las especies puedan coexistir a pesar de mostrar cierto grado de solapamiento o similitud entre sus nichos (May y MacArthur 1972, Pianka 1974, Prins et al. 2006).

El proceso competitivo puede producirse mediante dos mecanismos distintos: competencia por interferencia o por explotación (Begon et al. 1999). En el primero de los casos, la competencia implica una privación directa del acceso a los recursos (p.e. tróficos o espaciales) por medio de actos de agresión o de otro tipo. Por su parte, la competencia por explotación ocurre de forma indirecta y resulta en la disminución o limitación de la disponibilidad o abundancia de un recurso debido a la explotación (consumo) común del mismo. Así, el uso de un recurso por un individuo u especie, reduce la disponibilidad del recurso para otro/a. Estas formas de competencia pueden ocurrir tanto a nivel intra- como inter-específico. En el caso de los grandes herbívoros, la competencia suele darse de forma indirecta por explotación de los mismos recursos (Owen-Smith 2002) sin que se produzcan agresiones directas entre individuos, por lo que estas interacciones no siempre son claras ni fáciles de medir, detectar e interpretar (Homewood y Rodgers 1991, Marshal et al. 2008). A esto se le añade la dificultad de realizar experimentos con especies salvajes (Kie et al. 1991, Hobbs et al. 1996a, b, Stewart et al. 2002), lo que explica la dificultad para extraer conclusiones sólidas cuando se estudian estas comunidades.

El papel determinante de la competencia interespecífica en la partición de nichos ha sido un tema tradicionalmente estudiado por la ecología de comunidades (p.e. Rosenzweig 1981, Prins y Olff 1998, Morris 2009, Tarjuelo et al. 2016). Sin embargo, determinar si la segregación de hábitat y recursos tróficos que se observa actualmente en comunidades estructuradas evolutivamente se debe realmente a diferencias en sus preferencias o a un proceso de competencia en el pasado (el fantasma de la competencia pasada, sensu Connell 1980) continúa siendo una cuestión difícil de desentrañar.

El proceso de segregación de nicho ocurre en tiempo evolutivo, por lo que la introducción de una nueva especie en un ecosistema estructurado puede provocar el desequilibrio del mismo y desencadenar procesos de competencia interespecífica, sobre todo cuando la especie introducida es similar en tamaño, selección de hábitat y estrategia de alimentación a las especies nativas (Schoener 1974, Belovsky 1986). Este es uno de los principales problemas que ocurre tras la introducción de la ganadería en zonas donde existen todavía poblaciones de ungulados silvestres, como se expone más adelante.

Depredación

La depredación es otro de los factores que influye en la estructura y funcionamiento de las comunidades animales. En concreto, el riesgo de depredación afecta al comportamiento, la selección de hábitat y el uso del espacio de las presas (p.e. Brown 1999, Thaker et al. 2011, Laundré et al. 2014).

La relación en tiempo evolutivo entre depredadores y presas ha generado una serie de respuestas comportamentales en estas que se pueden manifestar intensamente incluso en ausencia de depredadores (Byers 1997). Entre las respuestas antidepredatorias más importantes se pueden citar el aumento del tiempo dedicado a la vigilancia (Childress y Lung 2003), la reducción en el tiempo de forrajeo (Lima y Dill 1990, Childress y Lung 2003), incrementos del tamaño de grupo (Creel y Winnie 2005) o cambios en el uso del hábitat (Creel et al. 2005).

En el caso concreto de los ungulados, el hecho de que modifiquen su uso del hábitat y comportamiento como respuesta al riesgo de depredación ha sido ampliamente estudiado (p.e. Brown 1999, Creel et al. 2005, Laundré et al. 2014). Sin embargo, los mecanismos subyacentes todavía no se conocen bien. Laundré et al. (2001) propusieron el concepto de "paisaje del miedo" para referirse al proceso por el cual las presas ajustan constantemente su comportamiento en respuesta al riesgo de depredación. Según estos autores, tanto la presencia de depredadores (riesgo real), como otros elementos relacionados con la estructura del hábitat (riesgo percibido) generan un paisaje del miedo en las presas, característico de cada lugar y momento. El paisaje del miedo, por tanto, es específico para cada especie y depende de factores como la estrategia de caza de sus depredadores, la estructura del hábitat o la densidad de conspecificos (Laundré et al. 2001, Thaker 2010).

En este paisaje, los animales responden al nivel de miedo pudiendo reducir el tiempo dedicado a alimentarse, moviéndose a zonas con menor disponibilidad o calidad de alimento para reducir el riesgo de ser depredados (Lima y Dill 1990, Acebes et al. 2013) o aumentando la vigilancia en zonas de mayor riesgo (Brown 1999). La estructura del hábitat juega un papel importante en las interacciones depredador-presa, afectando tanto a la probabilidad de supervivencia de la presa como al éxito de captura del depredador (Lima y Dill 1990, Kauffman et al. 2007). Por tanto, cómo se comporta cada presa frente a determinadas características del hábitat es una respuesta específica de la especie, modulada por el tipo de depredación al que está expuesta (Thaker 2010). Así, en el caso de depredadores que cazan al acecho y no persiguen durante largas distancias a su presa, una rápida detección es crucial para aumentar la probabilidad de supervivencia (Lima 1995, Childress y

Lung 2003). Por otra parte, en el caso de depredadores que cazan en manada persiguiendo a su presa, estas se benefician de los efectos de confusión y dilución que les proporcionan vivir en grandes rebaños (Pulliam y Caraco 1984, Roberts 1996). Es decir, las presas ajustan su comportamiento a las condiciones ambientales y estructura del hábitat en cada momento (Brown et al. 1999, Laundré et al. 2001, Laundré 2010) y experimentan un compromiso entre la necesidad de alimentarse y la de reducir el riesgo de ser cazadas.

1.3 Vida en grupo

Los organismos se agregan formando grupos como respuesta ante factores evolutivos y ecológicos. Entre los factores evolutivos a los que responde la formación de grupos se encuentran, por ejemplo, la estrategia vital o la historia de vida. Estos aspectos, sin duda muy interesantes en la formación y evolución de la sociabilidad animal, se hayan más allá de los objetivos de la presente tesis doctoral, por lo que son los aspectos ecológicos los que se van a desarrollar sucintamente a continuación.

Muchas especies presentan un comportamiento social y viven en grupos de tamaños muy diversos, desde pequeños grupos familiares hasta grandes rebaños mixtos como en el caso de los grandes ungulados africanos (Voeten y Prins 1999). En todo el gradiente entre estas situaciones, los individuos experimentan un compromiso entre los beneficios y los costes de vivir en grupo.

Desde el punto de vista ecológico, el riesgo de depredación, la estructura del hábitat y la densidad de las poblaciones se consideran los factores principales que determinan el tamaño y formación de grupos y son a los que más atención se les ha prestado en la literatura (Hamilton 1971, Jarman 1974, Lima 1995, Childress y Lung 2003). De acuerdo con Jarman (1974), la formación de grupos sociales es una adaptación biológica innata en los individuos que responde a los factores citados anteriormente. Así, en hábitats cerrados, un herbívoro reduce la probabilidad de ser detectado por un depredador siendo discreto y viviendo en pequeños grupos. Por el contrario, en hábitats abiertos, donde las presas son más fácilmente detectables por los depredadores, la formación de grandes grupos proporciona mayor protección contra los depredadores ya que, en el caso de ataque, la probabilidad de ser la presa focal disminuye al aumentar el tamaño de grupo (Hamilton 1971). Además, los animales que viven en grupos grandes se benefician de la vigilancia cooperativa (Pulliam 1973, Lima 1995) y reducen el riesgo de depredación mediante los procesos de dilución y confusión (Pulliam y Caraco

1984, Roberts 1996). Es decir, los animales se benefician al vivir en grupos de un menor riesgo de depredación. Sin embargo, la vida en grupos también tiene unos costes asociados relacionados con la competencia por los recursos tróficos y las interacciones agresivas derivadas de esta competencia entre los miembros del grupo. En este sentido, Jarman (1974) propuso que la distribución espacial de los recursos establece el tamaño máximo de grupo. Así, los herbívoros ramoneadores agotan los recursos al alimentarse (partes concretas de una planta), por lo que según se alimentan aumentan la distancia entre individuos y se favorece la formación de grupos pequeños. Por el contrario, las especies de estrategia pastadora al alimentarse reducen la disponibilidad de alimento, pero no lo agotan, por lo que la distribución espacial de los recursos se mantiene constante y del mismo modo la de los herbívoros. Es, por tanto, este compromiso entre costes y beneficios el que determina que un individuo permanezca o no en un grupo.

Frente a esta visión de la formación de grupos como respuesta a factores ecológicos, algunos autores consideran que es un proceso puramente mecánico que ocurre por fusión y fisión de grupos y que depende de la visibilidad del hábitat y la densidad de animales (Gerard 2002). Bajo esta perspectiva, los grupos son unidades temporales no permanentes. En este caso no se esperan interacciones sociales más allá de las ocurridas en los momentos de co-ocurrencia, ni la aparición de comportamientos de grupo. Además, este autor sugiere que a nivel de individuo los costes de pertenecer a un grupo pueden ser superiores a sus beneficios.

Probablemente, no existe una explicación única para la formación de grupos y así, tanto la visión adaptativa como la mecánica pueden explicar los patrones que se encuentran en la naturaleza. Además, entre especies y en una misma especie puede explicarse la formación de grupos por uno, otro o una combinación de ambos procesos (Gerard 2002, Marino y Baldi 2014).

1.4 Efectos antrópicos sobre la biodiversidad y la conservación de la naturaleza

El hombre ha desempeñado un papel fundamental en la pérdida de biodiversidad que estamos viviendo hoy en día. La actividad humana tiene un gran impacto en la naturaleza, provocando numerosas extinciones y amenazando la supervivencia de muchas especies y ecosistemas (Evaluación de los Ecosistemas de Milenio 2005, Gordon 2009). Los efectos negativos del hombre son múltiples: pérdida y modificación del hábitat, fragmentación, introducción

1.4. Efectos antrópicos sobre la biodiversidad y la conservación de la naturaleza

de especies invasoras, sobreexplotación, contaminación y cambio climático; y se manifiestan a todas las escalas, desde la global hasta la local.

Los grandes herbívoros no están exentos de esta amenaza. Su distribución se ha reducido notablemente en las últimas décadas y muchas poblaciones se encuentran al borde de la extinción (Prins 1992). Entre los factores que amenazan a estas especies se encuentran la caza furtiva, la destrucción y fragmentación de hábitat o la introducción de ganado que compite con los herbívoros silvestres, desplazándolos por lo general hacia hábitats subóptimos o inadecuados (Voeten y Prins 1999, Mishra et al 2004, Borgnia et al. 2008, Kutt y Gordon 2012).

Frente a esta situación de pérdida de biodiversidad general, se han llevado a cabo diversas medidas de conservación encaminadas a reducir y mitigar los efectos antrópicos sobre los ecosistemas y poblaciones naturales. Entre estas acciones destaca la creación de espacios protegidos, cuyo objetivo fundamental a medio y largo plazo es la protección de la naturaleza, y en los que se regulan, en distinta medida, las actividades antrópicas (Fall y Jackson 2002, Hansen y DeFries 2007). No obstante, para que la conservación sea efectiva se requiere de un correcto conocimiento de los mecanismos y procesos ecológicos subyacentes en la naturaleza, siendo fundamental una investigación básica que aporte este tipo de información. Además, en muchas ocasiones es necesario extender los objetivos de conservación más allá de los límites de las áreas protegidas para asegurar el mantenimiento de poblaciones viables a largo plazo (Meffe y Carroll 1994, Hutton et al. 2005).

Un aspecto al que sólo recientemente se está prestando atención, es que las medidas de conservación pueden ser exitosas y provocar el crecimiento y expansión de las poblaciones silvestres más allá de los límites administrativos de los espacios protegidos, resultando en causa potencial de conflictos con los ejes de desarrollo socioeconómico de las áreas limítrofes (Simonetti 1995, Distefano 2005, du Toit 2010). Esta situación se da con demasiada frecuencia en aquellas zonas donde las poblaciones de ungulados silvestres co-ocurren con prácticas ganaderas (Dawson y Ellis 1994, Voeten y Prins 1999, Bagchi et al. 2004, Sitters et al. 2009, Suryawanshi et al. 2010), y llega a ser especialmente problemática en el entorno de las áreas protegidas en las se protegen ungulados nativos. Estos, al salir fuera de las reservas generan conflictos por competencia interespecífica por los recursos tróficos o espaciales con el ganado. Por tanto, es necesario extender los objetivos de conservación fuera de los espacios protegidos a la vez que conocer y monitorizar el estado de las poblaciones silvestres de cara a poder establecer políticas de conservación

y/o gestión de estas especies que disminuyan el conflicto con las prácticas ganaderas (Gordon 2009).

En una situación como la que se describe se ha construido esta tesis doctoral, apoyada en el hecho de disponer de un “experimento natural” con una zona protegida y su entorno que difieren básicamente en la presencia de ganado junto con especies silvestres, lo que permite testar diversas hipótesis ecológicas relacionadas con la teoría de nicho.

1.5 El guanaco como modelo de estudio

Biología del guanaco

El guanaco (*Lama guanicoe* Müller 1776) es el mayor de las cuatro especies de camélidos sudamericanos que existen. Junto con la vicuña (*Vicugna vicugna* Molina 1782) son las dos especies silvestres, de las que proceden las dos especies domésticas: la llama (*Lama glama*), y la alpaca (*Vicugna pacos*). Es una especie característica de zonas áridas o semiáridas con vegetación baja y abierta (Puig et al. 2008, Acebes 2010), aunque en Tierra del Fuego también aparece en hábitats cerrados y bosques templados de *Nothofagus* (Puig 1995, Montes et al. 2000, González et al. 2006a).

Desde el punto de vista de su dieta, se considera un herbívoro rumiante generalista de carácter mixto, es decir, que se puede comportar como pastador o ramoneador según la disponibilidad de recursos tróficos (Hofmann 1989, Puig et al. 2001, Baldi et al. 2004), presentando su dieta una amplia variedad de especies vegetales. Se alimenta fundamentalmente de gramíneas, herbáceas o arbustos en función de la disponibilidad (Puig et al. 1997, Puig et al. 2001, Baldi et al. 2004) pero puede llegar a alimentarse incluso de líquenes y cactáceas en lugares con gran escasez de alimento (Raedeke y Simonetti 1988, Reus et al. 2014). El guanaco presenta un alto solapamiento trófico con las especies domésticas introducidas en su rango de distribución, fundamentalmente la oveja, pero también con otras especies de ganado como vacas, cabras, caballos o burros (Bonino y Pelliza-Sbriller 1991, Puig et al. 2001, Baldi et al. 2004, Reus et al. 2014), lo que incrementa el potencial para la competencia entre estas especies.

El guanaco es un ungulado sexualmente monomórfico (Franklin 1983, Sarno y Franklin 1999) cuya altura varía entre 1,6 y 1,8m y peso entre 80 y 120 kg (González et al. 2006a). El guanaco presenta una estructura social flexible (Franklin 1983, González et al. 2006a). Durante el periodo reproductivo se pueden distinguir cuatro tipos de grupos sociales: (i) grupos familiares, formados por un macho territorial (relincho) y un número variable de

hembras con sus crías del año (chulengos) o del año anterior (juveniles); (ii) grupos de machos inmaduros y machos maduros no territoriales; (iii) machos solitarios territoriales que defienden un territorio sin hembras y; (iv) grupos de hembras con o sin crías que no se encuentran asociadas a ningún macho territorial (Franklin 1982).

Fuera del periodo reproductivo se han descrito distintos comportamientos para poblaciones localizadas en zonas con diferencias marcadas en las condiciones climáticas en invierno. Así, las poblaciones de lugares con inviernos suaves tienden a ser sedentarias y la estructura social se mantiene estable a lo largo de todo el año (Franklin 1983, Acebes 2010). En zonas con inviernos fríos, donde se puede producir una reducción importante en la disponibilidad de alimento, los guanacos realizan movimientos estacionales pseudo-migratorios (Ortega y Franklin 1995); en estas condiciones los guanacos tienden a formar grupos mixtos constituidos por individuos de los dos sexos y todas las edades, si bien, el resto de unidades sociales también pueden mantenerse (Franklin 1983, Ortega y Franklin 1995).

El sistema reproductor es de tipo poligínico con defensa de recursos (Franklin 1982), aunque se ha descrito poliginia con defensa de hembras en poblaciones de lugares extremadamente áridos y con recursos escasos y no agregados (Acebes et al. 2013). Tras 11,5 meses de gestación las hembras dan a luz una sola cría que permanecerá con la madre hasta el año o año y medio de edad, momento en que son expulsadas por la madre o el relincho del grupo familiar (Sarno y Franklin 1999). El macho presenta un carácter filopátrico marcado volviendo año tras año al mismo lugar para establecer su territorio (Young y Franklin 2004a). Tanto machos como hembras suelen volver en años consecutivos a los mismos lugares de cría (Bank et al. 2003).

El puma (*Puma concolor*) es el principal depredador del guanaco (Franklin et al. 1999, Bank et al. 2003), si bien, los chulengos también pueden ser atacados por zorros culpeos (*Lycalopex culpaeus*; Novaro et al. 2009) y jaurías de perros asilvestrados.

Distribución y estado de conservación

El guanaco es, de los camélidos sudamericanos, el de más amplia distribución, pues se puede encontrar en un amplio rango altitudinal (0-4600 m) y latitudinal. Su distribución actual abarca desde el norte de Perú hasta el sur de Chile y Argentina, a ambos lados de la cordillera de los Andes y en la Patagonia, aunque esta distribución es discontinua (Baldi et al. 2016). Actualmente se reconoce la existencia de dos subespecies (*L. g. cacsilensis* y *L.*

g. guanicoe) distribuidas geográficamente y la presencia de una zona donde ambas subespecies solapan y pueden hibridar (Marín et al. 2013). La subespecie *cacsilensis* se localiza en la vertiente oeste de los Andes desde Perú hasta el norte de Chile. Por su parte, la subespecie *guanicoe* es la de más amplia distribución, encontrándose por toda la Patagonia y hasta el extremo austral del continente. La zona de contacto geográfico de ambas subespecies se extiende por el centro de Chile, noroeste de Argentina y sur de Bolivia (Marín et al. 2013).

Antes de la conquista española se estima que existían entre 30 y 50 millones de individuos ocupando gran parte de Perú, Bolivia y Paraguay, y casi la totalidad de Chile y Argentina (Raedeke 1979). Desde entonces, la especie ha sufrido un importante declive poblacional atribuido a la competencia con el ganado, la caza furtiva, el deterioro y fragmentación del hábitat y el comercio ilegal (Puig 1995, Baldi et al. 2016). Actualmente, la UICN (Baldi et al. 2016) estima la población total en unos 1.500.000-2.200.000 individuos (cálculo basado en tablas de vida de Raedeke 1979, Fritz y Franklin 1994) que se encuentran ocupando sólo el 26% de su distribución original (Baldi et al. 2016).

Debido a su amplio rango de distribución, su aún relativamente abundante población y su presencia en numerosas áreas protegidas, la especie está catalogada a nivel continental como de "preocupación menor" de acuerdo a las categorías de protección de la UICN. En Chile, donde se encuentra entre el 14% y el 18% de la población total de guanacos (Baldi et al. 2016), la especie está catalogada como vulnerable en el norte y centro, y de preocupación menor en el sur del país (Baldi et al. 2016).

1.6 Zona de estudio: Parque Nacional Torres del Paine y su entorno

La Patagonia Sur Chilena y en concreto el área que comprende el Parque Nacional de Torres del Paine y su entorno (Fig 1.1; Región de Magallanes y Antártica Chilena) constituye un espacio natural en el que confluyen los intereses socioeconómicos y la conservación de la fauna silvestre. La principal fuente de ingresos de la zona es la ganadería; muestra de ello es que en apenas 250.000 ha existen más de 130.000 cabezas de ganado ovino y varios miles de bovino y caballo (Soto 2001). En los últimos años el turismo generado por y alrededor del Parque Nacional se ha constituido en una fuente complementaria de ingresos.

1.6. El Parque Nacional Torres del Paine y su entorno

La oveja (*Ovis aries*) fue introducida en la Patagonia chilena a finales del siglo XIX con la llegada de los primeros colonos europeos. Su número se incrementó rápidamente hasta alcanzar los 22 millones de ejemplares en 1950 (Soriano y Movia 1986). De forma paralela se produjo un descenso importante en las poblaciones de herbívoros nativos, especialmente el guanaco, debido a la competencia con el ganado, la caza furtiva y la degradación del hábitat (Raedeke 1982). En la actualidad existen unos 2,2 millones de ovejas en la Patagonia Chilena en un sistema de pastoreo extensivo en semilibertad. La raza más abundante de ovino es la raza corridale cuyo aprovechamiento es la obtención de lana y carne. La ganadería de ovino se combina en la Patagonia con ganado vacuno (*Bos taurus*; fundamentalmente raza Angus) y caballo (*Equus caballus*), aunque las densidades de estas especies son mucho menores.



Figura 1.1. Localización de la zona de estudio. El área sombreada corresponde a la superficie muestreada.

El Parque Nacional Torres del Paine fue creado en 1959. En 1975, gracias a una donación particular, se amplió su superficie hasta las casi 280.000 ha actuales y fue en este momento en que recibió el nombre por el que se lo

1. INTRODUCCIÓN

conoce hoy en día. Posteriormente, la Unesco lo declaró Reserva de la Biosfera en 1978. A lo largo de su historia, entre sus objetivos se ha contado la conservación de fauna nativa silvestre como el guanaco, el huemul (*Hippocamelus bisulcus*) o el ñandú (*Pterocnemia pennata*). En los últimos veinte años, como resultado de la gestión dedicada a la potenciación de las poblaciones de fauna silvestre, se ha producido un importante crecimiento demográfico del guanaco en el interior del espacio protegido. Así, a principios de los años 80 apenas había unos centenares (Franklin 1982), en los años 90 se censaron cerca de 2.700 ejemplares (CONAF 1992) y en 2006 se estimaron en torno a 4.000 animales en un área limitada del Parque (González 2006b). Este crecimiento demográfico ha provocado su expansión hacia las fincas ganaderas limítrofes (Sarno y Franklin 1999) originando el conflicto entre conservación y actividad económica. En los últimos años, los propietarios de estos terrenos han mostrado su preocupación ante este fenómeno de expansión de los guanacos ya que consideran que pueden reducir la oferta trófica para su ganado (i.e. proceso competitivo) al alimentarse en sus campos, disminuyendo la producción ganadera (Soto 2001).

El área de estudio corresponde a la zona de transición bosque-estepa con clima templado-frío y lluvioso, sin temporada seca según la clasificación de Köppen, con una precipitación anual que varía entre 250 y 800 mm y temperatura media anual entre 4,9 y 5,7°C (González et al., en preparación). Los veranos son frescos y muy ventosos con temperaturas máximas de 15°C y los inviernos fríos, generalmente sin viento y con mínimas de -6°C, siendo frecuente que las precipitaciones sucedan en esta época en forma de nieve (CONAF 2011).

El interior del Parque Nacional Torres del Paine presenta gran heterogeneidad orográfica que hace que las condiciones climáticas en su interior sean muy variables, aunque los guanacos evitan las zonas montañosas y prefieren ocupar las áreas de transición hacia la típica estepa patagónica. El entorno del Parque Nacional está formado por grandes llanuras y amplios valles y es menos montañoso que el interior, lo que contribuye a que el clima sea más estable. Los asentamientos humanos son escasos y distantes, correspondiendo fundamentalmente a pequeñas estancias en las que viven una o varias familias. La actividad humana ha transformado el entorno del Parque Nacional para crear pastos para el ganado (Heusser 1994, Huber y Markraft 2003), y en la actualidad se están sembrando campos de especies forrajeras para alimentar al ganado en los periodos de escasez durante el invierno.

En su conjunto, el área de estudio se caracteriza por su alta diversidad paisajística influida por las condiciones topográficas y climáticas. La presen-

cia casi continua de fuertes vientos durante el verano da lugar a comunidades vegetales muy adaptadas a estas condiciones y al estrés hídrico. En concreto, se pueden diferenciar cuatro zonas ecológicas bien definidas (Pisano 1974):

- Estepa Patagónica: se encuentra en llanuras y mesetas sometidas a un clima semiárido y frío, con escasas precipitaciones. Corresponde a comunidades de gramíneas perennes, de altura baja a media, conocidas muchas de ellas como coirón (géneros *Stipa* y *Festuca*).
- Formaciones arbustivas y de matorrales en mesetas y llanuras. Las especies predominantes son mata negra (*Junellia tridens*), mata barrosa (*Mulinum spinosum*) y calafate (*Berberis microphylla*).
- Bosque Magallánico Deciduo: Pertenecen a este ecosistema todas las comunidades arbóreas y arborescentes del género *Nothofagus* entre las que se cuentan el ñirre (*N. antarcticus*), la lenga (*N. pumilio*) y el coigue (*N. betuloides*). Estas formaciones se encuentran fundamentalmente limitadas al interior del Parque Nacional.
- Desierto andino: zonas de gran aridez con muy baja cobertura vegetal (entre el 30 y el 0%).

Además de estas formaciones características, existen otras comunidades vegetales de relevancia por ser fuente de alimento para las especies en la zona de estudio, como las *vegas* (prados temporalmente encharcados con predominio de los géneros *Carex* y *Juncus* que suelen aparecer en fondos de valle y valles colgados) y los prados de herbáceas y gramíneas. Fuera del Parque Nacional, como se ha indicado anteriormente, está aumentando la presencia de cultivos forrajeros para alimentación del ganado.

La comunidad de especies nativas en la zona de estudio (tanto dentro como fuera del Parque Nacional) está constituida por el guanaco, el ñandú y el caiquén (*Chloephaga picta*) entre las especies de herbívoros de medio-gran tamaño; de ellas, el guanaco es con diferencia la especie más abundante. Dentro del Parque Nacional destaca la población de huemul, pero su presencia está restringida a las zonas boscosas, por lo que su distribución no solapa con la del resto de herbívoros nativos. Por su parte, la comunidad de carnívoros está formada por el puma, el zorro culpeo y el zorro gris o zorro chilla (*Lycalopex griseus*). Por último, hay que destacar la presencia generalizada de la liebre europea (*Lepus europaeus*) que se ha naturalizado en la zona.

La presencia de ganado se restringe al exterior del Parque Nacional, donde se encuentra en un sistema de pastoreo extensivo en semilibertad dentro

1. INTRODUCCIÓN

de potreros (fincas) cuya superficie alcanza varios cientos e incluso un par de miles de hectáreas. Normalmente se produce una rotación entre potreros dos veces al año, trasladando los animales de los pastos de invierno a los de verano, momento que se aprovecha para esquila a las ovejas y marcar los corderos nacidos durante la primavera. A parte de en estos momentos, el ganado es visitado episódicamente por los pastores.



Figura 1.2. Formaciones vegetales características de la zona de estudio. De izquierda a derecha y de arriba a abajo: estepa patagónica; guanacos en matorrales de *Mulinum spinosum*; formación de mata negra (*Junellia tridens*); bosque de lengas (*Nothofagus pumilio*); zona sin vegetación; vega en fondo de valle.

1.7 Objetivos y estructura de la presente tesis doctoral

De acuerdo con el marco teórico expuesto, en una comunidad de especies nativas, los procesos de disponibilidad y distribución de los recursos tróficos y el riesgo de depredación son los factores fundamentales que dirigen la selección de hábitat y el nicho de las especies ya que, al coexistir en tiempo evolutivo, se espera que entre ellas se haya producido un proceso de partición de recursos (segregación de sus nichos), de forma que, salvo en periodos de escasez de recursos o grandes incrementos en las densidades poblacionales, las especies puedan coexistir con una mínima intensidad de competencia interespecífica (Putman 1996). La introducción reciente de especies exóticas en este ensamblaje original podría dar lugar a una intensificación de los procesos de competencia interespecífica, ya que los mecanismos evolutivos de partición de recursos no han tenido tiempo para desarrollarse (Voeten y Prins 1999, Owen-Smith 2002). Este potencial para la competencia es mayor cuando las especies introducidas comparten estrategia de forrajeo y poseen un tamaño corporal similar al de las especies silvestres, como ocurre en el caso del ganado. Además, si la densidad de los nuevos competidores es elevada y estos se ven favorecidos por el hombre, el desenlace puede ser el desplazamiento competitivo de las especies silvestres (Prins y Olff 1998, Stewart et al. 2002, Borgnia et al. 2008).

En este contexto se plantea la presente tesis doctoral, englobada dentro de un programa de investigación comenzado en 2008 por el equipo investigador Universidad Autónoma de Madrid-Universidad de Chile. El objetivo del programa se dirige a conocer diversos aspectos de la ecología del guanaco y profundizar en el conocimiento de la red de interacciones ecológicas y sociales en la zona de Torres del Paine y su entorno. Esta red incluye especies de herbívoros autóctonos y exóticos, sus depredadores, y también los actores sociales implicados, vinculados todos ellos por mecanismos de competencia/coexistencia, depredación, caza furtiva e interés para la conservación en el Parque Nacional Torres del Paine y su entorno. En concreto, la presente tesis doctoral se centra en profundizar en aspectos concretos de la ecología del guanaco, determinar el estado de su población y examinar las interacciones interespecíficas de la comunidad de especies nativas y exóticas de la que el guanaco forma parte.

En definitiva, el incremento en la abundancia y área de ocupación del guanaco, a consecuencia de la expansión demográfica experimentada en el interior del Parque Nacional durante los últimos años, podría dar lugar a un

1. INTRODUCCIÓN

proceso de competencia por los recursos con el ganado en el exterior del Parque Nacional. Para determinar la existencia de estos procesos de competencia es necesario conocer el tamaño y la densidad de la población de guanacos, así como los factores que contribuyen a explicar la distribución de los animales, aspectos que se afrontarán en el CAPITULO 2. Desde el punto de vista aplicado, esta información podrá ser utilizada por los organismos responsables de Conservación de cara a adaptar las políticas de gestión del guanaco a la situación actual de la población. Además, para determinar si existe potencial para la competencia es necesario realizar una aproximación al uso de los recursos mediante el análisis de la selección de hábitat del guanaco y de la oveja. Esto permitirá conocer el uso del hábitat del guanaco en simpatria con la oveja y en condiciones "naturales" sin oveja (dentro del Parque Nacional) para determinar si el guanaco modifica su patrón de selección en presencia de ganado y si se pueden detectar procesos de competencia o desplazamiento competitivo. Este objetivo será abordado en el CAPITULO 3.

A pesar de poner el foco de la investigación en estas dos especies, no hay que olvidar que ambas se encuentran formando parte de una comunidad de especies silvestres en la que se ha introducido recientemente el ganado, por lo que los procesos de solapamiento y segregación de nicho debidos a la competencia se pueden extender más allá de la relación guanaco-oveja. Para abordar los efectos a nivel de comunidad de la introducción de ganado, así como detectar cambios en las dimensiones del nicho debidos a competencia intra- e interespecífica, en el CAPITULO 4 se lleva a cabo un análisis de amplitud y solapamiento de nicho entre todas las especies de herbívoros presentes en la zona de estudio. Como se ha expuesto en los primeros apartados de la introducción, el nicho de una especie es el resultado de los procesos de competencia y depredación modulados por la estructura del hábitat. Así, una vez determinado el papel de la competencia en el nicho del guanaco, en el CAPITULO 5 se abordarán los efectos del riesgo de depredación y la estructura del hábitat en el comportamiento social y los patrones de actividad de guanaco.

Los capítulos 2-5 reproducen el texto íntegro de manuscritos originales que se encuentran en diferentes fases de publicación, por lo que se presentan en inglés por ser el idioma en el que han sido publicados o enviados a publicar. En concreto, el capítulo 2 se encuentra enviado a Mammal Research. El capítulo 3 corresponde a una publicación en la revista PlosOne (Iranzo et al. 2013). El capítulo 4 se encuentra en fase de segunda revisión en Oikos, mientras que el capítulo 5 se encuentra en fase final de elaboración. Para finalizar,

1.7. Objetivos y estructura de la presente tesis doctoral

el CAPITULO 6 recoge la discusión general de los resultados obtenidos en la tesis, así como las conclusiones generales.

CAPÍTULO 2

Diffusive dispersal in a guanaco growing population: an example of ungulate expansion beyond the limits of protected areas

Esperanza C. Iranzo, Pablo Acebes, Cristián F. Estades, Benito A. González, Cristina Mata, Juan E. Malo and Juan Traba ¹

¹Manuscrito enviado como: Iranzo, E.C., Acebes, P., Estades, C.F., González, B.A., Mata, C., Malo, J.E. and Traba, J. Diffusive dispersal in a guanaco growing population: expansion beyond the limits of the protected areas.

Abstract

Wild ungulate population growth within protected areas can cause an expansion and colonization of surrounding non-protected areas. In the late phase of the colonization, animal abundance is expected to be associated with environmental variables, as the proportion of adequate habitats or food availability, and animal density reduces, and juvenile proportion increases, with increasing distance from the source of animals. Besides, demographic structure becomes similar throughout the whole occupation area. Here we analyse the current status of the colonization process of a guanaco population after its recovery within a protected area in Chilean Patagonia, and expansion to surrounding ranches. We compare animal abundance and social structure between the protected and non-protected areas, and evaluate the effect of several environmental factors on guanaco abundance, proportion of family groups and reproductive success during three consecutive years. Guanaco abundance significantly declined with increasing distance to the centroid of the distribution, both in summer and winter, and showed some association with environmental variables. This is the situation expected under a late phase of the dispersal process. Besides, social structure did show no relevant differences between the protected area and its surroundings, excepting for the proportion of male groups, also pointing to a diffusive dispersal pattern. All these results together suggest that the guanaco population is in a late phase of the colonization process and has potential to growth and continue expanding its distribution. In addition, the methodology presented here can be used to evaluate the state of wild ungulate populations colonizing new areas.

Keywords: Population abundance, density, population dynamics, population structure, mammal dispersal

2.1 Introduction

Animal conservation programs are successful in reversing negative population trends once the pressures involved in the decline of animal populations are removed. In this sense, protected areas play a vital role for the recovery of threatened species (Fall and Jackson 2002, Hansen and DeFries 2007). In the case of species with large home ranges, like many ungulates, the movement of animals into surrounding non-protected areas is the natural outcome when populations increase within protected areas (Simonetti 1995, Gurd et al. 2001, Kowalczyk et al. 2013).

Regarding this dispersal process, large territorial ungulates frequently show an ideal-despotic distribution (Fretwell 1972). In these cases, agonistic behavior among conspecifics is greater at high densities or in more favorable habitats. As a result, dominant individuals, occupying the highest quality territories, force subordinates to disperse to unoccupied, usually less favorable areas (Fretwell 1972). Under this assumption, and in the early stages of the dispersal, recently colonised areas show (i) a higher proportion of juvenile males, as they usually comprise the first wave of individuals that are dispersed and colonize new areas; and (ii) a lower density of families than in the source areas, since they are the dominant groups (Greenwood 1980, Dobson 1982, Clutton-Brock and Coulson 2002). In this case, neither animal density nor social structure of the population are dependent on environmental factors. Later in the colonization process, when the population is near settled, the spreading adopts a diffusive pattern (Darmon et al. 2007), in which (i) animals tend to be primarily concentrated nearby the source of dispersing animals fitting a normal distribution (Skellam 1951); and (ii) demographic structure and sex/age ratios become similar throughout the whole occupation area. In this situation, extrinsic factors like local resource availability, interspecific competition and predation, as well as intrinsic factors such intraspecific competition, are crucial in determining animal density and spatial structure of populations (Andersen et al. 2004, Darmon et al. 2007).

Therefore, social and demographic structure differs between in-expansion and settled populations. Under the ideal-despotic scenario, an increase of population density can trigger the rate of agonistic interaction between territorial males and juveniles, forcing the dispersal of the latter to the expanding edge of the range (Greenwood 1980, Dobson 1982, Howard 1986, Berger 1987, Clutton-Brock and Coulson 2002). As a result, social structure on the expansion area will be characterized by a higher proportion of juvenile males (forming male groups in some ungulate species, see

2. GUANACO EXPANSION BEYOND PROTECTED AREAS

below) while a lower proportion of families. Moreover, reproductive rate in the dispersal area could be lower if the area is more stressful (e.g. due to competition with livestock or human pressure) or less productive than in the core of the distribution. In addition to these stressing factors, the settlement of a stable population is finally dependent on the species' ability to cope with human-derived effects, like competition with livestock or poaching. As a result of the dispersal and colonization process, human-wildlife conflicts can emerge in the expansion areas, especially with livestock farming (Simonetti 1995, Mishra et al. 2004, Distefano 2005, du Toit 2010), and they can trigger negative pressures precluding wild population settlement.

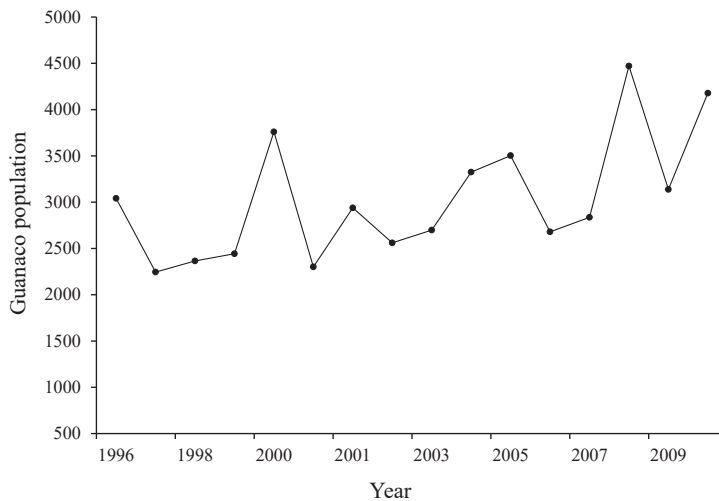


Figure 2.1. Guanaco population censused in Torres del Paine National Park (TdPNP) between 1996 and 2010 (annual growth rate $r=0.052$).

The guanaco (*Lama guanicoe*) is the largest South American ungulate, a wild camelid with resource defence polygyny and a flexible social structure (Franklin 1983, González et al. 2006a). Guanacos suffered a steep population decline after the Spanish arrival to South America attributed to over-hunting, competition with domestic species and habitat degradation (Puig 1995, Baldi et al. 2016). During the last decades, guanaco conservation programs have contributed to the recovery of the global population (Baldi et al. 2016). Currently, the main populations are located within protected areas of Patagonia and Tierra del Fuego, both in Argentina and Chile (Baldi et al. 2016). Of particular interest is the guanaco population located in Torres

del Paine National Park, TdPNP hereinafter (Magallanes region, Chile). The species was near to extinction in this region in mid-70s (Franklin 1982). However, guanaco protection policies since then allowed a large population increase, from less than 100 individuals in 1975 (Franklin 1982), to around 4200 in 2010 (Fig. 2.1). It is currently the second most important guanaco population, after the Tierra del Fuego population. This within-TdPNP population growth has occurred while causing an expansion outside of the protected area, where the species was many decades absent (Franklin 1982, Iranzo et al. 2013).

In this context, TdPNP and its surroundings offer a particular situation where factors affecting to the dispersal process of an ungulate species can be evaluated. Specifically, we aimed: i) to evaluate the effects of distance to the centroid of animal distribution, NDVI, proportion of suitable habitats, abundance of livestock and relative abundance of puma on guanaco abundance, social structure and reproductive success along the whole colonizing area, and ii) to test if guanacos inhabiting ranches surrounding TdPNP are yet in an expansion process or they are already settled. This last objective will be addressed through the comparison of guanaco abundance, density and social structure within TdPNP and the surroundings. In the case of population during the early phase of dispersal, we expect to find no relationships between abundance and environmental or demographic factors, a higher proportion of family groups in the core area and a higher proportion of dispersers (male groups) toward the edges of the distribution; whereas in the case of a population in diffusive dispersal, that is in the late phase of the colonization, we would expect to find that animal abundance, proportion of families and reproductive success to be associated with context variables, as the proportion of adequate habitats or primary productivity. Besides, populations in diffusive dispersal tend to show a normal distribution with respect to the origin of the individuals, which means that the animal density would be higher in the core than in the edges of the distribution (Skellam 1951). Finally, if the population in the surroundings is settled, we expected to find no differences in social and demographic structure throughout the guanaco occupation area. In addition, updated population size estimation, both in the protected area and in the surroundings, is provided.

The knowledge of the current status of the population (settled vs expansion) and the ecological cues shaping guanaco distribution can provide useful tools for its management and reflects the possible outcome of a wild ungulate population protected within a reserve that recovers from its initial low numbers.

2.2 Materials and methods

Study area

This study was conducted in Torres del Paine National Park and its surroundings, Southern Chile (51°30'S 72°55'W; Fig. 2.2). The study area covered approximately 1,090 km² (284 km² within TdPNP and 806 km² belonging to neighbouring ranches). Climate is considered temperate-cool without a pronounced dry season. Annual rainfall varied between 300 mm and 1,000 mm while mean temperatures averaged 2°C in winter and 10.8°C in summer (Vidal and Reif 2011). Vegetation in the study area is dominated by steppe-like grasslands and shrublands (Pisano 1974); a detailed description of distinct vegetation communities can be found in Iranzo et al. (2013).

No livestock occurs within TdPNP. Oppositely, surrounding privately owned ranches are dedicated to extensive livestock farming, consisting mainly of sheep (see below). TdPNP is delimited by 1.2 m-high wire fences, which restrict livestock movements but act only as a semipermeable barrier to wildlife movement (Rey et al. 2012).

Animal data collection

Two-person observer teams with binoculars conducted field surveys to estimate abundance and social structure of guanacos within and outside TdPNP during the austral winter (July) and late spring-summer (December) of three consecutive years (2009-2011). Observer teams surveyed all roads, tracks and footpaths existing within (N transect = 15; total transect length = 114.8 km) and outside TdPNP (N transect = 17; total transect length = 221.8 km) during both season and year. Surveys took place during daylight hours avoiding periods of poor visibility during dawn and dusk. Surveys along roads were conducted by car driven at a nearly constant speed of 15 km/h, while tracks and paths (22.5 km only within TdPNP) were surveyed on foot. Both methods are considered comparable since they do not disturb animal behavior or habitat selection in the study area, where animals show short flight distances (Malo et al. 2009, see also Iranzo et al. 2013, Traba et al. under review, for similar procedure). From a conservative perspective, assuming a 400m band width with complete detection on either side of the road (Pedrana et al. 2009), sampled area corresponds to 24.7 % of the total study area (Fig. 2.2).

Following distance sampling protocols (Buckland et al. 2001) we recorded locations for every guanaco (solitary individuals and social groups)

encountered using a GPS, measured distances to the central point of groups using a laser rangefinder (Leica 1200 m), and determined the appropriate angle of our observations with a precision compass, for an accurate localization of each observation. In addition, we recorded group size, sex, and age class of all individuals. Individuals were classified into three age classes: adults (2 years and older), yearlings or juveniles (between 1 and 2 years) and chulengos (calves up to 1 year old) (Franklin 1983). According to Franklin (1982), we assigned observations of guanacos to one of four social groups: i) family groups formed by a territorial male with females and their offspring; ii) solitary territorial males; iii) groups of immature and mature non-territorial

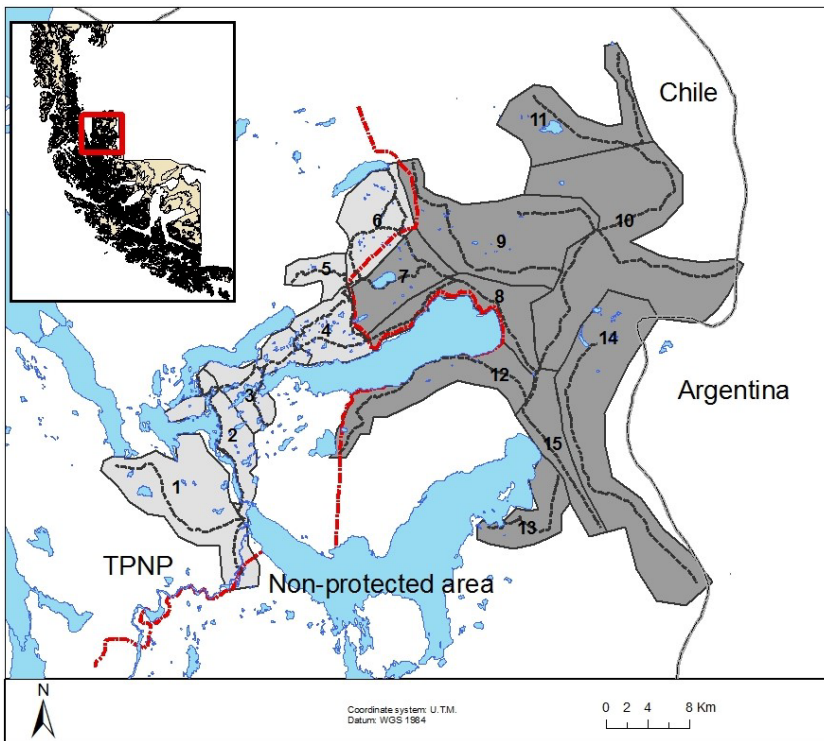


Figure 2.2. Location of study area (shaded area) in the Comuna Torres del Paine (Region of Magallanes, Chile). Red dashed line indicates Torres del Paine National Park (TPNP) boundary. Black dashed lines represent the surveyed road network within (light grey) and outside (dark grey) the protected area. Solid lines indicate different sectors (1-15).

males; and iv) female groups consisting of adult females with or without chulengos or yearling females without an adult male. During the non-breeding season guanacos tend to form large mixed herds composed of adults of both sexes, yearlings and chulengos (Franklin 1982, González et al. 2006a), although all four social units mentioned above may still be encountered. In our study area we recorded solitary males, male groups, female groups and mixed groups during winter.

The guanaco is a sexually monomorphic ungulate (Sarno and Franklin 1999) and sexual assignments are thus dependent on the corroboration of the presence of testicles and by reproductive behavior, as tail rising (Franklin 1983, Ortega and Franklin 1995). Thus, despite guanaco groups can be seen and accurately located at long distance (more than 1200 m, own data), sexual (and age) correct assignments are subject to high uncertainty above 400 m (Pedrana et al. 2009). Consequently, all observations above this threshold were used for density estimations, but removed from social structure analyses.

Environmental data

In order to estimate the effect of both density-related (intra- and interspecific competition), and environmental factors (resource availability, predation risk and proximity to the protected area) to explain guanaco abundance, social structure and reproductive success (chulengo/adult ratio), we recorded data on (i) primary productivity, (ii) habitat suitability, (iii) puma (*Puma concolor*) relative abundance (predation pressure) and (iv) livestock abundance (proxy of anthropic perturbations and interspecific competition). Previously, we divided the study area into 15 different sectors, attending to topographic and physiognomic similarity. Each sector included 1 to 4 of the above mentioned transects (see Fig. 2.2). Each sector was big enough to have a good representation of the different habitats present in the study area and to have a large enough number of animals to adequately test the hypotheses (see Traba et al. under review for a similar procedure for sector selection).

To account for the potential effect of primary productivity on guanaco abundance and distribution we used the Normalized Difference Vegetation Index (NDVI) value. NDVI values were obtained using MODIS-Terra images (MOD13Q1/Terra Vegetation Index 16 Day L3 Global 250 m SIN Grid V005) acquired during a 16-day period in December 2012 and July 2013 for summer and winter data, respectively. The persistent cloud cover prevented from using the same period as that for field sampling. However, it should have no effect on our results since the analysis is focused to inter-sector differences.

Grasslands (both natural and artificial) and vegas (meadows in the proximity of shallow wetlands) are considered the most suitable and optimal habitats for guanaco in the study area (Iranzo et al. 2013) due to their productivity and good visibility to detect predators (Bank et al. 2003). To estimate the cover of suitable habitat we located two control sampling points every 1000 m of each transect alternately right/left at 250 and 100 m distance from it (N = 194 sampling points in TdPNP, N = 394 sampling points in non-protected area in winter; N = 222 sampling points in TdPNP and N = 366 points in non-protected area in summer). At each sampling point we described the proportion (percentage of cover) of the above mentioned suitable habitats in a plot of 50 m radius (see Iranzo et al. 2013 for more details).

Puma surveys were conducted using footprints on snow during 2011 and 2012 winters along the same roads used to guanaco surveys. A 200 m perpendicular straight line was walked every 5000 m of each transect and road and all marks of puma presence were recorded to build an index of kilometric abundance (KAI) of puma per sector. Puma home ranges in the study area are small (19-84.5 km²) and tend to remain spatially constant throughout the year (Barrera et al. 2010), thus allowing us to use the winter data as a proxy of puma relative abundance also in summer, when footprints surveys are impossible to undertake.

Livestock abundance was recorded during guanaco surveys. Location and group size of livestock herds were used to calculate KAI of livestock per transect, year and season. Similarly, we used guanaco sightings to calculate KAI of guanaco per transect, year and season.

Statistical analysis

Factors influencing guanaco abundance, social structure and reproductive success

Factors influencing guanaco abundance, proportion of family groups and reproductive success among the 15 sectors were analyzed through General Linear Models (GLM) fitted for the following response variables: abundance of guanacos in each season and, only for summer data, percentage of family groups and chulengo/adult ratio of families (Table 2.1). Abundance of guanacos and sheep per sector was estimated by averaging transect and year KAIs to estimate mean KAI for each sector and season. In a similar way, the average percentage of family groups and chulengo/adult ratio of family groups was estimated for each sector only in summer. We also computed the average

NDVI for each sector and season in a 400m buffer around each transect. This is the same area used to estimate guanaco and sheep KAIs. A similar procedure was used to estimate puma relative abundance, although in this case we only have one estimate for both seasons. Habitat suitability was included as the mean proportion of grasslands and vegas per sector, averaging data from control points. We averaged the response and explanatory variables per sector when data from several years were available (Table 2.1).

In order to evaluate the effect of the distance of each observation to the core of animal distribution, we first estimated the geographical centroid of all animal observations weighted by group size for each season. We then calculated the distance from each observation to this seasonal centroid, using ArcGis 9.3 (ESRI) for both calculations. Finally, and to obtain a unique value per sector, we averaged all the distances per sector and season (Table 2.1).

We obtained models for each response variable (guanaco abundance, proportion of family groups and guanaco reproductive success - chulengo/adult ratio-) by performing GLM forward-backward stepwise regression on all the predictors that were included in each predictor-set model (Márquez et al. 2011). For each response variable, the full model included the distance to the centroid of animal distribution, NDVI, proportion of suitable habitats, abundance of livestock and relative abundance of puma. Inclusion of variables in the stepwise procedure was based on significance testing, comparing consecutive models by ANOVA test. If no significant differences between models were found, we selected the most parsimonious one. The stepwise approach has recently been described as one of the best methods to describe species distributions based on different sets of predictors (Barnagaud et al. 2012). All variables were transformed to meet normality assumptions and standardised. Percentage variables were arc-sin transformed, count variables were square root transformed and continuous variables were log-transformed. We used *lme4* library, on the free software R version 3.2.1 (R Core Team 2014).

Social Structure

Groups that included individuals with unknown sex or age (undetermined groups, hereinafter) were excluded from the analyses; they accounted for 23% of the observed groups in winter (corresponding to 16% of all animals) and 11% in summer (12% of all animals). These proportions are similar to those provided by Pedrana et al. (2009) for large-scale road surveys.

Table 2.1. Raw values for the response and environmental explanatory variables per sector for the factors influencing guanaco abundance, proportion of family groups and reproductive success analyses. Family group, proportion of family groups in summer. C/A ratio, chulengo/adult ratio in summer. Optimal habitat, proportion of grasslands and vegas. Dist centr winter, distance to the centroid of the observations during winter (km). Dist centr summer, distance to the centroid of the observations during summer (km). Guanaco winter, Kilometric abundance index (KAI) of guanacos in winter (animal/km). Guanaco summer, KAI of guanacos in summer (animal/km). Sheep winter, KAI of livestock in winter (animal/km). Sheep summer, KAI of livestock in summer (animal/km). Puma, relative puma abundance (KAI; animal/km).

Sector	Zone	Lenght (km)	Family group	C/A ratio	NDVI winter	NDVI summer	Optimal habitat	Dist centr. winter	Dist centr. summer	Guanaco winter	Guanaco summer	Sheep winter	Sheep summer	Puma
1	within TdPNP	22.2	0	0	0.312	0.424	26.58	36.606	31.865	0	0	0	0	1.528
2	within TdPNP	20.35	1.000	0.386	0.520	0.640	5.13	30.845	24.883	0.147	0.803	0	0	1.111
3	within TdPNP	17	0.190	0.241	0.227	0.424	8.36	26.189	18.828	11.902	1.745	0	0	6.250
4	within TdPNP	25.7	0.262	0.259	0.306	0.391	21.56	18.447	10.482	26.472	26.939	0	0	2.083
5	within TdPNP	7.5	0	0	0.345	0.405	58.47	20.003	8.648	22.889	0.267	0	0	5.000
6	within TdPNP	22	0.167	0.214	0.313	0.481	33.29	17.093	4.434	48.182	31.182	0	0	1.587
7	outside TdPNP	18.4	0.341	0.352	0.352	0.540	29.57	12.592	2.857	10.399	50.779	4.275	0	0.556
8	outside TdPNP	23.8	0.203	0.100	0.377	0.614	26.61	4.453	8.785	34.468	8.754	89.832	3.866	0.556
9	outside TdPNP	33.2	0.413	0.388	0.311	0.560	46.36	8.657	9.128	21.335	9.849	83.444	54.709	0
10	outside TdPNP	47.2	0	0	0.336	0.459	30.30	11.773	20.643	6.723	1.363	85.438	129.534	0
11	outside TdPNP	22.4	0.500	0.071	0.259	0.489	44.25	19.801	20.600	20.030	6.012	93.095	171.964	0
12	outside TdPNP	26.2	0.280	0.364	0.352	0.443	31.99	10.845	13.419	25.051	11.552	35.331	110.191	0
13	outside TdPNP	13.5	0.100	0.167	0.397	0.432	50.75	18.750	27.772	37.877	44.000	125.210	16.000	0
14	outside TdPNP	18.6	0	0	0.319	0.544	32.14	15.238	27.456	1.828	0.215	93.602	151.075	0
15	outside TdPNP	18.5	0.333	0.333	0.317	0.533	63.63	12.607	23.419	16.901	5.225	79.423	229.820	0.185

Firstly, we described typical group size. According to White et al. (2012), this metric complements mean group size and provides more information about grouping trends. Then, we tested for basic differences in social structure. We used factorial ANOVA and a posteriori Tukey test to evaluate differences in group size for each social group among years, seasons and zones (within/outside TdPNP). In addition, we tested for differences in guanaco reproductive success (chulengo/adult ratio of family groups) among years and zones by factorial ANOVA and a posteriori Tukey test, only with summer data. All data were transformed to meet test assumptions. However, untransformed data are shown to facilitate interpretation.

We used generalized linear models (GLM) with a binomial distribution to test for differences in social structure (i.e. proportion of each type of social unit) among years, seasons and zones. We built four different response variables: (i) family groups vs. all other groups; (ii) solitary males vs. all other groups; (iii) male groups vs. all other groups; and (iv) female groups vs. all other groups. We included three different explanatory factors: year (2009, 2010, 2011), season (winter, summer) and zone (within and outside TdPNP), and their biologically relevant interaction, season*zone, in the analyses. We confirmed that model assumptions were met and selected the best model for each response variable based on Akaike Information Criterion (AIC; Akaike 1974). These statistical analyses were performed with INFOSTAT 2013 (Di Rienzo et al. 2011).

Population Abundance and Density

Finally, we used program DISTANCE (version 6.0; Thomas et al. 2010) to obtain updated estimates of abundance (N) and population density (D) of guanacos. We estimated population parameters separately for each year, season and zone (within and outside TdPNP). We further screened our data for additional possible bias in detection probabilities related to road survey or animal behavior following Thomas et al. (2010) and removed all observations farther than 1200 m (above the range of the rangefinder) from DISTANCE analyses.

We analyzed distance data using conventional (CDS) and multiple covariate (MCDS) methods (Buckland et al. 2001) and considered three functions in density estimation: uniform, half-normal and hazard-rate (Buckland et al. 2001). We used the cosine adjustment function for all analyses. We built models both using exact perpendicular distances, and by grouping perpendicular distances into intervals of 50 and 100 m in order to

improve model fit. We included the number of individuals in each sighting as a covariate since detectability can vary depending on group size. Model selection was based on AIC (Akaike 1974). Differences in abundance and density among years, seasons and zones (within and outside TdPNP) were analyzed via factorial ANOVA, only for main effects, using INFOSTAT 2013 (Di Rienzo et al. 2011).

2.3 Results

Factors influencing guanaco abundance, social structure and reproductive success

Distance to summer guanaco centroid and puma abundance were included in the final model to explain guanaco abundance during summer (adjusted $R^2 = 0.404$; $F_{2,11} = 5.397$; $p = 0.023$; Table 2.2). During summer, guanaco abundance was negatively related to the distance to the summer distribution centroid (Fig. 2.3a). In addition, guanaco abundance was negatively related to puma abundance, though just marginally significant (Fig. 2.3b). No other factors affected guanaco abundance during this season.

Final model to explain guanaco abundance during winter included three variables (distance to winter centroid, NDVI and cover of optimal habitats), and was less explanatory than summer model and only marginally significant (adjusted $R^2 = 0.313$; $F_{3,11} = 3.127$; $p = 0.070$; Table 2.2). During winter, guanaco abundance was marginally and negatively related to the distance to the centroid of the winter distribution (Fig. 2.3c). Other factors showed no relationship with guanaco abundance. Both summer and winter centroids of observations were located outside the TdPNP, 3km and 400m away from the administrative limit, respectively. During summer, the proportion of family groups and the chulengo/adult ratio (averaging 0.22 at a global scale) showed no relationship with any of the considered factors.

Table 2.2. GLM results for guanaco abundance during winter and summer.

		Estimate	Std. error	t value	p
Summer	Intercept	2.369	0.493	4.802	<0.001
	Dist to centroid	-1.119	0.401	-2.790	0.018
	Puma	-0.894	0.426	-2.096	0.060
Winter	Intercept	2.943	1.093	2.692	0.021
	Dist to centroid	-1.096	0.535	-2.049	0.065

Social structure

After excluding undetermined groups, solitary males were the most frequent social unit in summer (55%), followed by family groups (26%), male groups (17%) and female groups (2%). In winter, mixed groups were the most frequent social units (54%), followed by solitary males (25%), male groups (15%) and female groups (6%). Family groups gathered the highest proportion of animals in summer (64% of all animals), and mixed groups in winter (94% of all animals), followed by male groups (29% and 4% of all animals in summer and winter respectively). Solitary males represented 6% of all animals in summer and 1% in winter, while female groups were rarely observed.

Proportion of family groups varied among zones (Table 2.3). It was higher outside (mean \pm SE = 0.43 ± 0.03) than within TdPNP (mean = 0.36 ± 0.02). Proportion of male groups differed between zones. It was higher outside (mean = 0.20 ± 0.02) than within TdPNP (mean = 0.13 ± 0.02 ; Table 2.3). Proportion of solitary males was higher within TdPNP (mean = 0.56 ± 0.03) than outside (mean = 0.32 ± 0.03) and in summer (mean = 0.54 ± 0.02) than in winter (mean = 0.25 ± 0.03 ; Table 2.3). Finally, proportion of female groups was higher in winter (mean = 0.06 ± 0.004) than in summer (mean = 0.01 ± 0.02 ; Table 2.3).

Regarding family groups in summer, mean group size ranged between 2 and 90 guanacos (mean = 16.6 ± 0.8 ; median = 11) and it did not vary between zones or years. In these groups, number of adults ranged between 2 and 66 adults (mean = 13.5 ± 0.9 ; median = 9); number of chulengos varied between 0 and 26 (mean = 3.5 ± 0.2 ; median = 2); and number of yearlings varied between 0 and 8 (mean = 0.6 ± 0.08 ; median = 0). Typical family group size was 38.6 animals, composed of 25.1 adults, 9.8 chulengos and 3.7 yearlings. During this season, the chulengo/adult ratio showed differences among years (ANOVA: $F_{3,201} = 8.39$, $p < 0.001$) and marginal differences between zones (ANOVA: $F_{3,201} = 3.79$, $p = 0.053$). This ratio was larger in 2009 and 2010 (mean = 0.34 ± 0.03 ; and mean = 0.32 ± 0.02 , respectively) than in 2011 (mean = 0.20 ± 0.03), and slightly outside (mean = 0.32 ± 0.02) than within TdPNP (mean = 0.26 ± 0.02). Male group size, although highly variable (mean = 13.16 ± 2.4 ; median = 3; range 2-210 guanacos; typical size = 92.1) did not differ between zones, seasons, nor years (ANOVA: $F_{4,167} = 1.03$, $p = 0.391$). Finally, female group size (mean = 5.1 ± 1 ; median = 3; range 2-25 guanacos) did not show differences between zones, seasons, nor years (ANOVA: $F_{4,24} = 1.55$, $p = 0.220$).

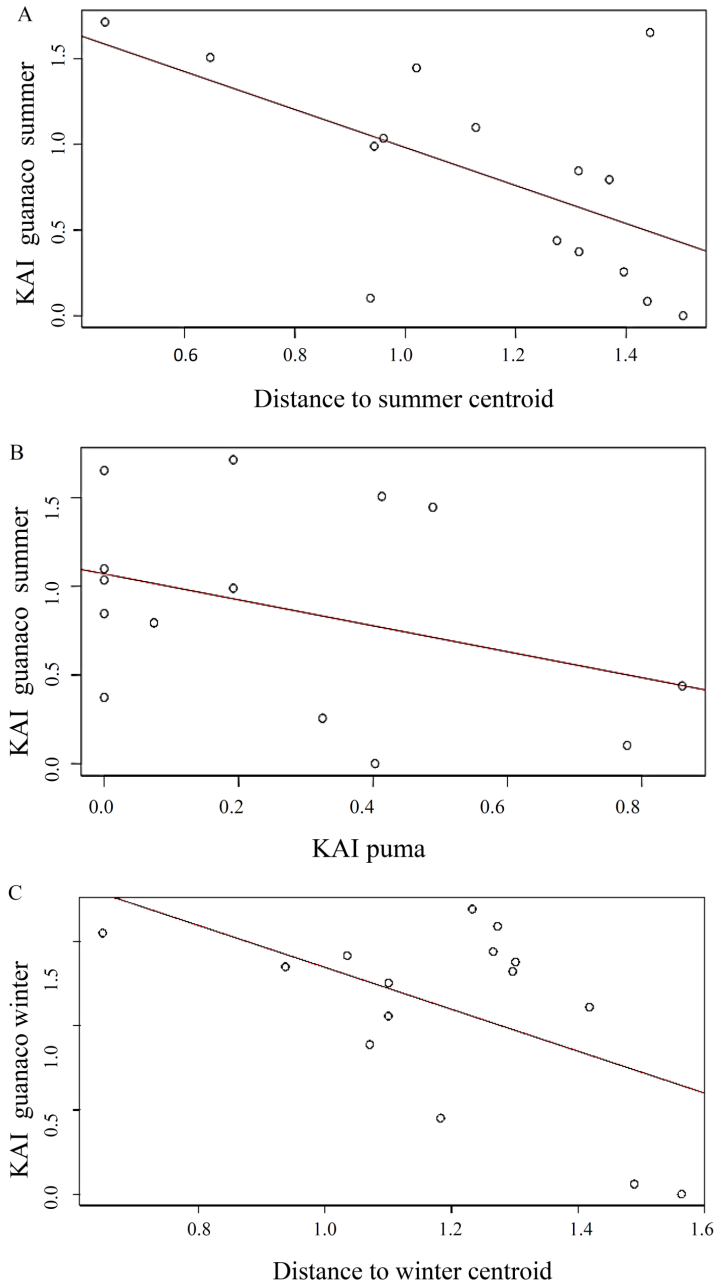


Figure 2.3. Relations of guanaco abundance with A) distance to summer distribution centroid; B) puma abundance; C) distance to winter distribution centroid. Fitted lines from linear regression are shown.

Population Abundance and Density

Over six seasons, 2,121 groups of guanacos were sighted, with a total of 30,515 individuals counted. Total seasonal number of sighted animals varied from 3,187 to 4,561 individuals during summer (mean = $4,038 \pm 743$) and 5,570 to 6,697 individuals during winter (mean = $6,134 \pm 564$; Table 2.4). During all surveys, we recorded more animals outside than within TdPNP. Regarding the number of sightings, more groups were detected in summer than in winter (Table 2.4).

The estimated total abundance of guanaco ranged from 12,800 animals to almost 19,000 in summer and from 13,000 to almost 22,000 animals in winter (Table 2.5). Estimates of guanaco abundance did not show any significant differences among years ($F = 0.07$; $p = 0.933$), seasons ($F = 0.188$; $p = 0.678$) or zones ($F = 1.429$; $p = 0.271$).

Estimates of population density varied across years and seasons (range summer = 10.2-25.6 individuals/km²; range winter = 8.3-36.6 individuals/km²; Table 2.5), although no significant differences were found (among years: $F = 0.31$; $p = 0.743$; between seasons: $F = 0.789$; $p = 0.404$). Differences in guanaco density between within and outside TdPNP were significant, being larger within TdPNP than outside ($F = 12.008$; $p < 0.01$; range within = 16.3-36.6 individuals/km²; range outside = 8.3-15.4 individuals/km²; Table 2.5).

2.4 Discussion

Our results support the existence of a diffusive dispersal pattern in the guanaco population of Torres del Paine National Park and its surroundings. In general, guanaco abundance declined with increasing distance to the geographic centroid of the distribution, both in summer and winter, and showed some association with environmental variables as expected under a late phase of the dispersal process (Skellam 1951, Darmon et al. 2007). Analysis of social structure also reinforces this result, as we found no differences between the source and the colonization area, excepting for the proportion of male groups.

Under a late phase of the dispersal, we expected to find relationship between environmental factors as habitat productivity and suitability and guanaco abundance, proportion of families or reproductive success, as they are traditionally considered crucial factors explaining ungulate abundance (Andersen et al. 2004). Our results find some marginal association between

guanaco and puma abundance during summer, and some relevance of other environmental factors during winter, which points to a population in late dispersal. The guanaco is a generalist herbivore that can occupy low resource habitats and be subjected to harsh conditions (González et al. 2006a, Puig et al. 2008). NDVI and cover of optimal habitats, though non-significant, were included in the winter model, which suggest the relevance of this factors in explaining the distribution of animals in the whole area. The negative relationship between guanaco and puma abundance during summer points to an avoidance of higher predation risk areas (Acebes et al. 2013). Summer is the birth season, when predation on chulengos is higher and guanaco try to reduce predation risk (Acebes et al. 2013). However, further analyses should help to identify other important environmental variables involved in guanaco abundance and reproductive success.

Table 2.3. Factors affecting proportion of each type of social unit of guanacos within and outside Torres del Paine National Park (Chile) in winter and summer during 2009-2011.

	Model	Chi2	p
Family group	Intercept	0.07	
	year	2.54	0.24
	zone	8.31	0.004
Male group	Intercept	1.77	
	year	4.77	0.09
	season	1.09	0.30
	zone	9.53	0.002
	season*zone	1.87	0.17
Solitary males	Intercept	0.79	
	year	1.81	0.45
	season	65.34	<0.001
	zone	26.41	<0.001
	season*zone	0.04	0.85
Female group	Intercept	2.70	
	year	3.28	0.19
	season	13.93	<0.001
	zone	0.13	0.72
	season*zone	3.3	0.07

Table 2.4. Guanacos (and groups) recorded in each social unit sighted within and outside Torres del Paine National Park (TdPNP) in winter and summer during 2009-2011.

Year	Season	Zone	Family group	Male group	Solitary males	Female group	Undetermined group	Total/zone	Total/season
2009	Winter	within TdPNP	1,534 (22)	41 (6)	16 (16)	16 (3)	480 (20)	2,087 (67)	5,570 (225)
		outside TdPNP	1,033 (41)	68 (7)	6 (6)	31 (5)	2,345 (99)	3,483 (158)	
	Summer	within TdPNP	1,202 (46)	395 (23)	126 (126)	5 (2)	30 (5)	1,758 (202)	4,365 (462)
		outside TdPNP	1,125 (81)	809 (44)	91 (91)	10 (4)	572 (40)	2,607 (260)	
2010	Winter	within TdPNP	2,626 (41)	32 (8)	14 (14)	0 (0)	133 (11)	2,805 (74)	6,697 (262)
		outside TdPNP	2,056 (71)	70 (7)	28 (28)	8 (3)	1,730 (79)	3,892 (188)	
	Summer	within TdPNP	888 (42)	272 (17)	122 (122)	14 (5)	174 (21)	1,470 (207)	4,561 (503)
		outside TdPNP	1,364 (81)	244 (26)	79 (79)	2 (1)	1,402 (109)	3,091 (296)	
2011	Winter	within TdPNP	1,292 (24)	13 (5)	16 (16)	13 (2)	259 (20)	1,593 (67)	6,135 (223)
		outside TdPNP	1,752 (41)	129 (11)	17 (17)	29 (3)	2615 (84)	4,542 (156)	
	Summer	within TdPNP	667 (38)	311 (25)	97 (97)	6 (4)	54 (18)	1,135 (182)	3,187 (446)
		outside TdPNP	804 (48)	249 (26)	56 (56)	0 (0)	943 (134)	2,052 (264)	

Table 2.5. Density (animals/km²) and abundance estimated of guanaco within and outside Torres del Paine National Park (Chile) in winter and summer during 2009-2011. Final DISTANCE model selected; n, number of detections; D, guanaco density (guanaco/km²); CV, per cent coefficient of variation of density estimated; N, abundance estimated; CI 95%, confidence interval of guanaco abundance, for each year, season and zone.

Year	Season	Zone	Selected model	n	D	CV	N	CI (95%)
2009	winter	within TdPNP	Hazard-rate interv 100m	65	17.6	54	4,983	1,815-13,676
		outside TdPNP	Hazard-rate	113	9.9	35	7,983	4,055-15,720
	summer	within TdPNP	Hazard-rate interv 100m	200	23	40	6,514	2,892-14,673
		outside TdPNP	Hazard-rate interv 100m	191	15.4	42	12,429	5,590-27,635
2010	winter	within TdPNP	Hazard-rate interv 100m cluster size ^a	73	36.6	-	10,379	-
		outside TdPNP	Hazard-rate interv 100m cluster size ^a	155	8.3	-	6,672	-
	summer	within TdPNP	Hazard-rate interv 100m	206	25.6	42	7,264	3,139-16,805
		outside TdPNP	Hazard-rate interv 100m	243	10.8	34	8,668	4,468-16,815
2011	winter	within TdPNP	Hazard-rate cluster size ^a	66	36.3	-	10,298	-
		outside TdPNP	Hazard-rate cluster size ^a	143	14.5	-	11,668	-
	summer	within TdPNP	Hazard-rate interv 100m	183	16.3	46	4,626	1,853-11,548
		outside TdPNP	Hazard-rate interv 100m	219	10.2	34	8,175	4,144-16,127

^a Models with cluster size as covariate do not provide CI (95%)

Analyses of social structure offer contradictory results. The reported mean and typical family group size in summer are between the highest ever described for the species (Puig and Videla 2007, Rey et al. 2009, Taraborelli et al. 2012). This, together with the high animal density found within the protected area, inform that a high density crowding effect could be occurring in the TdPNP (Sutherland and Norris 2002, Marino et al. 2016). High aggregation of animals is expected to increase agonistic interactions among them, forcing juveniles and subordinates to disperse (Greenwood 1980, Lawson Handley and Perrin 2007). Therefore, the proportion of male groups was higher outside TdPNP as expected for an early-phase dispersal population under an ideal-despotic scenario (Fretwell 1972), and their size was similar between zones and comparable to those previously observed in Torres del Paine (Ortega and Franklin 1995).

Contrarily to this, the proportion of family groups tend to be higher outside TdPNP than within it, which suggests a later stage of the dispersal process, with reproductive units already settled in the expansion area, probably as a consequence of a saturation effect within the protected area. The chulengo/adult ratio during summer, although relatively low compared to other populations (see p.e. Acebes et al. 2013), was slightly larger outside TdPNP, pointing again to a well-established population here and therefore, that population growth would be expected to continue. This expectation of a still growing population is also reinforced by the increase in the population reported here within TdPNP with respect to that described in previous years by CONAF (Fig. 2.1), and the fact that densities estimated within TdPNP (16.3-36.6 guanacos/km²) are among the highest ever reported for the guanaco (Sarno and Franklin 1999, Burgi et al. 2012).

The aggregated spatial distribution of animals can address to biases in DISTANCE software outcomes (Thomas et al. 2010), which results in a wide interval of confidence for the abundance estimation. Despite this, distance sampling method is recommended against total counts or fixed-width strip transect methods that tend to underestimate population numbers (Buckland et al. 1993). Therefore, we consider that our estimates provide updated and useful global abundance estimations for the whole area, especially when compared with guanaco numbers actually sighted each season (see also Olson et al. 2005, Durant et al. 2011, Travaini et al. 2015).

Besides, a large proportion of the whole population is inhabiting the neighbouring ranches of TdPNP. Guanaco abundance was greater, while density was lower outside than within the protected area. Even so, density reported outside TdPNP (8.3-15.4 guanacos/km²) is again among the highest

mentioned for guanaco populations (Burgi et al. 2012, Schroeder et al. 2014). Our results reinforce the idea of colonization from the protected area towards the surroundings in less than 40 years with a more than 100-fold increase in abundance (Franklin 1982, Sarno and Franklin 1999). Although no definitive conclusion about the actual origin of the living-outside animals can be extracted from our results, movements from protected areas towards surrounding ranches after a population growth have already been reported in other wild ungulate species (Baldi et al. 2001, Madhusudan 2004, Plumb et al. 2009, Kowalczyk et al. 2013), suggesting a similar phenomenon in this case, as reported by Sarno and Franklin (1999).

The use of demographic parameters and the centroid approximation can be used to evaluate the state of wild ungulate populations whose protection within protected areas has been effective, and populations are colonizing the surrounding areas. With this set of parameters and the reported results, it is possible to conclude with some certainty that guanacos are perfectly established outside the protected area (larger proportion of family groups), and the population has potential to grow and continue expanding its distribution (similar reproductive success outside than within TdPNP). Therefore, management program of the species should extend beyond the limits of the protected area, in order to reduce the predictable conflict with livestock farming, the most widespread socio-economic activity in the area.

2.5 Acknowledgements

We thank CONAF (Corporación Nacional Forestal) and SAG (Servicio Agrícola Ganadero- Government of Chile) for sharing the data presented in the introduction, permission and support to conduct this study. Specially thanks to N. Soto and A. Kroeger, the staff at the Torres del Paine National Park and ranchers from Torres del Paine municipality (XII Region, Chile) for their collaboration, and to volunteers for their assistance with fieldwork. The manuscript was improved by the helpful review of H. Wittmer and two anonymous referees. This research was funded by an Interuniversity Cooperation Program from Agencia Española de Cooperación Internacional para el Desarrollo (A/016431/08 and A/024945/09), Interuniversity Cooperation Project UAM-Santander and a Cooperation Agreement between UAM and SAG. Partial support for UAM researchers is provided by the Remedial-3 research network (S-2013/MAE-2719) and by Universidad de Chile. E. Iranzo is funded by a FPU grant from the Ministerio de Educación Cultura y Deporte (Government of Spain).

CAPÍTULO 3

Niche segregation between wild and domestic herbivores in Chilean Patagonia

Esperanza C. Iranzo, Juan Traba, Pablo Acebes, Benito A. González, Cristina Mata, Cristián F. Estades and Juan E. Malo ¹

¹Manuscrito publicado como: Iranzo, E.C., Traba, J., Acebes, P., González, B.A., Mata, C., Estades, C.F. and Malo, J.E., 2013. Niche segregation between wild and domestic herbivores in Chilean Patagonia. PloSOne, 8(3), p.e59326.

Abstract

Competition arises when two co-occurring species share a limiting resource. Potential for competition is higher when species have co-existed for a short time, as it is the case for herbivores and livestock introduced in natural systems. Sheep, introduced in the late 19th century in Patagonia, bear a great resemblance in size and diet to the guanaco, the main native herbivore in Patagonia. In such circumstances, it could be expected that the two species compete and one of them could be displaced. We investigated spatial overlap and habitat selection by coexisting sheep and guanaco in winter and in summer. Additionally, we studied habitat selection of the guanaco in a control situation free from sheep, both in summer and winter. We also determined overlap between species in areas with different intensity of use (named preferred and marginal areas) in order to further detect the potential level of competition in the case of overlapping. Guanaco and sheep showed significantly different habitat preferences through all seasons, in spite of their spatial overlap at landscape scale. Additionally, the habitat used by guanaco was similar regardless of the presence or absence of livestock, which further indicates that sheep is not displacing guanaco where they coexist. These results suggest that habitat segregation between guanaco and sheep is due to a differential habitat selection and not to a competitive displacement process. Therefore, the potential for competition is considered low, contrary to what has been previously observed, although this could be a density-dependent result.

3.1 Introduction

Animal community structure results from multiple interactions among biotic and abiotic factors that determine different species habitat selection (Prins 2000, Shea and Chesson 2002, Bailey and Provenza 2008). Resource availability, distribution and quality are essential factors to explain spatial distribution of species (Owen-Smith 2002, Bailey and Provenza 2008). In addition, for large herbivores, key habitat-selection factors include interspecific competition (Putman 1996, Arsenault and Owen-Smith 2002) and predation risk (Sinclair 1985).

Interactions between large herbivores are not easy to detect, measure and interpret (Prins 2000, Owen-Smith 2002, Mishra et al. 2004). Interspecific competition can occur by interference (direct competition) or by exploitation of the same resources (indirect competition; Prins 2000, Owen-Smith 2002). Furthermore, spatial and temporal scales in which such interactions take place usually difficult their study, especially in the absence of control situations and/or when variable species densities are involved (Hobbs et al. 1996b, Owen-Smith 2002, Stewart et al. 2002).

According to ecological theory, two species compete when they overlap in their use of limiting spatial and trophic resources (Wiens 1989, Boer and Prins 1990, Prins 2000). When species coexist through evolutionary time, resource partitioning mechanisms can evolve to minimize competition and, thus, to enable coexistence (Wiens 1989, Boer and Prins 1990, Putman 1996). However, the recent introduction of domestic species into an original assemblage may trigger processes of interspecific competition with native ones, although the intensity of these processes depends on the level of overlap between species and the generalist or specialist character of them (Voeten and Prins 1999, Baldi et al. 2001, Owen-Smith 2002). When competition occurs, it is expected to be more severe between species with similar foraging strategy and size (Owen-Smith 2002), and it is expected to trigger changes in the patterns of resource use of one or all of the species involved at the cost of a partial displacement away from their optimum (Wiens 1989, Prins 2000, Arsenault and Owen-Smith 2002). In these cases, animals may be lead to occupy habitats different to the preferred ones (sub-optimal habitats). In addition, competing species may show an apparent lack of competition due to competitive exclusion, often resulting in ambiguous spatial patterns (Borgnia et al. 2008). Conflict between sympatric species can increase when man favours one of them, which is the case where wild species coexist with domestic livestock (Voeten and Prins 1999, Mishra et al. 2004, Namgail et al.

2007). In such cases, populations of native species can suffer negative impacts ranging from competitive displacement to poorer areas, demographic effects, or even local extinction (Mishra et al. 2002, 2004, Namgail et al. 2007, Kutt and Gordon 2012). Besides, in these circumstances it is difficult to tease apart the direct effect of livestock on the native herbivore from that of human management of the grazing area.

The guanaco (*Lama guanicoe*) is the only large native herbivore widely distributed throughout Patagonia. Since the introduction of sheep in the late 19th century, this species has suffered a dramatic population decline attributed to competition with livestock, poaching and habitat degradation and fragmentation (Raedeke 1982, González et al. 2006a, Baldi et al. 2008). Currently, the IUCN estimates a total guanaco population of about 600000 individuals, of which 9% are in Chile (Baldi et al. 2008). Meanwhile, the number of sheep in Patagonia increased rapidly, reaching 22 million heads in 1950 (Soriano and Movia 1986). Today there are yet about 4 million sheep under an extensive free grazing system, being a study case for potential competition with guanaco.

Guanaco has been described as a generalist herbivore that shows preference for grasslands and open ranges with short vegetation. Its diet varies along its geographic distribution and it has been characterized as a mixed feeder (Raedeke 1982, Puig et al. 2001, González et al. 2006a, Acebes et al. 2010). Sheep is also characterized as a generalist herbivore which shows some preference for grasses (Baldi et al. 2004). Previous studies in Patagonia have shown that both species overlap in their niches (Raedeke 1982, Baldi et al. 2001) and exhibit high similarity in the composition of their diets (up to 80%), in fact, two grass species constitute the 40% of both guanaco and sheep diets (Bonino and Pelliza-Sbriller 1991, Baldi et al. 2001, Puig et al. 2001, Baldi et al. 2004). These facts point to a high potential for competition in places where both species coexist (Raedeke 1982, Baldi et al. 2004). To unravel this question it could be useful to investigate how habitat selection of native species varies in the presence and absence of the introduced one. For this objective, the presence of protected areas without livestock within a matrix of ranching areas in which both species coexist arises as an ideal natural field experiment.

The aim of this paper is to evaluate habitat selection and the degree of overlap between two recently sympatric species: guanaco and sheep. The study area allowed to analyse species coexistence in an environment inhabited by both species (hereafter non-protected area) and to compare these results with an adjacent control area where only the guanaco is present

(Torres del Paine National Park, hereafter TPNP). This, therefore, will allow to accurately assess the habitat preferences of the native herbivore in the absence of the introduced one. On the framework of competition and coexistence developed above, we discuss the recent entry of a domestic herbivore in a native assemblage, given high similarity in size, diet and requirements to the native species (guanaco) following next premises: 1) in the absence of sheep, inside the TPNP, the guanaco will select open areas with low-size vegetation; 2) where both species coexist, in the non-protected area, the guanaco will modify its habitat selection towards less preferred areas with regard to those in TPNP. In this case, it is expected to find segregation between preferred areas for both species, but some overlap between marginal and preferred areas may be detected.

3.2 Materials and methods

Ethics Statement

The present study did not need the capture or handling of protected or endangered animals. All data about species' locations were collected by observation at distance using binoculars. The described field studies were carried out on a protected area and on privately-owned farms with the permission of both, CONAF (Corporación Nacional Forestal de Chile) and farmers.

Study area

The study was carried out inside and around the Torres del Paine National Park (51°3'S 72°55'W, Última Esperanza province, Region of Magallanes, Chile; Fig. 3.1), particularly in an area of 1090 km² (284 km² inside the TPNP and 806 km² of the neighbouring farms). Study area belongs to the transition zone forest-steppe. According to the Köppen climate classification system, climate is temperate-cool without dry season. Annual rainfall varies between 300 and 1000 mm, mean temperature ranging from 2°C in winter to 10.8°C in summer. This study differentiated 10 habitats types (Table 3.1), most of them defined by plant communities (Pisano 1974, Ortega and Franklin 1995).

TPNP is only inhabited by wild animal populations, guanaco is the most abundant herbivore and hare (*Lepus europaeus*) and upland goose (*Chloephaga picta*) are present with lower densities. Rhea (*Pterocnemia pennata*) and huemul (*Hippocamelus bisulcus*) are also present but rare. The

3. NICHE SEGREGATION BETWEEN GUANACO AND SHEEP IN CHILEAN PATAGONIA

TPNP surroundings are private owned lands dedicated to extensive livestock farming, mainly sheep but also cattle and horses. Sheep graze freely in large pasture lots of several square kilometers without the continuous presence of shepherds. They are moved between pasture lots twice a year and shepherds occasionally visit flocks to verify that the animals are in good condition. In this area, livestock coexists with wild guanaco populations and other less abundant herbivore species such as rhea, upland goose or hare.

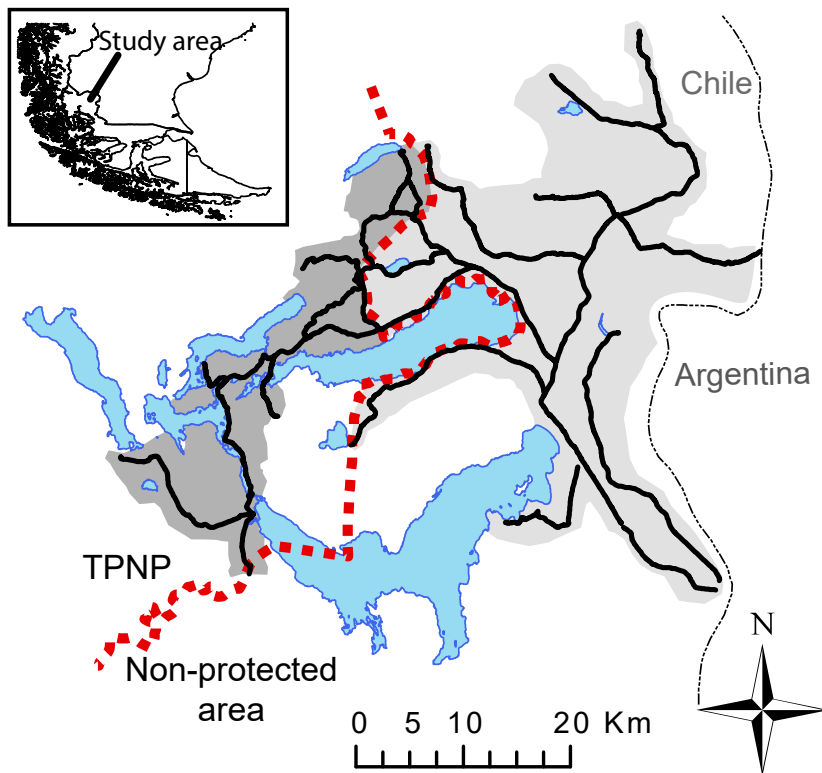


Figure 3.1. Location of study area (shaded area) in the Comuna Torres del Paine (Region of Magallanes, Chile). Red dashed line indicates Torres del Paine National Park (TPNP) boundary. Black solid lines represent the surveyed road network.

Table 3.1. Variables recorded for each guanaco (*Lama guanicoe*) and sheep (*Ovis aries*) sighting, and to estimate habitat availability at each control point.

	Variable*	Description
Topographic	Slope	Three levels: low (<5%), medium (5-45%), high (>45%)
	Topographic position Roughness	Four levels: valley bottom, lower half of hillside, upper half of hillside, peak Three levels: low (good visibility), medium (reduced visibility in some direction), high (low visibility)
Physiognomy	Mean vegetation height Maximum vegetation height	Medium vegetation height in cm Maximum vegetation height in cm
Habitat	Water	Bodies of running water (rivers or streams) or stagnant water (lakes and ponds)
	Bare soil	Without vegetation ground cover or rocks
	Natural grassland	Unmanaged grasslands dominated by native herbaceous species
	Managed grassland	Grasslands sown with fodder species
	Coironal	Steppe-like grasslands dominated by tufted grasses from genera <i>Festuca</i> and <i>Stipa</i>
	Wetland	Vegetation of shallow wetlands or flooded depressions with predominance of genera <i>Carex</i> and <i>Juncus</i>
	Xerophytic scrub	Small-sized scrubs, forming cushions and adapted to water deficit and strong winds. The most frequent species are <i>Mulinum spinosum</i> and <i>Senecio patagonicus</i>
	Mata Negra	Midheight woody shrub. This species (<i>Junellia tridens</i>) forms dense communities
	Mesophytic scrub	Robust scrubs reaching 4m in height. Characterized by <i>Berberis microphylla</i> that require higher precipitation and wind protection
Woods	Lenga (<i>Nothofagus pumilio</i>) and/or Nirre (<i>Nothofagus antarctica</i>) forest patches	

* Each variable was measured for a 50m radius from the animal or the centroid of the group.

Data collection

Sampling of herbivores was conducted during the winters and summers of 2009 and 2010, corresponding with times of minimum and maximum abundance of trophic resources, respectively. In each of the four sampling seasons, all existing roads and paths in the TPNP were travelled by vehicle or on foot (N=12; 76.6 km), as well as those in the non-protected area (N=17; 221.8 km). Both methods are considered comparable since they do not disturb animal behaviour or habitat selection in the study area, where animals show short flight distances (Malo et al. 2009). Sampling was carried out during daylight hours, avoiding sunrise and sunset. For each animal or group of animals encountered the centroid of the group was located and the point was recorded with a GPS. Considering a 50m radius around the centroid, the following descriptors were recorded: habitat composition (coverage (%) of different vegetation types), topography and physiognomy of the location of the sighting (Table 3.1).

To determine habitat availability, the same roads and paths were travelled in winter and summer, and the environmental variables were measured independently of the presence of animals. Two control sampling points (pseudo-absences) were located every 1000m, at 100m and 250m on each side of the road alternately (N=194 sampling points in TPNP, N=394 sampling points in non-protected area in winter; N=222 sampling points in TPNP and N=366 points in non-protected area in summer). At each sampling point a plot of 50m radius was established and the same variables described for herbivore sightings were measured (Table 3.1). Control plots have been classified as either inside or outside TPNP to take account in the analyses for differences in habitat availability between areas.

Data analysis

Firstly, we performed a point pattern analysis for each season and year in order to analyze the spatial pattern of landscape use by both species and detect their spatial overlap at intermediate (landscape) scale. We used a mathematic transformation of K-Ripley analysis, the bivariate function $L(r)$, in order to test the spatial aggregation between guanaco and sheep locations at scales from 0 to 2000 m in the non-protected area. If there is spatial overlap at that scale, there is some potential for competition. These analyses were performed with Passage software version 2 (Rosenberg and Anderson 2011).

Habitat selection analysis at a fine scale was performed in several sequential steps on habitat variables measured at a 50m radius scale for each observation. Firstly, general discriminant analyses (GDA) were used to determine whether the habitats used by both species were different from each another and from the availability, or whether guanaco and sheep showed overlap in resource use by selecting similar habitats. GDA combines predictor variables on a reduced number of axes, orthogonal to each other, and allows the detection of differences between a priori defined groups (see below). These axes can be interpreted as niche dimensions, as they include information of original variables related not only to habitat used by animals but also to habitat availability. To test the relative weight of each axis to the overall discrimination power of the model, 1-Wilks' λ statistic was used. Values of 1-Wilks' λ indicate the discriminatory power of models in the range of 1 (perfect discrimination) to 0 (no discrimination) for the whole model as well as for the sub-models obtained after removing the respective axis. Analyses were performed separately for each season in order to detect temporal overlap in habitats used. To assess differences in habitat selection of guanaco attributable to the presence of sheep in the non-protected area, guanaco observations inside and outside TPNP were treated independently, thus considering 5 different groups for analyses: Habitat availability (controls in TPNP/controls in non-protected area), guanaco (TPNP/non-protected area) and sheep (just in non-protected area).

Complementarily, to test which groups differed from others in their position on the discriminant axes, a MANOVA test was performed for each season using the coordinates on the canonical axes to define the multivariate space of the test and the group as a factor. Differences between groups were determined by post-hoc Unequal-N HSD tests. These analyses were performed with STATISTICA 8 (StatSoft 2007).

In order to detect differences in the overlap between guanaco and sheep related to preferred areas (defined as habitats of maximum utilization) and marginal areas (defined as habitats of marginal use), an analysis based on kernel functions was conducted on the points (observations) within the two-dimensional space defined by GDA axes. This analysis follows the assumption that animals can occupy sub-optimal or less preferred areas where they are more liable to overlap with the other species. Preferred and marginal areas were determined for guanacos and sheep in the non-protected area using an adaptive kernel (Worton 1989) from the coordinates for each species in discriminant axes. The kernel density estimator is used to describe the intensity of use on a two-dimensional representation of the relative frequency

distribution of animals' locations over a specified period of time (Van Winkle 1975). Therefore, it is a good estimator of preferred areas, since it minimizes the influence of isolated points (Worton 1995). Kernel estimates can be visualized as a sum of 'bumps' placed over the individual locations, so that the density estimate will show large bumps in areas of the GDA space where concentrations of points occur (Worton 1989). Preferred areas were calculated by the commonly used kernel 50% isopleth (Worton 1989, Cimino and Lovari 2003) and sightings within it defined as of preferred area. The remaining sightings of each species were classified as occupying marginal areas. ArcView 3.3 (ESRI) was used to define preferred and marginal areas of each species. To determine whether preferred areas of both species overlapped, new MANOVA and post-hoc Unequal-N HSD tests on the coordinates of the canonical axis were performed for each season and year using species as factor. Similar tests were performed to detect overlap between marginal areas and between preferred and marginal ones. These analyses were performed with STATISTICA 8 (StatSoft 2007).

3.3 Results

Throughout the four seasons 1446 groups of guanacos were sighted ($N_{TPNP}=550$, $N_{non-protectedarea}=896$) totalling 20,958 individuals ($N_{TPNP}=7,938$, $N_{non-protectedarea}=13,020$), and 561 groups of sheep (82,339 animals).

Point pattern analyses showed an aggregated pattern between guanaco and sheep for three of the four seasons (summer 2009, winter 2010 and summer 2010) at spatial scales lesser than 500m. During winter 2009, both species showed a random pattern at these scales (Fig. 3.2).

In relation with the GDA analyses, the whole models discriminated clearly between groups, both in winter and in summer. According to Wilks' λ , in both seasons the discriminatory power of the models (defined as 1-Wilks' λ) was largely determined by the first two axes (Table 3.2), while the remaining axes achieved an average of 9-12 % of discriminatory information present in habitat variables.

Winter

In winter, habitats used by both species and habitat availability were differentiated by the full set of discriminant axes (canonical $r=0.486$; $p<0.001$). Of the five significant axes, the first two included 67% of the

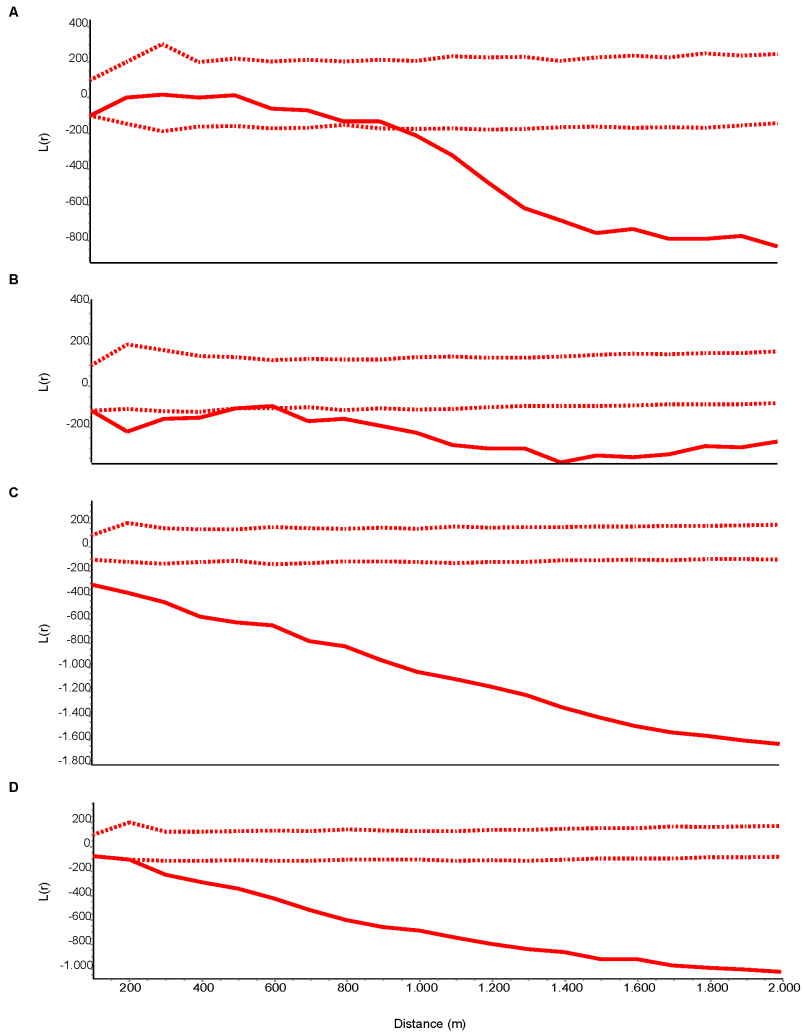


Figure 3.2. Spatial pattern of aggregation between guanaco and sheep in non-protected areas up to 2000m. Bivariate function $L(r)$ calculated for (A) winter 2009; (B) summer 2009; (C) winter 2010; (D) summer 2010. The dotted lines represent the 95% confidence interval of a standard complete spatial randomness of the same intensity. For this representation, values below the confidence interval indicate aggregation between guanaco and sheep, while higher values indicate segregation.

3. NICHE SEGREGATION BETWEEN GUANACO AND SHEEP IN CHILEAN PATAGONIA

information contained in habitat variables (Table 3.2), so that subsequent analyses were based on them. The most important variables to discriminate between groups were topographic position (valley bottom), roughness (low), xerophytic scrub cover, mata negra and bare soil for the first axis; and slope (flat), topographic position (valley bottom) and cover of water, xerophytic scrub and woods for the second (Table 3.3). The first axis discriminated between sites used by guanaco and habitat availability inside the TPNP, and the sites used by sheep and habitat availability in the non-protected area ($F_{MANOVA}=55.38$; $p<0.001$). The second axis separated habitat availability within the TPNP from everything else ($F_{MANOVA}=17.11$; $p<0.001$).

Habitat availability inside TPNP and in the non-protected area (expressed in terms of control sampling points in each zone; Table 3.4) differed significantly on both axes (Fig. 3.3). Sites used by sheep could not be discriminated from habitat availability in non-protected area on any of the axes or years (Fig. 3.3). However, they were segregated from the sites selected by guanaco in the non-protected area in both axes and years, and from those used by guanaco inside the TPNP on axis 1 (Fig. 3.3). Guanacos in TPNP and in non-protected area did not show significant differences on any axis in 2009 or on the first axis in 2010 (Fig. 3.3). Lastly, inside the TPNP, sites selected by guanacos were different from availability only on the second axis (Fig. 3.3), while guanacos in the non-protected area showed significant differences with habitat availability in that area on both axes (Fig. 3.3).

Table 3.2. Main results of GDA per season to test the presence of differences in habitat variables among groups.

Season	Model*	Discriminatory power (1- Wilks' λ)	p
Winter	whole model	0.393	<0.001
	after removal of axis 1	0.206	<0.001
	after removal of axes 1 and 2	0.130	<0.001
Summer	whole model	0.463	<0.001
	after removal of axis 1	0.264	<0.001
	after removal of axes 1 and 2	0.191	<0.001

* Results of general discriminant analysis (GDA) per season to test whether groups of observations (i.e. availability in Torres del Paine National Park and in non-protected area, and sites selected by guanaco and sheep) could be distinguished on the basis of habitat variables. Values of 1-Wilks' λ indicate the discriminatory power of models in the range of 1 (perfect discrimination) to 0 (no discrimination) for the whole model as well as for the sub-models obtained by removing the respective axis.

Assessing possible overlap in winter between preferred and marginal areas, MANOVA test identified significant differences between preferred areas of guanaco and sheep during both years and on both GDA axes ($F_{2009}=$

13.51; d.f: 2,253; $p < 0.001$; and $F_{2010} = 5.79$; d.f: 2,334; $p = 0.003$) (Fig. 3.4), while for marginal areas significant differences were found on axis 1, during both years (Fig. 3.4). Besides, guanaco marginal areas and sheep preferred areas showed significant differences during both winters, though only for axis 1 (Unequal-N HSD test, $p < 0.001$).

Table 3.3. Matrix of structure coefficients for discriminant axes in each season.

	Winter		Summer	
	Axis 1	Axis 2	Axis 1	Axis 2
Slope (low)	0.376	-0.375	-0.510	-0.185
Slope (medium)	-0.116	0.191	0.267	0.238
Topographic Position (valley bottom)	0.438	-0.311	-0.359	-0.222
Topographic Position (lower hillside)	0.062	0.224	-0.114	-0.221
Topographic Position (upper hillside)	-0.143	0.215	0.194	0.106
Roughness (low)	0.577	0.112	-0.463	-0.237
Roughness (medium)	-0.266	0.230	0.198	0.019
Mean vegetation height	-0.029	-0.153	-0.083	0.487
Maximum vegetation height	0.008	-0.236	-0.051	0.141
Water	-0.071	-0.496	-0.040	0.256
Ground cover	-0.513	-0.056	0.393	0.072
Natural grassland	0.314	0.117	-0.326	-0.083
Managed grassland	0.119	-0.029	-0.169	0.190
Coironal	0.192	-0.109	-0.290	-0.167
Wetland	-0.012	-0.274	0.010	-0.459
Xerophytic scrub	-0.568	0.493	0.696	-0.017
Mata Negra	0.424	0.063	-0.381	0.353
Mesophytic scrub	-0.056	-0.171	-0.024	0.085
Woods	-0.115	-0.441	-0.036	0.383

Absolute values indicate correlation of predictor variables with the respective discriminant axes.

Summer

During summer, habitats selected by guanaco and sheep, as well as those described by the controls inside TPNP and non-protected area, were discriminated by the set of discriminant axes (canonical $r = 0.520$; $p < 0.001$). Of the 6 significant axes, only the first two were chosen owing to their high share (69%) of discriminant power (Table 3.2). Topographic variables (slope -flat-, position -valley bottom- and roughness -low-) and three coverage types (bare soil, xerophytic scrub cover and mata negra) were the most important variables to discriminate among groups in the first axis (Table 3.3). In the second, the variables with the greatest weight were wetlands, woods and mata negra, and mean vegetation height (Table 3.3). As

3. NICHE SEGREGATION BETWEEN GUANACO AND SHEEP IN CHILEAN PATAGONIA

in winter, the first axis segregated the sites selected by guanacos and the habitat availability inside the TPNP from those selected by sheep and from the availability in the non-protected area ($F_{MANOVA}=94.56$; $p<0.001$). The second axis discriminated between habitat selection of both species and environmental availability ($F_{MANOVA}=25.07$; $p<0.001$).

Summer habitat availability (in terms of control sampling points in each zone; Table 3.4) was different between TPNP and non-protected areas (differences attributed to axis 1; Fig. 3.5). The sites used by sheep only showed significant differences with habitat availability in non-protected areas on axis 2, both in 2009 and 2010 (Fig. 3.5). In addition, they segregated of the sites selected by guanaco (inside TPNP and in non-protected area) on axis 1 in both years (Fig. 3.5). Sites used by guanaco in non-protected area did not differ between years, and inside the TPNP inter-annual differences were found only on the first axis (Fig. 3.5). Finally, sites selected by guanacos were significantly different from habitat availability in

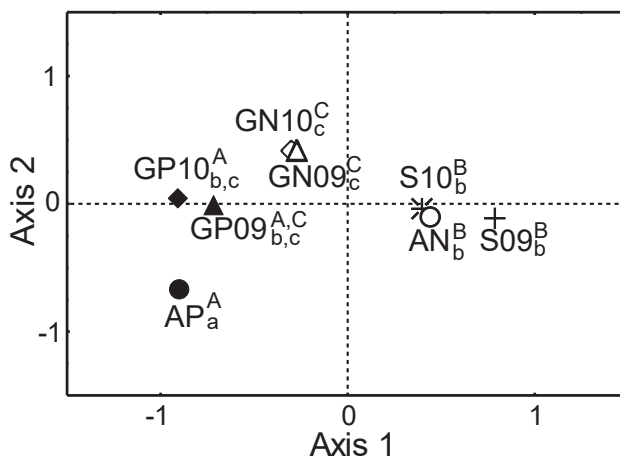


Figure 3.3. Results of the General Discriminant Analysis (GDA) in winter. Centroids of the observation groups are shown in the space defined by the first two discriminant axes of GDA. AP: Habitat availability in Torres del Paine National Park (TPNP); AN: Habitat availability in non-protected area; GP09: guanaco in TPNP in 2009; GP10: guanaco in TPNP in 2010; GN09: guanaco in non-protected area in 2009; GN10: guanaco in non-protected area in 2010; S09: sheep in non-protected area in 2009; S10: sheep in non-protected area in 2010. Different letters indicate significant differences between groups in first (superscript) and second axis (subscript) in MANOVA analysis according to the Unequal-N HSD post-hoc test ($p<0.05$).

both areas and years (except in the case of guanacos in the TPNP in 2010, which showed significant differences with habitat availability only on axis 2; Fig. 3.5).

Assessing possible overlap in summer between species in preferred and marginal areas, the emerging pattern displayed significant differences between guanaco and sheep in their preferred areas in both years restricted to the first axis ($F_{2009}=18.17$; d.f: 2,387; $p<0.001$; and $F_{2010}=11.42$; d.f: 2,452; $p<0.001$; Fig. 3.6). In the case of marginal areas, species differed in the two axes in 2009 and on the first axis in 2010 (Fig. 3.6).

3.4 Discussion

The results show that habitat selection by guanaco in summer and in winter differs from sheep selection at a fine scale, in spite of their spatial aggregation

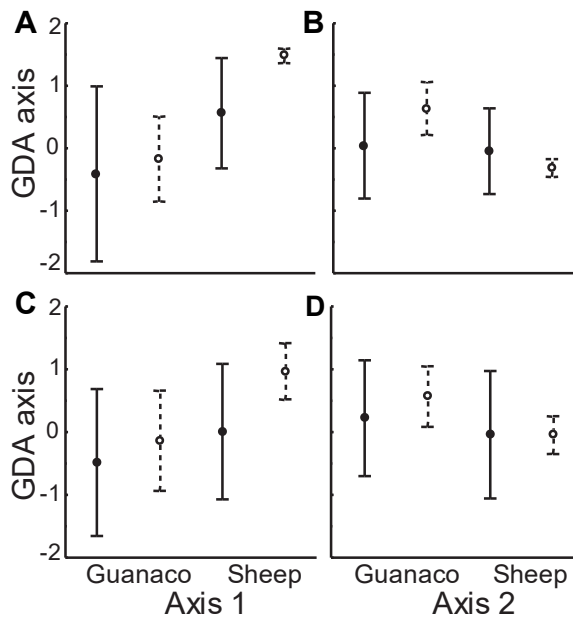


Figure 3.4. Habitats used by guanaco and sheep in winter. Means and standard deviations of canonical scores for preferred and marginal areas of guanaco and sheep in the first two axes defined by GDA in non-protected areas in winter 2009 (A, B) and winter 2010 (C, D). Filled circle and solid line represent marginal areas. Open circles and dotted line represent preferred areas.

3. NICHE SEGREGATION BETWEEN GUANACO AND SHEEP IN CHILEAN PATAGONIA

at a landscape scale during three of the four seasons. In addition, this study allows a comparison of guanaco habitat selection in presence and absence of livestock, thanks to the presence of a control situation (inside TPNP) where the domestic species is absent. Thus, we found that guanaco did not modify its habitat selection in the presence of sheep, suggesting that the potential for competition between these species is low.

The spatial aggregation at landscape scale showed by guanaco and sheep, at least for three of the four seasons analysed, suggests the possibility for competition between both species at that scale. However, differential habitat use at a fine scale and selectivity in comparison with availability by the two species points to a low intensity of interaction between them in the present situation. Sheep displayed generalist behaviour, selecting in accordance with the available habitat, and, on a scale of tens of meters, habitats used by sheep differed from those of guanaco. On the contrary, habitats selected by guanacos differed from availability and they were similar both inside and outside the TPNP. These facts suggest a competition-free habitat selection by the wild herbivore.

The observed differences in habitat selection of co-occurring species have been attributed to different mechanisms: competitive displacement,

Table 3.4. Seasonal habitat availability in Torres del Paine National Park (TPNP) and in the non-protected area.

	Winter		Summer	
	TPNP	Non-protected area	TPNP	Non-protected area
Slope (classes 1-3)	1.68	1.45	1.73	1.42
Topographic position (classes 1-4)	2.27	1.91	2.14	1.85
Roughness (classes 1-3)	1.66	1.20	1.64	1.22
Mean vegetation height (cm)	33.4	29.7	37.6	39.4
Maximum vegetation height (cm)	93.0	80.9	107.5	101.1
Water (%)	6.83	2.70	2.64	1.23
Ground cover (%)	15.83	6.35	11.16	7.24
Natural grassland (%)	19.64	32.65	28.58	36.91
Managed grassland (%)	0.00	0.92	0.00	3.42
Coironal (%)	12.04	17.11	9.49	11.51
Wetland (%)	5.15	1.97	3.30	1.42
Xerophytic scrub (%)	31.24	17.42	29.24	15.96
Mata Negra (%)	0.60	16.94	8.10	15.86
Mesophytic scrub (%)	4.15	2.54	4.22	4.30
Woods (%)	4.51	1.42	3.27	2.15

Values are expressed as percentages, except topographic and physiognomic variables.

plasticity or differential selection, among others (Stewart et al. 2002, Sitters et al. 2009). However, the absence of control situations in most studies makes it impossible to determine whether the apparent displacement of wild species towards suboptimal areas actually responds to some of them or to factors related to human activity difficult to quantify (Pedrana et al. 2010, Soler Esteban et al. 2012). It has been reported that large herbivores modify their behaviour, diet and/or habitat selection in the presence of livestock, trying to avoid it (Baldi et al. 2001, Namgail et al. 2007, Borgnia et al. 2008). In this sense, a clear advantage of the present study is that it was possible to compare the guanaco habitat selection in both scenarios (with and without sheep) at one time and place. Guanaco showed a pattern of habitat selection consistent between years and seasons. According to previous studies, it selected open areas with abundant bare soil and small-size vegetation where a trade-off is reached between food availability and good visibility to reduce predation risk (Raedeke 1982, Bank et al. 2003, Sosa and Sarasola 2005,

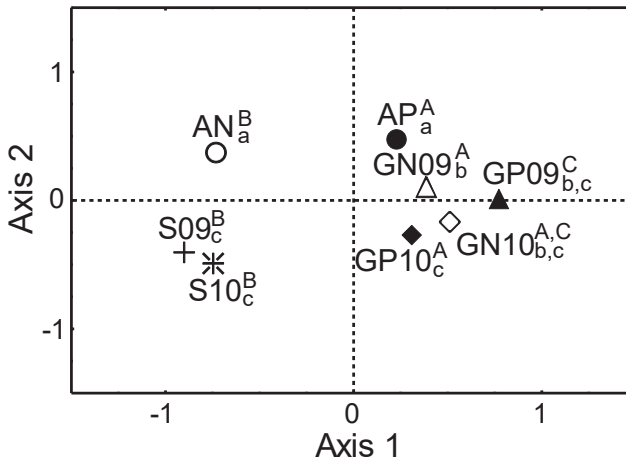


Figure 3.5. Results of the General Discriminant Analysis (GDA) in summer. Centroids of the observation groups are shown in the space defined by the first two discriminant axes of GDA. AP: Habitat availability in Torres del Paine National Park (TPNP); AN: Habitat availability in non-protected area; GP09: guanaco in TPNP in 2009; GP10: guanaco in TPNP in 2010; GN09: guanaco in non-protected area in 2009; GN10: guanaco in non-protected area in 2010; S09: sheep in non-protected area in 2009; S10: sheep in non-protected area in 2010. Different letters indicate significant differences between groups in first (superscript) and second axis (subscript) according to Unequal-N HSD post-hoc test ($p < 0.05$).

3. NICHE SEGREGATION BETWEEN GUANACO AND SHEEP IN CHILEAN PATAGONIA

Acebes et al. 2010). This selection pattern was similar in TPNP and in non-protected area, indicating that guanaco did not modify its habitat selection despite the presence of livestock (Ovejero et al. 2011, Acebes et al. 2012, Soler Esteban et al. 2012). Nevertheless, the use of hillsides and sloppy terrain, rather than the flattest areas, could reflect some undetected factor that, at least in the non-protected area, may be associated with poaching or other human activity (see discussion below).

The low level of overlap between species in habitat selection at a fine scale shown here may be due to the fact that habitat diversity in the area allows them to make differential exploitation of available resources (Sitters et al. 2009, Soler Esteban et al. 2012). Segregation at this scale was maintained throughout the year, even in winter, when the reduced availability of trophic resources could lead to a higher overlap in habitat use (Soler Esteban et al. 2012). Segregation was found between guanaco and sheep both in pre-

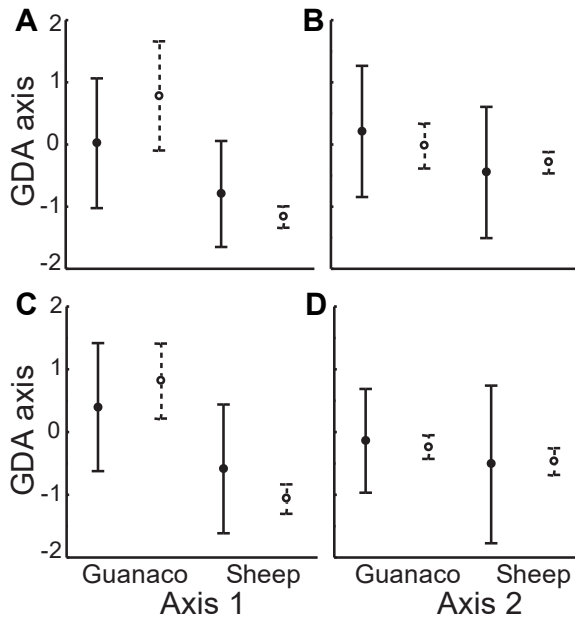


Figure 3.6. Habitats used by guanaco and sheep in summer. Means and standard deviations of canonical scores for preferred and marginal areas of guanaco and sheep in the first two axes defined by GDA in non-protected areas in summer 2009 (A, B) and summer 2010 (C, D). Filled circle and solid line represent marginal areas. Open circles and dotted line represent preferred areas.

ferred and marginal areas, as well as between guanaco marginal and sheep preferred areas. Hypothetically, this segregation pattern could be attributed to a high plasticity in resource use by guanaco, which could have shifted its realized niche towards habitats unused by sheep. However, the similarity between guanaco selection both inside and outside the protected area supports that guanaco did not modify its habitat selection due to livestock.

On the other hand, it does not appear that, in this case, the lack of interaction is due to low densities of the species, as suggested by Acebes et al. (2012). In fact, the density of guanacos in the non-protected area (10.4 animals/km²; Iranzo et al., unpublished data) falls within the range described in other areas of Patagonia where these two species coexist (Baldi et al. 2001, Soto 2010, Thüngen and Lanari 2010), and the density of sheep is close to the sustainable stocking density in the area (Soto (SAG) pers. com.). This fact supports the idea that conditions are adequate in our study area to detect potential for competition between species, should this occur. Moreover, Patagonia has suffered an important desertification process as a consequence of the excessive density of sheep since the end of the 19th century (Soriano and Movia 1986, Adler et al. 2005, Chartier and Rostagno 2006, Thüngen and Lanari 2010). A side effect of this has been a considerable loss of stocking capacity in the system, affecting the livestock production system as well as wildlife. In this context, studies such as this one, conducted in natural conditions with relatively high herbivore densities, are of particular interest in learning about the dynamics of ecosystems (Acebes et al. 2012, Burgi et al. 2012).

This study, therefore, provides a new perspective: differences in habitat use at a fine scale by sympatric guanaco and sheep in Patagonia reflect a differential selection process. These results, based on habitat use, complement studies on diet that showed a high degree of coincidence between both species (Bonino and Pelliza-Sbriller 1991, Puig et al. 2001, Baldi et al. 2004), and indicate that they may share trophic but not spatial resources at least under relatively high habitat heterogeneity. Nevertheless, it should be noted that habitat selection may be somewhat affected by pressure exerted by shepherds on the native species (Pedrana et al. 2010, Burgi et al. 2012). Such harassment takes the form of poaching or persecution, which could lead guanacos to avoid some habitats and move to sub-optimal areas where human pressure is lower (Baldi et al. 2001, Pedrana et al. 2010, Acebes et al. 2012, Burgi et al. 2012). Malo et al. (2009) showed that the flight distance of guanacos in little-frequented areas was much greater than that of those in more

frequented areas, which points to a certain harassment effect from farmers and some degree of habituation to TPNP visitors by guanacos.

Finally, it must be taken into account that studies in natural conditions, such as this one, are subject to certain limitations that must be assumed as unavoidable since it is the only feasible way to study the interaction between large vertebrates, and the effects of livestock farming on wildlife (Baldi et al. 2001, Mishra et al. 2004, Kutt and Gordon 2012). These limitations are reflected, in this case, in certain differences in the proportions of available habitats inside the TPNP and the non-protected area, although this is not considered to have relevant impacts on the results obtained given consistency in guanaco habitat selection between zones and throughout the seasons and the vast area covered by the study.

In conclusion, the results show that there is low overlap between habitat used by guanaco and sheep at a fine scale, suggesting that, at present, there is low potential for competition between them. However, under different conditions, such as in sites with low habitat heterogeneity or with higher livestock pressure, as happened a few decades ago, the potential for competition may increase up to the triggering of demographic consequences on the species. Therefore, it would be interesting to further study the dynamics of the system in the face of potential future changes.

3.5 Acknowledgements

We would like to thank CONAF (Corporación Nacional Forestal) and SAG (Servicio Agrícola y Ganadero, Ministerio de Agricultura, Chile) for their permission and support to conduct this study. Specially thanks to N. Soto and A. Kroeger for their collaboration and M.A. Vukasovic and N. Fuentes for their great help in the fieldwork. We are also grateful to the staff at the Torres del Paine National Park, ranchers from Torres del Paine municipality (XII Region, Chile), everyone else who helped us in fieldwork and the two anonymous reviewers who provided useful comments for the manuscript.

CAPÍTULO 4

Realised niche changes in a native herbivore assemblage associated to the presence of livestock

Juan Traba, Esperanza C. Iranzo, Carlos P. Carmona and Juan E. Malo ¹

¹Manuscrito en segunda revisión: Traba, J.; Iranzo, E.C.*; Carmona, C.P. and Malo, J.E. (under review) Realised niche changes in a native herbivore assemblage associated to the presence of livestock. *Oikos*.

Abstract

Habitat partitioning is a common ecological mechanism to avoid competition among coexisting species and species introduction in already conformed assemblages can increase competitive pressures. However, comparable situations of species in allopatry and sympatry are scarce and consequently to discern whether niche segregation arises from competition or from different habitat preferences is usually unfeasible.

Here, we analyse niche relationships in an assemblage of native and introduced herbivores in Southern Patagonia. We test if niche overlap is higher between native and domestic herbivores than between natives as expected from the relatively short time of coexistence and we evaluate the effect of intra and interspecific competition in niche breadth. We have used a probabilistic multidimensional approach and null models to evaluate overlap and changes in niche dimensions.

Overlap among native species was low as expected for species coexisting in evolutionary time. The overlap between native-domestic species pairs was higher than between only natives, although showing a niche segregation that suggests niche differentiation in ecological time. Moreover, the introduction of domestic species caused niche narrowing of both native and introduced species, revealing interspecific density-dependent effects on their habitat niche during resource shortage periods.

Keywords: Competition, Habitat segregation, Niche breadth

4.1 Introduction

Competition is a main force driving ecological and evolutionary changes of community structure and organization (MacArthur and Wilson 1967, Chase and Leibold 2003). Under the selective pressures imposed by competition, species can diverge in key factors such as habitat use or trophic preferences (Chase and Leibold 2003, Bolnick et al. 2010). As a result, niche segregation and resource or time partitioning may allow the stable coexistence of species (Chesson 2000, Di Bitetti et al. 2009) and those coexisting in evolutionary time can show substantial differences in critical dimensions of their niches (niche compression hypothesis, sensu MacArthur and Wilson 1967). Such niche differences can also be accompanied by phenotypic shifts of the species which further facilitate their ecological segregation (Prins and Olf 1998, Chesson 2000).

Habitat partitioning is one of the most common ecological mechanisms to reduce overlap and avoid competition among coexisting species (Rosenzweig 1981, Morris 2009, Traba et al. 2015). Habitat selection drives the distribution of organisms among habitats depending on their preferences on biotic and abiotic factors, including foraging, competing and antipredatory strategies (Chase and Leibold 2003), and these factors can be considered independent niche dimensions (Schoener 1989, Holt 2009). Consequently, habitats can be interpreted in terms of multidimensional realised niches (sensu Hutchinson 1957, Soberón 2007, Traba et al. 2015). In the case of species coexisting in evolutionary time, habitat segregation with no apparent interaction can mirror competition in the past (Rosenzweig 1981, Morris 1988, Prins and Olf 1998). However, apparent non-competitive coexistence can be observed when asymmetric competition occurs, i.e. when species differ in their respective competitive abilities, one being the dominant and other the subordinate, leading to an unequal fitness output (Morris 1988, Mayfield and Levine 2010). Thus, subordinate species can be completely displaced towards one particular habitat (Codron et al. 2011, Zhang et al. 2015), masking current competition, especially when species show large morphological differences (Mayfield et al. 2010).

Low niche overlap between similar coexisting species can therefore be due either to past competition or to competition operating in ecological time, and observed patterns of species segregation can wrongly lead to the conclusion that competition is no longer operating. Although this is a common ground in theoretical ecology, discerning whether observed habitat segregation arises from context driven differences of habitat selection or from evolutionary divergence of habitat use in response to past competition is not

usually feasible (the ghost of competition past, Connell 1980). In these cases, a single estimation of niche overlap among coexisting species does not yield sufficient information, and species niches must be analysed in different scenarios to unravel the intensity of current competition.

Niche theory states that niche breadth also varies according to a balance between intra and interspecific competition. While the first one would force niche expansion (Bolnick 2001, Morris 1988, Svanbäck and Bolnick 2007), interspecific competition would constrain it and facilitate coexistence between competitors (Rosenzweig 1981, Schoener 1989). For instance, the ecological release from a competitor is expected to cause niche expansion in the remaining species, because of the potential to use additional resources previously inaccessible (Schoener 1989, Bolnick et al. 2010). Conversely, increases in the density of heterospecific competitors reduce habitat niche breadth due to a lower proportional use of shared habitats (Morris 2009).

Changes in niche dimensions due to competition can be analysed by comparing allopatric and sympatric situations, since competition modifies the proportional use of habitats by species and it sometimes leads to the exclusion from some of them (Adams 2004, Codron et al. 2011). However, niche segregation between competitors is not always absolute and a variable degree of niche overlap can be observed in nature even under heavy competition (May and MacArthur 1972, Codron et al. 2011). Thus, the degree of niche overlap between competing species can be informative of the intensity of interspecific competition (Chesson 2000).

Accordingly, only experimentation either by removal or by introduction of competitor species could help to solve this issue, but such experiments cannot be conducted in most ecological communities. Valuable pseudo-experimental exceptions are those of reported introductions, where allochthonous species have been inserted during recent times in native assemblages (Stewart et al. 2002, Madhusudan 2004, Stuart et al. 2014). When non-affected remnant areas persist, variations in the realised niche of the autochthonous species assemblage between contrasting situations can be analysed, and hypothesis about niche changes tested.

Here, we analyse niche relationships in a complex assemblage of native and introduced herbivores in Southern Patagonia. During the last years of nineteenth century, the first hundreds of sheep were introduced in Southern Patagonia (Soriano and Movia 1986). Seventy years after the introduction, sheep population had grown steeply until 50 million individuals, and populations of native herbivores, especially guanaco (*Lama guanicoe*), dramatically decreased in parallel due to competition with livestock, poaching

and habitat degradation (Raedeke 1982). Nowadays, no more than 2.2 million sheep remain in the Chilean Patagonia. Populations of guanaco and other native herbivores are experiencing a steadily increase, especially in the protected areas where livestock is excluded, allowing the recolonization of their surroundings (E. C. Iranzo et al. unpublished manuscript). In some areas of Magallanes (Chile) a semi-natural experiment can be analysed: within the protected areas, only wild herbivores are found, while in the surroundings, autochthonous and allochthonous herbivores live in sympatry in different densities.

Methods for measuring niche breadth and overlap have rapidly evolved over the last years (Mouillot et al. 2005, Geange et al. 2011, Blonder et al. 2014, Carmona et al. 2016a, Tarjuelo et al. 2016). Specifically, multivariate kernel density estimation (KDE) techniques allow comparison among several niche dimensions simultaneously (the niche concept sensu Hutchinson 1957, see also Soberón 2007), being then more realistic since they incorporate the multiple interacting niche dimensions that truly modulate species coexistence (Carmona et al. 2016a). In addition, KDE can deal with non-normal distributions and covariance between niche dimensions (Mouillot et al. 2005, Geange et al. 2011, Laughlin and Messier 2015). So, quantification of niche relationships in complex assemblages may be better understood from multi-dimensional niches, whenever these niche dimensions have ecological meaning and are not redundant for the species (Blonder et al. 2014).

We use a multidimensional approach based on KDE and null models to evaluate changes in the niche associated to the presence of domestic competitors in an herbivore assemblage where livestock was introduced 130 years ago. In addition, and for the two most common species, we analyse niche changes in a set of contrasting situations regarding differences in their densities. Based on the "niche compression hypothesis" (MacArthur and Wilson 1967), we predict: i) the presence of niche segregation among wild autochthonous species, as expected for an assemblage competitively structured under an evolutionary time scenario. Anyway, ii) some degree of niche overlap will exist between these species, and this will be larger under more stressing conditions as resource shortage. In addition, iii) we predict a larger niche overlap between native and domestic species, due to the relatively short time of coexistence among them. Accordingly, niche overlap between native and domestic species will be larger under more stressing conditions.

We then analyse if guanaco's niche experiences ecological release by measuring changes on niche breadth between situations of allopatry and sympatry with its main domestic competitor, sheep. In this case, we expect iv) larger

guanaco's niche breadth in the absence of sheep due to the removal of competitive restrictions to habitat use. On the contrary, and following again the "niche compression hypothesis", we expect that v) both the native, guanaco, and the domestic species will show narrower niches due to a reduction in habitat use when they are in sympatry (MacArthur and Wilson 1967), being this modulated by the density of con- and hetero-specifics. Increased density of conspecifics should increase niche breadth, while increased density of the competitor species should decrease it, due to lower proportional use of the shared habitat (Morris 2009).

4.2 Materials and Methods

Study area

The study was conducted in Torres del Paine National Park (TPNP) and its surroundings (Fig. 4.1; Magallanes Region, Chile, 51°3'S 72°55'W). The study area is around 1090 km² (284 km² within the TPNP and 806 km² of the neighbouring ranches), with a temperate-cool climate without dry season. Annual rainfall varies between 300 and 1000 mm and mean temperature ranges from 2°C in winter to 10.8°C in summer (Vidal and Reif 2011). Dominant vegetation consists of steppe-like grasslands and shrublands. This study differentiated 10 habitat types (Supplementary material Appendix A Table A.1), most of them defined by plant communities. A detailed description of habitats can be found in Iranzo et al. (2013).

While no livestock is found within TPNP, the surroundings are private owned ranches dedicated to extensive livestock farming, mainly sheep (*Ovis aries*), with a density of 57-84 sheep/km², although varying across sectors (E. C. Iranzo et al. unpublished manuscript). Cattle (*Bos taurus*) and horses (*Equus caballus*) can be also found, although in much lower densities. Sheep graze freely in large pasture paddocks up to several square kilometers without the continuous presence of shepherds. They are moved between pasture paddocks twice a year and shepherds occasionally visit flocks to verify that animals are in good condition. Both within and outside the protected area, a native assemblage of medium- to big-sized herbivores can be found, especially guanaco, lesser rhea or ñandú (*Pterocnemia pennata*) and upland goose or caiquén (*Chloephaga picta*). European hare (*Lepus europaeus*) is also present in the study area as an introduced and naturalised species. However, it has been deliberately excluded from the study because of its nocturnal habits. A 1-1.2 m fence, which allows movements of wildlife but

not livestock, encircle the protected area. Wild herbivores thus coexist with livestock only outside TPNP. Guanaco density varies from 36.6 (within) to 8.8 (outside TPNP) animal/km² (E. C. Iranzo et al. unpublished manuscript) and the density of other wild herbivores is much lower.

Species and habitat data

Sampling of herbivores was conducted during the winters and summers of 2009- 2011. Winter is the season with shortage of resources due to harsh climate conditions, whereas in summer the situation reverses. In each of the six sampling seasons, all existing roads and paths in the TPNP were travelled by vehicle or on foot (N=12; 76.6 km/season), as well as those in the non-

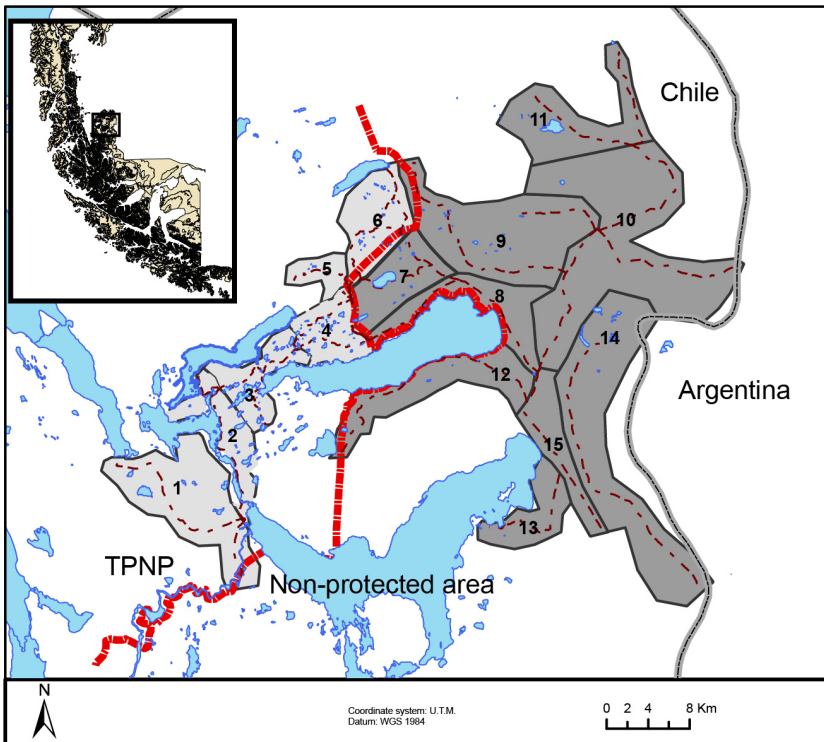


Figure 4.1. Location of study area (shaded area) in the Comuna Torres del Paine (Region of Magallanes, Chile). Red dashed line indicates Torres del Paine National Park (TPNP) boundary. Black dashed lines show the surveyed road network. Solid lines indicate different sectors (1-15).

protected area (N=17; 221.8 km/season). Both driving or on foot methods are considered comparable since they do not disturb animal behaviour or habitat selection in the study area, where animals show short flight distances (Malo et al. 2011). Sampling was carried out during daylight hours, avoiding sunrise and sunset. Each animal or group of animals was georeferenced with a GPS. To describe habitat use by each animal or group of animals, we considered a 50m radius around the centroid of the point where they were initially observed, and recorded the following descriptors: habitat composition (percentage cover of 10 different habitat or vegetation types), topography (3 categorical variables) and physiognomy (2 continuous variables, Supplementary material Appendix A. Table A.1).

To determine habitat availability and the total habitat niche available, both in winter and summer, and both within and outside the protected area, we travelled the same roads and paths, measuring the same environmental variables independently of animal presence. Every 1000 m we sampled two control points, at 100 m and 250 m on each side of the road-path alternately (194 and 394 sampling points in winter in TPNP and non-protected area, respectively; 222 and 366 sampling points in summer in TPNP and non-protected area, respectively). Habitat description in control points followed the sampling procedure described above. Control plots were classified as either winter or summer, and within or outside TPNP to test for differences in habitat availability between seasons and areas.

Niche dimensions

We performed a General Discriminant Analysis (GDA; Anderson and Robinson 2003) with habitat variables in order to summarise habitat variation across all study sites and years and to unravel ecological gradients which could be interpreted as niche dimensions for the species. GDA combines predictor variables on a reduced number of axes, orthogonal to each other, and allows the detection of differences between a priori defined groups. These axes can be interpreted as niche dimensions, as they include information of original variables related to the habitat used by animals. To know the relative weight of each axis to the overall discrimination power of the model, 1-Wilks' λ statistic was used. Values of 1-Wilks' λ indicate the discriminatory power of models in the range of 1 (perfect discrimination) to 0 (no discrimination). Axes contributing more than 10% of total discriminatory power were retained for further analyses. GDA analyses were performed separately for each season due to the strong differences in habitat availability

and animal use between winter and summer. Guanaco observations within and outside TPNP were treated independently in order to assess differences in niche dimensions of guanaco attributable to the presence of domestic species in the non-protected area. The analysis thus considered 7 different groups: guanaco within TPNP; guanaco outside TPNP; sheep, cattle and horse (just in the non-protected area); lesser rhea and upland goose (indistinctively within or outside, due to the relatively low number of sightings).

We calculated a probabilistic niche (Carmona et al. 2016a) for each of the 7 groups of analysis and seasons (summer and winter) using KDEs (Duong 2016, Carmona et al. 2016a). The use of KDEs generates smooth probability functions that avoid the assumption that the values of species in the GDA axes are normally distributed, and provide a better estimation of the niche breadth and overlap than Gaussian distributions (Mouillot et al. 2005, Geange et al. 2011). We used the R package 'ks' (Duong 2016) to estimate diagonal and unconstrained data-driven bandwidth matrices for the tree-dimensional KDEs. To account for the uneven size of observations and modulate the relevance given to very large groups, KDEs were weighted by the log of the number of individuals in each observation. We applied a 5% threshold to the resulting probability density function for each group, thus retaining a 95% of the total probability in order to avoid the influence of outlier observations (e.g. Blonder et al. 2014, Traba et al. 2015), and setting the probability of all the rest of the niche space to 0. After applying the threshold, the probability density functions were rescaled so that they integrated to 1, thus easing the interpretation of niche overlap between species. Overall, this approach may better reflect the process of individual habitat choice than single-variable niche spaces (one-dimensional KDE) used in other studies (e.g. Benítez-López et al. 2014, Traba et al. 2015, Tarjuelo et al. 2016).

We then used these probability density functions to estimate the niche breadth of each group, as well as niche overlap between groups. Niche breadth was calculated as the size of the region of the niche space where the rescaled probability density function is greater than zero, indicating a relevant probability for the considered species to be present in such conditions (this corresponds with functional richness in Carmona et al. 2016a). Niche overlap was estimated as the sum of the (rescaled) probabilities associated to the smaller of the considered species' specific probability density functions at each point of the GDA space (i.e. the probability under the smaller of different species' specific density functions, Mouillot et al. 2005, Carmona et

al. 2016a). A value of 0 indicates no overlap whereas a value of 1 reflects complete niche overlap. Overlap data are presented as percentages.

In order to evaluate the predicted effect of conspecifics (expansion) and heterospecifics (contraction) on the niche breadth of guanaco and sheep, we used the procedure described above to calculate niche breadth for both species in 15 different sectors in the study area. These sectors were defined attending to geographical, topographical and physiognomic similarity, and showed differences in herbivore abundances (Fig. 4.1; Supplementary material Appendix B. Tables B.1 to B.3). We used only guanaco and sheep data, the main herbivore species in the area, as the number of observations per sector for the rest of the species was too low. We excluded sectors with less than 10 observations of the considered species in order to avoid the potential effect of a low number of observations on the niche dimensional volume. No significant correlation was found between niche breadth and number of observations in the retained dataset (winter: Pearson $r = -0.051$; $n=15$; $p = 0.857$; summer: Pearson $r = -0.343$; $n=11$; $p = 0.303$), suggesting that the niche breadth estimated for each sector was not constrained by the number of observations in it. Individual sectors included an average of 76% (winter) and 78% (summer) available habitat according to the GDAs.

Statistical analysis

We evaluated changes in niche overlap between pairs of species and we also compared guanaco within and guanaco outside the protected area to inform the sympatry vs. allopatry change. Overlap among species was computed according to the procedure described in Carmona et al (2016a). In order to evaluate if an observed overlap was different from random, we followed the null-modelling approach proposed by Geange et al. (2011). For each comparison, the observations from both species were thus pooled and the species' labels randomised. We performed a total of 200 randomizations for each comparison, calculating each time the overlap between the simulated probability density distributions. This procedure allowed us to assign a raw p-value to each comparison by ranking the observed overlap value against the simulated ones, and final p-values were computed using the Hochberg correction (Legendre and Legendre 2012). Significant differences for a given pair imply that the observed overlap is significantly smaller than that expected by random (i.e. segregation occurs). All calculations were performed in the R environment (v.3.2.0, R Core Team 2015).

We estimated the effect of herbivore abundance (both con- and heterospecific) on habitat niche breadth of guanaco and sheep using General

Linear Models (GLMs) with Gaussian error distribution. The value of niche breadth of each species per sector was included as response variable, and guanaco and sheep abundances per sector as explanatory variables. We used the guanaco and sheep kilometric abundance index (KAI, number of observed animals/km) for each of the 15 sectors as an estimate of herbivore abundance. We selected explanatory variables using a backward stepwise procedure. We performed analysis for winter and summer separately due to differences in resource availability between seasons (Iranzo et al. 2013). GLMs were done with "lme4" package in the R environment (v.3.2.0, R Core Team 2015). Residuals of GLMs were tested a posteriori for the presence of spatial autocorrelation using a Moran's-I correlogram. We found no such spatial relationship, so we could discard any effect of spatial autocorrelation in our results. Specifically, neither in guanaco nor in sheep niches, the Moran's-I correlogram reached significance thresholds at any of the 5000m wide lag distance classes used. We assumed randomly distributed data and carried out permutation tests with 999 permutations. We ran these tests under Passage software (Rosenberg and Anderson 2011). To facilitate the understanding of the set of statistical analyses done, we summarised the process in the Supplementary material Appendix C. Fig. C.1.

4.3 Results

Throughout the six seasons, 3,051 groups of animals of the six species were sighted, totaling more than 146,700 animals (Supplementary material Appendix D. Table D.1). The more abundant species was sheep (in average 135 groups, with 21,133 animals, in summer by year; 162 groups, with 16,840 animals in each winter). Guanaco was the second in abundance (268 groups, with 2,527 animals in average by summer; 167 groups, with 4,004 animals in each winter). Other species were much less abundant (Supplementary material Appendix D. Table D.1).

GDA analysis - habitat niche dimensions

According to Wilks' λ , the discriminatory power of the GDAs in both seasons was determined by the first three axes (Supplementary material Appendix E. Table E.1). GDA models allowed clear discrimination between all species both in winter and in summer, as previously reported in an evaluation of habitat selection by guanaco and sheep in the same area (Iranzo et al. 2013).

In winter, habitats used by all species were differentiated by the full set of discriminant axes (canonical $r=0.530$; $p<0.0001$). Of the five significant axes, the first three retained 91.2% of the variance (canonical $r = 0.328$; $p<0.0001$; Supplementary material Appendix E. Table E.1). In winter, the first GDA axis (winter GDA 1) was positively correlated with natural grasslands, on flat, valley bottom positions, and negatively with xerophytic scrub. The second axis (winter GDA 2) was positively correlated with the presence of water, and negatively with mata negra shrubs. Finally, the third axis (winter GDA 3) showed a gradient from natural to managed grasslands, mata negra and water presence (Supplementary material Appendix F. Table F.1).

In summer, habitats were differentiated by the full set of discriminant axes (canonical $r = 0.657$; $p<0.0001$). Again, the first three axes were very explicative, absorbing 95.3% of the variance (canonical $r = 0.438$; $p<0.0001$; Supplementary material Appendix E. Table E.1). In summer, the first GDA axis (summer GDA 1) was positively correlated with water, on flat, valley bottom positions, and negatively with xerophytic scrub. The second axis (summer GDA 2) was again positively correlated with water, and negatively with mata negra, and the third axis (summer GDA 3) showed a gradient from forests to coironal (Supplementary material Appendix F. Table F.1).

Both for winter and summer, the first three GDA axes reflected the most important habitats used by the species and year was a non-relevant variable. Therefore, we built a probability density function for each species and season, which we used to evaluate niche overlap and breadth in these three niche dimensions.

Niche compression and ghost of competition past hypotheses

Inter-seasonal mean niche overlap between native and domestic herbivores (44.2%) was higher than that among only native species (30.2%), as expected in a non-evolutionary assemblage (Table 4.1).

Native species were anyhow not completely segregated, as expected in the niche overlap hypothesis. Mean overlap between pairs of native species was higher in summer (34.3%) than in winter (26.0%). However, the whole wild assemblage overlapped only in 8.7%, indicating that the shared niche among the three native species was remarkably low (Fig. 4.2). Besides, all the comparisons between pairs of native species showed a significantly lower overlap than expected by chance (Table 4.2), both for winter and summer, as expected in a competitively segregated assemblage.

Mean overlap between domestic species was higher than between natives, and it was larger in winter than in summer (Table 4.1; Supplementary

material Appendix G. Fig G.1). However, nearly all comparisons between domestic species, both for winter and summer, showed an overlap significantly lower than expected (Table 4.2).

Contrary to our expectations, nearly all comparisons between native and domestic species showed a significant lower overlap than expected by random (Table 4.1). Only the comparison between lesser rhea and sheep, both for winter and summer, and between lesser rhea and cattle, only for winter, showed a degree of overlap similar to random expectation (Table 4.2).

Effect of habitat availability

Habitat availability differed between seasons, and between the protected area and the surroundings, as the overlap in niche availability was lower than expected by random. Despite these differences, available niche overlap between within and outside locations was near 50% (Table 4.2). Remarkably, habitat availability outside the TPNP did not differ from the overall habitat availability (Table 4.2), thus suggesting that no restrictions of habitat availability in the sympatric situation underlie in our results.

During winter, sheep showed non-significant segregation with habitat availability suggesting a non-selective habitat selection during this season. During summer, however, the three domestic species overlapped less than expected by random, indicating a differential habitat selection.

All the comparisons between native species and habitat availability, both during winter and summer, showed habitat selection different from availability, as suggested by the lower overlap with habitat availability than expected by random.

Contraction-release of niche breadth

During winter, guanaco showed a large and significant niche contraction when coexisting with sheep, as compared with the situation in allopatry

Table 4.1. Seasonal mean overlap between species calculated for all the possible species pairs.

	Winter	Summer	Mean
Native-Native	26.0	34.3	30.2
Domestic-Domestic	60.1	41.2	50.6
Native-Domestic	45.5	43.0	44.2

(53.63 vs 26.95 GDA units; $p < 0.001$). During summer, small and non-significant differences were found between guanaco niche breadth in allopatry and in sympatry with sheep (26.95 vs 24.04).

Effects of intra and interspecific abundance in niche breadth

During winter, guanaco niche breadth showed some tendency to decrease in areas with higher sheep abundance (KAI sheep: estimate = -0.179; $p = 0.088$) (Fig. 4.3A), although the model was only marginally significant (adjusted $R^2 = 0.19$; $p = 0.088$). During summer, the niche breadth of guanaco

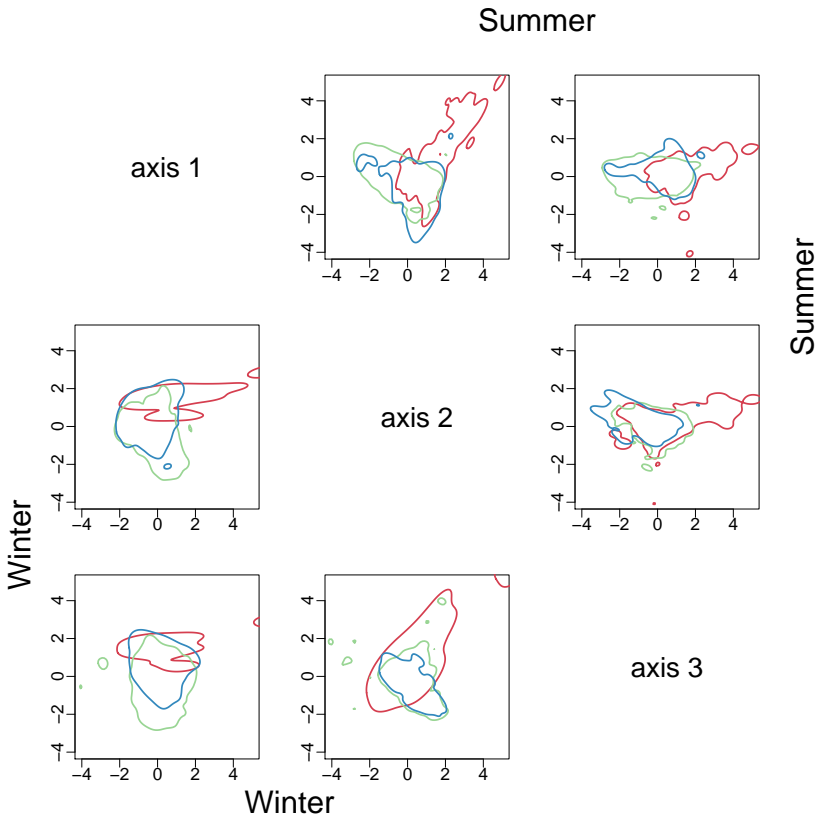


Figure 4.2. Niche overlap among native species both for winter and summer. Red line represents caiquén (*Chloephaga picta*); green line, guanaco (*Lama guanicoe*) and blue line, ñandú (*Pterocnemia pennata*).

showed no changes in relation neither with guanaco nor sheep abundance (adjusted $R^2 = -0.06$; $p = 0.516$).

In the case of sheep, winter niche breadth significantly decreased where guanaco abundance was larger (KAI guanaco: estimate = -0.838 ; $p < 0.05$), being the model very explicative and near significant (adjusted $R^2 = 0.45$; $p = 0.097$) (Fig. 4.3B). During summer, the niche breadth of sheep showed a tendency to decrease at increasing guanaco abundances (KAI guanaco: estimate = -0.318 ; $p = 0.081$), although the model was not significant (adjusted $R^2 = 0.305$; $p = 0.174$).

Table 4.2. Niche overlap between species pairs measured and significance of overlap data according to the null-modelling. P-values were computed using the Hochberg correction.

Assemblages	Pairs of species	Winter		Summer	
		Overlap	p-value	Overlap	p-value
Native-Native	Caiquén - guanaco	0.092	0.030	0.227	0.015
	Caiquén - ñandú	0.274	0.030	0.414	0.015
	Guanaco - ñandú	0.403	0.030	0.374	0.015
	Guanaco within - guanaco outside	0.668	0.030	0.760	0.015
Domestic-Domestic	Cattle - horse	0.625	0.725	0.339	0.015
	Cattle - sheep	0.615	0.030	0.322	0.015
	Horse - sheep	0.582	0.030	0.545	0.015
Native-Domestic	Caiquén - cattle	0.373	0.030	0.360	0.015
	Caiquén - horse	0.317	0.030	0.469	0.015
	Caiquén - sheep	0.261	0.030	0.471	0.015
	Ñandú - cattle	0.611	0.725	0.354	0.015
	Ñandú - horse	0.561	0.030	0.491	0.015
	Ñandú - sheep	0.697	0.725	0.700	0.580
	Guanaco outside - cattle	0.360	0.030	0.216	0.015
	Guanaco outside - horse	0.378	0.030	0.355	0.015
	Guanaco outside - sheep	0.514	0.030	0.351	0.015
	Native-Control	Caiquén - control (total)	0.164	0.030	0.243
Ñandú - control (total)		0.438	0.030	0.345	0.015
Guanaco (total) - control (total)		0.541	0.030	0.483	0.015
Guanaco within - control within		0.451	0.030	0.331	0.015
Guanaco outside - control outside		0.556	0.030	0.440	0.015
Domestic-Control	Cattle - control outside	0.464	0.030	0.370	0.015
	Horse - control outside	0.433	0.030	0.399	0.015
	Sheep - control outside	0.606	0.725	0.419	0.015
Control-Control	Control (total) - control within	0.680	0.030	0.681	0.015
	Control (total) - Control outside	0.801	0.725	0.800	0.580
	Control within- Control outside	0.499	0.030	0.498	0.015

NOTE: Significant differences for a given pair imply that the observed overlap is significantly smaller than that expected by random (i.e. segregation). In bold, non-significant differences

4.4 Discussion

Our main objective was to evaluate how autochthonous species occupy the niche space in an herbivore assemblage, and whether the relatively recent introduction of livestock modifies this occupation. Our analysis of hypervolume habitat niches shows that the native assemblage displayed

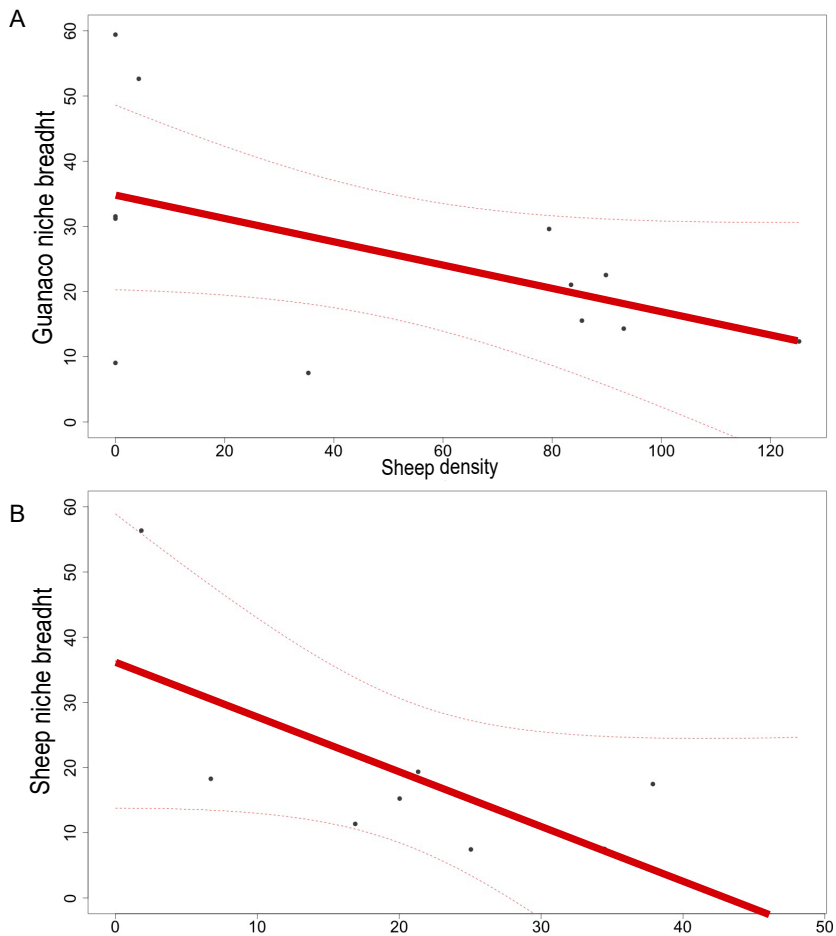


Figure 4.3. A) Effect of winter sheep abundance (KAI sheep by sector) on winter guanaco niche breadth (adjusted $R^2 = 0.19$; $p = 0.088$); B) Effect of winter guanaco abundance (KAI guanaco by sector) on winter sheep niche breadth (adjusted $R^2 = 0.45$; $p = 0.097$).

a pattern consistent with a long-term competitive configuration, as expected for species coexisting in an evolutionary time. Besides, our results exemplify how the recent-time introduction of species in already structured assemblages increases niche overlap between native and domestic species, as predicted. Nevertheless, the consideration of multiple niche axes revealed niche segregation among species even in this case. The segregation detected between nearly all the analysed species in both seasons suggests that herbivores somewhat accommodate their realised niches when in sympatry to share resources.

In addition, we provide empirical evidence of niche contraction of species under competitive pressures. Niche narrowing and segregation seemed to be interspecific density-dependent, while we found no effect of intraspecific niche expansion. In this respect, the differences between seasons suggest that non-competitive coexistence could be occurring during summer, when resource availability is high, but that this situation reverses during the resource-shortage season.

The primary assumption of this work is that habitat is a main component of the ecological niche (Schoener 1989, Chase and Leibold 2003). Interspecific competition is a driver of species coexistence, leading to differential habitat selection after evolutionary time (Rosenzweig 1981, Morris 1988, Stewart et al. 2002). In this sense, long-term coexisting species should show small niche overlap, depicting an apparent non-competitive coexistence (Connell 1980, Rosenzweig 1981, Prins 2000). In our case, the whole native assemblage overlapped only in 8.7% of the niche volume. As predicted, this result shows that native species apparently conform a competitively structured assemblage, according to a scenario of niche compression and segregation associated to a competition past (Rosenzweig 1974, Fischer and Gates 2005). Overlap among pairs of native species was higher during summer than in winter (34.3 vs. 26.0% as an average), a situation related to the higher resource availability during summer. Higher resource availability would reduce the importance of competitive interactions between species, thus allowing an increased overlap among potentially competing species (Ahrestani et al. 2012, Darmon et al. 2012). The lack of effect of the factor "year" indicates the high interannual concordance in habitat selection, and suggests the evolutionary character of this process. In the case of guanaco, within and outside niches showed significantly lower overlap than expected by random, despite the overall overlap was high (71.4%). This was also the case for many other species pairs, which suggests that species segregation is

more easily detected when multidimensional niches are considered (Di Bitetti et al. 2009, Darmon et al. 2012, Djagoun et al. 2013).

The introduction of species in already conformed competitive assemblages could lead to high competitive pressures (Stewart et al. 2002). Accordingly, habitat selection theory states that competition between coexisting species decreases by habitat segregation (Rosenzweig 1981, Morris 1988). We predicted a higher niche overlap between native and domestic herbivores than between pairs of natives as a result of the relatively short time for coexistence, and our expectation was fully met since the overlap between pairs of native and domestic species (44.2% as an average) was higher than between natives (30.2%). Moreover, the overlap between domestic and native species' niches was remarkably high in several cases (Table 4.2), although almost all the comparisons showed niche segregation. Although low overlap can be generally expected when considering multiple niche dimensions (Rosenfeld 2002, Blonder et al. 2014, Carmona et al. 2016a), this result suggests that ecological adjustments are faster than expected and they can be observed even in cases of short-term coincidence of species. Effectively, this means that species quickly modulate their habitat utilization in order to reduce the effects of competition (Madhusudan 2004, Svanbäck and Bolnick 2007, Darmon et al. 2012). This is in agreement with a previous study in the same area showing that guanaco and sheep use different habitats (Iranzo et al. 2013). Interestingly, interseasonal differences in overlap among introduced species (41.2% in summer; 60.1% in winter) runned contrarily to those observed for the native assemblage. This could be a response to human influence, since ranchers move the livestock to lower altitude paddocks in winter, effectively reducing the range of habitats available for domestic animals. However, this could also point to a subadaptation of domestic herbivores to harsh climatic and plant conditions, forcing the animal to share the few good pastures remaining during winter.

In the absence of a control situation, this pattern of differential habitat selection could be interpreted as a non-competitive situation (sensu Connell 1980), where the species assemblage is governed by a "distinct habitat preference organization" (Morris 1988). The guanaco-sheep coexistence would be in this case coincidental, non-competitive (Iranzo et al. 2013). Fortunately, our results comparing allopatric and sympatric situations reveal the niche compression effect of coexistence on both main competing species. Guanaco niche widened in allopatry and compressed in sympatry, although only during resource shortage. This suggests that guanaco modifies its habitat use when it is in sympatry with domestic herbivores, indicating a quick

effect on wild species niche parameters of coexistence with competitors. This also fits the "niche overlap hypothesis" (Pianka 1974), with the niche breadth of competing species narrowing when in coexistence, and expanding after the release from the competitor (Schoener 1989). Different habitat use between protected and non-protected areas could be due to different habitat availability, but total and only-outside habitat availability were similar (Table 4.2) suggesting the absence of habitat restrictions when guanaco and sheep are in sympatry.

Despite we have no similar allopatric situation for sheep, both guanaco and sheep niches showed a tendency to contract due to heterospecific abundance, suggesting that competition is a two-sided process in our study case (Morris 2009). The density-dependent niche contraction of both guanaco and sheep would agree with niche theory's prediction of negative relationships between niche breadth and overlap and the density of heterospecifics, which is indicative of interspecific competition intensity (May and MacArthur 1972, Mwasi et al. 2013). In parallel, density dependent intraspecific competition may lead to the use of suboptimal less-preferred habitats, thus causing a widening of habitat niche (Svanbäck and Bolnick 2007, Tarjuelo et al. 2016). Although we detected no effect of intraspecific competition in niche breadth, the population increase of guanaco observed in sectors allopatric with-sheep (E.C. Iranzo et al. unpublished manuscript) could change this situation in the near future, and these effects would deserve further analysis.

Despite sheep move freely within grazing paddocks across the study area, competition between guanaco and sheep could be modulated by ranchers, as they decide the paddocks to be grazed by livestock. However, both the scale used in this study to estimate habitat use (50m around the centroid of each observation, a microhabitat scale sensu Morris 1988) and the size of grazing paddocks (usually over 2000 ha) reduce this potential effect. Moreover, sheep get scarce attention by ranchers during long time periods and guanaco show unlimited movement within and among paddocks. Thus, both species move freely at the scale of interest in the study with a minimum potential influence of ranchers on the observed habitat use patterns. Other confounding factors like predator density and hunting could modify guanaco habitat selection patterns. The density of puma is higher within the National Park than in the surrounding ranches and that of culpeo fox shows the reverse pattern, but no significant effect of predator densities on guanaco habitat selection pattern has been found (Iranzo et al. in prep.). Regarding hunting, puma and guanaco are protected but subject to some poaching. However,

habitat selection by guanaco seems independent of proximity to villages and to shepherds facilities (pers. obs.; Iranzo et al. in prep.).

The methodology used here, a hypervolume approach to realised niches (Carmona et al. 2016a), allows estimating the niche as a probabilistic multidimensional volume, as originally conceived by Hutchinson (1957). This approach seems to be effective and useful for the quantification of species niches as well as for hypothesis-focused niche experiments and observational studies. It skips problems related to hypervolume shape and reduces the importance of outliers in the estimation of niche overlap, thus allowing setting a probability threshold to delineate niche boundaries (Carmona et al. 2016b). Finally, it is an operational method for null hypothesis modelling. However, like most methods used to estimate multidimensional niches this approach is sensitive to sample size. This issue is of special concern when considering multiple dimensions, as the number of points required to adequately characterise the niche increases exponentially with dimensionality (Qiao et al. 2016). Therefore, the results concerning species with fewer observations should be taken with caution, as niche estimations for them are likely less precise. Indeed, habitat is only one of the multiple dimensions of the niche (*sensu* Hutchinson 1957), and more research is needed on other complementary aspects (i.e. trophic niche within habitats). However, species overlap-segregation on habitats is crucial to understand the relevance of competition on shaping natural communities (Blonder et al. 2014), and the effect of species introduction on natural assemblages.

This is one of the first studies evaluating interspecific density-dependent competition, habitat use and species niche adjustments from a probabilistic multidimensional niche perspective (see Traba et al. 2015, Tarjuelo et al. 2016), and our results suggest that the native herbivore assemblage configuration depends on competitive processes. Moreover, we have shown that the introduction of domestic species causes niche narrowing on native species (and on the introduced one too), revealing interspecific density-dependent effects on habitat niche. This process can have potential negative effects for the conservation of native species, especially when conflict between conservation and socioeconomics are emerging due to the recent demographic recovery of native species.

4.5 Acknowledgements

Many people participated in field data collection. We expressly wish to thank among them to P. Acebes, C. Estades, B. González, C. Mata, and M.A. Vukaso-

vic. Corporación Nacional Forestal CONAF-Magallanes and specifically the staff of Torres del Paine National Park kindly provided support and logistics. We also thank three anonymous reviewers for their critical comments on this work. Funding was provided by several organisms and institutions: Program UAM-CEAL-Santander Bank 2011-2012, 2013-2014 and 2015-2016; Foreign Affairs Ministry, Spanish Agency for Development and International Cooperation (A/9875/07, A/016431/08 and A/024945/09); Agriculture Ministry and Environment Ministry, Chile, Servicio Agrícola y Ganadero 2011-2012, and the REMEDINAL 3CM network (S2013/MAE-2719). ECI was supported by a PhD grant from the Spanish Minister of Education (FPU). CPC was supported by a Marie Curie Intra-European Fellowship within the 7th European Community Framework Programme (TANDEM; project id. 626392).

4.6 Supplementary Material

Appendix A

Table A.1. Variables recorded to estimate habitat availability at each animal sighting and control points. Each variable was measured within a 50m circle centred at the animal or the centroid of the sighting/control point.

Variable	Description
Habitat type:	
Water body	Rivers, streams, lakes or ponds
Bare soil	Soil without plant cover or with rocks
Natural grassland	Grasslands dominated by native herbaceous species
Managed grassland	Grasslands seeded with fodder species
Coironal	Steppe-like grasslands dominated by tuft grasses from genera <i>Festuca</i> and <i>Stipa</i>
Vega	Vegetation of shallow wetlands or flooded depressions with predominance of genera <i>Carex</i> and <i>Juncus</i>
Xerophytic scrub	Small-sized cushion-like scrubs. Mainly <i>Mulinum spinosum</i> and <i>Senecio patagonicus</i>
Mata Negra	Midheight woody scrub of <i>Junellia tridens</i>
Mesophytic scrub	Dense scrubs reaching up to 4m height dominated by <i>Berberis microphylla</i>
Forest	Lenga (<i>Nothofagus pumilio</i>) and/or Nirre (<i>Nothofagus antarctica</i>) forest patches
Topography:	
Slope	Three classes: low (<5%), medium (5-45%), high degree (>45%)
Topographic position	Four classes: valley bottom, lower half of hillside, upper half of hillside, peak
Visibility	Three classes: good visibility, medium or reduced in some direction, low visibility
Physiognomy:	
Mean vegetation height	Medium vegetation height in cm
Max vegetation height	Maximum vegetation height in cm

Appendix B

Table B.1. Relevant descriptive data from the 15 sectors defined in the study area attending to their geographical, topographical and physiognomic similarity. Sector position in relation to the protected area (within, outside), length (km), and seasonal abundance of the main herbivores (KAI, kilometric abundance index averaged across years) are shown.

Sector ID	Location	Length	KAI Winter		KAI Summer	
			Guanaco	Sheep	Guanaco	Sheep
1	within	22.2	0.00	0.00	0.00	0.00
2	within	20.4	0.15	0.00	0.80	0.00
3	within	17.0	11.90	0.00	1.75	0.00
4	within	25.7	26.47	0.00	26.94	0.00
5	within	7.5	22.89	0.00	0.27	0.00
6	within	22.0	48.18	0.00	31.18	0.00
7	outside	18.4	10.40	4.28	50.78	0.00
8	outside	23.8	34.47	89.83	8.75	3.87
9	outside	33.2	21.34	83.44	9.85	54.71
10	outside	47.2	6.72	85.44	1.36	129.53
11	outside	22.4	20.03	93.10	6.01	171.96
12	outside	26.2	25.05	35.33	11.55	110.19
13	outside	13.5	37.88	125.21	44.00	16.00
14	outside	18.6	1.83	93.60	0.22	151.08
15	outside	18.5	16.90	79.42	5.23	229.82

Table B.2. Mean habitat availability for each of the 15 sectors in winter.

Sector ID	Slope	Topogr position	Visib	Water	Bare soil	Natural grassland	Managed grassland	Coironal Vega	Xeroph scrub	Mata negra	Mesoph scrub	Forest	Mean veg height	Max veg height
1	1.33	1.35	1.30	1.31	3.59	19.40	0.00	35.60	0.00	0.01	16.52	23.57	95.57	267.84
2	1.69	1.93	1.74	16.61	11.39	18.33	0.00	1.48	1.76	0.00	22.96	12.41	92.30	230.31
3	1.65	2.51	1.88	11.74	25.40	3.14	0.00	9.07	3.60	0.12	7.98	4.35	32.84	71.74
4	1.47	2.38	1.69	2.44	20.71	9.47	0.00	17.99	8.82	3.43	3.01	0.94	26.32	58.33
5	1.27	1.77	1.50	0.00	6.38	49.50	0.00	1.23	3.85	3.58	3.58	21.42	73.27	206.35
6	1.69	2.39	1.31	1.21	7.34	17.50	0.00	20.00	5.48	1.45	4.00	2.98	27.10	133.79
7	1.49	2.02	1.27	8.06	10.45	23.63	0.00	6.51	3.47	18.06	1.43	0.00	26.12	59.18
8	1.33	2.03	1.34	0.00	10.04	26.04	0.00	18.81	0.00	21.84	1.72	0.00	26.66	76.57
9	1.54	2.09	1.04	1.85	8.00	29.85	0.00	9.63	1.76	20.13	2.76	0.74	29.65	95.09
10	1.33	1.81	1.14	0.00	2.93	25.94	1.14	23.38	0.68	39.32	2.31	0.00	35.34	87.05
11	1.61	1.81	1.28	0.00	7.28	22.78	0.00	39.86	14.03	0.28	2.97	0.00	14.31	39.58
12	1.38	1.55	1.27	6.63	4.75	33.45	0.00	3.09	0.27	0.57	4.21	14.20	72.54	158.26
13	1.38	1.92	1.29	3.33	2.29	52.42	0.00	23.67	0.83	0.42	3.13	0.00	11.00	57.63
14	1.69	2.03	1.17	0.83	10.00	26.89	0.00	16.53	0.00	23.06	5.44	0.00	34.86	82.92
15	1.13	1.52	1.11	0.42	6.18	58.39	3.99	15.73	0.00	0.14	2.04	0.00	11.76	45.34

Table B.3. Mean habitat availability for each of the 15 sectors in summer.

Sector ID	Slope	Topogr position	Visib	Water	Bare soil	Natural grassland	Managed grassland	Coironal Vega	Xeroph scrub	Mata negra	Mesoph scrub	Forest	Mean veg height	Max veg height
1	1.21	1.18	1.26	1.28	1.62	22.56	20.77	20.13	2.82	0.00	4.74	24.03	140.64	304.49
2	2.08	2.23	2.15	3.65	14.42	17.50	0.00	1.73	0.00	0.00	23.08	10.77	60.77	282.31
3	2.00	2.10	1.70	10.00	17.30	9.00	0.00	23.20	6.00	0.00	0.00	6.50	29.50	123.50
4	1.81	2.35	1.83	3.40	15.49	18.88	0.00	6.80	4.27	9.53	2.27	0.53	26.27	67.73
5	1.42	1.75	1.42	0.00	2.08	69.58	0.00	0.00	0.00	0.00	7.92	10.00	36.67	205.00
6	1.57	1.97	1.37	1.33	6.10	38.73	0.00	12.63	2.75	10.37	3.37	4.67	51.92	131.58
7	1.69	1.97	1.31	1.56	16.09	30.16	0.00	1.56	7.81	17.03	1.41	0.00	22.81	58.91
9	1.40	1.68	1.20	0.17	4.25	32.77	1.67	6.32	1.50	23.63	3.18	3.25	49.33	130.58
10	1.22	1.86	1.11	0.11	6.25	32.42	1.14	15.99	0.00	32.63	3.45	0.11	41.42	91.65
11	1.55	1.98	1.36	0.12	4.64	52.07	1.19	22.12	2.38	3.33	5.10	0.00	18.81	52.74
12	1.54	1.88	1.34	5.50	13.00	26.36	4.80	1.60	0.20	0.30	8.54	11.64	78.60	206.80
13	1.17	2.08	1.17	4.17	5.83	46.46	1.79	27.92	0.00	0.42	2.63	0.00	19.79	61.46
14	1.74	2.24	1.34	0.00	6.58	37.11	0.00	14.66	0.00	20.58	3.29	0.00	30.66	91.63
15	1.19	1.16	1.03	0.00	2.97	52.97	22.50	4.38	2.19	1.41	6.41	0.00	21.56	52.34

Appendix C

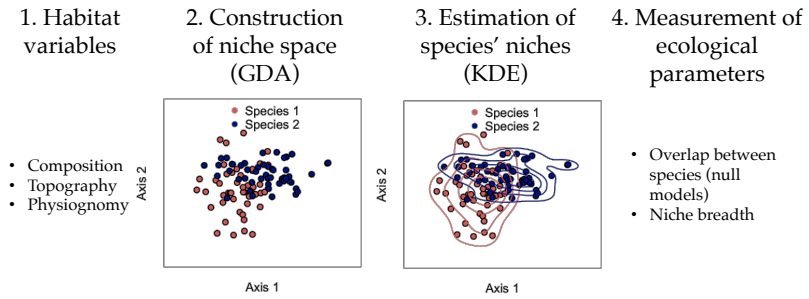


Figure C.1. Summary of the analytical process followed in the paper.

Appendix D

Table D.1. Total number of individuals and number of groups (in brackets) recorded during the six field surveys.

	2009	Winter 2010	2011	2009	Summer 2010	2011
Guanaco	3577 (158)	3893 (188)	4542 (156)	2609 (260)	2991 (293)	1982 (251)
Ñandú	419 (65)	431 (66)	351 (67)	513 (72)	416 (69)	197 (44)
Caiquén	1188 (7)	622 (10)	1047 (11)	583 (34)	1030 (77)	593 (63)
Sheep	15413 (100)	20411 (161)	14695 (134)	24098 (134)	22274 (164)	17027 (106)
Cattle	930 (26)	747 (37)	993 (43)	234 (11)	583 (28)	797 (29)
Horse	216 (24)	282 (36)	377 (43)	222 (21)	266 (32)	204 (31)

Appendix E

Table E.1. Main results of the GDAs built per season to resume the variability in habitat use among species.

Season	Model	Discriminatory power (1- Wilks' λ)	p
Winter	whole model	0.424	<0.001
	after removal of axis 1	0.199	<0.001
	after removal of axes 1 and 2	0.102	<0.001
	after removal of axis 1, 2 and 3	0.053	<0.001
Summer	whole model	0.612	<0.001
	after removal of axis 1	0.318	<0.001
	after removal of axes 1 and 2	0.155	<0.001
	after removal of axis 1, 2 and 3	0.052	<0.001

NOTE: Values of 1-Wilks' λ indicate the discriminatory power of models in the range of 1 (perfect discrimination) to 0 (no discrimination) for the whole model as well as for the sub-models obtained by removing the respective axes.

Appendix F

Table F.1. Matrix of structure coefficients for discriminant axes of GDAs from each season.

	Winter			Summer		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Year (2009)	-0.109	-0.045	0.084	-0.073	-0.165	0.176
Year (2010)	-0.060	-0.073	0.103	0.045	-0.045	0.090
Water	0.137	0.587	0.381	0.438	0.645	0.164
Bare soil	-0.380	0.265	0.272	-0.250	0.275	0.064
Natural grassland	0.432	0.084	-0.347	0.264	-0.172	-0.035
Managed grassland	0.126	0.307	0.3245	0.072	-0.148	-0.057
Coironal	0.100	-0.392	0.125	0.058	-0.356	0.235
Vega	0.270	0.210	-0.097	0.251	0.076	-0.047
Xerophytic scrub	-0.734	0.229	-0.123	-0.681	0.341	0.051
Mata Negra	0.052	-0.496	0.400	0.022	-0.474	0.116
Mesophytic scrub	-0.047	0.039	-0.133	-0.011	-0.049	-0.336
Forest	0.053	0.287	-0.549	0.055	0.009	-0.862
Slope (low)	0.545	-0.012	0.130	0.563	-0.158	0.045
Slope (medium)	-0.155	-0.032	-0.227	-0.289	0.098	-0.083
Topogr(valley bottom)	0.640	0.070	0.114	0.575	-0.056	-0.018
Topogr(lower hillside)	-0.058	-0.078	-0.210	-0.086	-0.174	-0.077
Topogr(upper hillside)	-0.159	-0.005	-0.082	-0.198	0.091	0.018
Visibility (good)	0.364	0.022	0.051	0.346	-0.209	0.082
Visibility (medium)	-0.197	0.006	-0.176	-0.199	0.130	-0.064
Mean veg height	-0.253	-0.192	0.027	-0.143	-0.091	-0.221
Max vegetation height	0.015	-0.041	-0.372	0.0729	-0.094	-0.547

Absolute values indicate correlation of predictor variables with the respective discriminant axes.

Appendix G

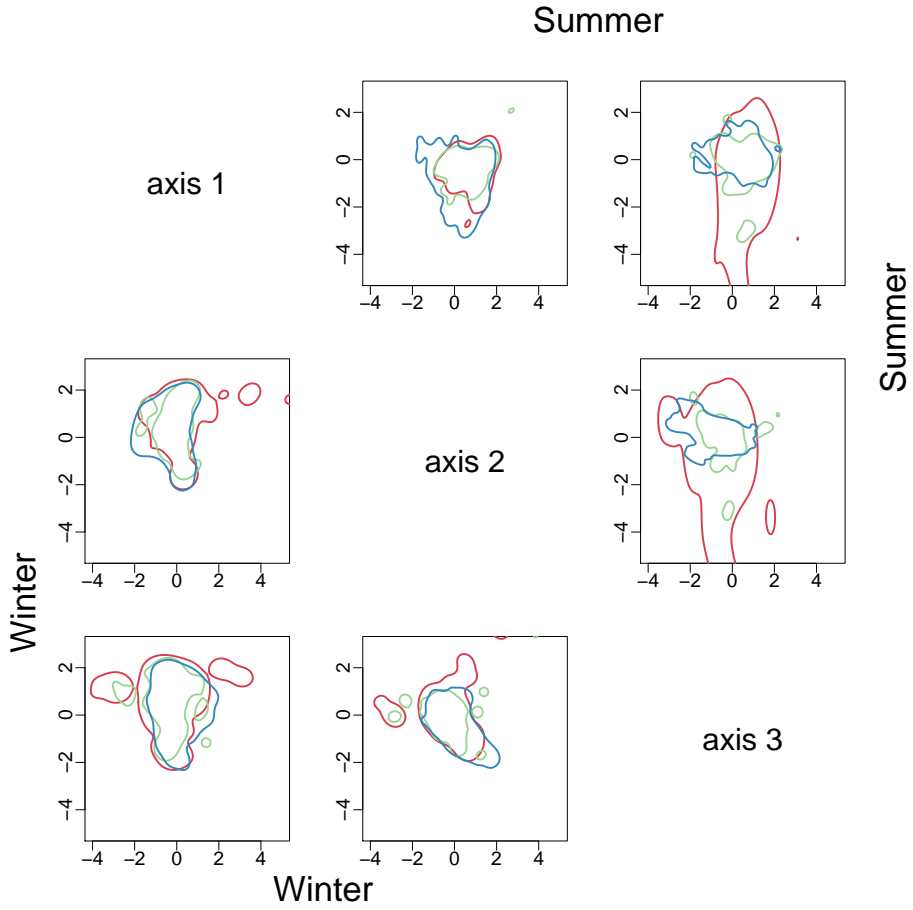


Figure G.1. Niche overlap among domestic species both for winter and summer. Cattle (*Bos taurus*) is represented with red line, horse (*Equus caballus*) in green, and sheep (*Ovis aries*) in blue.

CAPÍTULO 5

Effect of predator abundance and perceived predation risk on guanaco antipredator behavior: vigilance, group size and cohesion

Esperanza C. Iranzo, Heiko Wittmer, Juan Traba, Pablo Acebes, Cristina Mata and Juan E. Malo ¹

¹Manuscrito en preparación como: Iranzo, E.C., Wittmer, H., Traba, J., Acebes, P., Mata, C. and Malo, J.E. Effect of predator abundance and perceived predation risk on guanaco antipredator behavior: vigilance, group size and cohesion.

Abstract

Social ungulates respond to predation risk by modifying their behavior. Antipredator behavior may be adjusted as a function of predator abundance or changes in perceived predation risk associated with group size or density, group composition and habitat structure. We studied antipredator behavior of guanaco (*Lama guanicoe*) family groups in Chilean Patagonia during the calving season over a total of three years to determine their behavioral responses to variation in actual or perceived predation risk. We measured two common (group size and vigilance) and one novel (group cohesion) behavioral responses of guanaco during road surveys. We then used generalized linear mixed models (GLMM) and model averaging to evaluate the responses of family groups to variation in predator abundance, conspecific density and habitat structure (perceived predation risk). Predator abundance affected group size and cohesion. Guanaco families were larger in areas with greater relative puma abundance, while they responded to both predators relative abundance increasing group cohesion. This increase in cohesion may help improve detection of predators and reduce reaction time to approaching predators. Group cohesion also increased with declining family group size and conspecific density suggesting that perceived predation risk was higher when prey were sparsely distributed. Furthermore, group size was larger in open habitats and lower in areas with low visibility, highlighting a potential trade-off between food availability and predator avoidance. Oppositely, vigilance of guanacos appeared unrelated to predation risk, at least during daytime. Our results highlight how family groups in social ungulates respond to predation risk and adapt their antipredator behavior to both presence of predators and perceived risk.

Keywords: Predation risk, antipredator behavior, group size, vigilance, guanaco, perceived predation risk.

5.1 Introduction

Predation risk is one of the main factors shaping grouping behavior in ungulates (Jarman 1974, Kie 1999). Social ungulates respond to predation risk by modifying group size or vigilance rate (Childress and Lung 2003, Roberts 1996). Laundré et al. (2001) proposed that both the presence of predators (actual risk) and elements related to habitat structure (perceived risk) generate a "landscape of fear", in which prey constantly have to adjust their behavior. Behavioral responses of preys to landscapes of fear depend on factors such as predator hunting strategy, habitat structure, density of conspecifics and group size (Kie 1999, Laundré et al. 2001, Heithaus et al. 2009). Besides, predation risk may be perceived by individuals regardless of the actual presence of predators, but as a function of the above-mentioned landscape of fear. In this sense, decreasing in the time dedicated to vigilance of individuals within large groups may reflect a reduction in the individual perceived predation risk (Pulliam 1973, Lima and Dill 1990, Roberts 1996). Despite the reduction in individual vigilance in large groups, total group vigilance increases or remains constant with increasing group size (Kie 1999, Childress and Lung 2003, Marino and Baldi 2008). Other individual factors such as sex, age or the presence of offspring can also influence perceived predation risk and, accordingly, grouping pattern and other associated antipredator behaviors (Kie 1999, Childress and Lung 2003, Lung and Childress 2007, Marino and Baldi 2008, Haswell et al. 2016).

Grouping behavior is also affected by factors other than predation risk including habitat structure and density of conspecifics (Jarman 1974, Kie 1999). Social ungulates thus experience a trade-off between benefits and costs of living in groups. Benefits are related to the reduction of predation risk through early predator detection (collective detection hypothesis; Pulliam 1973, Lima 1995, Kie 1999), vigilance reduction of individuals and a reduced individual predation risk through dilution and confusion effects (Pulliam and Caraco 1984, Roberts 1996). Costs are associated with resource partitioning that result in a decrease in food availability and thus an increase in competition and aggressive interactions among group members (Jarman 1974, Marino 2010). Jarman (1974) suggested that habitat openness and food availability will set the maximum group size, while predation risk will establish the minimum size. Grazing ungulates form larger herds in open grasslands where food is homogeneously distributed and predators are easily detectable. Oppositely, browsing ungulates tend to gather in smaller groups in closed habitats due to the distribution and patchiness of their forage. Ungulates with a mixed feeding strategy typically inhabit complex landscapes

composed of open and close habitats, and must balance group benefits of managing predation risk in larger groups with costs of increased competition with conspecifics (Jarman 1974, Marino 2010).

Guanacos (*Lama guanicoe*) are monomorphic wild ungulates from South America. Guanacos are mixed feeders, display a flexible social organization and a polygynous resource-defense mating system (Franklin 1982, Gonzalez et al. 2006a). During the breeding season, the most important social units are family groups, which are typically formed by a territorial male and several females with their offspring. In areas with temperate climate, family groups remain stable year-round. Contrarily, in areas with severe winters on the other hand, guanacos tend to aggregate into large mixed groups during winter (Franklin 1982, Ortega and Franklin 1995, Gonzalez et al. 2006a). Guanacos give birth in late austral spring and early summer. The birthing season is considered the most stressful period due to the high predation risk experienced by calves (Bank et al. 2002). While the social organization of guanacos has been the focus of much research (e.g., Franklin 1982, Ortega and Franklin 1995, Acebes et al. 2013, Schroeder et al. 2014), there remains uncertainty regarding the factors that determine composition of family groups in populations where families do not persist year-round. Guanaco populations showing such flexibility in grouping behavior are primarily located in protected areas in the southernmost part of their distribution in Patagonia and Tierra del Fuego (Baldi et al. 2016).

In Chilean Patagonia, guanaco have two native predators: culpeo foxes (*Lycalopex culpaeus*) and pumas (*Puma concolor*). Culpeo foxes are opportunistic cursorial predators that have been shown to prey on chulengos (guanaco calves up to 1 year; Novaro et al. 2009). Pumas prey on both young and adult guanacos (Franklin et al. 1999, Bank et al. 2002, Elbroch and Wittmer 2012). Pumas are stalking and stealth predators that rely on vegetation cover and terrain to approach their prey before attacking (Bank and Franklin 1998, Franklin et al. 1999, Elbroch and Wittmer 2012). Thus, shrub cover and fine-scale terrain roughness are important factors for successful hunting.

We evaluated antipredator behavior of guanaco family groups during the birthing season to determine their response to predation risk. We focused on group size, group cohesion, and group vigilance as the main antipredator behaviors in social ungulates. The birthing season is considered the most critical period since calves are more vulnerable and typically experience the highest rates of predation (Bank et al. 2002) and antipredator behaviors should thus be most pronounced.

We considered responses to both presence of predators and perceived predation risk (habitat structure and conspecific density). If guanacos respond to predation pressure, we expect to find larger, more cohesive groups as well as higher vigilance rates in areas with greater predator abundance. On the other hand, if guanacos respond to perceived predation risk, we expect smaller, more cohesive groups as well as higher vigilance in areas with higher shrub cover and low visibility because these will be perceived as riskier habitats independent of predator abundance and are less favorable habitats in terms of the quality and availability of food. Assuming that presence of conspecific relaxes the perceived risk, we also expected a decrease in group cohesion and vigilance with increasing conspecific density.

5.2 Materials and methods

Study area and study case

We conducted our study in the Comuna Torres del Paine (51°3'S; 72°55'W) in the Última Esperanza Province, Region of Magallanes, Chile. Our study area covered approximately 1090 km²; 284 km² were located within Torres del Paine National Park (TPNP) and 806 km² were part of several neighbouring private ranches (Fig. 5.1). Annual rainfall in the area varies between 300 and 1000 mm, and mean temperature ranges from 2.0°C in winter to 10.8°C in summer (Vidal and Reif 2011). Vegetation is dominated by steppe-like grass and shrublands (Pisano 1974). TPNP is separated from surrounding ranches by a 1.2 m high wire fence. The fence restricts livestock movements from private ranches into the National Park, but allows wildlife movements, although guanacos occasionally die entangled (Rey et al. 2012).

Guanacos are the most abundant large-bodied native herbivore in the study area. Estimated guanaco densities currently vary from 36.6 (within TPNP) to 8.8 (outside TPNP) individuals/km² (Iranzo et al. submitted). Other medium to large bodied native herbivores found in our study area include lesser rhea (*Pterocnemia pennata*) and upland geese (*Chloephaga picta*), both of which occur at low densities compared to guanacos. Introduced European hares (*Lepus europaeus*) were abundant and present throughout the study area. Pumas and culpeo foxes occurred at variable densities throughout the study area. Reported puma densities within TPNP are high compared to density estimates from other areas of their distribution (Franklin et al. 1999, but see Rinehart et al. 2014) and decline in the surrounding areas (own unpublished data). Culpeo foxes within TPNP occur at an estimated density of 1.2 individuals/km² (Lucherini 2016).

Data collection

We carried out field surveys to determine size, cohesion and vigilance of guanaco family groups. We conducted surveys during the breeding season in December (i.e., during late austral spring) of three consecutive years (2009, 2010 and 2011). Each year, two surveyors equipped with binoculars drove by car along the existing network of roads in the study area (total road length surveyed = 336.4 km/year) and recorded all guanacos (individuals and groups) they encountered. A detailed description of survey methodology is provided in Iranzo et al. (2013).

We recorded the GPS location for every family detected, and determined its size and composition (sex and age: adult, juvenile or calf). To evaluate group cohesion (a surrogate of animal density per family group), we visually estimated the area (maximum length and width) it occupied. Using instantaneous scan sampling, we quantified the number of adults with heads up

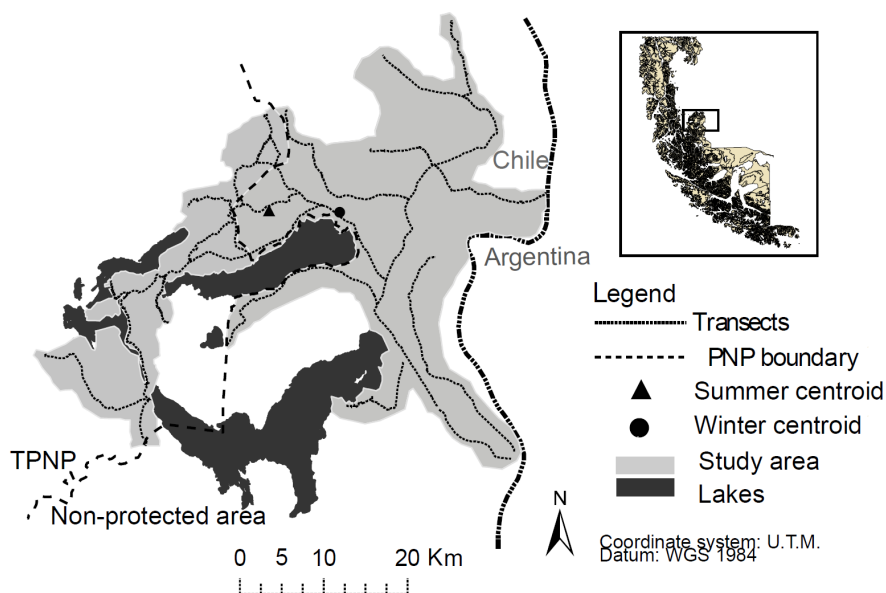


Figure 5.1. Location of study area (shaded area) in the Comuna Torres del Paine (Region of Magallanes, Chile). Dashed line indicates Torres del Paine National Park (TPNP) boundary. Black solid lines represent the surveyed road network within and outside the protected area.

(above the shoulder level) at the time of our first observation, avoiding any kind of disturbance by the observers, and used this ratio as an approximation of vigilance dedication (Childress and Lung 2003). To assess perceived predation risk, we visually estimated shrub cover and visibility within a 50 m radius buffer around the group centroid. Visibility was assessed based on vegetation structure, rocks and terrain roughness, and classified into three categories: high (no visual restriction in any direction), medium (reduced visibility in some direction), and low (low visibility in all directions). During surveys, we also recorded the location and size of bachelor groups, female groups and solitary guanacos in order to estimate total guanaco density (Iranzo et al. submitted).

To determine the influence of predators (puma and culpeo fox) on guanaco behavior we attempted to estimate their relative abundances in the study area using two methods. First, we conducted snow track surveys during austral winters of 2011 and 2012. Pumas in the area have relatively small home ranges, remaining in their territories year round (19-84.5 km²; Barrera et al. 2010; see also Franklin et al. 1999); we thus considered winter surveys as a valid proxy of their relative abundances during summer. Due to the lack of reliable information about movement and territory size for culpeo fox, we decided to apply the same criteria for the utilization of winter data to estimate summer relative abundance. Surveys were conducted by two observers walking 200 m long linear transects every 5 km along the same set of roads and paths used to survey guanacos (year 2011: n = 40 transects, 8km in total; year 2012: n = 54 transects, 10.8 km) recording all signs of puma and culpeo fox presence (feces, tracks). We also deployed remote cameras to record predators along the road network used for guanaco surveys. Specifically, we installed three scent-stations (Long et al. 2003) every 5 km (n = 40); each camera within a station was separated by 500 m. At each scent station, we placed a Cuddeback Digital-camera (Cuddeback Digital, Non Typical Inc., Park Falls, WI, USA) with the infrared beam passing over the center of the scent station, where the attractant was located. We used a small synthetic sponge (0.05 m above the ground) impregnated with bobcat urine as a lure. Cameras were active 24 hours. We then converted predator records from both surveys into estimates of relative abundances using MaxEnt software (Phillips et al. 2006; see below).

Statistical analysis

We used generalized linear mixed models (GLMM) to evaluate the responses of guanaco family groups to both predator abundance and perceived pre-

dition risk. We used group size, group cohesion and vigilance as response variables. Group cohesion was calculated as the density of guanacos within a group (number of guanacos/group area; where group area is the area of the rectangle that contained the group). For group vigilance, we excluded the number of calves as they do not contribute to predator detection. To test vigilance, and in order to avoid the potential relationship between vigilance ratio and group size, we first fitted a negative binomial regression between the number of scanning adults and the total number of adults per group. Then, we used the standardized residuals of this regression as the response variable for the vigilance analysis. Residuals provide information about the intensity of group vigilance: positive regression residuals indicate groups more vigilant than the mean, while negative residuals mean under-expected vigilant groups (Fig 5.2).

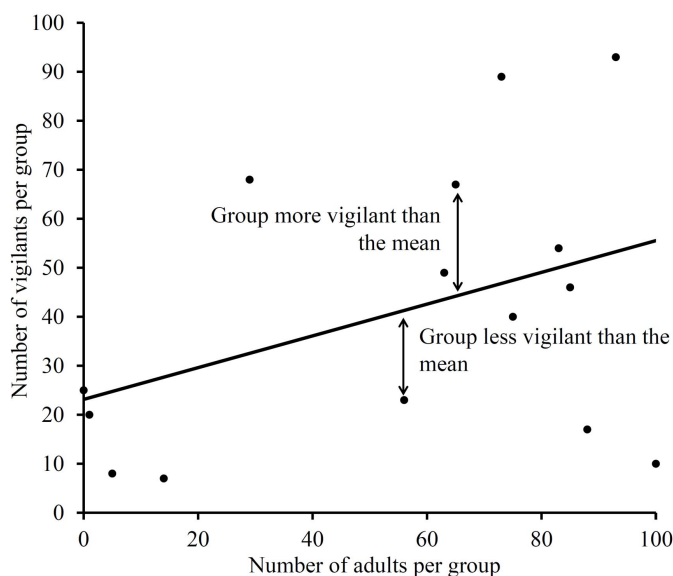


Figure 5.2. Example of the interpretation of the intensity of group vigilance using the residuals of a negative binomial regression between the number of scanning adults and the total number of adults per family group.

We evaluated each response variable as a function of the following set of explanatory variables: percentage of shrub cover, visibility, conspecific density (i.e., perceived predation risk) and puma and culpeo fox relative abundances (i.e. actual predation pressure). We included calf/adult ratio as an

explanatory variable for group cohesion and vigilance analyses, and group size for group cohesion analysis. Although group vigilance is usually related to group size, we did not incorporate the latter in the analysis since it was included in the response variable through the residuals of the regression. We included year as a random effect. Because of the limited number of groups recorded in areas with low visibility, we grouped medium and low visibility levels for our analysis.

To assess actual predation pressure, we built a model aimed at estimating relative abundances of pumas and culpeo foxes using data from predator surveys. We built a model for each species using MaxEnt (Phillips et al. 2006). We used presence of either predator as the response variable, and a set of climatic and topographic variables as explanatory variables (Table S.1 Supplementary Material). Climatic variables were obtained from WorldClim database and topographic variables from Digital Terrain Model ASTER GDEM (METI & NASA). We used Boosted Regression Trees to reduce the initial number of explanatory variables (Elith et al. 2008) before building MaxEnt models. In the same way, we used all guanaco observations to build a model of relative abundance of guanacos as a proxy of conspecific density, variable that affects perceived predation risk.

We standardized explanatory variables prior to conducting the GLMM and transformed response variables when necessary. We used model averaging (Burnham and Anderson 2002) to obtain an averaged model in which the parameters for each variable are averaged across the range of possible models. We first built the complete set of possible models and we ranked them according to their AIC values and then we selected the plausible ones as those whose AIC weights were included in a 95% confidence set of models (the set of models that would include the best model in 95% of the cases). Then we applied model-averaging over the selected set of models, obtaining for each predictor the weighted value of its estimator, the unconditional standard error based on Burnham and Anderson's revised formula (2004) and its z and p values, identifying those significant effects. We performed our analyses using R packages *lme4* (Bates et al. 2011), *MuMIn* (Bartón 2012) and *MASS* (Venables and Ripley 2002).

5.3 Results

We observed 314 families of guanacos over the 3 years of our study. Family group size ranged from 2 to 60 individuals (mean \pm SE = 14.6 ± 0.6 indi-

5. EFFECTS OF PREDATION RISK ON GUANACO ANTIPREDATOR BEHAVIOR

viduals), with a mean of 11 ± 0.5 adults, 0.5 ± 0.1 juveniles, and 3.1 ± 0.2 calves.

Group size, defined as the number of adults within a family group, was explained by an averaged model including puma relative abundance, visibility and shrub cover as explanatory variables (Table 5.1). Group size significantly increased with puma relative abundance and decreased with low visibility or higher proportion of shrub cover.

Table 5.1. Results of the model averaged for guanaco family group size in summer. Model estimates, adjusted standard error, estimate of the z test and its associated p value are presented.

	Estimate	Adjusted SE	z value	p
Intercept	15.466	1.076	14.379	<0.001***
Shrub cover	-1.227	0.617	1.988	0.047*
Puma abundance	2.096	0.629	3.332	0.001***
Visibility	-2.786	1.275	2.184	0.028*
Culpeo abundance	0.417	0.695	0.600	0.549
Guanaco abundance	0.043	0.685	0.063	0.949

Mean group cohesion was 0.26 ± 4.9 animals/ha. Group cohesion was explained by both predator and conspecific relative abundances and by group size (Table 5.2). Group cohesion significantly increased with both puma and culpeo fox relative abundances and decreased with group size and guanaco relative abundance.

Table 5.2. Results of the model averaged for guanaco family group cohesion in summer. Model estimates, adjusted standard error, estimate of the z test and its associated p value are presented. C/A ratio: calf/adult ratio.

	Estimate	Adjusted SE	z value	p
Intercept	-5.093	0.082	61.85	<0.001***
Culpeo abundance	0.244	0.094	2.59	0.01**
Guanaco abundance	-0.468	0.107	4.391	<0.001***
Group size	-0.372	0.081	4.589	<0.001***
Puma abundance	0.425	0.083	51.222	<0.001***
C/A ratio	-0.112	0.08	1.401	0.161
Visibility	-0.045	0.172	0.262	0.793
Shrub cover	0.095	0.081	1.18	0.238

Group vigilance was variable; 56.4% of the groups were not vigilant upon first encounter and 43.6% of the groups contained at least one vigilant individual. Overall, mean group vigilance (of the total number of groups) was

$10.2 \pm 0.01\%$ of the adults and juveniles, translating into an average of 0.95 ± 0.1 vigilant animals per group (min = 0, max = 13 guanacos). In groups that contained vigilant individuals, the mean percentage of vigilance was $23.4 \pm 0.02\%$ of adults and juveniles. In these groups, the mean number of vigilant animals per group was 2.18 ± 0.2 animals (min = 1, max = 13).

Observed differences in vigilance were explained by a model that only included visibility as marginally significant variable (Table 5.3). No other variables showed significant relationship with vigilance ratio.

Table 5.3. Results of the model averaged for guanaco family group vigilance in summer. Model estimates, adjusted standard error, estimate of the z test and its associated p value are presented. C/A ratio: calf/adult ratio.

	Estimate	Adjusted SE	z value	p
Intercept	-0.409	0.127	3.209	0.001*
Visibility	0.188	0.099	1.893	0.058.
C/A ratio	0.051	0.050	1.018	0.309
Puma abundance	-0.050	0.049	1.033	0.301
Guanaco abundance	-0.0126	0.049	0.255	0.799
Shrub cover	-0.118	0.049	0.242	0.809
Culpeo abundance	0.002	0.050	0.034	0.973

5.4 Discussion

Our results suggest that guanaco family groups respond to predation risk and adapt their antipredator behavior to both the presence of predators and the perceived predation risk (Laundré et al. 2001). Both, group size and cohesion were influenced by actual predation pressure (i.e., to the presence of predators; Berger 1999). Group cohesion partially responded to perceived predation risk, specifically to conspecific density and group size. Vigilance behavior was variable and appeared to increase in areas with low visibility.

Aggregation and changes in prey group size as a response to the presence of predators have previously been reported in many species of herbivores (e.g., Lima 1990, Banks 2001, Hebblewhite and Fletscher 2002). As expected, actual predation risk thus also affected group size and cohesion in guanacos. Specifically, guanaco families were larger in areas with greater relative puma abundances and also exhibited increased group cohesion as response to both predators. Increasing group cohesion may help improve detection of an approaching predator and thus provide guanacos with greater re-

response time (Taraborelli et al. 2012). Similarly, Marino and Baldi (2014) reported larger family groups of guanacos in populations coexisting with pumas than in predator-free reserves. Since pumas hunt by stalking their prey, an early detection will increase the likelihood of escape. Thus guanacos benefit from forming large groups, in which is easier to detect predators (collective vigilance hypothesis; Pulliam 1973, Pulliam and Caraco 1984, Taraborelli et al. 2012). However, the response to predation risk is also influenced by the particular predator hunting strategy (Thaker et al. 2010, Samelius et al. 2013, Haswell et al. 2016). A response based on early detection and escape may not be effective against cursorial predators such as culpeo foxes (Novaro et al. 2009). Therefore guanacos respond to culpeo fox relative abundance increasing group cohesion, which allows a faster group response, but not group size.

Perceived predation risk had no effect on guanaco group size or vigilance behavior and only partially influenced group cohesion. Group cohesion increased with a decrease in group size and conspecific density, suggesting that perceived predation risk increase when group members are sparsely distributed. Shrub cover and visibility did not influence group cohesion. Therefore, group cohesion only partially supports the perceived predation risk predictions. Interestingly, group cohesion has been sometimes included as an independent variable for vigilance and antipredator response analyses (Marino and Baldi 2008, Taraborelli et al. 2012). However, there are no studies analyzing it as an anti-predator response variable itself. Our findings suggest that this new approach complements and adds information to the traditional study of group size as antipredator response. Specifically, the response of group cohesion to actual predator abundance, conspecific density and group size suggest that guanacos are risk sensitive and may adapt their individual distance to others group members according to actual and perceived predation risk. The lack of response to habitat structure suggests the possible effect of other ecological cues shaping group composition. Besides, guanaco family group size was not related to conspecific density, suggesting that plasticity of these social units could be relatively low, as reported by Marino and Baldi (2014).

Of particular interest were responses in vigilance. According to Jarman (1974) and the collective vigilance hypothesis (Pulliam 1973), group size was larger in open and high visibility habitats with high puma abundance and it reduced in areas with higher shrub cover and low visibility. In shrublands, guanacos experience a trade-off between early predator detection and fit their energetic and food requirements in a patched and low-quality habitat.

Marino (2010) reported a high rate of aggressions among females on family groups feeding in shrublands and this rate increased rapidly with group size, suggesting that intra-group competition costs constrain family group size in those habitats. Although we did not measure aggression rates, our results could respond to an interference competition among group members that would limit the shorter distance among animals (Jarman 1974, Marino 2010). These results suggest that habitat structure might be related to food availability, which influences grouping behavior in guanacos, but not with perceived predation risk. Similar response to forage abundance and distribution rather than predation risk was reported by Creel and Winnie (2005) for an elk (*Cervus elaphus*) population. Therefore, guanaco family groups fit Jarman's theory (1974) suggesting that group size is an adaptive response to ecological conditions.

Group vigilance is often analyzed using different response variables (group scan level, group vigilance in Childress and Lung 2003; collective vigilance in Marino and Baldi 2008), and results are not always in the same direction. As a consequence, different interpretations have been proposed to vigilance behavior (antipredatory response vs social monitoring; Laundré et al. 2001, Lung and Childress 2007). Guanaco group vigilance was unrelated to predator abundance, calf/adult ratio and shrubs cover, but it was marginally affected by visibility. As occurs in our study area, no pattern was detected for elk and bison (*Bison bison*) vigilant behavior in Yellowstone National Park (Laundré et al. 2001). This result could suggest that guanaco vigilance is an evolutionarily fixed behavior or that it responds to other ecological factors not included in the study.

Our lack of results could reflect an independence of external factors in family group vigilance (Lima 1995, Laundré et al. 2001). It could be due to the high energy requirements during the breeding season that cause an increase in foraging rate to the detriment of vigilance (Young and Franklin 2004, Marino and Baldi 2008). Another complementary reason is that, in areas with larger shrub cover, where we expected higher vigilance rate, the patchy distribution and low quality of vegetation forced guanacos to increase their investment in foraging and decrease the time spent vigilant. A third non-competing explanation is that anti-predator benefits of grouping were reached at a size smaller than the reported group size, so we did not detect differences. Thus the level of group vigilance would have reached its maximum, although low, and seemed independent of predation risk. It should be noted that puma is most active at dusk and dawn (Franklin et al. 1999), therefore guanacos could increase their vigilance rate during those

hours and decrease the time spent on vigilance during daytime, when this study was conducted, as reported by Young and Franklin (2004) for guanaco males. Besides, it could be that vigilance reported acts as social monitoring rather than antipredator response (Laundré et al. 2001, Lung and Childress 2007). However, social monitoring is generally carried out by the male to defend its territory and the harem, so this explanation seems unlikely (Lung and Childress 2007, Marino 2012). Finally, it could be due to the choice of a non-enough-sensitive variable to analyze group vigilance.

Calf/adult ratio did not affect group cohesion and vigilance. Whereas male individual vigilance increases in association to the presence of calves (Marino and Baldi 2008), these authors detected that the number of calves present in the group decreased collective vigilance because of females vigilance behavior. In our study the male vigilance effect may be diluted because we are studying family groups. These family groups are formed by only one male and several females and thus, female behaviour is the dominant one we registered. So, our results could be related to the low time invest in vigilance by females (Barri and Fernandez 2011, Marino and Baldi 2008). In addition, Acebes et al. (2013) did not detect effect of calves presence in habitat use by family groups and propose that guanaco prioritizes reducing predation risk using the least productive but also less risky areas during the breeding season.

In conclusion, guanaco family groups adapt their anti-predatory behavior to the predation pressure and perceived predation risk. The reported responses are for family groups during breeding season, and therefore, it would be necessary to further investigate the anti-predatory behavior of guanacos in other social groups and seasons.

5.5 Acknowledgements

We thank all collaborators who participated in field data collection, and most particularly, M.A. Vukasovic, N. Fuentes and D. Valencia. Corporación Nacional Forestal CONAF-Magallanes and specifically the staff of Torres del Paine National Park kindly provided support and logistics. We are also grateful to J. Seoane for valuable advices during the analysis process. Funding was provided by several organisms and institutions: Program UAM-CEAL-Santander Bank 2011-2012, 2013-2014 and 2015-2016; Foreign Affairs Ministry, Spanish Agency for Development and International Cooperation (A/9875/07, A/016431/08 and A/024945/09); Agriculture Ministry and Environment Ministry, Chile, Servicio Agrícola y Ganadero 2011-2012,

and the REMEDINAL 3CM network (S2013/MAE-2719). ECI was supported by a PhD grant from the Spanish Minister of Education (FPU).

5.6 Supplementary Material

Table S.1. List of variables used and those selected to build the model for each species after applying BRT (+). Predator and prey abundance variables are the result of the MaxEnt model for each of these species (average model).

Variables		Puma	Culpeo
Topographic	Mean altitude		
	Standard deviation of altitude		+
	Mean gradient		
	Standard deviation of gradient		
	Mean roughness		
	Standard deviation of roughness		+
Location	Distance to protect area	+	
	Distance to water bodies		
	Distance to hydrographic network		+
	Distance to settlements		+
Climatic	Annual Mean Temperature	Bio1	+
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Bio2	
	Isothermality (BIO2/BIO7) (* 100)	Bio3	+
	Temperature Seasonality (standard deviation *100)	Bio4	+
	Max Temperature of Warmest Month	Bio5	
	Min Temperature of Coldest Month	Bio6	
	Temperature Annual Range (BIO5-BIO6)	Bio7	
	Mean Temperature of Wettest Quarter	Bio8	
	Mean Temperature of Driest Quarter	Bio9	+
	Mean Temperature of Warmest Quarter	Bio10	
	Mean Temperature of Coldest Quarter	Bio11	
	Annual Precipitation	Bio12	
	Precipitation of Wettest Month	Bio13	
	Precipitation of Driest Month	Bio14	
	Precipitation Seasonality (Coefficient of Variation)	Bio15	
	Precipitation of Wettest Quarter	Bio16	
	Precipitation of Driest Quarter	Bio17	
	Precipitation of Warmest Quarter	Bio18	
	Precipitation of Coldest Quarter	Bio19	
Vegetation	The Normalized Difference Vegetation Index	NDVI	+
Prey abundance	Guanaco average abundance	+	+
	Cattle average abundance	+	+
Predator abundance	Puma average abundance		+

CAPÍTULO 6

Discusión general

En la presente tesis doctoral se han abordado diversos aspectos de la ecología de una población de guanacos localizada en un espacio natural protegido y sus alrededores en la Patagonia chilena, así como de la estructura de la comunidad de herbívoros nativos y domésticos de la que forma parte. La población de guanacos de Torres del Paine se cuenta entre las mayores de toda su área de distribución junto con la población de Tierra del Fuego y algunas localizadas en áreas protegidas de la Patagonia argentina. Esto ha permitido testar hipótesis ecológicas en una población bien asentada y evitar posibles sesgos que pueden derivarse de estudiar poblaciones pequeñas o aisladas. Además, la presencia de otros herbívoros nativos y sus depredadores en la zona de estudio (o al menos en parte de ella, ver discusión más adelante) proporciona el mantenimiento del funcionamiento ecológico del que carecen otras zonas, como Tierra del Fuego, por la ausencia de depredadores naturales. Además, el conocimiento generado en esta tesis doctoral sobre el comportamiento de esta población respecto a sus condicionantes y perturbaciones antrópicas brinda información de interés de cara a anticipar y prever lo que podría ocurrir en otras poblaciones de ungulados silvestres que se encuentran bajo protección y que co-ocurren con prácticas ganaderas.

En concreto, en la presente tesis doctoral se ha estimado el tamaño poblacional y la densidad de guanacos en el Parque Nacional Torres del Paine y su entorno. Se han aportado datos sobre la estructura social y demográfica de dicha población y se han descrito los factores que influyen en su distribución y estructura social (CAPITULO 2). En este mismo capítulo, además, se ha estudiado el patrón de dispersión del guanaco y se ha descrito la fase actual de este proceso de expansión de los animales desde el interior del Parque Nacional hacia las fincas ganaderas limítrofes. Una vez determinados

estos aspectos, la pregunta se dirigió hacia las posibles consecuencias de la expansión del guanaco hacia las zonas ganaderas y su potencial para la competencia con la oveja. En el CAPITULO 3 se describe la selección de hábitat de ambas especies en simpatría, y la del guanaco en alopatría en los momentos de mayor y menor abundancia de recursos, es decir, final de primavera - principio de verano, e invierno. Complementariamente, en el CAPITULO 4 se ha determinado la amplitud y solapamiento de nicho para toda la comunidad de herbívoros de medio y gran tamaño tanto silvestres como domésticos también en ambas estaciones, analizando el efecto que la coexistencia entre herbívoros silvestres y domésticos tiene sobre el nicho realizado de las especies. Por último, en el CAPITULO 5 se ha evaluado el papel del riesgo de depredación en el comportamiento social del guanaco, en concreto, de los grupos familiares durante la época de cría, cuando son más vulnerables por la presencia de recién nacidos, y por tanto se espera que las respuestas antidepredatorias sean más acusadas. A continuación, se discuten de forma conjunta los resultados más importantes de la presente tesis doctoral.

La estimación del tamaño y densidad de la población de guanacos actualiza la información disponible hasta el momento dentro del Parque Nacional y proporciona nuevos datos para su entorno. La abundancia de guanacos estimada dentro (4.600-10.300) y fuera (6.700-12.500) del Parque, así como la tendencia respecto a datos propios y ajenos de años previos, sugiere que la población se encuentra en crecimiento, con una importante fracción de la misma asentada en el exterior del espacio protegido. Además, las densidades estimadas para ambas zonas se encuentran entre las más altas descritas para la especie (Sarno y Franklin 1999, Burgi et al. 2012, Schroeder et al. 2014).

La relevancia que ha mostrado el centroide de la distribución de guanacos en la explicación del patrón de abundancia indica que el núcleo de la población ya se ha desplazado desde el interior hacia el exterior del Parque Nacional, y que el proceso de dispersión hacia el exterior continúa, como ya fue observado por Sarno y Franklin (1999). La estructura social descrita, por su parte, sugiere que los guanacos en todo el área de estudio forman una única población que se encuentra próxima a una fase tardía del proceso dispersivo.

Una vez conocido el tamaño de la población de guanacos, confirmada su dispersión hacia el exterior del espacio protegido y estimado el contingente de guanacos que existe fuera del mismo, ya establecidos y formando una única población con los guanacos del interior del Parque Nacional, parece natural y necesario estudiar si en estas zonas ganaderas el guanaco compite con el ganado por los recursos. Al ser el ganado ovino el más abundante y

extendido en los alrededores del Parque, fue en este, como especie doméstica, en el que se centró el estudio de la selección de hábitat para determinar el potencial para la competencia entre ambas especies. El estudio de la selección de hábitat de guanaco y oveja se hizo en función de 10 comunidades vegetales bien definidas (Pisano 1974) y tres variables topográficas consideradas relevantes en los procesos de uso y selección de hábitat (pendiente, posición topográfica y visibilidad/rugosidad del entorno).

Las diferencias observadas en la selección de hábitats entre especies que coexisten se han atribuido a diferentes mecanismos: desplazamiento competitivo, plasticidad o selección diferencial, entre otros (Stewart et al. 2002, Sitters et al 2009). La ventaja de contar con un experimento natural, que proporciona una situación "control" de ausencia de ganado (el interior del Parque Nacional), es que permite determinar si el uso aparente de áreas subóptimas por las especies silvestres responde realmente a alguno de ellos o a factores relacionados con la actividad humana difíciles de cuantificar (Pedrana et al. 2010, Soler Esteban et al. 2012).

Los resultados del análisis de la selección de hábitat indican que guanaco y oveja mostraron diferentes preferencias de hábitat tanto en verano como en invierno a pesar de su agregación espacial a escala de paisaje. Contrariamente a la hipótesis de partida, el guanaco no modificó su uso del hábitat en presencia de oveja, lo que sugeriría que no está siendo desplazado por esta donde coexisten, como indican otros trabajos de coexistencia entre guanaco y especies domésticas (p.e. Ovejero et al. 2011, Acebes et al. 2012, Esteban et al. 2012), por lo que la segregación detectada se debería a una selección diferencial de hábitat y no a un proceso de desplazamiento competitivo. No obstante, esta segregación puede ser consecuencia de una compactación del nicho como se discute más adelante. El guanaco mostró un proceso activo de selección de hábitat, correspondiendo estos a los descritos como preferidos, es decir, zonas abiertas con vegetación de bajo porte donde puede alcanzar un compromiso óptimo entre disponibilidad de alimento y una buena visibilidad que reduzca el riesgo de depredación (Raedeke 1982, Bank et al. 2003, Sosa y Sarasola 2005, Acebes et al. 2010). Por su parte, la oveja presentó un comportamiento generalista en cuanto al uso del hábitat.

Estos resultados enfocan las interacciones entre guanaco y oveja desde una nueva perspectiva: en situaciones de una heterogeneidad de hábitat relativamente alta y a una escala de estudio media, guanaco y oveja podrían coexistir mediante un uso diferencial del hábitat, lo que hace que el potencial para la competencia entre estas especies sea relativamente bajo en dichas circunstancias. No obstante, cabe señalar que la selección de hábitat es un

proceso denso-dependiente y que por tanto se puede modificar en función de cambios en la densidad de las especies. Además, la selección de hábitat de las especies nativas puede verse afectada en cierta medida por la presión ejercida por los ganaderos que pueden desplazarlas hacia hábitats subóptimos (Pedrana et al. 2010, Burgi et al. 2012). Por otra parte, esta aproximación a las interacciones interespecíficas a través de la selección de hábitat, aunque muy utilizada, podría no reflejar adecuadamente otros procesos que acontecen sobre el nicho efectivo de las especies implicadas. Por tanto, es necesario utilizar otras alternativas al análisis de la coexistencia, como pueden ser el estudio de los cambios en la amplitud o el solapamiento de nicho de las especies.

Un estudio local sobre la dieta del guanaco y la oveja sería necesario para complementar este análisis de selección de hábitat, ya que frecuentemente se ha señalado el alto grado de coincidencia en la alimentación entre ambas especies (Bonino y Pelliza-Sbriller 1991, Puig et al. 2001, Baldi et al. 2004). Aunque este punto no ha sido abordado en la presente tesis doctoral, se han realizado análisis preliminares de la dieta de ambas especies durante dos inviernos consecutivos a través de análisis microhistológico. Estos análisis indican que existe un grado relativamente alto de solapamiento en la composición florística de la dieta de guanaco y oveja, pero existen diferencias significativas en cuanto a las proporciones de las especies encontradas en las muestras de cada herbívoro, lo que podría sugerir que, más allá de una diferenciación en los hábitats de alimentación, está teniendo lugar un proceso de segregación trófica (datos propios sin publicar).

Una vez determinado el escaso solapamiento, y por tanto, bajo potencial para la competencia entre guanaco y oveja, se evaluó la manera en que se estructura la comunidad de especies silvestres nativas, así como los potenciales efectos sobre el nicho de estas especies cuando están en co-ocurrencia con herbívoros domésticos introducidos en tiempo ecológico. La inclusión del conjunto de especies de vertebrados herbívoros presentes en la zona de estudio (con la excepción de la liebre europea), así como la condición de "experimento natural" del Parque Nacional, donde no hay herbívoros domésticos, nos han permitido determinar la partición de nichos de la comunidad de especies nativas evolutivamente estructurada, y si la introducción relativamente reciente de ganado modifica esta partición de nichos.

De acuerdo con la teoría de nicho, debido a una larga fase de coexistencia competitiva en tiempo evolutivo, la comunidad de herbívoros nativos debería presentar una segregación de sus nichos de forma que los procesos de competencia entre ellos sean mínimos (MacArthur and Wilson 1967, Rosenzweig

1981, Chase and Leibold 2003). Por otra parte, la introducción de especies exóticas en esta comunidad puede provocar un incremento de las tensiones competitivas debido al solapamiento de sus nichos ecológicos, producido por el escaso tiempo de coexistencia (Stewart et al. 2002). Cumpliendo estas predicciones, el solapamiento encontrado entre las especies nativas fue bajo, sugiriendo que forman una comunidad competitivamente estructurada de acuerdo a un proceso de segregación y compresión de nicho asociado a la competencia en el pasado (Rosenzweig 1974, Connell 1980).

Los resultados del análisis de solapamiento de nicho mostraron un mayor solapamiento entre especies domésticas y nativas que entre especies nativas, lo que refleja cómo la introducción reciente de especies en comunidades ya estructuradas aumenta el solapamiento de nichos entre especies nativas y domésticas. Sin embargo, casi todas las especies mostraron cierta segregación de nicho que sugiere una modificación y adaptación de los nichos en tiempo ecológico.

Se ha mencionado que la consideración de múltiples dimensiones de nicho facilita encontrar dicha segregación entre especies (Rosenfeld 2002, Blonder et al. 2014, Carmona et al. 2016). Sin embargo, nuestros resultados sugieren que los ajustes ecológicos ocurren incluso a corto plazo, es decir, que las especies modulan su uso del hábitat para reducir los efectos de la competencia (Madhusudan 2004, Svanbäck y Bolnick 2007, Darmon et al. 2012). En este sentido esta segregación de nicho entre guanaco y oveja concuerda con las diferencias en la selección de hábitat detectadas en el CAPITULO 3, pero apuntan a que la coexistencia entre ganado y especies silvestres sí tiene un efecto negativo sobre estas últimas, ya que reduce el nicho efectivo de las especies implicadas.

Efectivamente, la comparación de situaciones de alopatría y simpatría reveló una compresión de nicho derivada de la coexistencia tanto en guanaco como en oveja. El nicho del guanaco se amplió en alopatría y se comprimó en simpatría, aunque sólo en los periodos de escasez de recursos (invierno). Es decir, el guanaco muestra una respuesta en tiempo ecológico a la presencia de ganado modificando su nicho de acuerdo con lo establecido por la hipótesis de solapamiento de nicho (Pianka 1974). Del mismo modo, el nicho de la oveja mostró una tendencia a contraerse con la abundancia de guanaco, lo que sugiere que la competencia es un proceso bilateral en nuestro caso de estudio (Morris 2009). Los efectos últimos de esta compactación denso-dependiente del nicho están aún por dilucidar, ya que los procesos de competencia, cuando existen, deben suponer impactos negativos sobre el fitness de las especies implicadas.

Por último, retomando uno de los resultados obtenidos, que postulan al riesgo de depredación como un elemento importante en la selección de hábitat, se evaluó más a fondo el efecto de los depredadores y del riesgo de depredación en el comportamiento y estructura social del guanaco. Estos análisis se centraron en el periodo reproductivo, cuando los chulengos son más vulnerables.

Los grupos familiares respondieron al riesgo de depredación y adaptaron su comportamiento antidepredatorio a la presencia de depredadores y a la estructura del hábitat, mostrando una respuesta tanto al riesgo de depredación real como al percibido. En este sentido, tanto el tamaño como la cohesión de los grupos respondieron al riesgo real de depredación, es decir, a la presencia de depredadores. Así, en áreas con mayor abundancia de puma los grupos fueron más grandes y mostraron mayor cohesión como respuesta a la presencia de depredadores (Lima 1990, Thaker et al. 2010).

El tamaño de grupo fue mayor en zonas abiertas y de buena visibilidad con alta abundancia de puma, de acuerdo con las tesis de Jarman (1974) y la hipótesis de la vigilancia colectiva (Pulliam 1973), y se redujo en zonas con mayor cobertura de matorral. En estos hábitats de menor visibilidad, los guanacos experimentan un compromiso entre la detección temprana de depredadores (que favorecería un mayor tamaño de grupo) y los requerimientos energéticos y alimentarios. Así, la distribución parcheada de los recursos (matorrales y menor disponibilidad de herbáceas) y la posible competencia por interferencia entre los miembros del grupo (Marino et al. 2010) podrían estar limitando el tamaño del grupo familiar en estas zonas.

Por otra parte, la cohesión de grupo también respondió, al menos en parte, al riesgo percibido, aumentando al disminuir el tamaño de grupo y la densidad de coespecíficos. Esto sugiere que los guanacos adaptan su distancia con otros miembros del grupo en función del riesgo. Contrariamente a lo esperado, la cohesión no aumentó en zonas con mayor cobertura de matorral y peor visibilidad donde se espera que la percepción del riesgo sea mayor. Esta falta de respuesta podría indicar de nuevo la existencia de procesos de competencia entre los miembros del grupo por el alimento, lo que limitaría la distancia mínima entre individuos (Jarman 1974, Marino 2010).

Por último, no detectamos respuesta en la vigilancia de los grupos ni al riesgo real ni al percibido. Esto puede tener dos explicaciones, o bien es un comportamiento innato e independiente de factores externos como han sugerido algunos autores (Lima 1995, Laundré et al. 2001); o la forma de medir la vigilancia no permitió determinar la tasa real de vigilancia.

Como broche final para entender el entramado de interacciones ecológicas y sociales, sería necesario evaluar la percepción de la realidad que tienen los actores sociales implicados en este ecosistema, es decir, ganaderos y gestores del espacio natural y de las poblaciones silvestres fuera del mismo. A pesar de que esta evaluación no se ha incluido en la presente tesis doctoral, análisis preliminares indican cierto desajuste entre las interacciones reales entre fauna nativa y ganado (abundancia de herbívoros y depredadores silvestres, y uso del hábitat) y la percepción que los actores sociales tienen de las mismas. Estos, independientemente de su posición (ganadero/gestor) expresan una actitud positiva hacia el Parque Nacional y consideran necesario aceptar o tolerar cierto grado de pérdidas económicas por competencia y/o depredación de cara a conservar la fauna nativa. Sin embargo, en el caso de los ganaderos esta aceptación disminuye cuando la pregunta se dirige directamente a su persona en lugar de ser un concepto abstracto. Además, tanto ganaderos como gestores de fauna perciben un conflicto fauna silvestre - ganado mayor del que los resultados de la presente tesis doctoral arrojan, sugiriendo un desacople entre la percepción y los procesos reales. Por otra parte, todos ellos expresaron su interés por ampliar sus fuentes de ingresos más allá de la ganadería e incluir el ecoturismo como vía alternativa y complementaria de la ganadería (Iranzo et al. en prep.). Esto sugiere que existe una vía abierta para compaginar ganadería y conservación de la biodiversidad en el entorno del Parque Nacional Torres del Paine, en la que es necesario seguir trabajando.

Por otro lado, se ha iniciado recientemente un proceso de control de la población de guanacos por el Servicio Agrícola y Ganadero, que responde a una exigencia por parte de los ganaderos acerca de la necesidad de control de las poblaciones naturales (Servicio Agrícola y Ganadero 2016). Aunque los resultados de esta tesis sugieren que el nivel de competencia real por el pasto entre guanacos y ovejas es aún escaso, debido a procesos de selección diferencial o por partición competitiva de nicho, es indudable que este fenómeno es denso-dependiente. La abundancia de guanaco y la estructura social de los grupos presentes en el exterior del Parque, apuntan a que los procesos de tensión competitiva real o percibida van a seguir incrementándose en el futuro. En este contexto es posible que el control de poblaciones sea una herramienta necesaria, dadas las disfunciones existentes en el funcionamiento natural del ecosistema provocadas a su vez por la alteración antrópica del equilibrio depredador-presa con la introducción de ganado y la persecución y práctica erradicación de los depredadores fuera del espacio protegido. Esto ha llevado a que los mecanismos de regulación de la población hayan perdido su

funcionamiento natural y la presencia de depredadores, fundamentalmente puma, casi exclusivamente sólo dentro del espacio protegido, no sea suficiente para controlar la población de guanacos. No obstante, deben considerarse otras estrategias de gestión, como la utilización de mecanismos disuasorios de la depredación sobre herbívoros domésticos (perros de guarda, pastores eléctricos, etc.), que permitan redirigir la presión de depredación de nuevo sobre los herbívoros silvestres, facilitando la convivencia de los objetivos de conservación y desarrollo.

Implicaciones para la conservación y gestión de la especie

El tamaño de la población de guanacos en la zona de estudio indica la elevada capacidad de recuperación poblacional de la especie en un periodo breve del tiempo, siempre que se establezcan las medidas necesarias para evitar la caza furtiva y otras amenazas. Este crecimiento poblacional ha venido acompañado de procesos de dispersión y colonización desde la fuente (el Parque Nacional) hacia el exterior, por lo que es necesario tener en cuenta este hecho a la hora de elaborar planes de conservación y programas de manejo de cara a evitar posibles conflictos con los usos humanos asentados en la zona no protegida.

Hasta el momento, y con las densidades poblacionales actuales, no se ha encontrado competencia activa entre guanaco y oveja por el uso de los recursos, lo que sugiere la posibilidad de una co-ocurrencia entre ambas especies, sea por selección diferencial, sea por compresión competitiva del nicho, aunque este proceso puede ser denso-dependiente y alterarse con cambios en las densidades de alguna de las especies o debido a escasez de recursos tróficos. No obstante, la contracción de los nichos de ambas especies cuando están en presencia de la otra, sugiere un efecto negativo derivado de su coexistencia. En este punto es necesario resaltar que hay lugares específicos en los que el potencial para la competencia es mucho mayor, como son los campos cultivados de alfalfa. Estas zonas contribuyen notablemente al sesgo en la percepción de los ganaderos sobre la competencia entre guanaco y ganado. Los campos de alfalfa, aunque escasos, son especialmente productivos y seleccionados por algunos grupos de guanacos, con el consiguiente conflicto con los ganaderos. Sin embargo, no hay que olvidar que se trata de un caso particular para el que se podrían tomar medidas de gestión concretas y puntuales.

Además, los resultados de la presente tesis doctoral indican que el guanaco responde al riesgo de depredación modificando su comportamiento social, al menos en ciertos aspectos. El guanaco es la presa preferida del puma (Barrera et al 2010, datos propios), por lo que una población estable de este depredador en la zona, junto con las medidas necesarias para redirigir su presión de depredación sobre el guanaco en lugar de sobre el ganado, podría colaborar al restablecimiento del equilibrio natural del ecosistema. Esto, además de reducir el conflicto percibido entre guanaco y ganado, actuaría como control natural de la población de guanacos que de otra forma necesita ser controlada por el hombre.

Conclusiones

- Existe una gran población de guanacos en la zona de estudio estimada entre 12.800 y casi 22.000 animales, buena parte de los cuales habitan en el exterior del Parque Nacional Torres del Paine.
- Las densidades estimadas están entre las más altas descritas para la especie, tanto dentro del Parque Nacional como fuera, donde el guanaco co-ocurre con prácticas ganaderas.
- La estructura demográfica descrita apunta a que los guanacos del Parque Nacional y su entorno constituyen una única población bien establecida incluso fuera de los límites del espacio protegido. Esta población se encuentra en una fase tardía del proceso dispersivo hacia el exterior del Parque Nacional.
- La estructura social de esta población de guanacos coincide con la descrita en otras zonas de la Patagonia, a pesar de que el tamaño de los grupos familiares se halla entre los mayores descritos para la especie.
- El guanaco selecciona de forma activa zonas abiertas con vegetación de bajo porte en busca de un compromiso óptimo entre disponibilidad de alimento y una buena visibilidad que reduzca el riesgo de depredación.
- Los grupos familiares de guanaco responden a la presencia de depredadores aumentando el tamaño y la cohesión de los grupos. La cohesión también aumenta al disminuir el tamaño del grupo y la densidad de coespecíficos, lo que sugiere una respuesta al riesgo percibido. La ausencia de respuesta a la estructura del hábitat probablemente se debe a un compromiso entre disminuir el riesgo de depredación y la disponibilidad y distribución del alimento.

- El solapamiento de nicho encontrado entre los herbívoros nativos es bajo, sugiriendo que forman una comunidad competitivamente estructurada de acuerdo a un proceso de segregación y compresión de nicho asociado a la competencia en el pasado.
- El solapamiento de nicho entre especies domésticas y nativas es mayor que entre especies nativas. Sin embargo, la consideración de múltiples dimensiones permite detectar cierta segregación de nicho entre especies, lo que sugiere una rápida adaptación y modificación de nicho en tiempo ecológico.
- Guanaco y oveja muestran diferencias en su selección de hábitat, lo que parece sugerir que, a mesoescala, el potencial para la competencia es bajo, aunque este proceso puede ser denso-dependiente y la situación puede cambiar si se produce un incremento en la densidad de las especies o se reduce la disponibilidad de recursos.
- La presencia de oveja provoca una contracción del nicho del guanaco y viceversa, lo que sugiere que, en este caso, la competencia es un proceso bilateral y denso-dependiente.
- Los resultados de esta tesis doctoral apuntan a que es necesario llevar a cabo medidas de gestión de la población de guanacos de cara a evitar posibles conflictos con el desarrollo socioeconómico del entorno del Parque Nacional.

Conclusions

- There is a large guanaco population in the study area, estimated to be between 12,800 and 22,000 animals, most of them living outside Torres del Paine National Park.
- Estimated densities are among the highest reported for the species, both within and outside the National Park, where guanaco co-occurs with livestock.
- The reported demographic structure points to a single well-established guanaco population throughout the study area encompassing both the National Park and its surroundings. This population is close to a late stage of the dispersive process towards surrounding ranches.
- The social structure of this guanaco population is similar to that described in other areas of Patagonia, although the size of the family groups is among the largest described.
- Guanaco actively selects open areas with small-size vegetation in search of a trade-off between food availability and a good visibility that reduces predation risk.
- Guanaco family groups respond to the presence of predators by increasing group size and cohesion. Group cohesion also increases as group size and co-specific density decreases suggesting a response to perceived risk. There is a lack of response to habitat structure that is probably due to a trade-off between decreasing predation risk and the availability and distribution of trophic resources.
- Niche overlap among native herbivores is low, suggesting that they belong to a competitively structured community according to a process of niche segregation and compression associated with the competition in the past.

- Niche overlap between pairs of domestic and native species is larger than between pairs of natives. However, considering multiple dimensions allows detection of some niche segregation between species, suggesting a niche differentiation in ecological time.
- Guanaco and sheep show differences in habitat selection, pointing to a low potential for competition, although this process may be density-dependent and the situation may change if there is an increase in the density of either species or a reduction in resources availability.
- Sheep abundance causes a niche contraction of the guanaco and vice versa, suggesting that competition is a bilateral and density-dependent process in this case.
- Results of this doctoral thesis suggest that it is necessary to manage the guanaco population in order to avoid possible conflicts with socioeconomic development in the surroundings of the National Park.

Bibliografía

- Abramsky, Z., Rosenzweig, M. L., and Subach, A. (2002). The costs of apprehensive foraging. *Ecology* 83, 1330-1340.
- Acebes Vives, P. (2010). Ecología del guanaco (*Lama guanicoe*) en el Monte hiperárido argentino: uso del espacio, selección de hábitat e interacciones con ungulados exóticos y turistas. PhD dissertation, Universidad Autónoma de Madrid.
- Acebes, P., Traba, J., Malo, J. E., Ovejero, R., and Borghi, C. E. (2010). Density and habitat use at different spatial scales of a guanaco population (*Lama guanicoe*) in the Monte desert of Argentina. *Mammalia* 74, 57-62.
- Acebes, P., Traba, J., and Malo, J. E. (2012). Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *Journal of Arid Environments* 77, 39-44.
- Acebes, P., Malo, J. E., and Traba, J. (2013). Trade-offs between food availability and predation risk in desert environments: The case of polygynous monomorphic guanaco (*Lama guanicoe*). *Journal of Arid Environments* 97, 136-142.
- Adams, D. C. (2004). Character displacement via aggressive interference in Appalachian salamanders. *Ecology* 85, 2664-2670.
- Adler, P. B., Milchunas, D. G., Sala, O. E., Burke, I. C., and Lauenroth, W. K. (2005). Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. *Ecological Applications* 15, 774-792.
- Ahrestani, F. S., Heitkönig, I. M. A., and Prins, H. H. T. (2012). Diet and habitat-niche relationships within an assemblage of large herbivores in a seasonal tropical forest. *Journal of Tropical Ecology* 28, 385-394.
- Akaike, H. (1974). A new look at the statistical model identification. *Automatic Control, IEEE Transactions on* 19, 716-723.
- Andersen, R., Herfindel, I., Sæther, B. E., Linnell, J. D., Oddén, J., and Liberg, O. (2004). When range expansion rate is faster in marginal habitats. *Oikos* 107, 210-214.
- Anderson, M. J. and Robinson, J. (2003). Generalized discriminant analysis based on distances. *Australian & New Zealand Journal of Statistics* 45, 301-318.
- Arsenault, R. and Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. *Oikos* 97, 313-318.

- Bagchi, S., Mishra, C., and Bhatnagar, Y. V. (2004). Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan mountains. *Animal Conservation* 7, 121-128.
- Bailey, D. W. and Provenza, F. D. (2008). Mechanisms Determining Large-Herbivore Distribution. In 'Resource Ecology'. (Eds H. H. T. Prins and F. Langevelde) pp. 7-28. (Springer Netherlands: Netherlands.)
- Baldi, R., Albon, S. D., and Elston, D. A. (2001). Guanacos and sheep: evidence for continuing competition in arid Patagonia. *Oecologia* 129, 561-570.
- Baldi, R., Pelliza-Sbriller, A., Elston, D., and Albon, S. (2004). High potential for competition between guanacos and sheep in Patagonia. *Journal of Wildlife Management* 68, 924-938.
- Baldi, R., Lichtenstein G., González, B., Funes, M., Cuéllar, E., Villalba, L., Hoces, D. and Puig, S. (2008). *Lama guanicoe*. In 'IUCN Red List of Threatened Species'. (Ed. I. 2012). (IUCN.)
- Baldi, R., Acebes, P., Cuéllar, E., Funes, M., Hoces, D., Puig, S., and Franklin, W. L. (2016). *Lama guanicoe*. In 'IUCN Red List of Threatened Species' (Ed. IUCN 2016) <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T11186A18540211.en>. Downloaded on 19 August 2016.
- Bank, M. and Franklin, W. (1998). Puma (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). *Mammalia* 62, 599-605.
- Bank, M. S., Sarno, R. J., Campbell, N. K., and Franklin, W. L. (2002). Predation of guanacos (*Lama guanicoe*) by southernmost mountain lions (*Puma concolor*) during a historically severe winter in Torres del Paine National Park, Chile. *Journal of Zoology* 258, 215-222.
- Bank, M. S., Sarno, R. J., and Franklin, W. L. (2003). Spatial distribution of guanaco mating sites in southern Chile: conservation implications. *Biological Conservation* 112, 427-434.
- Banks, P. B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal behaviour* 61, 1013-1021.
- Barnagaud, J.-Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Viol, I., and Archaux, F. (2012). Relating habitat and climatic niches in birds. *PloS one* 7, e32819.
- Barrera, K., Soto, N., Cabello, J., and Antúnez, D. (2010). 'El puma. Antecedentes para su conservación y manejo en Magallanes'. (Servicio Agrícola y Ganadero. Punta Arenas. Chile).
- Barri, F. and Fernández, M. (2011). Foraging and vigilance time allocation in a guanaco (*Lama guanicoe*) population reintroduced in Quebrada del Condorito National Park (Córdoba, Argentina). *Acta ethologica* 14, 103-107.
- Bartón, K. (2012). MuMIn: Multi-model inference. R package version 1.7. 11.)
- Bates, D., M. Machler, and B. Bolker (2011). lme4: Linear mixed-effects models using s4 classes. <http://cran.R-project.org/package=lme4>. R package version 0.999375-42
- Begon, M., J. L. Harper, and C. R. Townsend. (1999). *Ecología*. (Omega, Barcelona, Spain).

-
- Belovsky, G. E. (1986). Generalist herbivore foraging and its role in competitive interactions. *American Zoologist*, 51-69.
- Benítez-López, A., Viñuela, J., Suárez, F., Hervás, I., and García, J. T. (2014). Niche-habitat mechanisms and biotic interactions explain the coexistence and abundance of congeneric sandgrouse species. *Oecologia* 176, 193-206.
- Berger, J. (1987). Reproductive fates of dispersers in a harem-dwelling ungulate: the wild horse. *Mammalian dispersal patterns* (Ed. BD Chepko-Sade & ZT Halpin), 41-54.
- Berger, J. (1999). Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proceedings of the Royal Society of London B: Biological Sciences* 266, 2261-2267.
- Blonder, B., Lamanna, C., Violle, C., and Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography* 23, 595-609.
- Boer, W. F. and Prins, H. H. T. (1990). Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82, 264-274.
- Bolnick, D. I. (2001). Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature* 410, 463-466.
- Bolnick, D. I., Ingram, T., Stutz, W. E., Snowberg, L. K., Lau, O. L., and Paull, J. S. (2010). Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society of London B: Biological Sciences* 277, 1789-1797.
- Bonino, N., Pelliza-Sbriller, A (1991). Comparación de las dietas del guanaco, ovino y bovino en Tierra del Fuego, Argentina. *Turrialba* 41, 6.
- Borgnia, M., Vilá, B. L., and Cassini, M. H. (2008). Interaction between wild camelids and livestock in an Andean semi-desert. *Journal of Arid Environments* 72, 2150-2158.
- Brown, J. S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* 1, 49-71.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (1993) 'Distance sampling: estimating abundance of biological populations.' (Chapman & Hall.)
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., and Thomas, L. (2001) 'Introduction to Distance Sampling.' (Oxford University Press: London.)
- Burgi, M. V., Marino, A., Rodriguez, M. V., Pazos, G., and Baldi, R. (2012). Response of guanacos *Lama guanicoe* to changes in land management in Peninsula Valdes, Argentine Patagonia: conservation implications. *Oryx* 46, 99-105.
- Burnham, K. P. and Anderson, D. R. (2002) 'Model selection and multimodel inference: a practical information-theoretic approach.' (Springer.)
- Burnham, K. P. and Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in model selection. *Sociological methods & research* 33, 261-304.
- Byers, J. A. (1997) 'American pronghorn: social adaptations and the ghosts of predators past.' (University of Chicago Press.)

- Carmona, C. P., de Bello, F., Mason, N. W., and Leps, J. (2016a). Traits without borders: integrating functional diversity across scales. *Trends in Ecology & Evolution* 31, 382-394.
- Carmona, C. P., de Bello, F., Mason, N. W., and Leps, J. (2016b). The Density Awakens: A Reply to Blonder. *Ecol. Lett* 17, 771-784.
- Chartier, M. P. and Rostagno, C. M. (2006). Soil erosion thresholds and alternative states in northeastern patagonian rangelands. *Rangeland Ecology & Management* 59, 616-624.
- Chase, J. M. and Leibold, M. A. (2003) 'Ecological niches: linking classical and contemporary approaches.' (University of Chicago Press.)
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics* 31, 343-366.
- Childress, M. J. and Lung, M. A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal behaviour* 66, 389-398.
- Cimino, L. and Lovari, S. (2003). The effects of food or cover removal on spacing patterns and habitat use in roe deer (*Capreolus capreolus*). *Journal of Zoology* 261, 299-305.
- Clutton-Brock, T. and Coulson, T. (2002). Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357, 1285-1298.
- Codron, D., Hull, J., Brink, J. S., Codron, J., Ward, D., and Clauss, M. (2011). Effect of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis. *Evolutionary Ecology Research* 13, 217-235.
- CONAF. (1992). Manejo productivo y sustentable del guanaco en su medio natural. Isla Tierra de Fuego, XII Región, Chile. Departamento Técnico, Programa Patrimonio Silvestre.
- CONAF. (2011). Parque Nacional Torres del Paine. www.conaf.cl/parques/ficha-parque-nacional-torres-del-paine-39.html. Acceso el 11/01/11
- Connell, J. H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 131-138.
- Creel, S. and Winnie, J. A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal behaviour* 69, 1181-1189.
- Darmon, G., Calenge, C., Loison, A., Maillard, D., and Jullien, J.-M. (2007). Social and spatial patterns determine the population structure and colonization processes in mouflon. *Canadian Journal of Zoology* 85, 634-643.
- Darmon, G., Calenge, C., Loison, A., Jullien, J. M., Maillard, D., and Lopez, J. F. (2012). Spatial distribution and habitat selection in coexisting species of mountain ungulates. *Ecography* 35, 44-53.
- Dawson, T. J. and Ellis, B. A. (1994). Diets of mammalian herbivores in Australian arid shrublands: seasonal effects on overlap between red kangaroos, sheep and

-
- rabbits and on dietary niche breadths and electivities. *Journal of Arid Environments* 26, 257-271.
- Delgado, M. P., Sanza, M. A., Morales, M. B., Traba, J., and Rivera, D. (2013). Habitat selection and coexistence in wintering passerine steppe birds. *Journal of Ornithology* 154, 469-479.
- Di Bitetti, M. S., Di Blanco, Y. E., Pereira, J. A., Paviolo, A., and Pérez, I. J. (2009). Time Partitioning Favors the Coexistence of Sympatric Crab-Eating Foxes (*Cerdocyon thous*) and Pampas Foxes (*Lycalopex gymnocercus*). *Journal of Mammalogy* 90, 479-490.
- Di Rienzo, J. A., Casanoves, F., Balzarini, M. G., Gonzalez, L., Tablada, M., and Robledo, C. W. (2011). InfoStat.
- Distefano, E. (2005). Human-Wildlife Conflict worldwide: collection of case studies, analysis of management strategies and good practices. Food and Agricultural Organization of the United Nations (FAO), Sustainable Agriculture and Rural Development Initiative (SARDI), Rome, Italy. Available from: FAO Corporate Document repository <http://www.fao.org/documents>.
- Djagoun, C. A., Kassa, B., Mensah, G. A., and Sinsin, B. A. (2013). Seasonal habitat and diet partitioning between two sympatric bovid species in Pendjari Biosphere Reserve (northern Benin): waterbuck and western kob. *African Zoology* 48, 279-289.
- Dobson, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal behaviour* 30, 1183-1192.
- du Toit, J. T. (2010). Addressing the Mismatches between Livestock Production and Wildlife Conservation across Spatio-temporal Scales and Institutional Levels. *Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystems*, 30. Duong, T. (2016). ks: Kernel smoothing. R package version 1.10.2.
- Durant, S. M., Craft, M. E., Hilborn, R., Bashir, S., Hando, J., and Thomas, L. (2011). Long-term trends in carnivore abundance using distance sampling in Serengeti National Park, Tanzania. *Journal of Applied Ecology* 48, 1490-1500.
- Elbroch, L. M. and Wittmer, H. U. (2012). Puma spatial ecology in open habitats with aggregate prey. *Mammalian Biology-Zeitschrift für Säugetierkunde* 77, 377-384.
- Elith, J., Leathwick, J. R., and Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology* 77, 802-813.
- ESRI ArcGIS: A Complete Integrated System. (<http://www.esri.com/software/arcgis>)
- Evaluación de los Ecosistemas del Milenio 2005. (2005). *Ecosystems and human well-being: biodiversity synthesis*. World resources institute, Washington, DC, 86.
- Fall, M. W. and Jackson, W. B. (2002). The tools and techniques of wildlife damage management-changing needs: an introduction. *International biodeterioration & biodegradation* 49, 87-91.
- Fischer, L. A. and Gates, C. C. (2005). Competition potential between sympatric woodland caribou and wood bison in southwestern Yukon, Canada. *Canadian Journal of Zoology* 83, 1162-1173.

- Franklin, W. L. (1982). Biology, ecology, and relationship to man of the South American camelids. *Mammalian Biology in South America* 6, 457-489.
- Franklin, W. L. (1983). Contrasting socioecologies of South America's wild camelids: the vicuña and guanaco. In 'Advances in the Study of Mammalian Behavior'. (Ed. J. F. K. Eisenberg, D.G.) pp. 573-629. (The American Society of Mammalogists: USA.)
- Franklin, W. L., Johnson, W. E., Sarno, R. J., and Iriarte, J. A. (1999). Ecology of the Patagonia puma *Felis concolor patagonica* in southern Chile. *Biological Conservation* 90, 33-40.
- Fretwell, S. D. (1972) 'Populations in a seasonal environment.' (Princeton University Press.)
- Fretwell, S. D. and Lucas, H. L., Jr. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta biotheorica* 19, 16-36.
- Fritz, M. and Franklin, W. (1994). First estimates of guanaco male group harvestability in the Patagonia of South America. *Vida Silvestre Neotrop* 3, 84-90.
- Gause, G. (1934). *The struggle for existence.* (Ed. Williams & Wilkins) Baltimore. USA. 163pp.
- Geange, S. W., Pledger, S., Burns, K. C., and Shima, J. S. (2011). A unified analysis of niche overlap incorporating data of different types. *Methods in Ecology and Evolution* 2, 175-184.
- Gerard, J.-F., Bideau, E., Maublanc, M.-L., Loisel, P., and Marchal, C. (2002). Herd size in large herbivores: encoded in the individual or emergent? *The Biological Bulletin* 202, 275-282.
- González, B. A., Palma, R. E., Zapata, B., and Marín, J. C. (2006a). Taxonomic and biogeographical status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae). *Mammal Review* 36, 157-178.
- González, B.A. (2006b). Efecto del incendio del año 2005 sobre la biodiversidad de fauna en el Parque Nacional Torres del Paine. Estudios específicos en aves acuáticas, aves terrestres, ñandú y guanaco. Informe Técnico preparado para CONAF y GTZ.
- Gordon, I. J. (2009). What is the Future for Wild, Large Herbivores in Human-Modified Agricultural Landscapes? *Wildlife Biology* 15, 1-9.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal behaviour* 28, 1140-1162.
- Gurd, D. B., Nudds, T. D., and Rivard, D. H. (2001). Conservation of mammals in eastern North American wildlife reserves: how small is too small? *Conservation Biology* 15, 1355-1363.
- Hall, L. S., Krausman, P. R., and Morrison, M. L. (1997). The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin*, 173-182.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of theoretical Biology* 31, 295-311.
- Hansen, A. J. and DeFries, R. (2007). Ecological mechanisms linking protected areas to surrounding lands. *Ecological Applications* 17, 974-988.

-
- Haswell, P. M., Kusak, J., and Hayward, M. W. (2016). Large carnivore impacts are context-dependent. *Food Webs*.
- Hebblewhite, M., Pletscher, D. H., and Paquet, P. C. (2002). Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology* 80, 789-799.
- Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., and Dill, L. M. (2009). Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78, 556-562.
- Heusser, C. (1994). Paleoindians and fire during the late Quaternary in southern South America. *Revista Chilena de Historia Natural* 67, 435-443.
- Hobbs, N. T., Baker, D. L., Bear, G. D., and Bowden, D. C. (1996a). Ungulate grazing in sagebrush grassland: Effects of resource competition on secondary production. *Ecological Applications* 6, 218-227.
- Hobbs, N. T., Baker, D. L., Bear, G. D., and Bowden, D. C. (1996b). Ungulate grazing in sagebrush grassland: Mechanisms of resource competition. *Ecological Applications* 6, 200-217.
- Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78, 443-457.
- Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106, 19659-19665.
- Homewood, K. and Rodgers, W. (1991). Maasailand ecology: pastoralist development and wildlife conservation in Ngorongoro, Tanzania. *Maasailand ecology: pastoralist development and wildlife conservation in Ngorongoro, Tanzania*.
- Howard, P. C. (1986). Spatial organization of common reedbuck with special reference to the role of juvenile dispersal in population regulation. *African Journal of Ecology* 24, 155-171.
- Huber, U. M. and Markgraf, V. (2003). European impact on fire regimes and vegetation dynamics at the steppe-forest ecotone of southern Patagonia. *The Holocene* 13, 567-579.
- Hutchinson, G. E. (1957). Cold spring harbor symposium on quantitative biology. Concluding remarks 22, 415-427.
- Hutton, J., Adams, W. M., and Murombedzi, J. C. Back to the barriers? Changing narratives in biodiversity conservation. 2005 pp. 341-370. (Taylor & Francis.)
- Iranzo, E. C., Traba, J., Acebes, P., González, B. A., Mata, C., Estades, C. F., and Malo, J. E. (2013). Niche Segregation between wild and domestic herbivores in Chilean patagonia. *PloS one* 8, e59326.
- Jarman, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* 48, 215-267.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65-71.

- Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., and Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology letters* 10, 690-700.
- Kie, J. G. (1999). Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* 80, 1114-1129.
- Kie, J. G., Evans, C. J., Loft, E. R., and Menke, J. W. (1991). Foraging behavior by mule deer: the influence of cattle grazing. *Journal of Wildlife Management* 55, 665-674.
- Kowalczyk, R., Krasíńska, M., Kamiński, T., Górny, M., Struś, P., Hofman-Kamińska, E., and Krasíński, Z. A. (2013). Movements of European bison (*Bison bonasus*) beyond the Białowieża Forest (NE Poland): range expansion or partial migrations? *Acta theriologica* 58, 391-401.
- Kutt, A. S. and Gordon, I. J. (2012). Variation in terrestrial mammal abundance on pastoral and conservation land tenures in north-eastern Australian tropical savannas. *Animal Conservation*, 15, 416-425.
- Laughlin, D. C. and Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution* 30, 487-496.
- Laundré, J. W. (2010). Behavioral response races, predator-prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology* 91, 2995-3007.
- Laundré, J. W., Hernández, L., and Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79, 1401-1409.
- Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P., and Browning, D. M. (2014). The landscape of fear: the missing link to understand top?down and bottom?up controls of prey abundance? *Ecology* 95, 1141-1152.
- Lawlor, L. R. and Smith, J. M. (1976). The coevolution and stability of competing species. *The American Naturalist* 110, 79-99.
- Lawson Handley, L. and Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology* 16, 1559-1578.
- Legendre, P. and Legendre, L. F. (2012) 'Numerical ecology.' (Elsevier.)
- Lima, S. (1990). The influence of models on the interpretation of vigilance. In 'Interpretation and Explanation in the Study of Animal Behavior: Vol. 2: Explanation, Evolution and Adaptation'. (eds M. Bekoff and D. Jamieson.) pp. 246-267. (Westview Press: Boulder, CO).
- Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal behaviour* 49, 11-20.
- Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68, 619-640.
- Long, E. S., Fecske, D. M., Sweitzer, R. A., Jenks, J. A., Pierce, B. M., and Bleich, V. C. (2003). Efficacy of photographic scent stations to detect mountain lions. *Western North American Naturalist* 63, 529-532.

-
- Lucherini, M. (2016). *Lycalopex culpaeus*. The IUCN Red List of Threatened Species 2016: e.T6929A85324366. Downloaded on 25 December 2016.
- Lung, M. A. and Childress, M. J. (2007). The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behavioral Ecology* 18, 12-20.
- MacArthur, R. H. and Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist* 100, 603-609.
- MacArthur, R.H. and Wilson, E.O. (1967). Reprinted 2001. *The theory of island biogeography*. (Princeton University Press).
- Madhusudan, M. (2004). Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* 41, 858-869.
- Malo, J., González, B., Traba, J., Estades, C., Acebes, P., Galaz, J., and Zapata, O. (2009). Modulation of guanaco (*Lama guanicoe*) flight behaviour by tourist use in Torres del Paine Region. In 10th international mammalogical congress, Mendoza, Argentina. pp. 134-135.
- Malo, J. E., Acebes, P., Giannoni, S. M., and Traba, J. (2011). Feral livestock threatens landscapes dominated by columnar cacti. *Acta Oecologica-International Journal of Ecology* 37, 249-255.
- Marin, J. C., González, B. A., Poulin, E., Casey, C. S., and Johnson, W. E. (2013). The influence of the arid Andean high plateau on the phylogeography and population genetics of guanaco (*Lama guanicoe*) in South America. *Molecular Ecology* 22, 463-482.
- Marino, A. (2010). Costs and benefits of sociality differ between female guanacos living in contrasting ecological conditions. *Ethology* 116, 999-1010.
- Marino, A. (2012). Indirect measures of reproductive effort in a resource-defense polygynous ungulate: territorial defense by male guanacos. *Journal of ethology* 30, 83-91.
- Marino, A. and Baldi, R. (2008). Vigilance patterns of territorial guanacos (*Lama guanicoe*): The role of reproductive interests and predation risk. *Ethology* 114, 413-423.
- Marino, A. and Baldi, R. (2014). Ecological Correlates of Group-Size Variation in a Resource-Defense Ungulate, the Sedentary Guanaco. *PloS one* 9, e89060.
- Marino, A., Rodríguez, V., and Pazos, G. (2016). Resource-defense polygyny and self-limitation of population density in free-ranging guanacos. *Behavioral Ecology* 27, 757-765.
- Márquez, A. L., Real, R., Olivero, J., and Estrada, A. (2011). Combining climate with other influential factors for modelling the impact of climate change on species distribution. *Climatic Change* 108, 135-157.
- Marshal, J. P., Bleich, V. C., and Andrew, N. G. (2008). Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment. *Wildlife Biology* 14, 228-236.
- May, R. M. (1974). Ecosystem patterns in randomly fluctuating environments. *Progress in theoretical biology* 3, 1-50.

- May, R. M. and Mac Arthur, R. H. (1972). Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences* 69, 1109-1113.
- Mayfield, M. M., Bonser, S. P., Morgan, J. W., Aubin, I., McNamara, S., and Vesk, P. A. (2010). What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography* 19, 423-431.
- Mayfield, M. M. and Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology letters* 13, 1085-1093.
- Meffe, G. and Carroll, C. (1994). *Principles of conservation biology*. (Sinauer Associates: Massachusetts.).
- Mishra, C., Wieren, S. E., Heitkönig, I. M. A., and Prins, H. H. T. (2002). A theoretical analysis of competitive exclusion in a Trans-Himalayan large-herbivore assemblage. *Animal Conservation* 5, 251-258.
- Mishra, C., Van Wieren, S. E., Ketner, P., Heitkönig, I. M. A., and Prins, H. H. T. (2004). Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *Journal of Applied Ecology* 41, 344-354.
- Montes, C., De Lamo, D. A., and Zavatti, J. (2000). Distribución de abundancias de guanacos (*Lama guanicoe*) en los distintos ambientes de Tierra del Fuego, Argentina. *Mastozoología Neotropical* 7, 5-14.
- Morris, D. W. (1988). Habitat-dependent population regulation and community structure. *Evolutionary Ecology* 2, 253-269.
- Morris, D. W. (2009). Apparent predation risk: tests of habitat selection theory reveal unexpected effects of competition. *Evolutionary Ecology Research* 11, 209-225.
- Mouillot, D., Stubbs, W., Faure, M., Dumay, O., Tomasini, J. A., Wilson, J. B., and Do Chi, T. (2005). Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. *Oecologia* 145, 345-353.
- Mwasi, S. M., Van, S. E., and Ignas MA, H. (2013). Seasonal resource use and niche breadth in an assemblage of coexisting grazers in a fenced Park. *Open Journal of Ecology* 2013.
- Namgail, T., Fox, J., and Bhatnagar, Y. (2007). Habitat shift and time budget of the Tibetan argali: the influence of livestock grazing. *Ecological Research* 22, 25-31.
- Novaro, A. J., Moraga, C. A., Briceño, C., Funes, M. C., and Marino, A. (2009). First records of culpeo (*Lycalopex culpaeus*) attacks and cooperative defense by guanacos (*Lama guanicoe*). *Mammalia* 73, 148-150.
- Olson, K. A., Fuller, T. K., Schaller, G. B., Odonkhuu, D., and Murray, M. G. (2005). Estimating the population density of Mongolian gazelles *Procapra gutturosa* by driving long-distance transects. *Oryx* 39, 164-169.
- Ortega, I. M. and Franklin, W. L. (1995). Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. *Revista Chilena de Historia Natural* 68, 489-500.
- Ovejero, R. J. A., Acebes, P., Malo, J. E., Traba, J., Torres, M. E., and Borghi, C. E. (2011). Lack of feral livestock interference with native guanaco during the dry

-
- season in a South American desert. *European Journal of Wildlife Research* 57, 1007-1015.
- Owen-Smith, R. N. (2002) 'Adaptive herbivore ecology : from resources to populations in variable environments.' (Cambridge University Press: Cambridge.)
- Pedrana, J., Rodríguez, A., Bustamante, J., Travaini, A., and Zanón Martínez, J. I. (2009). Failure to estimate reliable sex ratios of guanaco from road-survey data. *Canadian Journal of Zoology* 87, 886-894.
- Pedrana, J., Bustamante, J., Travaini, A., and Rodríguez, A. (2010). Factors influencing guanaco distribution in southern Argentine Patagonia and implications for its sustainable use. *Biodiversity and Conservation* 19, 3499-3512.
- Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological modelling* 190, 231-259.
- Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences* 71, 2141-2145.
- Pisano, E. (1974). Estudio ecológico de la región continental sur del área andino patagónica. II Contribución a la fitogeografía de la zona del Parque Nacional Torres del Paine. In 'Anales del Instituto de la Patagonia' pp. 59-104.)
- Plumb, G. E., White, P. J., Coughenour, M. B., and Wallen, R. L. (2009). Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation* 142, 2377-2387.
- Prins, H. H. (1992). The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19, 117-123.
- Prins, H. H. T. (2000). Competition between Wildlife and Livestock in Africa. In 'Wildlife conservation by sustainable use'. (Ed. G. J. Prins HHT, Dolan TT) pp. 51-80. (Kluwer Academic Publishers: Boston.)
- Prins, H. H. T. and Olf, H. (1998). Species richness of African grazer assemblages: towards a functional explanation. In 'Dynamics of tropical communities'. (Ed. D. M. Newbery, Prins, H.H.T., Brown, N.D. (eds.)) pp. 449-490. (Blackwells Scientific: Oxford, UK.)
- Prins, H. H., De Boer, W. F., Van Oeveren, H., Correia, A., Mafuca, J., and Olf, H. (2006). Coexistence and niche segregation of three small bovid species in southern Mozambique. *African Journal of Ecology* 44, 186-198.
- Puig, S. (1995) 'Técnicas para el manejo del guanaco.' (IUCN: Buenos Aires, Argentina.)
- Puig, S. and Videla, F. (2007). Distribución, densidades y estado de conservación de los camélidos. In 'Diversidad biológica y cultural de los altos andes centrales de Argentina'. (Ed. E. Martínez Carretero) pp. 198. (Editorial Fundación Universidad Nacional de San Juan: Argentina.)
- Puig, S., Videla, F. and Cona, M.I. (1997). Diet and abundance of the guanaco (*Lama guanicoe* Muller 1776) in four habitats of northern Patagonia, Argentina. *Journal of Arid Environments* 36, 343-357

- Puig, S., Videla, F., Cona, M. I., and Monge, S. A. (2001). Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). *Journal of Arid Environments* 47, 291-308.
- Puig, S., Videla, F., Cona, M. I., and Roig, V. G. (2008). Habitat use-by guanacos (*Lama guanicoe*, Camelidae) in northern Patagonia (Mendoza, Argentina). *Studies on Neotropical Fauna and Environment* 43, 1-9.
- Pulliam, R. H. (1973). On the advantage of flocking. *J. Theor. Biol.* 38, 419-422.
- Pulliam, H. and Caraco, T. (1984). Living in groups: is there an optimal group size?. *Behavioural Ecology: an evolutionary approach.* (JR Krebs & NB Davies, Eds.) pp. 122-148. (Blackwell Scientific Publications, Oxford.)
- Putman, R. J. (1996) 'Competition and resource partitioning in temperate ungulate assemblies.' 1°ed. (Chapman & Hall: London.)
- Qiao, H., Escobar, L. E., Saupe, E. E., Ji, L., and Soberón, J. (2016). A cautionary note on the use of hypervolume kernel density estimators in ecological niche modelling. *Global Ecology and Biogeography*.
- R Core Team. (2014). R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Raedeke, K. (1979) Population dynamics and socioecology of the guanaco (*Lama guanicoe*) of Magallanes, Chile. (University of Washington: Seattle.)
- Raedeke, K. J. (1982). Habitat use by guanacos (*Lama guanicoe*) and sheep on common range, Tierra del Fuego, Chile. *Turrialba* 32, 6.
- Raedeke, K. J. and Simonetti, J. A. (1988). Food habits of *Lama guanicoe* in Atacama Desert of northern Chile. *Journal of Mammalogy* 69, 4.
- Reus, M. L., Cappa, F. M., Andino, N., Campos, V. E., de los Ríos, C., and Campos, C. M. (2014). Trophic interactions between the native guanaco (*Lama guanicoe*) and the exotic donkey (*Equus asinus*) in the hyper-arid Monte desert (Ischigualasto Park, Argentina). *Studies on Neotropical Fauna and Environment* 49, 159-168.
- Rey, A., Carmanchahi, P. D., Puig, S., and Guichón, M. L. (2009). Densidad, estructura social, actividad y manejo de guanacos silvestres (*Lama guanicoe*) en el sur del Neuquén, Argentina. *Mastozoología Neotropical* 16, 389-401.
- Rey, A., Novaro, A. J., and Guichón, M. L. (2012). Guanaco (*Lama guanicoe*) mortality by entanglement in wire fences. *Journal for Nature Conservation* 20, 280-283.
- Ricklefs, R. and Schluter, D. (1993). Species diversity in ecological communities: historical and geographical perspectives.
- Rinehart, K.A., Elbroch, L.M. and Wittmer, H.U. (2014). Common biases in density estimation based on home range overlap with reference to pumas in Patagonia. *Wildlife Biology* 20, 19-26.
- Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal behaviour* 51, 1077-1086.
- Rosenberg, M. S. and Anderson, C. D. (2011). PASSaGE: Pattern Analysis, Spatial Statistics and Geographic Exegesis. Version 2. *Methods in Ecology and Evolution* 2, 229-232.

-
- Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos* 98, 156-162.
- Rosenzweig, M. L. (1974). On the evolution of habitat selection. In *Proceedings of the first international congress of ecology* 401, 404.
- Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology* 62, 327-335.
- Samelius, G., Andrén, H., Kjellander, P, and Liberg, O. (2013). Habitat selection and risk of predation: re-colonization by lynx had limited impact on habitat selection by roe deer. *PloS one* 8, e75469.
- Sarno, R. J. and Franklin, W. L. (1999). Population density and annual variation in birth mass of guanacos in southern Chile. *Journal of Mammalogy* 80, 1158-1162.
- Schoener, T. W. (1974). Competition and the form of habitat shift. *Theoretical population biology* 6, 265-307.
- Schoener, T. W. (1989). The ecological niche. In 'Ecological concepts'. (Ed. J. M. Cherret) pp 79-113. (Blackwell).
- Schroeder, N. M., Matteucci, S. D., Moreno, P. G., Gregorio, P., Ovejero, R., Taraborelli, P., and Carmanchahi, P. D. (2014). Spatial and seasonal dynamic of abundance and distribution of guanaco and livestock: insights from using density surface and null models. *PloS one* 9, e85960.
- Servicio Agrícola y Ganadero. (2016). Resolución exenta No:272/2016. Autorización a la empresa comercial Mac Lean y cía. Ltda. Cuota de caza de guanacos (*Lama guanicoe*) en la Comuna Torres del Paine, Provincia Última Esperanza, con fines de uso sustentable. (SAG Magallanes y Antártica Chilena)
- Shea, K. and Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17, 170-176.
- Simonetti, J. A. (1995). Wildlife conservation outside parks is a disease-mediated task. *Conservation Biology* 9, 454-456.
- Sinclair, A. R. E. (1985). Does interspecific competition or predation shape the african ungulate community? *Journal of Animal Ecology* 54, 20.
- Sitters, J., Heitkönig, I. M. A., Holmgren, M., and Ojwang', G. S. O. (2009). Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. *Biological Conservation* 142, 738-750.
- Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika* 38, 196-218.
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology letters* 10, 1115-1123.
- Soberon, J. and Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiv. Inform* 2, 1-10.
- Soler Esteban, R., Martínez Pastur, G., Lencinas, M., and Borrelli, L. (2012). Differential forage use between large native and domestic herbivores in Southern Patagonian *Nothofagus* forests. *Agroforestry Systems* 85, 397-409.
- Soriano, A. and Movia, C. P. (1986). Erosión y desertización en la Patagonia. *Interciencia* 11, 7.

- Sosa, R. A. and Sarasola, J. H. (2005). Habitat use and social structure of an isolated population of guanacos (*Lama guanicoe*) in the Monte Desert, Argentina. *European Journal of Wildlife Research* 51, 207-209.
- Soto, N. (2001). Impacto de la fauna silvestre en la producción agropecuaria de Magallanes. Informe técnico: Servicio Agrícola y Ganadero (Punta Arenas).
- Soto, N. (2010) Distribución y abundancia de la población de guanacos (*Lama guanicoe*, Muller 1776) en el área agropecuaria de Tierra del Fuego (Chile) y su relación de carga animal con la ganadería ovina. (Universidad Internacional de Andalucía: Punta Arenas, Chile.)
- Southwood, T. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46, 337-365.
- StatSoft, I. (2007). STATISTICA (data analysis software system), version 8.0. (www.statsoft.com.)
- Stewart, K. M., Bowyer, R. T., Kie, J. G., Cimon, N. J., and Johnson, B. K. (2002). Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *Journal of Mammalogy* 83, 229-244.
- Stuart, Y. E., Campbell, T., Hohenlohe, P., Reynolds, R. G., Revell, L., and Losos, J. (2014). Rapid evolution of a native species following invasion by a congener. *Science* 346, 463-466.
- Suryawanshi, K. R., Bhatnagar, Y. V., and Mishra, C. (2010). Why should a grazer browse? Livestock impact on winter resource use by bharal *Pseudois nayaur*. *Oecologia* 162, 453-462.
- Sutherland, W. J. and Norris, K. (2002). Behavioural models of population growth rates: implications for conservation and prediction. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 357, 1273-1284.
- Svanbäck, R. and Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society of London B: Biological Sciences* 274, 839-844.
- Taraborelli, P., Gregorio, P., Moreno, P., Novaro, A., and Carmanchahi, P. (2012). Cooperative vigilance: The guanaco's (*Lama guanicoe*) key antipredator mechanism. *Behavioural processes* 91, 82-89.
- Tarjuelo, R., Traba, J., Morales, M. B., and Morris, D. W. (2016). Isodars unveil asymmetric effects on habitat use caused by competition between two endangered species. *Oikos*.
- Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., and Slotow, R. (2010). Group dynamics of zebra and wildebeest in a woodland savanna: effects of predation risk and habitat density. *PloS one* 5, e12758.
- Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., and Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92, 398-407.
- Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., and Burnham, K. P. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47, 5-14.

-
- Thüngen, J. and Lanari, M. R. (2010). Profitability of sheep farming and wildlife management in Patagonia. *Pastoralism* 1, 17.
- Traba, J., Morales, M., Carmona, C., and Delgado, M. P. (2015). Resource partitioning and niche segregation in a steppe bird assemblage. *Community Ecology* 16, 178-188.
- Travaini, A., Zapata, S. C., Bustamante, J., Pedrana, J., Zanón, J. I., and Rodríguez, A. (2015). Guanaco abundance and monitoring in Southern Patagonia: distance sampling reveals substantially greater numbers than previously reported. *Zoological Studies* 54, 23.
- Van Winkle, W. (1975). Comparison of several probabilistic home-range models. *Journal of Wildlife Management* 39, 6.
- Venables, W. N. and Ripley, B. D. (2002). *Modern Applied Statistics with S*. Fourth Edition. (Springer, New York).
- Vidal, O. J. and Reif, A. (2011). Effect of a tourist-ignited wildfire on *Nothofagus pumilio* forests at Torres del Paine biosphere reserve, Chile (Southern Patagonia). *Bosque* 32, 64-76.
- Voeten, M. M. and Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120, 287-294.
- White, P., Gower, C. N., Davis, T. L., Sheldon, J. W., and White, J. R. (2012). Group dynamics of Yellowstone pronghorn. *Journal of Mammalogy* 93, 1129-1138.
- Wiens, J. A. (1986). Spatial scale and temporal variation in studies of shrubsteppe birds. *Community ecology*. Harper and Row, New York, 154-172.
- Wiens, J. A. (1989). *The ecology of birds communities*. Vol 1: Foundations and patterns. (Cambridge University Press: Reino Unido.)
- Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology* 70, 164-168.
- Worton, B.J. (1995). Using Monte Carlo simulation to evaluate kernelbased home range estimators. *Journal of Wildlife Management* 59,794-880.
- Young, J. K. and Franklin, W. L. (2004a). Activity budget patterns in family-group and solitary territorial male guanacos. *Revista Chilena de Historia Natural* 77, 617-625.
- Young, J. K. and Franklin, W. L. (2004b). Territorial fidelity of male guanacos in the Patagonia of southern Chile. *Journal of Mammalogy* 85, 72-78.
- Zhang, Y., Cao, Q. S., Rubenstein, D. I., Zang, S., Songer, M., Leimgruber, P., Chu, H., Cao, J., Li, K., and Hu, D. (2015). Water Use Patterns of Sympatric Przewalski's Horse and Khulan: Interspecific Comparison Reveals Niche Differences. *PLoS one* 10, e0132094.