UNIVERSIDAD AUTÓNOMA DE MADRID
FACULTAD DE CIENCIAS
Departamento de Ecología

Ecología del guanaco (Lama guanicoe) en el Monte hiperárido argentino: uso del espacio, selección de hábitat e interacciones con ungulados exóticos y turistas.

TESIS DOCTORAL
Pablo Acebes Vives
Madrid, 2010

UNIVERSIDAD AUTÓNOMA DE MADRID
FACULTAD DE CIENCIAS
Departamento de Ecología

Ecología del guanaco (*Lama guanicoe*) en el Monte hiperárido argentino: uso del espacio, selección de hábitat e interacciones con ungulados exóticos y turistas.

Memoria presentada por **Pablo Acebes Vives** para optar al Grado de Doctor
en Ecología y Medio Ambiente por la Universidad Autónoma de Madrid

Bajo la dirección de los doctores:

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, junio de 2010

La presente Tesis Doctoral ha sido desarrollada en el marco del proyecto INTERMARG "*Interacciones entre especies autóctonas amenazadas, herbívoros exóticos y visitantes en áreas protegidas del Monte árido argentino. Implicaciones para la conservación y directrices de gestión*" financiado por la **Fundación BBVA** en su 1ª convocatoria de ayudas en Biología de la Conservación (Biocon 03).

Fundación BBVA

InterMArg

A mi madre

Au fond de l´Inconnu puor trouver du nouveau

C. BAUDELAIRE

El verdadero incordio de este mundo nuestro es parecer un poquito más matemático y regular de lo que es; su exactitud resulta obvia, pero su inexactitud está escondida: lo salvaje yace a la espera.

G. K. CHESTERTON

AGRADECIMIENTOS

Afrontar los agradecimientos a estas alturas no resulta sencillo. Cinco años de trabajo y numerosa gente han hecho posible que esta tesis doctoral llegue a buen puerto. Mis más sinceras disculpas de antemano si me olvido de alguna persona.

Mis comienzos en el Departamento de Ecología fueron bien distintos a los que me han llevado a concluir esta tesis doctoral. De la mano de Juan Malo, Juan Traba y Quico Suárez abandoné el apasionante universo de lo microscópico e intangible de las bacterias, por el fascinante mundo (y ciertamente más tangible) de los vertebrados terrestres. A ellos les debo muchísimas cosas. Juan Traba y Juan Malo, mis directores de tesis y amigos, me han enseñado a caminar por el excitante y tortuoso mundo de la Ciencia. Hemos intercambiado jugosas ideas y hemos discutido con intesidad muchos de los temas que figuran en esta tesis. Hemos compartido también muchos días de calor y frío en Argentina (y ahora en Chile), y muchos “salamines”, nuestra “deliciosa dieta” durante las largas temporadas de campo. Y es que resulta extraño que unos directores pasen tanto tiempo con el doctorando; por eso no me extraña que en alguna ocasión (o en muchas) acabaran hasta el gorro de mí. Y por muchas cosas que no terminaría de enumerar, muchas gracias. A Quico me une gran amistad, a prueba de las tórridas arenas saharianas. Siempre ha estado ahí, con una sonrisa (y un cigarrito), pendiente de un servidor, en los buenos y sobretodo en los malos momentos. Un tipo generoso y simpático donde los haya (quizá en algunos cuentos).

Y ya que he descendido al sotano del edificio de Biológicas con Quico, quiero recordar y dejar plasmado la amistad que me une a Juan Oñate, Patri, Isra y Edu. Un despacho de lo más divertido, con gente siempre dispuesta a escuchar (que no es muy frecuente). Y de un salto me planto en mi despacho. Allí hemos compartido largas horas Manolo Morales, Eladio y Paula, además del mencionado Traba. Con Manolo he compartido interesantes charlas sobre algunos de los capítulos de esta tesis y ha sido fuente de numerosas consultas y de buenas risotadas. Eladio, además de un extraordinario compañero, es una persona que ha estado siempre dispuesto a echar una mano. Gracias Eladín. Y con Paulita he compartido muchos ratos, conversaciones y desencuentros, pero sobretodo buenos momentos. Irene Guerrero es un personajillo peculiar que aunque no sea del despacho es como si lo fuese. Me ayudado con temas relacionados con la teledetección y hemos compartido muchos 714 divertidos. Y tampoco quiero olvidar a Jesús Herranz y a Begoña Peco con quienes también he pasado buenos momentos a lo largo de estos años.

En el departamento de Ecología he pasado grandes momentos de la mano de muchos “precarios” a lo largo de estos años: Iker, Isa, Irene Lozano, Carmencita, Susanita, los Pedros, Berta, Pablo Manzano, Erik, Luis, los Diegos, Bea, Jorge, Cristina Mata, Paco, Driss, Paloma, Carlos, Desi, Nacho...y por supuesto Zipi (Sergio Velasco).

En Argentina, mi segunda patria durante los tres años del proyecto, conocí a mucha gente que hicieron sentirme como en casa. En *Guachilasto* pasé largas y divertidas temporadas con los chicos del parque (Pedro, "Pichón", el "Turco", "Chuna", Gustavo, Dino, Iván, Liliana, Fredi, Richard, Lidio, Carlitos y muchos más) con quienes compartí innumerables asados, chivitos y damajuanas. Emilio Fernandez y Eduardo Cortez, los responsables del parque por aquel tiempo se mostraron siempre amables y dispuestos a ayudar en lo que fuese. Del fantasmágórico pueblo de Baldecitos no me puedo olvidar del "Turco" Molina y su familia, nuestros vecinos de la casa de Vialidad; de la familia Herrera (Dante, doña Alba y sus deliciosas comidas); de don Emeldo y su mujer; del gomero y de la familia Aróstica (Carlos, Javier, Ariel,…). Y por supuesto de todos los chicos y chicas del Museo, con quienes compartimos casa y muchos momentos buenos. También en Argentina coseché buenas amistades como las de Ramiro Ovejero y Martín Almirón, con quienes pasé largas jornadas de campo, y me recibieron siempre con los brazos abiertos en sus respectivas moradas. En el Museo Nacional de Ciencias Naturales de San Juan, también conocí a gente amable y quisiera ahora agradecerles su ayuda. Nuestros compañeros de proyecto Carlos, Stella y Claudia nos "interiorizaron" en la vida sanjuanina y nos ofrecieron su casa en nuestros primeros viajes.

Como no queríamos dejar el continente americano, decidimos embarcarnos en una nueva aventura científica, esta vez en la Patagonia chilena, gracias a la cual conocimos a nuestros nuevos colegas y amigos Cristián Estades, Benito González y Beatriz Zapata, además del ya conocido José Luis Galaz. Con ellos hemos seguido compartiendo la pasión por los guanacos…

Y quizá en un ataque de locura (o de extremada sensatez) debo agradecer a mi tortuga Paula haber compartido mi encierro y final de tesis, habiendo soportado estoica e indiferentemente mis charlas, con la única ilusión de que le diese comida y la sacase a corretear por casa.

Los amigos de toda la vida, de la Universidad, las supernenas y los amigos más recientes han sido mi válvula de escape durante todos estos años. Espero que, con esta tesis, todos ellos sepan de una vez qué es un guanaco ¡Por favor no digáis más 'guallaco', guacamayo ni tantos otros nombres impronunciables!

Para finalizar mi más sincero agradecimiento a mi familia por su apoyo y cariño: la del centro peninsular y la de tierra de Guanches. Y a mi hermano Juan, a Manolo y a mi madre.

Hay una persona que transita silenciosamente a lo largo de esta tesis y que dejó una huella imborrable en mi vida. Mi padre. Ejemplo de honestidad, sencillez y generosidad. Pero a quien más tengo que agradecer en esta vida es a mi madre. Por eso, esta tesis está dedicada a ella.

ÍNDICE

Agradecimientos

CAPÍTULO I.
Introducción general

FACTORES QUE REGULAN LA DISTRIBUCIÓN Y ABUNDANCIA DE LOS UNGULADOS

Los grandes herbívoros están presentes en cerca de la mitad de la superficie terrestre y son importantes ecológica y económicamente (Owen-Smith 1988), pero su diversidad está siendo amenazada por las actividades humanas (Prins 1992), quedando sus mejores poblaciones confinadas a unas cuantas áreas protegidas (Harris et al. 2009). En ausencia de perturbaciones de origen antrópico, los herbívoros están regulados mediante mecanismos de arriba abajo (top-down), como la depredación (Sinclair et al. 2003, Hopcraft et al. 2010), o a través de restricciones de abajo a arriba (botton-up) en la producción primaria (McNaughton et al. 1989, Hopcraft et al. 2010). Que prevalezca la regulación de arriba abajo o de abajo a arriba dependerá tanto de las restricciones abióticas que determinen la disponibilidad de forraje, como del tamaño corporal, puesto que el tamaño afecta al riesgo de depredación y a los requerimientos tróficos de los herbívoros (Hopcraft et al. 2010).

Sin embargo, hay otros factores que regulan la mayoría de las poblaciones de grandes herbívoros y cuyo principal responsable es el hombre, como ya se ha mencionado, alterando los procesos naturales de abajo a arriba y de arriba a abajo. Entre dichos factores se pueden citar la caza furtiva o las actividades agrarias y ganaderas, que provocan la destrucción y fragmentación de sus hábitats, o la competencia y desplazamiento por las especies introducidas, quedando las poblaciones de herbívoros silvestres relegadas a hábitats menos favorables. Recientemente se está haciendo énfasis en el efecto que determinadas actividades humanas de recreo tienen sobre las poblaciones silvestres.

Por lo tanto, en función de las condiciones particulares en las que se encuentran las poblaciones de herbívoros silvestres es necesario generar un marco teórico, que permita bosquejar cuáles son los condicionantes que rigen la dinámica de dichas poblaciones, y contrastarlo con datos de campo, para poder implementar políticas de conservación eficaces.

La teoría de nicho: una primera aproximación teórica

Hutchinson (1957) definió el nicho como la suma de todos los factores ambientales que actúan sobre un organismo, es decir, como una región en un hipervolumen *n*-dimensional. Para cada especie, un número explícito (n) de factores limitantes podría ser determinado definiendo el rango de condiciones en el que una especie podría existir. Hutchinson también introdujo las diferencias entre el *nicho fundamental* (todos los condicionantes en el hipervolumen *n*-dimensional en ausencia de otras especies) y el *nicho realizado*, como el subespacio del nicho fundamental en el que una especie queda restringida por las interacciones interespecíficas. MacArthur (1958), Levin (1968) y otros científicos desarrollaron la teoría de Hutchinson, haciendo énfasis en el papel de la competencia interespecífica como factor principal en la estructuración de las comunidades. Posteriormente, los modelos desarrollados fueron criticados por ausencia de rigurosidad estadística y ausencia de contraste frente a modelos nulos (ver revisión en Chase y Leibold 2003). Como quiera que sea, hoy en día convergen diversas aproximaciones en la literatura científica que incluyen varios aspectos en el nicho de las especies: las interacciones competitivas, el efecto de la depredación y la heterogeneidad espacial y temporal (Kotler y Brown 1999, Chesson 2000a, 2000b, Ritchie 2002). Recientemente Chase y Leibold (2003) han propuesto una nueva definición de nicho: "Las condiciones ambientales que permiten satisfacer los requerimientos mínimos de una especie (de manera que la tasa de natalidad de una población determinada es igual o mayor que su tasa de mortalidad), junto con el conjunto de efectos *per capita* de esa especie en esas condiciones ambientales".

En cualquier caso, es una definición teórica o restringida a estudios observacionales o experimentos a pequeña escala, y no ha sido todavía comprobada en las comunidades ungulados. Por lo tanto, todavía hay que aplicar una aproximación más general en la que se explore cómo las especies se posicionan a lo largo de unos pocos ejes (Van Wieren y Van Langevelde 2008). En los sucesivos apartados se analizarán algunos de los factores que determinan el nicho de los ungulados y que centran el contenido experimental de la presente tesis doctoral.

Abundancia, calidad y distribución de los recursos

Los mecanismos comportamentales que rigen los patrones de uso del espacio y selección de hábitat de los ungulados están determinados principalmente por la abundancia, calidad y distribución espacio-temporal de los recursos (Senft et al. 1987, Bailey et al. 1996). Pero ¿qué entendemos por recursos? Una definición interesante es la que ofrecen Prins y Van Langevelde (2008): "un recurso es la energía utilizable o cualquier sustancia biótica o abiótica explotada por un organismo, y que incluye alimento, nutrientes, agua, luz, refugio, espacio, etc. y cuyo uso puede conducir a un agotamiento (temporal) del mismo". La esencia del concepto es que los organismos pueden competir por un recurso y que éste puede limitar el crecimiento de un individuo o de una población (Prins y Van Langevelde 2008). En el caso de los ungulados, el forrajeo es una actividad central y la vegetación es el recurso fundamental (Owen-Smith 2002), pero también existen factores abióticos que afectan a sus patrones de forrajeo como son la topografía (pendiente), la temperatura, la distancia a puntos de agua, el viento o barreras físicas como acantilados o cercados (Bailey et al. 1996).

Los ungulados están generalmente condicionados por las variaciones estacionales, espaciales y climáticas en la disponibilidad de los recursos, especialmente en ecosistemas áridos y semiáridos, donde las variaciones son extremas (Illius 2007). Los ungulados deben afrontar dichos cambios modificando su selección de hábitat, estableciendo desplazamientos de corta distancia o movimientos migratorios en busca de hábitats que ofrezcan mayor calidad y/o abundancia de recursos (Owen-Smith 2002). En los ecosistemas áridos con una estacionalidad marcada, la alternancia de estaciones húmedas y secas marca un ciclo en la fenología de las plantas, que se traduce en un ciclo de abundancia y calidad de forraje. Así, en la estación húmeda los recursos son generalmente abundantes y nutritivos, y los ungulados pueden ser muy selectivos en la dieta, alimentándose de plantas o partes de plantas de gran valor nutritivo (Illius 2006). Durante la estación seca los recursos van progresivamente reduciéndose y los ungulados deben ampliar su dieta incorporando forraje poco nutritivo para satisfacer sus requerimientos energéticos (Sinclair 1975, Fryxell 1987).

Reparto de recursos: competencia *versus* coexistencia

La importancia de la competencia como factor estructurador de las comunidades de ungulados ha sido ampliamente reconocida, a pesar de que en pocas ocasiones ha sido demostrada (Owen-Smith 2002). De hecho, la competencia interespecífica no es el único factor que afecta a las comunidades, no debiéndose descartar los efectos de los procesos históricos y geográficos (Ricklefs y Schluter 1993). Desde un enfoque evolutivo, una explicación plausible es que la competencia en el pasado (‘fantasma de la competencia en el pasado’, Connell 1980) ha devenido en una divergencia de nichos (reparto de recursos) que permite la coexistencia de distintas especies, teniendo por tanto una influencia menor en las poblaciones actuales, o manifestándose intermitentemente cuando los recursos tróficos se agotan temporalmente (Owen-Smith 1989). Determinar efectos competitivos es en parte difícil porque la competencia por interferencia (cuando una especie deniega el uso de recursos a otra a través de comportamientos agresivos) es rara entre grandes herbívoros (Prins 2000, Owen-Smith 2002, Ritchie 2002). La competencia generalmente tiene lugar por explotación de los recursos y sus efectos no se experimentan inmediatamente (Owen-Smith 2002).

La segregación en la dieta o en el hábitat son mecanismos que permiten la coexistencia y forman parte de las adaptaciones comportamentales o fenotíficas que muestran las especies para evitar competencia con otras especies (Van Wieren y Van Langevelde 2008). Sin embargo, la introducción reciente de ungulados exóticos en el ensamblaje de especies nativas puede producir procesos de competencia interespecífica, dado que no ha habido tiempo para que tenga lugar un reparto de recursos (Putman 1996; Voeten y Prins 1999). Así, especies simpátricas de ungulados exóticos y autóctonos con un tamaño corporal similar y estrategias de forrajeo parecidas pueden competir (Prins y Olff 1998, Owen-Smith 2002,). Pero para que haya competencia es necesario que las especies solapen en gran medida los recursos y que además éstos sean escasos, o bien que las densidades de las especies implicadas sean elevadas (Putman 1996, Prins y Olff 1998). Esta situación se da con frecuencia en zonas donde las poblaciones de ungulados silvestres co-ocurren con prácticas ganaderas tradicionales

(Fritz et al. 1996, Voeten y Prins 1999, Bagchi et al. 2004, Mishra et al. 2004, Sitters et al. 2009).

La depredación

La depredación constituye un mecanismo de regulación de las poblaciones de ungulados (Sinclair et al. 2003, Hopcraft et al. 2010) como se ha comentado más arriba, aunque su efecto real sea discutible fuera de los espacios protegidos, como consecuencia de la persecución a la que se ven sometidos los depredadores (Woodroffe 2000, Andersen et al. 2006). Sin embargo, la depredación genera una serie de respuestas comportamentales en los ungulados, incluso en situaciones en las que el efecto de control sea desdeñable. Byers (1997) sostiene que en ausencia de depredadores el comportamiento antidepredatorio está todavía presente en los ungulados porque han coevolucionado con sus depredadores durante miles de años, un fenómeno que ha denominado el ‘fantasma de la depredación en el pasado’.

Entre las respuestas comportamentales frente al riesgo de depredación se puede citar el aumento de la vigilancia, la reducción en el tiempo de forrajeo (Lima and Dill 1990), cambios en el tamaño de grupo (Creel y Winnie 2005) o en el uso del hábitat (Creel et al. 2005). Está generalmente aceptado que la selección favorecerá a aquellos individuos que compensen óptimamente los beneficios de reducir el riesgo de depredación frente a sus costes (Lima 1998, 2002). Así la selección de hábitat supone un compromiso entre maximizar los beneficios de forrajeo y minimizar el riesgo de depredación (Kie 1999, Heithaus y Dill 2002). Pero, los cambios en la selección de hábitat pueden alterar las dinámicas poblacionales, al acarrear costes en el estado físico de los individuos, reduciendo el número de efectivos más allá de los efectos directos de la depredación (Sinclair y Arcese 1995, Creel y Christianson 2008).

Efectos antrópicos

Las actividades humanas generan perturbaciones en las poblaciones de ungulados silvestres, algunas de las cuales producen impactos negativos directos (p.e. la caza furtiva), mientras que otras tienen efectos difusos, como el ecoturismo u otras actividades de recreo (Gill et al. 2006). Así, las perturbaciones generadas por el ser humano pueden afectar a los patrones de comportamiento de una especie, alterando por ejemplo el tiempo de forrajeo, la estructura social o el uso del hábitat (Stankowich 2008). Además, determinadas especies responden evitando la presencia del hombre, mientras que otras muestran una mayor tolerancia. Detrás de este efecto aparentemente inocuo puede haber factores que no permiten que los animales ocupen otras zonas. De hecho, el efecto que tiene la perturbación humana es similar al riesgo de depredación (Gill et al. 2001).

En las últimas décadas, disciplinas como la ecología del comportamiento, el comportamiento animal y la biología de la conservación tratan de analizar conjuntamente los efectos comportamentales que las distintas perturbaciones de origen antrópico tienen sobre la fauna silvestre, con el propósito de ofrecer soluciones que contribuyan a definir directrices de conservación y gestión de poblaciones silvestres y de espacios protegidos (Buchholz 2007), aunque todavía tengan un carácter eminentemente teórico (Caro 2007).

Dimensionando el nicho

En un esfuerzo por simplificar el nicho de un ungulado, se han expuesto algunos de los factores relevantes que pueden ser abordados en un trabajo de investigación. Así, la abundancia, calidad y distribución de los recursos, los procesos de competencia y coexistencia interespecíficos, el riesgo de depredación y el efecto que tiene el hombre sobre una población de ungulados en un espacio natural protegido serán objeto de estudio de la presente tesis doctoral. Una especie poco estudiada, si se la compara con otras especies de ungulados de tan amplia distribución, es el guanaco (*Lama guanicoe*), que es la especie elegida para analizar estos factores en un espacio protegido de Argentina.

EL GUANACO COMO ESPECIE MODELO

Origen y evolución

Cuatro son las especies de camélidos sudamericanos reconocidos hoy en día. Dos de ellas son silvestres: el guanaco (*Lama guanicoe* Müller 1776) y la vicuña (*Vicugna vicugna* Molina 1782), y las otras dos son domésticas: la llama (*Lama glama*), y la alpaca (*Vicugna pacos*), que proceden del guanaco y la vicuña respectivamente (Wheeler 1995, Kadwell et al. 2001). El guanaco y la vicuña junto con la extinta *Palaeolama* evolucionaron a partir de su antecesor común *Hemiauchenia* hace aproximadamente dos millones de años en Sudamérica. A finales del Pleistoceno y principios del Holoceno (13000-8500 años) tuvo lugar una gran extinción en la que desaparecieron *Hemiauchenia* y *Palaeolama*, siendo el guanaco y la vicuña los únicos representantes de la tribu Lamini que sobrevivieron (López Aranguren 1930, Webb 1978, Miotti y Salemme 1999). El otro grupo de la familia Camelidae que ha llegado hasta nuestros días es el de los camélidos del Viejo Mundo, pertenecientes a la tribu Camelini. Cuenta con dos especies, ambas domesticadas por el hombre: *Camelus dromedarius*, distribuido por el norte de África y el suroeste asiático, y *Camelus bactrianus*, cuyo rango de distribución abarca las desiertas y frías estepas de Mongolia y China. En la actualidad sólo el camello bactriano mantiene pequeñas poblaciones en estado salvaje (*C. bactrianus ferus*) en el desierto del Gobi (Kadwell et al. 2001).

Ambas tribus (Lamini y Camelini) tienen su antecesor común en Norteamérica, hace aproximadamente 45 millones de años, en el Eoceno (Stanley et al. 1994).

El guanaco, *Lama guanicoe*, es el camélido sudamericano de más amplia distribución (izquierda), mientras que la vicuña, *Vicugna vicugna*, presenta una distribución restringida a la Puna y pre-Puna (derecha). La fotografía del guanaco está hecha en el Parque Provincial Ischigualasto y la de la vicuña en el Parque Nacional San Guillermo, ambos situados en la provincia de San Juan, Argentina.

Distribución y estado de conservación

El guanaco es el camélido silvestre sudamericano de mayor tamaño, con una altura entre 1,6-1,8 m y un peso de unos 120 kg (González et al. 2006), y más amplia distribución. Su rango de distribución actual abarca desde los 8°S (Perú) hasta los 55° de latitud Sur en la Isla Navarino (Chile), y se extiende a lo largo de las laderas orientales y occidentales de la cordillera de los Andes y por la Patagonia (Franklin 1982, Puig 1995). En ese rango se han encontrado ejemplares desde el nivel del mar hasta los 4600 metros de altitud (Puig 1995) ocupando una gran cantidad de ecosistemas, generalmente áridos o semiáridos y abiertos (Cunazza 1991) (Figura 1).

La población de guanacos antes de la conquista española se cifraba entre 30 y 50 millones y ocupaba la casi totalidad de Chile y Argentina, y parte de Bolivia, Perú y Paraguay (Raedeke 1979). En la actualidad se estima que hay unos 600.000, ocupando el 40% de su distribución original (Baldi et al. 2008). Las causas de este fuerte declive son la competencia con el ganado, la pérdida de hábitat y la caza furtiva (Puig 1995, Baldi et al. 2008). Tradicionalmente se han reconocido cuatro subespecies de guanaco en función de su distribución geográfica, tamaño corporal y coloración (Wheeler 1995): *L. guanicoe guanicoe* Müller, 1776; *L. g. huanacus* Molina, 1782; *L. g. cacsilensis* Lönnberg, 1913 y; *L. g. voglii* Krumbiegel, 1944 (ver detalles en González el al. 2006). Sin embargo, estudios recientes basados en el citocromo-*b* del ADN mitocondrial no reconocen la existencia de subespecies a lo largo de su rango geográfico, si bien las poblaciones más septentrionales (Perú y norte de Chile) muestran cierto grado de diferenciación respecto a aquéllas de Argentina, Bolivia y resto de Chile (Marín et al. 2008). Esta situación, junto con su amplia distribución, la existencia de grandes poblaciones y su presencia en numerosas áreas protegidas, ha provocado que la especie pase a ser considerada a nivel continental como de "preocupación menor" de acuerdo a las categorías de la UICN (Baldi et al. 2008).

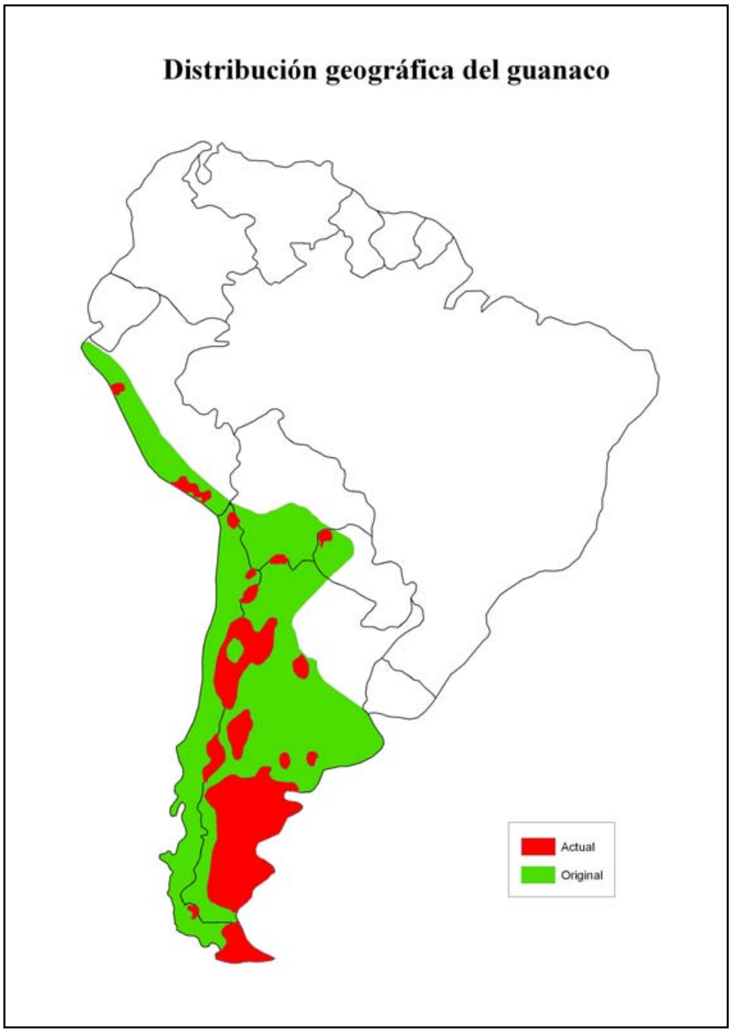

Figura 1. Distribución original (verde) y actual (rojo) del guanaco en Sudamérica (Modificado de Nugent et al. 2006).

Actualmente existen poblaciones en la región chaqueña de Paraguay y Bolivia y recientemente se ha descubierto una población en el Chaco árido del noroeste de Córdoba (Argentina). Hay guanacos en los desiertos costeros de Perú y norte de Chile, en la pre-Puna y Puna peruana, argentina y chilena y también en el desierto del Monte (Argentina). Las poblaciones más grandes se concentran en la estepa patagónica argentina y chilena (80% de los efectivos de la especie) y en menor medida en los bosques templados de *Nothofagus* de Tierra del Fuego e Isla Navarino (González et al. 2006). Por países, Argentina alberga el grueso de las poblaciones de guanaco (500.000 guanacos), seguido de Chile (66.000). Perú (3500), Bolivia (<200) y Paraguay (100) mantienen poblaciones con riesgo de desaparición (Baldi et al. 2008). Probablemente porque el gran contingente poblacional de guanacos está en la Patagonia, la práctica totalidad de trabajos sobre la especie se han realizado en esta zona (ver por ejemplo Sarno et al. 1999, Baldi et al. 2001, 2004, Puig et al. 2001, 2009, Bank et al. 2003, Young & Franlin 2004a, 2004b). El Desierto del Monte es el segundo bioma donde la especie es más abundante (Baldi et al. 2008) y, sin embargo, sólo existe un trabajo (Sosa y Sarasola 2005)

Comportamiento social y estrategias reproductivas

El guanaco es un ungulado social sexualmente monomórfico, en cuanto al tamaño corporal (Franklin 1983, Sarno y Franklin 1999). Durante el periodo reproductivo se pueden encontrar tres tipos de unidades sociales: (i) grupos familiares, constituidos por un macho territorial o *relincho* y un grupo variable de hembras y sus crías, entre las que se encuentran los *chulengos* (crías de menos de un año de edad) y juveniles (entre un año y año y medio de edad); (ii) grupos de machos no territoriales ni reproductivos de edad variable y; (iii) machos solitarios territoriales, que buscan territorios o defienden territorios sin hembras (Franklin 1983). Algunos autores han descrito grupos de hembras, aunque no hay consenso y puede que sólo aparezcan en poblaciones con altas densidades. Fuera del periodo reproductivo, las poblaciones sedentarias (aquéllas ubicadas en zonas donde las condiciones climáticas y la disponibilidad de forraje no oscilan mucho) tienden a mantenerse estables (Franklin 1983). En el sur de la Patagonia o en la cordillera de los Andes, donde los inviernos son fríos y nevosos, puede producirse una reducción drástica en los recursos tróficos disponibles, y los guanacos realizan migraciones de corta distancia (Ortega y Franklin 1995, Contreras et al. 2006). Las unidades sociales adquieren entonces laxitud y tienden a formar grupos mixtos, es decir, grupos formados por individuos de los dos sexos y de todas las edades (Franklin 1983, Ortega y Franklin 1995).

La estrategia reproductiva es de tipo poligínico basado en la defensa de recursos (Emlen y Oring 1977), en la que un macho adulto defiende un territorio con cuantioso forraje, apropiado para la cópula y con escasa abundancia de depredadores, siendo el puma (*Puma concolor*) su principal depredador (Franklin 1983, Bank et al. 2003). Los machos y hembras suelen volver a los mismos lugares de apareamiento y cría en años consecutivos (Bank et al. 2003), defendiendo los machos los mismos territorios durante 3 años en promedio (Young y Franklin 2004b). El periodo reproductivo varía latitudinalmente, teniendo lugar cuando las condicionales ambientales son más favorables, es decir, durante el periodo de lluvias (González et al. 2006). Tras 11,5 meses de gestación las hembras dan a luz una sola cría (Sarno y Franklin 1999).

La mayoría de trabajos sobre estrategias reproductivas y comportamiento territorial del guanaco se han realizado en el Parque Nacional Torres del Paine, en la Patagonia chilena (Ortega y Franklin 1995, Young y Franklin 2004a, 2004b) donde la densidad de guanacos es de unos 43 ind/km^2 (Sarno y Franklin 1999, Sarno et al. 1999), una de las más altas descritas para la especie. En esta zona, los principales hábitats defendidos durante el periodo reproductivo por los machos territoriales son las *vegas*, humedales temporales con elevada disponibilidad trófica y gran visibilidad (Bank et al. 2003), ambientes que también pueden encontrarse en la pre-Puna y la Puna (Cajal 1989). Sin embargo, no existen trabajos en zonas más áridas que no presentan estos hábitats y donde la densidad de guanacos es mucho menor.

Comportamiento de forrajeo

El guanaco es un herbívoro rumiante y su estómago sólo consta de tres cavidades (Cabrera 1935). Está considerado como pastador-ramoneador dependiendo de la disponibilidad espacial y temporal de los recursos tróficos (Puig 1995). En aquellas zonas en las que el estrato herbáceo es abundante, el guanaco se comporta como pastador, estando su dieta compuesta fundamentalmente por gramíneas y otras herbáceas (Puig et al. 2001, Baldi et al 2004). Sin embargo, si se produce un declive estacional en los pastos, o si el estrato arbustivo es predominante en el área de ocupación del guanaco, éste se comporta como ramoneador, incluyendo arbustos y hojas de árboles en su dieta (Bahamonde et al. 1986, Puig et al. 1997, Caviares y Fajardo 2005). En zonas extremadamente desérticas como el desierto de Atacama, su dieta se compone de líquenes, arbustos y cactáceas (Raedeke y Simonetti 1988).

EL MONTE HIPERÁRIDO ARGENTINO: UN ECOSISTEMA INTERESANTE PARA ANALIZAR PATRONES Y PROCESOS ECOLÓGICOS

El bioma del desierto del Monte comprende la franja árida del oeste argentino (2000 km). Se extiende latitudinalmente desde los 24º35`S en la provincia de Salta hasta los 44º20`S en el centro de la Patagonia, y desde los 62º54` en la Costa Atlántica (provincia de Chubut) hasta los 69º50`W en la zona preandina (Morello 1958) (Figura 2). Dentro de este bioma se han descrito dos ecorregiones diferenciadas principalmente por sus características geomorfológicas: el *Monte de Sierras y Bolsones*, que abarca la zona norte hasta el sur de la provincia de San Juan, y el *Monte de Llanuras y Mesetas*, que se extiende desde el sur de San Juan hasta la provincia de Chubut (Burkart et al. 1999). La primera ecorregión se caracteriza por la presencia de valles longitudinales que terminan en cuencas cerradas (bolsones) y por valles intermontanos. Carece de redes fluviales permanentes, siendo abrupta su topografía. La segunda ecorregión presenta paisajes más abiertos y homogéneos, con llanuras y extensas mesetas escalonadas. Tres son los ríos que atraviesan la región: el Desaguadero-Salado, el Colorado y el Negro (Burkart et al. 1999).

El clima es cálido y seco, con una gran amplitud térmica diaria y estacional, fluctuando latitudinalmente y de este a oeste. La estación seca dura un máximo de nueve meses, estando las lluvias restringidas durante el periodo estival, excepto en el sur, donde tienden a distribuirse más regularmente a lo largo del año. Las precipitaciones oscilan entre los 100 y los 350 mm anuales. La cordillera de los Andes ejerce una marcada influencia en la circulación de las masas de aire, cuyos efectos en las precipitaciones y temperaturas son patentes en el norte y centro del Monte, atenuándose en el sureste, debido a la influencia atlántica (Labra y Villalba 2008).

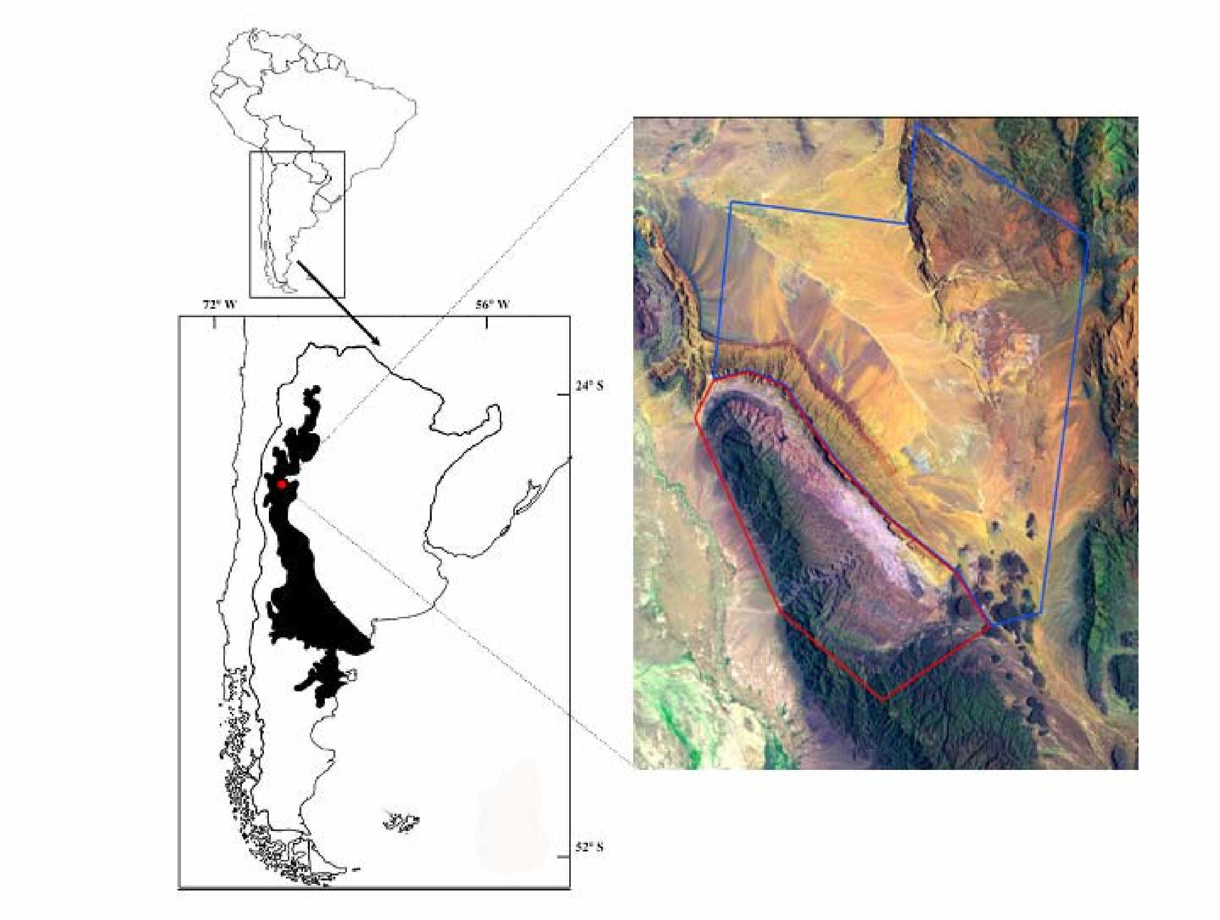

Figura 2. Distribución del Desierto del Monte argentino (negro) y localización y límites del Parque Provincial Ischigualasto (60.369 ha, San Juan) (rojo) y del Parque Nacional Talampaya (215.000 ha, La Rioja) (azul).

La fauna y flora del Monte cuenta con algunos géneros que muestran una gran similitud filogenética con taxones de los desiertos norteamericanos (Sonora y Mojave). Sin embargo, la mayoría de las especies están estrechamente relacionadas con los Biomas del Chaco y Patagónico, razón por la cual algunos autores consideran al desierto del Monte como una zona de transición. Aún así, al menos el 30% de su biota es endémica (Roig et al. 2008). La vegetación del desierto de Monte está fisonómicamente caracterizada por las estepas arbustivas perennifolias de la familia

Zigofiláceas, siendo los elementos típicos los jarillales (*Larrea* spp). En las laderas de solana aparecen Bromeliáceas y Cactáceas. En zonas en las que la capa freática está próxima a la superficie, bosquetes de algarrobos (*Prosopis* spp) y Quenopodiáceas (*Atriplex* spp, *Suaeda* spp) en cuencas endorreicas (Morello 1958). En cuanto a la fauna, el desierto del Monte alberga 73 especies de mamíferos, de los cuales el 55% son endémicos, lo que representa una endemicidad relativamente alta en comparación con otras zonas áridas y semiáridas (Ojeda et al. 2002). Es, además, el segundo bioma donde el guanaco es más abundante, después del patagónico.

Área de estudio

El Parque Provincial Ischigualasto (29º55´S, 68º05´ O; 60.369 ha) está situado en el noreste de la provincia de San Juan, limitando con la provincia de La Rioja (Argentina) donde se encuentra el Parque Nacional Talampaya (215.000 ha) (Figura 2). Ambos espacios colindantes están ubicados en la cuenca geológica Ischigualasto-Villa Unión, localizada en el ámbito geográfico de las Sierras Pampeanas Occidentales, en la región limítrofe con la Precordillera. Morfológicamente se trata de una depresión rodeada por sierras con diferentes características geológicas que constituyen afloramientos de basamento cristalino, rocas sedimentarias y volcánicas (Milana y Alcober 1994). Las condiciones climáticas son extremas debido al efecto de sombra de lluvias de la Precordillera, lo que convierte a esta zona en una de las más áridas del Desierto del Monte y de Argentina. El conjunto del área protegida Ischigualasto-Talampaya representa desde hace varias décadas un centro de importantes estudios geológicos y paleontológicos por presentar una secuencia completa de sedimentos continentales del Periodo Triásico (248-205 ma). En este importante yacimiento paleotológico se han descubierto algunos de los dinosauros más primitivos (*Eoraptor lunensis*, *Herrerasaurus ischigualastensis*), antecesores de los cocodrilos y de los mamíferos, así como una gran riqueza y diversidad de plantas. El valor de sus registros fósiles, la espectacularidad de sus formaciones geomorfológicas y las peculiaridades de su biota permitieron que en octubre de 2000 la UNESCO le otorgara el reconocimiento de Patrimonio de la Humanidad.

A pesar de dicho reconocimiento, en el momento del inicio del proyecto *Interacciones entre especies autóctonas amenazadas, herbívoros exóticos y visitantes en áreas protegidas del Monte árido argentino. Implicaciones para la conservación y directrices de gestión* (Fundación BBVA), proyecto en el que se enmarca la presente tesis doctoral, sólo existían dos publicaciones de ámbito regional en el área de Biología: una que versaba sobre aspectos florísticos del P. P. Ischigualasto (Márquez et al. 2005) y otra que ofrecía una lista preliminar de la mastofauna del parque y su estado de conservación (Acosta y Murúa 1999). Entre la fauna autóctona descrita se pueden citar los siguientes mamíferos: el guanaco (*Lama guanicoe*), el puma (*Puma concolor*), el zorro gris (*Pseudalopex griseus*), la mofeta o chingue (*Conepatus chinga*), el quirquincho (*Zaedyus pichiy*), la mara o liebre criolla (*Dolichotis patagonum*), la vizcacha (*Lagidium viscacia*), o el cuis (*Microcavia australis*), y varias especies de micromamíferos (*Octomys mimax*, *Eligmodontia moreni*, *Tympanoctomys barrerae*, etc). Entre las aves destaca el cóndor (*Vultur gryphus*), la martineta (*Eudromia elegans*), la chuña de patas negras (*Chunga burmeisteri*) o el ñandú (*Pterocnemia pennata*). La vegetación está fundamentalmente representada por elementos florísticos del bioma del Monte, estando enriquecida con diversas especies de cactáceas procedentes del bioma del Cardonal (Márquez et al. 2005).

Las características climáticas extremas, la escasez de recursos tróficos, la presencia de especies de vertebrados autóctonas sudamericanas en simpatría con especies introducidas y un turismo en auge convierten a este lugar en un excelente laboratorio natural para analizar los patrones de uso del espacio y selección de hábitat del guanaco. Teniendo además en cuenta que: (i) la mayoría de publicaciones sobre guanacos se han realizado en la Patagonia, donde los recursos tróficos son más abundantes; (ii) los trabajos que han evaluado el efecto de las especies introducidas sobre el guanaco se han realizado también en la Patagonia, donde la especie ganadera más abundante es la oveja, encontrándose en densidades muy superiores al guanaco (Baldi et al. 2001, Puig et al. 2001, Baldi et al. 2004) y; (iii) aunque existen estudios precedentes de efectos del turismo en ungulados (Stankowich 2008), no se ha evaluado hasta la fecha en el guanaco, este espacio protegido reúne unas condiciones interesantes cuyos resultados abordados en la presente tesis doctoral pueden ser extrapolables a otras zonas áridas de Sudamérica, como el noroeste argentino o algunas áreas del desierto costero chileno.

OBJETIVOS Y ESTRUCTURA DE LA TESIS

La presente tesis doctoral tiene como objetivo general aportar nuevas perspectivas sobre la ecología de un ungulado silvestre sudamericano, el guanaco, bajo un marco teórico amplio, que contemple distintas disciplinas de la moderna ciencia ecológica, a saber: la Ecología de Comunidades, la Ecología de los recursos, o la Ecología del comportamiento y la Biología de la Conservación. El propósito que se persigue es definir los patrones de uso del espacio y selección de hábitat de una población de guanacos, de gran interés para la conservación, situada en un ecosistema hiperárido del noroeste argentino, particularmente en un espacio protegido. Se analizarán los patrones de uso del espacio y selección de hábitat estacional e interanual del guanaco en función de su estructural social, de la abundancia de forraje y del riesgo de depredación. Asimismo, se analizarán los patrones de uso del espacio de dos especies introducidas, el burro (*Equus asinus*) y la vaca (*Bos taurus*), en relación con el guanaco y se examinará si existe algún efecto sobre este último. Por último, se evaluará si el ser humano tiene algún efecto en la distribución del guanaco y se analizarán los cambios en el comportamiento del guanaco asociados al uso turístico del espacio protegido.

Dada la escasa información disponible acerca de las comunidades vegetales la región más árida del desierto del Monte, en el **capítulo 2** se analizan las comunidades de plantas del Parque Provincial Ischigualasto en función de la estructura de la vegetación, de la composición florística y de la diversidad de especies incorporando variables ambientales como la pendiente, la cobertura de roca y suelo desnudo y de hojarasca. El objetivo es disponer de una información básica para poder entender y explicar los patrones de uso del espacio y selección de hábitat del guanaco. En el **capítulo 3** se realiza una estimación estacional (estación húmeda y seca) de la densidad de guanacos y de su tamaño poblacional por una parte y, por otra, se analiza el uso del hábitat del guanaco a dos escalas, comunidades de plantas y unidades geomorfológicas. Puesto que en ambos espacios protegidos los guanacos coexisten con burros y vacas, en el **capítulo 4** se analizan los patrones de uso del espacio (patrones de ocurrencia y de abundancia) de las tres especies de ungulados, a partir de datos de excrementos, para detectar posibles interferencias de las especies introducidas sobre el guanaco. Asimismo se explican los patrones de uso del espacio a partir de variables de hábitat, distancia a puntos de agua, y distancia a carreteras y pueblos cercanos. Una vez conocido el efecto que tienen las especies introducidas (burro y vaca), en el **capítulo 5** se describen las distintos tipos de organización social del guanaco a lo largo del periodo de estudio y se analizan los patrones de selección de hábitat estacional e interanual de las distintas unidades sociales del guanaco en función de la disponibilidad trófica y del riesgo de depredación. En el **capítulo 6** se evalúa la posible afección del uso turístico sobre la población de guanacos en el espacio protegido, analizando su respuesta comportamental. Por una parte se estima la distancia de huida del guanaco a turistas caminando y a vehículos. Por otra se calcula el umbral de número de visitantes al espacio protegido a partir del cual los guanacos pueden ser sensibles a dicha perturbación.

Los capítulos mencionados reproducen el texto íntegro de manuscritos originales en diferentes fases de publicación, por lo que se han presentado en el idioma en el que han sido publicados o enviados a publicar. Cada capítulo va acompañado de un resumen en castellano. Para finalizar, el **capítulo 7** recoge una discusión general de los resultados obtenidos a lo largo de la tesis, así como las conclusiones generales.

REFERENCIAS BIBLIOGRÁFICAS

Acosta JC y Murúa F. 1999. Lista preliminar y estado de conservación de la mastofauna del Parque Natural Ischigualasto, San Juan-Argentina. Multequina 8: 121-129.

Andersen R, Linnell JDC y Solberg EJ. 2006. The future role of large carnivores in terrestrial trophic interactions: the northern temperate view. En: Danell K, Bergström R, Duncan P y Pastor J (eds). Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Pp. 414-448. Cambridge University Press, New York.

Bahamonde N, Martin S y Pelliza Sbriller A. 1986. Diet of guanaco and red deer in Neuquen Province, Argentina. Journal of Range Management 39: 22-24.

Bailey DB, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM y Sims PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49: 386-400.

Baldi R, Albon S y Elston D. 2001. Guanacos and sheep: evidence for continuing competition in arid Patagonia. Oecologia 129: 561-570.

Baldi R, Pelliza-Sbriller A, Elston D y Albon S. 2004. High potential for competition between guanacos and sheep in Patagonia. Journal of Wildlife Management 68: 924-938.

Baldi B, Lichtenstein G, González B, Funes M, Cuéllar E, Villalba L, Hoces D y Puig S. 2008. Lama guanicoe. En: IUCN 2010. IUCN Red List of Threatened Species. <www.iucnredlist.org>

Bank MS, Sarno RJ y Franklin WL. 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biological Conservation 112: 427-434.

Buchholz R. 2007. Behavioural biology: an effective and relevant conservation tool. Trends in Ecology and Evolution 22: 401-407.

Byers JA. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago.

Cabrera A. 1935. Historial Natural. Vida de los animales, de las plantas y de la tierra. Instituto Gallach de librería y ediciones. Barcelona.

Cajal JL. 1989. Uso de habitat por vicunas y guanacos en la reserva San Guillermo, Argentina. Vida Silvestre Neotropical 2: 21-31.

Caro T. 2007. Behavior and conservation: a bridge too far? Trends in Ecology and Evolution 22: 394-400.

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

Chase JM y Leibold MA. 2003. Ecological niches: linking classical and ontemporary approaches. University of Chicago Press, Chicago.

Chesson P. 2000a. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58: 211-237.

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

Contreras M, González B y Novoa F. 2006. Patrón de migración altitudinal y rango de hogar de guanacos en un ambiente andino del centro norte de Chile. En: Camaño A, Castilla JC y Simonetti JA (eds). Minería y Biodiversidad. Pp.79-91. Publicaciones SONAMI, Chile.

Creel S y Winnie JA. 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.

Creel S, Winnie J, Maxwell B, Hamlin K y Creel M. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86: 3387-3397.

Creel S y Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23: 194-201.

Cunazza C. 1991. El guanaco, una especie de fauna Silvestre con futuro. Corporación Nacional Forestal, Gerencia Técnica, Santiago, Chile.

Emlen ST y Oring LW. 1977. Ecology, Sexual Selection and the Evolution of Mating Systems. Science 197: 215-223.

Feranec RS. 2003. Stable isotopes, hypsodonty, and the paleodiet of Hemiauchenia (Mammalia: Camelidae): a morphological specialization creating ecological generalization. Paleobiology 29: 230-242.

Franklin W. 1982. Biology, ecology and relationship to man of the South American camelids. En: Mares MA y Genoways HH (eds). Mammalian Biology in South America. Pp. 457-489. Vol. Pymatuning Symp. Ecol. Spec. Publ. 6, Pittsburg.

Franklin WL. 1983. Contrasting socioecologies of South American’s wild camelids: the vicuña and guanaco. En: Eisenberg JF y Kleiman DG (eds). Advances in the Study of Mammalian Behavior. Pp. 573-629. Special Publication No. 7. American Society of Mammalogists, Allen Press, Lawrence, Kansas.

Fryxell JM. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. Oecologia 72: 83-91.

González BA, Palma RE, Zapata B y Marín JC. 2006. Taxonomic and biogeographic status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae). Mammal Review 36: 157-178.

Harris G, Thirgood S, Hopcraft JGC, Cromsigt JPGM y Berger J. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7: 55-76.

Heithaus MR y Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83: 480-491.

Hopcraft JGC, Olff H y Sinclair ARE. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology and Evolution 25: 119-128.

Illius AW. 2006. Linking functional responses and foraging behaviour to population dynamics. En: Danell K, Bergström R, Duncan P y Pastor J (eds). Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Pp. 71-96. Cambridge University Press, New Cork.

Hutchinson GE. 1957. Concluding remarks: Cold Spring Harbor symposium. Cuantitative Biology 22: 415-427.

Kadwell M, Fernandez M, Stanley HF, Baldi R, Wheeler JC, Rosario R y Bruford MW. 2001. Genetic analysis reveals the wild ancestros of llama and the alpaca. Proceedings of the Royal Society of London 268: 2575-2584.

Kie JG. 1999. Optimal foraging risk of predation: effects on behavior and social structure in ungulates. Journal of Mammalogy 80: 1114-1129.

Kotler BP y Brown JS. 1999. Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. Journal of Mammalogy 80: 361-374.

Levins R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton.

Lima SL y Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lima SL. 1998. Nonlethal effects in the ecology of predator–prey interactions. BioScience 48: 25-34.

Lima SL. 2002. Putting predators back into predator–prey behavioral interactions. Trends in Ecology and Evolution 17: 70-75.

López Aranguren D. 1930. Camélidos fósiles Argentinos. Anales de la Sociedad Científica Argentina 59: 97-126.

Labra JC y Villalba R. 2009. Climate in the Monte Desert: Past trends, present conditions, and future projections. Journal of Arid Environments 73: 154-163.

MacArthur RH. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

Marín JC, Spotorno AE, González BA, Bonacic C, Wheeler JC, Casey CS, Bruford MW, Palma RE y Poulin E. 2008. Mitochondrial DNA variation and systematics of the guanaco (*Lama guanicoe*, Artiodactyla: Camelidae). Journal of Mammalogy 89: 269-281.

Márquez J, Martínez Carretero E, Dalmasso A, Pastrán G y Ortiz S. 2005. Las áreas protegidas de la provincia de San Juan (Argentina) II. La vegetación del Parque Provincial de Ischigualasto. Multequina 14: 1-27.

McNaughton SJ, Oesterheld M, Frank DA y Williams KJ. 1989. Ecosystem-level patterns of primary productiviy and herbivory in terrestrial habitats. Nature 341: 142-144.

Miotti L y Salemme M. 1999. Biodiversity, taxonomic richness and specialists-generalists during Late Pleistocene/Early Holocene times in Pampa and Patagonia (Argentina, Southern South America). Quaternary International 54: 53-68.

Mishra C, Van Wieren SE, Ketner P, Heitkönig IMA y Prins HHT. 2004. Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. Journal of Applied Ecology 41: 344-354.

Morello JH. 1958. La Provincia Fitogeográfica del Monte. Opera Lilloana II, Tucumán.

Novillo A y Ojeda RA. 2008. The exotic mammals of Argentina. Biological Invasions 10: 1333-1344.

Nugent P, Baldi R, Carmanchi P, De Lamo D, Puig S y Von Thüngen. 2006. Conservación del guanaco en la Argentina. Propuesta para un plan nacional de manejo. En: Bolkovic ML y Ramadori E (eds). Manejo de Fauna Silvestre en la Argentina. Programa de uso sustentable. Pp. 1-13. Dirección de fauna Silvestre. Secretaria de Ambiente y Desarrollo Sustentable. Buenos Aires.

Ojeda RA, Borghi CE y Roig VG. 2002. Mamíferos de Argentina. En: Ceballos G, Simonetti JA (eds). Diversidad y Conservación de los Mamíferos Neotropicales. Pp. 23-63.CONABIO-UNAM, México DF.

Ortega IM and Franklin WL. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural 68: 489-500.

Owen-Smith N. 1988. Megherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge.

Owen-Smith N. 1989. Megafaunal extintions: the conservation messag from 11,000 years BP. Conservation Biology 3: 405-412.

Owen-Smith N. 2002. Adaptative herbivore ecology. From resources to populations in variable environments. Wits University Press, Johannesburg, South Africa.

Prins HHT. 1992. The pastoralism road to extintion: competition between wildlife and traditional pastoralism in East Africa. Environmental Conservation 19: 117-123.

Prins HHT. 2000. Competition between wildlife and livestock in Africa. En: Prins HHT, Grootenhuis JG y Dolan TT (eds). Wildlife conservation by sustentable use. Pp. 51-80. Kluwer Academic Publishers, Boston.

Prins HHT, de Boer WK y Van Langevelde F. 2008. Comments on “Resource distribution and dynamics: mapping herbivore resources” . En: Van Langevelde F y Prins HHT (eds). Resource Ecology: Spatial and temporal dynamics of foraging. Pp. 79-80. Wageningen UR Frontis Series, vol. 23. Springer.

Puig S. 1995. Abundancia y distribución de las poblaciones de guanacos. En: Puig S (ed). Técnicas para el manejo del guanaco. Pp. 57-70. IUCN, Buenos Aires, Argentina.

Puig S. 1995. Uso de recurso ambientales por el guanaco. En: Puig S (ed). Técnicas para el manejo del guanaco. Pp. 119-134. IUCN, Buenos Aires, Argentina.

Puig S, Videla F y Cona MI. 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 MI y Monge 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 MI y Roig VG. Habitat use by guanacos (*Lama guanicoe*, Camelidae) in northern Patagonia (Mendoza, Argentina). Studies on Neotropical Fauna and Environment 43: 1-9.

Raedeke K. 1979. Population dynamics and socioecology of the guanaco (*Lama guanicoe*) of Magallanes, Chile. Doctoral Dissertation. College of Forest Resources University of Washington.

Raedeke K y Simonetti J. 1988. Food habits of *Lama guanicoe* in Atacama desert of northern Chile. Journal of Mammalogy 69: 198-201.

Ricklefs RE y Schluter D. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.

Ritchie ME. 2002. Competition and coexistence in mobile animals. En: Sommer U y Worm B (eds). Competition and coexistence. Pp. 127-141. Springer, Berlin.

Sarno RJ, Clark WR, Bank MS, Prexl WS, Behl MJ, Johnson WE y Franklin WL. 1999. Juvenile guanaco survival: management and conservation implications. Journal of Applied Ecology 36: 937-945.

Sarno RJ y Franklin WL. 1999. Maternal expenditure in the polygynous and monomorphic guanaco: suckling behavior, reproductive effort, yearly variation, and influence on juvenile survival. Behavioral Ecology 10: 41-47.

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE y Swift DM. 1987. Large foraging and ecological hierarchies. Bioscience 37: 789-799.

Sinclair ARE, Mduma S y Brashares JS. 2003. Patterns of predation in a diverse predator prey system. Nature 425: 288-290.

Sinclair ARE y Arcese P. 1995. Population consequences of predation sensitive foraging: the Serengeti wildebeest. Ecology 76: 882-891.

Sosa RA y Sarasola JH. 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.

Stankowich T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141: 2159-2173.

Stanley HF, Kadwell M y Wheeler JC. 1994. Molecular evolution of the family Camelidae: a mitochondrial DNA study. Proceedings of the Royal Society of London 256: 1-6.

Van Wieren SE y Van Langevelde F. 2008. Structuring herbivore communities. The role of habitat and diet. En: Van Langevelde F y Prins HHT (eds). Resource Ecology: Spatial and temporal dynamics of foraging. Pp. 237-262. Wageningen UR Frontis Series, vol. 23. Springer.

Webb SD. 1978. A history of savanna vertebrates in the new world: South America and the Great interchange. Annual Review of Ecology and Systematics 9: 393-426.

Wheeler JC. 1995. Evolution and present situation of the South American Camelidae. Biological journal of the Linnean Society 54: 271-295.

Young JK y Franklin WL. 2004a. Activity budget patterns infamily-group and solitary territorial male guanacos. Revista Chilena de Historia Natural 77: 617-625.

Young JK y Franklin WL. 2004b. Territorial fidelity of males guanacos in the Patagonia of southern Chile. Journal of Mammalogy 85: 72-78.

Woodroffe R. 2000. Predators and people: using human densities to interpret decline of large carnivores. Animal Conservation 3: 165-73.

CAPÍTULO II.

Las comunidades vegetales del Monte hiperárido argentino

Gradientes abióticos dirigen la composición florística y la estructura de las comunidades de plantas en el Desierto del Monte.

RESUMEN

La definición de comunidades discretas de plantas en zonas desérticas es complejo debido tanto a su homogeneidad a gran escala como a su heterogeneidad a pequeña escala, lo que acaba generando dificultades para la toma de decisiones de conservación. En este trabajo analizamos las comunidades de plantas del sector más árido del Desierto del Monte en función de su estructura y composición florística. Se han utilizado también variables ambientales estimadas a pequeña escala como la pendiente o la superficie de roca, suelo desnudo y hojarasca, así como variables que operan a mayor escala como la diversidad de especies, la composición florística y la similitud dentro y entre localidades. Los análisis de composición florística resaltaron la dificultad para segregar diferentes comunidades debido al elevado nivel de heterogeneidad interna y de solapamiento florístico entre las distintas localidades estudiadas. Sólo la comunidad situada en el extremo del gradiente de humedad edáfica, el algarrobal, se segregó del resto. La ordenación realizada sobre las variables estructurales en función del tipo de sustrato y de la cobertura arbórea y de matorral segregó mejor las diferentes comunidades. Nuestros resultados muestran la dificultad para diferenciar comunidades de plantas en desiertos templados, sugiriendo la existencia de ensamblajes de especies relativamente estables en los extremos de los gradientes y de una gran heterogeneidad dentro y entre localidades. Las comunidades de plantas, por tanto, no pueden ser definidas únicamente por variables florísticas, sino que es preciso incluir información ambiental.

Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert.

Acebes, P, Traba J, Peco B, Reus L, Giannoni SM y Malo JE. (in press). Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert. *Revista Chilena de Historia Natural.*

ABSTRACT

Defining plant communities in desert zones is difficult due to large scale homogeneity and small scale heterogeneity, thus making provision of systematic information for conservation decisions problematic. We analysed plant communities of the most arid sector of Monte Desert for structure, plant composition and environmental variables. Small-scale variables such as slope, rock cover, bare ground and litter, as well as large-scale ones such as species diversity, composition and similarity within and between sites were included. Analyses of floristic composition showed the difficulty of segregating distinct communities due to high internal heterogeneity and overlap between the different sites. Only mesquite woodlands, a community situated at the extreme of the soil moisture-gradient was segregated. Ordination on structural variables was somewhat more successful in segregating communities on the basis of substrate type and of tree and shrub cover. Our results showed the difficulty distinguishing plant communities in temperate deserts, suggesting the existence of relatively stable assemblages of species at the extremes of the gradients and of great heterogeneity within and between sites. They cannot be defined by floristic variables solely, but require environmental information also.

Key words: arid environment, heterogeneity, shrubland, similarity, species richness.

INTRODUCTION

Desert vegetation is relatively homogeneous on a large scale, but heterogeneous on a small scale, which makes it difficult for definition of plant communities for descriptive, scientific and practical purposes. Plant cover in ecosystems which are strongly water-limited is patchy and normally below 60% (Aguiar and Sala 1999). Thus the presence of surface or subterranean water plays a fundamental role in plant communities distribution (Jobbágy et al. 1996, León de la Luz et al. 2000, Zhang et al. 2005). Deserts have been defined as water-controlled ecosystems with infrequent, discrete and largely unpredictible water inputs (Noy-Meir 1973). Large spatial heterogeneity occurs and vegetation is not uniform on a small scale (Xu et al. 2006) but rather clumped where environmental conditions are more severe (Tirado and Pugnaire 2003). As a result, plant communities are structured around gradients of plant cover such that often they cannot be defined solely by floristic variables but require inclusion of environmental ones such as geomorphological and edaphic factors (Abd El-Ghani and Amer 2003, Bisigato et al. 2009).

The Monte Desert biome characterizes the arid fringe of western Argentina, from 24º35´S in Salta province to 44º20´S in central Patagonia, and from 62º54´ on the Atlantic coast to 69º50´W in the pre-Andean zone (Morello 1958). It represents one of the most interesting South American biomes due to its high plants and mammals endemicity. A few plant genera show a remarkable phylogenetic similarity with taxa of North American deserts (Mojave and Sonora), but most plant species are closely related to those in Chaco and Patagonian biomes, and some authors consider the Monte Desert as a part of the South American Transition Zone (Roig et al. 2009).

Most studies within the Monte Desert have been carried out in regions where climatological conditions are not as severe as in its hyper-arid region. These include studies of seed banks (López de Casenave et al. 1998, Marone et al. 2000), to certain woody species such as *Larrea* spp. (Rossi et al. 1999), *Prosopis* spp. (Rossi and Villagra 2003, Villagra and Cavagnaro 2006, Campos et al. 2007) and *Bulnesia retama* (Debandi et al. 2002) and plant/animal interactions (see review Bertiller et al. 2009). Studies of plant communities of the hype-arid Monte Desert are sparse and limited either to floral listings (Dalmasso and Márquez 1999) or to phytosociological studies (Márquez et al. 2005). As a result necessary information for adequate protection is insufficient and of concern since drylands constitute vulnerable ecosystems facing strong global change (Millennium Ecosystem Assessment 2005). Less than 4% of the Monte Desert is protected, significantly lower than the proposed 10% for each eco-region by 2010 in ‘2010 - The Global Biodiversity Challenge’ (Pol et al. 2006).

The present study reports on systematic analyses of the vegetation of a poorly known hyper-arid sector of the Monte Desert biome in order to determine whether plant communities can be identified there. We analyse vegetation units which differ in appearance (physiognomy) for floristic characters, and both structural and environmental variables, and compare patterns of diversity and similarity within and between communities.

MATERIALS AND METHODS

Study area

The work was conducted in the Ischigualasto Provincial Park (29º55´ S, 68º05´ O), in San Juan province, Argentina, a World Heritage Site together with the adjacent

Talampaya National Park (2000) in La Rioja province (Fig. 1). The park is over 60369 ha and has a mean altitude of 1300 m above sea level. The climate is as defined by W. Köeppen (Poblete and Minetti 1999) desert, with mean annual temperatures below 18ºC, a temperature range of -10º–45ºC, and mean annual precipitation of 80–140 mm: occurring mainly in summer (November to February). Particularly, when the study was carried out (March 2005) the hydrologic year was rather dry and hot (data not published). Triassic sandstones dominate the soils of the zone with variable salt content, and in some cases, interspersed coal deposits. Fine-textured silts and Quaternary sediments also occur, forming pebbly expanses of a diverse nature.

Figure 1. Location of Ischigualasto Provincial Park (IPP) and Talampaya National Park (TNP) in San Juan and La Rioja provinces, repectively (Argentina). Distribution of the Monte Desert biome.

Data collection

In order to maximise differences between the plant communities analysed six sites were selected. Two were defined on the basis of physiognomic characteristics: 1) columnar cactus slopes, dominated by *Trichocereus terscheckii*; and 2) barrens: mostly plantless zones. The other four were defined as a function of the apparently most abundant species: 3) saltbush: *Atriplex spegazzinii*; 4) creosote bush scrub: *Larrea cuneifolia*; 5) mesquite woodlands: *Prosopis chilensis*; and 6) chical: *Ramorinoa girolae,* a woody legume tree (Fabaceae) with almost leafless green stems. With respect to substrates, barrens, saltbush and mesquite woodlands are on fine sandy-silty soils, the columnar cactus and chical are on rocky, principally sandstones slopes and creosote bush scrub is on consolidated Quaternary deposits. Moreover, these sites are on a gradient of water availability, from mesquite woodlands located along ephemeral watercourses to barrens, the driest zone of the Monte Desert.

Within these sites 20 sampling plots (n=120 plots) were selected at random were separated by at least 30 m. At each sampling plot 13 2×2 m subplots were established along two perpendicular lines, the first at their intersection and the remainder at 2 m intervals totalling 52 m^2 sampling area per plot. The total sampling area was about 15 ha at each site with the exception of mesquite woodlands owing to its linear and discontinuous distribution along some of the dry watercourses.

In each subplot we estimated the following physiognomic variables: total plant cover at three strata (0.5 m, 1 m and canopy), rock cover, bare ground and litter cover; cover was assigned to the following categories (<5%; 5-10%; 11-25%; 25-50%; 50-75%; >75%). For floristic composition, the cover of each of the plant species was also estimated in each subplot (%).

Sampling was designed with the aim to: (i) obtain robust estimates of plant composition in plots; and (ii) avoid inflated variation of plant composition in them. Thus, 13 subplots were sampled instead of a larger contiguous unit in order to minimize sampling variance produced by plant aggregation in patches, and the 2×2 m subplot size was selected after measuring average shrub dimensions in the area (238±13 × 215±13 cm, mean±SE, N=120). Afterwards, a cumulative species analysis allowed us to estimate plant richness in 13 subplots (52 m^2) in order to obtain 80% species richness expected had we sampled 100 m^2 (25 subplots).

Data analysis

We used the midpoint of the cover class (i.e. 2.5%; 7.5%; 18%; 37.5%; 62.5%; 87.5%) to calculate the mean value and coefficient of variation for each variable at each sample point (plot), except for slope and altitude, which were recorded only at one point per plot, since they did not differ appreciably among the 13 sampling subplots (Table 1). Species richness was taken as the total number of species per sampling plot and per site. Within-site heterogeneity was calculated using Jaccard’s qualitative index for similarity between sampling plots at a given site and overall between sites.

Principal Component Analyses (PCAs) were carried out on environmental and structural variables and on floristic composition to obtain components (axes) enabling simple interpretation and avoiding the problems of colinearity detected among the original variables in an initial exploratory analysis. For floristic composition the covariance matrix based on mean-centered variables was chosen. It is appropriate when variables are measured in comparable units and differences in variance between them makes an important contribution to interpretation. For environmental and structural variables the correlation matrix based on variables standardized to zero mean and unit variance was chosen. It is necessary when variables are measured in very different units and differences between variances are ignored, i.e., slope, altitude, and plant, rock or litter cover (Quinn and Keough 2002).

The PCA results for the differences in environmental and structural variables on the one hand, and those relating to floristic composition on the other, were analysed by means of multivariate analyses of variance (MANOVAs) in which the positions obtained via PCAs were used as dependent variables and sites as the predictive variable. Tukey´s honestly significant difference test (HSD test) was used a posteriori to compare pairs of means. We selected this analytic approach to strengthen the differences in both floristic and environmental-structural variables among sites.

To determine significant differences in plant species among sites, Kruskal-Wallis tests of one factor (site) were carried out for each species, using mean plant cover per sampling plot as the dependent variable. False Discovery Rate (FDR) correction was employed to control alpha-inflation (García 2004). ANOVA test was used to compare total species richness per sampling plot between sites. Tukey´s honestly significant difference test (HSD test) was used a posteriori to compare pairs of means. All analyses were carried out with STATISTICA 8.0 (StatSoft Inc. 2007).

Table 1. Variables and their values recorded in the 2×2 m sampling subplots (n=1560). Each site had 20 sampling plots. The altitude and slope variables were taken at the centre of each sampling plot (n=120). Barrens (B), saltbush (S), creosote bush scrub (CB), mesquite woodlands (M), columnar cactus slopes (CS) and Chical (CH).

Variable		Code	B	S	CB	M	CS	CH
Environmental variables								
Altitude (m)		Alt	1283	1245	1351	1272	1271	1426
Slope (º)		Slope	21.05	0.61	0.91	0	8.4	11.95
Rock cover (%)	mean	MRC	16.55	6.31	70.63	6.06	75.17	54.19
	CV	RCCV	133.76	119.90	37.62	228.35	29.05	77.32
Bare cover (%)	mean	MBC	77.27	76.93	13.89	70.57	10.25	31.48
	CV	BCCV	23.90	25.18	133.62	36.05	142.96	128.45
Leaf litter cover (%)	mean	MLC	0.08	1.38	8.06	19.16	6.76	4.68
	CV	LCCV	29.33	180.20	170.17	133.93	167.54	162.91
Physiognomic variables								
Tree canopy (%)	mean	MTC	0.12	8.29	16.66	30.37	18.84	15.44
	CV	TCCV	30.13	196.06	156.48	124.45	135.32	139.81
Vegetation at 1m (%)	mean	V1M	0.12	7.63	15.23	18.57	17.0	14.06
	CV	V1CV	30.13	195.34	156.02	146.82	134.14	143.03
Vegetation at 0.5m (%)	mean	V0.5M	0.13	5.36	11.16	13.41	13.55	11.28
	CV	V0.5CV	48.16	183.81	162.28	157.07	143.32	139.10

RESULTS

Total species richness for the sampled sites was 69. The most abundant species, according to their frequency of occurrence in the six sites, were *L. cuneifolia*, *A. spegazzinii*, *Zuccagnia punctata*, *Prosopis torquata* and *B. retama* (see Appendix). The families represented by most species were the Cactaceae (12), Fabaceae (10), Solanaceae (7) and Poaceae (7). With respect to total cover, the families with the greatest cover were the Zygophyllaceae, Fabaceae, Chenopodiaceae and Cactaceae. Finally, including frequency of occurrence, the Bromeliaceae, with both terrestrial and epiphytic species, must be added to the last four families.

The most species-rich sites were mesquite woodlands, chical and columnar cactus slopes, with 36, 35 and 33 species, respectively. Only four species occurred in barrens (see Appendix). Species-richness per sampling plot showed significant differences among sites (ANOVA test; F=56.375; df=5; p<0.001). The a posteriori analysis revealed differences between barrens and saltbush with more species (15) in the latter, and among these two sites and all others. Chical also had a significantly larger number of species than creosote bush scrub (the latter had 23 species).

Floristic composition

The similarity index between pairs of sites showed generally low values. Sites can be ranked, with barrens at one extreme (mean similarity index < 0.02) and larger values (i.e. > 0.58) in comparisons between columnar cactus slopes with chical and creosote bush scrub. Other comparisons gave index values intermediate between the above mentioned (Table 2). The analysis of similarity within each site also produced low values. The most heterogeneous site was chical (mean±SD; 0.245±0.116), followed by mesquite woodlands (0.276±0.108) and columnar cactus slopes (0.248±0.124). Saltbush (0.304±0.216) and creosote bush scrub (0.347±0.149) were the most homogeneous.

Table 2. Values of floral similarity (Jaccard index) between the sampled sites.

	Columnar cactus slopes	Chical	Creosote bush scrub	Mesquite woodland	Saltbush
Barrens	0.03	0.02	0.00	0.03	0.00
Saltbush	0.23	0.20	0.18	0.21	
Mesquite woodlands	0.30	0.31	0.30		
Creosote bush scrub	0.58	0.48			
Chical	0.75				

The first two axes of the PCA relating to floristic composition, explained 58.45% of total variance (Fig. 2), indicating the existence of a dual floristic gradient and showed an initial segregation of sites. The MANOVA carried out on the first two axes of the PCA showed significant differences among sites (MANOVA test; F=22.464; df=10; p<0.001), confirming the detected pattern. The results of the a posteriori Tukey's test for axis 1 revealed significant differences only between mesquite woodlands and the remaining sites (p<0.001), separating the observations of the former from those of the others, with mesquite associated with *P. chilensis*, *Larrea divaricata*, *Atriplex lampa*, *Grabowskia obtusa*, *Senecio subulatus* and *Lycium chilense*. The same test for axis 2 separated barrens, saltbush and mesquite woodlands from creosote bush scrub and columnar cactus slopes ($p<0.001$, Fig. 3a), whereas chical shared characteristics with both groups. These tests showed that sites could not be differentiated purely on floristic criteria.

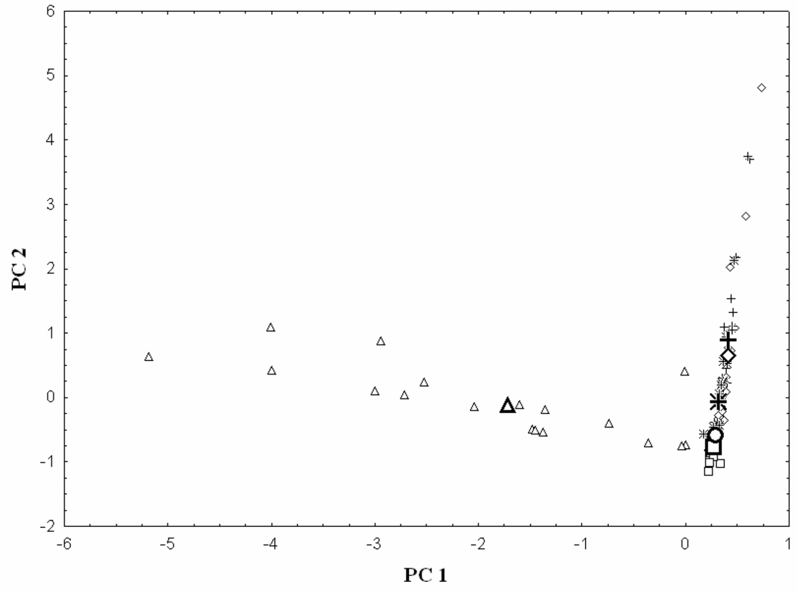

Figure 2. Principal Component Analysis of observations of all species in the six sites. Component 1 separates observations of mesquite woodlands (Δ) and component 2 represents the gradient of the rest of observations. Barrens (○), saltbush (□), creosote bush scrub (◊), columnar cactus slopes (+) and chical (*). Identical but larger symbols represent the centroids of observations of sites.

A second PCA on floristic composition, after omitting mesquite woodlands, yielded clearer results. The MANOVA performed on the first two axes of this second PCA (explained variance=51.64 %) once again showed significant differences between sites (MANOVA test; F=9.765; df=8; $p<0.001$). Post hoc Tukey's test for the first axis differentiated barrens and saltbush from creosote bush scrub and columnar cactus slopes ($p<0.001$), whereas gradient 2 separated creosote bush scrub from the others ($p<0.001$). Barrens and saltbush still remained undifferentiated and as well as chical with the rest.

Kruskal-Wallis tests showed differences in plant species cover among sites ($p<0.05$; see Appendix), confirming that some species were specific to sites, although overall communities were not clearly distinguishable with PCAs.

Vegetation structure and physiognomy

The PCA performed on the structural and physiognomic variables of the vegetation proved to be as explanatory as the PCA of floristic composition. Axis 1 (explained variance=30.9%) was associated positively with MBC and negatively with MRC and BCCV (Table 3), discriminating observations of large expanses of bare ground from those of large extents of rocky cover and large heterogeneity of bare ground. Axis 2 of PCA (explained variance=25.3%) showed positive correlations with MTC, V1M, V0.5M and MLC, distinguishing the presence of sites with high plant and litter cover.

Table 3. Results of the Principal Component Analyses carried out to synthesise the variation in environmental and structural characteristics at the sampling plots. Asterisks indicate the highest factor scores.

Variable	PC 1	PC 2
Altitude	-0.408	-0.131
Slope	0.353	-0.294
Mean tree canopy	-0.383	0.889*
Tree canopy CV	-0.591	-0.344
Mean vegetation at 1 m	-0.504	0.801*
Vegetation at 1m CV	-0.584	-0.277
Mean vegetation at 0.5 m	-0.508	0.769*
Vegetation at 0.5 m CV	-0.570	-0.229
Mean rock cover	-0.727*	-0.351
Rock cover CV	0.458	0.466
Mean bare ground	0.815*	0.188
Bare ground CV	-0.758*	-0.257
Mean leaf litter cover	-0.207	0.852*
Leaf litter cover CV	-0.594	-0.082
Variation explained (%)	30.89	25.32

The MANOVA carried out on the first two axes of PCA showed significant differences between sites (MANOVA; F=42.992; df=10; p<0.001). The a posteriori Tukey`s test on axis 1 differentiated barrens from the other sites (p<0.001), with very high values for bare ground (Table 1), whereas saltbush and mesquite woodlands were also segregated from the other sites. Columnar cactus slopes, creosote bush scrub and chical remained grouped together (Fig. 3b), due to high values for rocky cover and high variability of plant cover at different levels (Table 1). Axis 2 only segregated mesquite woodlands from the other sites, on the basis of the former’s high canopy and litter cover (Fig. 3b).

DISCUSSION

Our data represent the first quantitative description of the structure and composition of plant communities of the hyper-arid Monte Desert, a largely unknown South American temperate desert. They indicate a gradient of communities with a high level of intrinsic heterogeneity due to presence of many shared species with fairly well-defined extremes.

Characteristics of the plant communities of this part of Monte Desert are similar to those of other deserts (Orians and Solbrig 1977, Abd El-Ghani 2000). The vegetation is typically xerophytic, low in cover, and greatly heterogeneous in floristic composition. The clear dominance of woody species vs. herbs is possibly due to the ability of extensive root systems to exploit water at different soil depths (Abd El-Ghani 2000). In contrast, herbaceous plants, which are much more dependent on seasonal rain (Vidiella et al. 1999), were sparsely represented, despite sampling having accounted at the end of the rainy season.

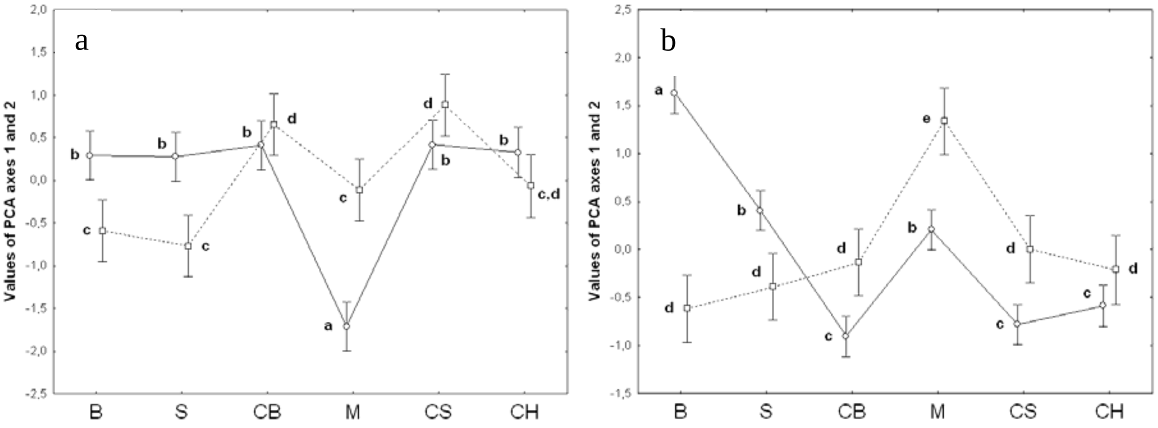

Figure 3. Means and standard deviations for the two dependent variables in the MANOVA test for floristic composition (a) and environmental and vegetation-structure variables (b) at the six sites. In both diagrams the continuous line corresponds to gradient 1 and the broken line to gradient 2 derived from the PCA. Different letters for values of the same factor indicate significant differences ($p<0.05$) between sites. Barrens (B), Saltbush (S), creosote bush scrub (CB), mesquite woodlands (M), columnar cactus slopes (CS) and chical (CH).

With respect to differentiation, the analyses of floristic composition showed the difficulty of segregating distinct communities, due to high levels of internal heterogeneity and overlap between the different sites. Floristic composition is clearly distinct at extremes of the moisture gradient with mesquite woodlands along margins of dry watercourses, which occasionally have water after heavy rains. They include species which are linked to water presence such as *P. chilensis*, *Baccharis salicifolia*, *Tessaria dodoneifolia* or *Schinus polygama.*

Ordination on structural variables helps shape this pattern, segregating communities on the basis of substrate type, and tree and shrub cover. Canopy cover segregated mesquite woodlands from the other communities, which indicates the high structural and physiognomic similarity of most plant communities in the Monte Desert. Furthermore, the multivariate analyses segregate sites situated on sandy or silty substrata (mesquite woodlands, saltbush and barren) from those on rocky and more heterogeneous substrata. Saltbush, dominated by zampa (*A. spegazzinii*), along with halophytic species such as *Suaeda divaricata, Plectrocarpa tetracantha* or *Prosopis strombulifera* occurred in communities on sandy-silty soils. This community is scattered and near dry riverbeds, and unlike other deserts, where saltbush communities were most often found on harder, stony soils (Fernandez-Gimenez and Allen-Diaz 2001), in the Monte Desert they associated with sandy and disaggregated soils. Barren areas occur in zones well away from influence of phreatic level. Surface is often eroded and of irregular topography; this impedes vegetation presence except at drainage points (Orians and Solbrig 1977). Only a few halophytic Crassulaceae, such as *Sclerophylax kurtzii* and *Halophytum ameghinoi*, grow there, being well-adapted to aridity and salinity.

The above-mentioned findings are consistent with deterministic models of vegetation distribution in arid regions, in which water availability is the essential factor in the structuring and functionality of distinguishable plant communities (Noy-Meir 1973, Jobbágy et al. 1996, León de la Luz et al. 2000, Zhang et al. 2005). As has been suggested for other desert zones, patchiness in soil types together with distance from water are the two principal factors which contribute to shaping the distribution of plant communities in deserts (Beyer et al. 1998, Fernandez-Gimenez and Allen-Diaz 2001), as a result of the redistribution of water, soil particles, propagules, and resources which create and maintain vegetation patches (Aguiar and Sala 1999). In Monte Desert, plant communities differentiated on the basis of floristic and physiognomic variables seem to result from the existence of a dual gradient – edaphic factors and distance from watercourses - producing significant differences in floristic composition as either one of them varies, as proposed in Fig. 4.

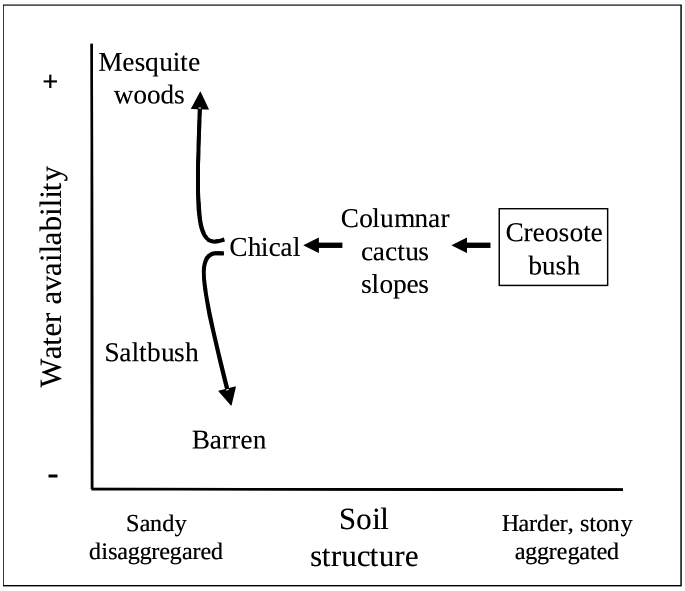

Figure 4. Conceptual diagram of the relationships of vegetation with soil structure and water availability in the Monte Desert.

The differentiation which we have shown should be considered within the context of a continuum of variation between plant communities, however. The floristic similarity data show a high number of species in common between creosote bush scrub, columnar cactus slopes and chical. Under the most usual conditions within the region, on harder, coarser and more heterogeneous soils, the predominant community of the hyper-arid Monte Desert is creosote bush scrub, which is principally characterized by the abundance of *L. cuneifolia* and *Z. punctata*. Creosote bush scrub shows small floristic differences when it is situated directly on bare rock, allowing the inclusion of physiognomically-prominent elements such as cacti and bromeliads including *T. strigosus*, *Echinopsis leucantha*, *O. sulphurea* or *Tephrocactu*s spp., and especially *Deuterocohnia longipetala* and *T. terscheckii*, although not so frequent to allow floristic differentiation of these sites. Differentiated sites such as columnar cactus slopes do not seem to be limited by water availability due to irregular topography and frequent fissures which retain some humidity and permit *R. girolae* on rocky substrates in some zones. The very low values of the intralocality similarity index in chical and columnar cactus slopes confirm this impression, pointing to the high degree of spatial heterogeneity which seems to be associated with a structuring of vegetation in bands dependent on watercourses (Aguiar and Sala 1999).

Unlike this small scale heterogeneity of lithological origin, creosote bush scrub and saltbush show higher intralocality similarity values. These communities are situated in flat areas where rainwater spreads more evenly and vegetation is more uniformly distributed. Vegetation here is structured in a leopard-spot pattern, where wind and animals are the principal factors responsible for its distribution (Aguiar and Sala 1999). Here, presence of scrub favours structuring in relatively dense patches, where spatial aggregation by facilitation phenomena are produced (Tirado and Pugnaire 2003).

The results of the species-richness analysis help to reinforce the patterns detected in the analyses of floristic composition and structural and physiognomic variables. The two communities at the extremities of the dryness gradient, saltbush and barren, had the lowest species diversity, confirming that species richness in arid areas increases with water availability (Cornwell and Grubb 2003), parallel to productivity (Waide et al. 1999). The greater plant cover in the columnar cactus slopes, mesquite woodlands and chical communities produces a concentration of water and nutrients beneath their canopies as well as shielding from intense solar radiation (Rossi and Villagra 2003), and results in an overall increase in productivity and diversity in arid zones (Sala and Aguiar 1996, Tirado and Pugnaire 2003).

Finally, like vegetation in Monte Desert is mainly organized in gradients, not being easy to define plant communities *sensu strico*, conservation targets should focus on increasing surface of protected areas in order to guarantee all the heterogeneity.

REFERENCES

Abd El-Ghani MM. 2000. Floristics and environmental relations in two extreme desert zones of western Egypt. Global Ecology and Biogeography 9: 499-516.

Abd El-Ghani MM and Amer WM. 2003. Soil–vegetation relationships in a coastal desert plain of southern Sinai, Egypt. Journal of Arid Environments 55: 607-628.

Aguiar MR and Sala OE. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14: 273-277.

Bertiller MB, Marone L, Baldi R and Ares JO. 2008. Biological interactions at different spatial scales in the Monte desert of Argentina. Journal of Arid Environments 73: 212-221.

Beyer L, Tielbörger K, Blume H-P, Pfisterer U, Pingpank K and Podlech D. 1998. Geo-ecological soil features and the vegetation pattern in an arid dune area in the Northern Negev, Israel. Zeitschrift für Pflanzenernährung und Bodenkunde (Germany) 161: 347-356.

Bisigato AJ, Villagra PE, Ares JO and BE Rossi. 2009. Vegetation heterogeneity in Monte Desert ecosystems: A multi-scale approach linking patterns and processes. Journal of Arid Environments 73: 182-191.

Cabrera AL. 1994. Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería. Tomo II. Fascículo I. Editorial ACME S.A.C.I.

Campos C, Giannoni S, Taraborelli P and Borghi CE. 2007. Removal of mesquite seeds by small rodents in the Monte desert, Argentina. Journal of Arid Environments 69: 228-236.

Cornwell WK and Grubb PJ. 2003. Regional and local patterns in plant species richness with respect to resource availability. Oikos 100: 417-428.

Dalmasso A and Márquez J. 1999. Vegetación actual de San Juan. In: Paredes JD, Suvires GM and Zambrano JV (eds). Síntesis del Cuaternario de la Provincia de San Juan. Argentina. CD-ROM Edition

Debandi G, Rossi B, Araníbar J, Ambrosetti JA and Peralta IE. 2002. Breeding system of *Bulnesia retama* (Gillies ex Hook & Arn.) Gris. (Zygophyllaceae) in the Central Monte Desert (Mendoza, Argentina). Journal of Arid Environments 5: 141-152.

Fernandez-Gimenez M and Allen-Diaz B. 2001. Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. Plant Ecology 157: 101-118.

García LV. 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos 105: 657-663.

Jobbágy EG, Paruelo JM and León RJC. 1996. Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia. Journal of Vegetation Science 7: 599-605.

León de la Luz JL, Pérez Navarro JJ and Preceda A. 2000. A transitional xerophitic tropical plant community of the Cape Region, Baja California. Journal of Vegetation Science 11: 555-564.

López de Casenave J, Cueto VR and Marone L. 1998. Granivory in the Monte desert: is it less intense than in other arid zones of the world? Global Ecology and

Biogeography Letters 7: 197-204.

Marone L, Horno ME and González del Solar R. 2000. Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years. Journal of Ecology 88: 940-949.

Márquez J, Martínez Carretero E, Dalmasso A, Pastrán G and Ortiz S. 2005. Las áreas protegidas de la provincia de San Juan (Argentina) II. La vegetación del Parque Provincial de Ischigualasto. Multequina 14: 1-27.

Milennium Ecosystem Assessment. 2005. Ecosystems and Human Well-Being: Synthesis. Island Pres, Washinton, DC, USA.

Morello JH. 1958. La Provincia Fitogeográfica del Monte. Opera Lilloana II. Tucumán. Argentina.

Noy-Meir I. 1973. Desert ecosystems: environments and producers. Annual Review of Ecology and Systematics 4: 25-51.

Orians GH and Solbrig OT. 1977. Convergent evolution in warm deserts. US/Synthesis series, 3. Dowden, Hutchinson and Ross, Inc. Pensylvania.

Poblete AG and Minetti JL. 1999. Atlas Climatológico de San Juan. Instituto de Geografía Aplicada. UNSJ. CD-ROM Edition. San Juan.

Pol RG, Camín SR and Astié AA. 2006. La situación ambiental de la Ecorregión del Monte. In: Brown A, Martinez Ortiz U, Acerbi M and Corcuera J (eds). La situación Ambiental Argentina. Pp. 227-239. Fundación Vida Silvestre Argentina, Argentina.

Quinn GP and Keough MJ. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.

Roig FA. 1960. Bosquejo fitogeográfico de las provincias de Cuyo. Publicación No 3. Facultad de Ciencia Agrarias. U.N.C. CAPERAS. Subcomité Zona Cuyo.

Roig FA, Roig-Juñent S and Corbalán V. 2009. Biogeography of the Monte Desert. Journal of Arid Environments 73: 164-172.

Rossi BE, Debandi GO, Peralta IE and Martínez Palle E. 1999. Comparative phenology and floral patterns in *Larrea* species (Zygophyllaceae) in the Monte desert (Mendoza, Argentina). Journal of Arid Environments 43: 213-226.

Rossi BE and Villagra PE. 2003. Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understorey species in arid Argentina. Journal of Vegetation Science 14: 543-550.

Sala OE and Aguiar MR. 1996. Origin, maintenance, and ecosystem effect of vegetation patches in arid lands. In: West N (ed). Rangelands in a Sustainable Biosphere. Pp 29-32.Proceedings of the Fifth International Rangeland Congress Vol. 2, Society for Range Management, Denver.

StatSoft Inc. 2007. STATISTICA (data analysis software system), version 8.0.

Tirado R and Pugnaire FI (2003) Shrub spatial aggregation and consequences for reproductive success. Oecologia 136: 296-301.

Vidiella PE, Armesto JJ and Gutiérrez JR. 1999. Vegetation changes and sequential flowering after rain in the southern Atacama desert. Journal of Arid Environments 43: 449–458.

Villagra PE and Cavagnaro JB. 2006. Water stress effects on the seedling growth of *Prosopis argentina* and *Prosopis alpataco*. Journal of Arid Environments 64: 390-400.

Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP and Parmenter R. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300.

Xu L, Liua H, Chuc X and Sua K. 2006. Desert vegetation patterns at the northern foot of Tianshan Mountains: The role of soil conditions. Flora 201: 44-50.

Zhang YM, Chen YN and Pan BR. 2005. Distribution and floristics of desert plant communities in the lower reaches of Tarim River southern Xinjiang, People´s Republic of China. Journal of Arid Environments 63: 772-784.

Appendix. Percentage cover (mean±SD) of all species in the six sampling sites. Plant cover species with differences among sites ($p<0.05$; Kruskal-Wallis test, corrected by FDR rule) are indicated in bold type. N=20 sampling plots each with 13 subplots in all cases.

Species list	Barrens	Saltbush	Creosote bush scrub	Mesquite woodlands	Columnar cactus slopes	Chical
Aristida mendocina	-	-	0.02±0.04	1.60±3.70	-	-
Atriplex lampa	-	0.12±0.52	-	0.45±0.80	-	-
Atriplex litophila	-	-	-	-	-	0.43±0.86
Atriplex spegazzinii	-	3.92±4.05	-	1.98±1.92	0.15±0.54	0.89±1.94
Baccharis salicifolia	-	-	-	1.55±3.49	-	0.33±1.43
Bulnesia retama	-	1.37±2.48	2.36±3.26	0.42±1.56	0.51±1.36	-
Capparis atamisquea	-	-	0.40±1.42	1.66±2.95	0.25±0.77	0.02±0.06
Cercidium praecox	-	-	0.08±0.34	0.72±1.83	0.27±0.73	0.11±0.36
Cereus aethiops	-	-	0.00±0.02	-	-	-
Clematis montevidensis	-	-	-	0.00±0.02	-	-
Cyclolepis genistoides	-	-	0.08±0.34	0.07±0.26	0.03±0.14	0.12±0.39
Denmoza rhodacantha	-	-	-	-	0.08±0.20	0.06±0.16
Deuterocohnia longipetala	-	-	-	-	1.70±2.58	-
Digitaria californica	-	-	-	-	0.02±0.06	-
Distichlis spicata	-	-	-	0.03±0.09	-	-
Ditaxis malpighipila	-	-	-	-	-	0.01±0.04
Echinopsis leucantha	-	-	0.05±0.17	-	0.13±0.16	0.02±0.06
Geoffroea decorticans	0.10± 0.43	-	-	0.55±1.50	0.35±1.07	0.04±0.11
Gomphrena pulchella	-	-	-	0.00±0.02	-	-
Grabowskia obtusa	-	-	-	0.08±0.24	-	-
Grahamia bracteata	-	-	-	0.00±0.02	-	-
Gymnocalycium bodenbenderianum	-	-	-	-	0.03±0.09	-
Gymnocalycium schickendantzii	-	-	0.00±0.02	-	0.01±0.04	-
Halophytum ameghinoi	0.00±0.02	-	-	-	-	-
Heterostachys ritteriana	-	-	-	-	-	0.09±0.27
Hoffmanseggia sp.	-	-	-	0.01±0.02	-	-
Larrea cuneifolia	-	0.00±0.02	5.17±5.11	0.46±1.53	3.24±3.63	1.15±2.54
Larrea divaricata	-	0.10±0.35	-	6.40±6.21	0.13±0.53	0.29±0.70
Lippia integrifolia	-	-	-	0.52±1.09	-	-
Lycium chilense	-	0.00±0.02	-	0.15±0.44	-	-
Lycium ciliatum	-	-	-	-	-	-
Lycium tenuispinosum	-	0.02±0.09	0.01±0.05	0.17±0.41	0.04±0.12	0.41±0.72
Maytenus viscifolia	-	-	0.13±0.42	-	0.83±2.56	-
Mimosa ephedroides	-	-	0.04±0.17	0.00±0.02	0.08±0.27	0.98±1.62
Monttea aphyla	-	-	-	-	0.44±1.18	0.48±0.90
Opuntia sulphurea	-	-	0.13±0.37	0.00±0.02	0.28±0.47	0.81±0.87
Pappophorum sp.	-	-	-	-	-	0.06±0.16
Philibertia gilliesii	-	-	-	-	-	0.00±0.02
Plectrocarpa tetracantha	-	2.16±3.96	0.55±1.69	0.32±1.17	0.10±0.26	0.05±0.18
Prosopis chilensis	-	-	-	14.4±12.9	-	-

Species list	Barrens	Saltbush	Creosote bush scrub	Mesquite woodlands	Columnar cactus slopes	Chical
Prosopis flexuosa	-	0.22±0.68	-	1.29±3.42	-	0.39±1.18
Prosopis strombulifera	-	0.34±1.04	-	-	-	-
Prosopis torquata	-	0.15±0.69	2.84±4.29	-	4.22±3.90	0.95±1.40
Ramorinoa girolae	-	-	-	-	-	1.88±3.83
Salvia gilliesii	0.01±0.05	-	-	-	-	-
Schinus polygama	-	-	-	0.33±1.01	-	-
Sclerophylax kurtzii	0.00±0.02	-	-	-	-	-
Senecio riojanus	-	-	-	-	-	0.06±0.19
Senecio subulatus	-	-	-	0.77±1.90	-	-
Senna aphyla	-	0.08±0.34	0.62±1.52	-	0.37±1.15	0.62±1.18
Sporobolus rigens	-	0.03±0.15	-	-	-	-
Suaeda divaricata	-	0.87±1.69	-	1.11±1.62	0.03±0.09	0.60±1.17
Tephrocactus alexanderi	-	-	0.07±0.26	-	0.95±1.47	0.15±0.37
Tephrocactus aoracanthus	-	-	0.28±0.52	0.00±0.02	-	0.13±0.33
Tephrocactus articulatus **var.** ***oligacanthus***	-	-	-	0.04±0.08	-	-
Tephrocactus halophilus	-	-	0.55±0.90	-	0.04±0.19	-
Tessaria absinthioides	-	0.08±0.34	-	-	-	-
Tessaria dodoneifolia	-	-	-	0.68±1.64	-	-
Tillandsia aizoides	-	-	0.05±0.06	0.00±0.02	0.02±0.03	0.01±0.02
Tillandsia bryoides	-	-	0.27±0.33	-	0.03±0.05	0.04±0.09
Tillandsia xiphioides	-	-	0.00±0.02	-	0.00±0.02	0.20±0.24
Trichloris crinita	-	-	-	-	0.00±0.02	-
Trichocereus strigosus	-	-	-	-	0.22±0.39	0.55±0.68
Trichocereus terscheckii	-	-	-	-	0.06±0.19	-
Tricomaria usillo	-	-	0.16±0.39	0.10±0.43	0.19±0.86	0.01±0.05
Tricycla spinosa	-	-	-	-	-	0.37±0.66
Tweedia brunonis	-	-	-	0.08±0.34	-	-
Wedelia glauca	-	-	-	0.01±0.03	-	-
Zuccagnia punctata	-	-	3.04±4.37	0.60±1.84	4.56±6.34	2.33±3.94

CAPÍTULO III.

Densidad y tamaño de población y uso del hábitat del guanaco

Densidad y uso de hábitat a diferentes escalas espaciales de una población de guanacos (*Lama guanicoe*) en el Desierto del Monte de Argentina.

RESUMEN

Se presentan las primeras estimas de densidad y el uso del hábitat a diferentes escalas espaciales de una población periférica de guanacos en un área protegida del desierto del Monte, Argentina. Para el cálculo de la densidad, se realizaron transectos en las estaciones húmeda y seca de 2005. Paralelamente, se llevaron a cabo recorridos sistemáticos a través de las carreteras y caminos del espacio protegido en los que se anotó la posición exacta (mediante GPS) y se identificó el hábitat en el que se encontraban los guanacos. El tamaño de grupo varió significativamente entre las estaciones húmeda y seca. La densidad poblacional estimada fue diferente para la estación húmeda (0.10–0.12 individuos/Km^2) que para la seca (0.60–0.75 individuos /Km^2). El tamaño poblacional estimado osciló entre los 75 individuos (estación seca) y los 388 individuos (estación húmeda). En cuanto al uso del hábitat, los guanacos mostraron un uso diferencial definido en primer lugar por factores abióticos como la topografía, las características del suelo o las condiciones microclimáticas. Así los guanacos usaron preferentemente sustratos rugosos y rocosos en la estación seca y zonas más llanas y abiertas en la estación húmeda. En segundo lugar, el uso del hábitat definido a partir de la ocupación de las distintas comunidades vegetales también mostró diferencias estacionales: en la estación húmeda los guanacos utilizaron preferentemente el jarillal mixto y el zampal, mientras que en la estación seca prefirieron el matorral abierto y la ladera cardón. El tamaño poblacional estimado para este espacio protegido es pequeño, aunque su densidad está dentro del rango de otras poblaciones, siendo relativamente alto para una zona tan árida.

Density and habitat use at different spatial scales of a guanaco population (*Lama guanicoe*) in the Monte desert of Argentina.

Acebes, P, Traba J, Malo JE, Ovejero R and Borghi CE. 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.

ABSTRACT

The first density estimates of a peripheral guanaco population and its habitat use at different spatial scales are presented for a protected area of Monte desert, Argentina. Transects were surveyed in the wet and dry seasons of 2005. All guanaco herds seen during systematic surveys using roads and tracks were GPS located and their habitat use identified. Herd size differed significantly between the dry and wet seasons. Population densities differed between wet (0.10–0.12 individuals/Km^2) and dry seasons (0.60–0.75 individuals/Km^2). The population estimates ranged from 75 individuals (dry season) to 388 individuals (wet season). Guanacos showed differential habitat use, the first determinant being abiotic factors such as topography, soil characteristics or microclimate conditions, animals being detected in rougher rocky substrata in the dry season and in open flat terrain in the wet season, followed by a mesoscale selection defined by plant communities. At the later scale guanaco preferentially used mixed creosote bushland and saltbush more intensively during the wet season, and open scrub and columnar-cactus slopes in the dry season. The estimated population of this protected area was small but its population density was within the range of other populations and relatively high for this dry and unproductive area.

Key words: arid environments, conservation, population estimates, protected areas, ungulates.

INTRODUCTION

Knowledge of the status of small populations of wild mammals and their main ecological needs is fundamental to taking proper conservation decisions (Groom et al. 2006). Density and total population estimations are associated with the likelihood of population persistence and characterization of habitat use helps to identify the key elements of the territory upon which they rely. With respect to habitat use it is important to note that it is determined not only by biotic factors such as food resources (Senft et al. 1987) or predation risk (Lima 2002, Creel et al. 2005) but also by abiotic factors such as topography and water availability, which frequently become determinants of broad-scale distribution patterns (Bailey et al. 1996). As a result some kind of spatial hierarchy in habitat use can be detected for many animal species (Senft et al. 1987, Kotliar and Wiens 1990, Turner et al. 1997) and attention should be paid to it in the management of protected areas.

The guanaco (*Lama guanicoe*, Müller 1776) is the largest of the wild South American camelids and it is distributed from 8°S in Perú to almost 55°S on Navarino island (Chile). Within this range it has been encountered from sea-level to 4600 m (Puig 1995). Towards the end of the 19th century, guanaco populations were present in nearly all Argentinean biomes, occupying open, scrub-dominated areas and open woodlands. Currently guanacos are abundant only on the Patagonian steppes and in the Andean foothills (Cunazza et al. 1995). The causes of this decline have not been well documented but they may include hunting, competition with domestic livestock and/or exotic herbivores, and loss or fragmentation of habitat resulting from agricultural development (Cunazza et al. 1995). Even so, there still remain some relict, isolated populations in restricted areas, generally within scarcely altered habitats in north-central Argentina (Sosa and Sarasola 2005). Among these, very little is known about the guanaco populations of the Monte desert biome, a temperate dry desert where guanacos depend for food on woody plants and cacti, as herbaceous plants are scarce (Acebes et al. unpubl. data).

This study presents the first density and population estimates from the arid extreme of the species' distribution within Argentina, in one of the most arid areas of South America. It also provides the first data on seasonal habitat use by guanacos at plant community (mesoscale) and landscape spatial scales.

MATERIALS AND METHODS

Study area

The study was carried out in Ischigualasto Provincial Park (29º55' S, 68º05' W), in San Juan Province, Argentina (Figure 1) which, together with Talampaya National Park, constitutes the Ischigualasto-Talampaya World Heritage Site (UNESCO). The park extends over 60 369 ha at a mean altitude of 1300 m asl. The climate is typical dry desert, with a mean annual temperature below 18ºC (range -10º to +45ºC) and a mean temperature over 22ºC during the hottest month. Mean annual precipitation ranges from 80–140 mm, concentrated during late spring and summer (November to February).

The Monte is the dominant biome of the protected area (Márquez et al. 2005). The vegetation is dominated by species of the families Zygophyllaceae (*Larrea* spp., *Zuccagnia punctata*, *Bulnesia retama* and *Plectrocarpa tetracantha*), Fabaceae (*Prosopis* spp., *Cercidium Praecox, Geoffroea decorticans, Senna aphylla*, *Ramorinoa* *girolae*) and Chenopodiacae (*Atriplex* spp. and *Suaeda divaricata*). Cacti (*Trichocereus* spp., *Tephrocactus* spp. and *Opuntia sulphurea*) and Bromeliads (*Deuterocohnia longipetala* and *Tillansia* spp.) are also abundant, but to a lesser extent. The average plant cover is low, less than 30%, with a seasonal and sparse herbaceous layer (Acebes et al. unpubl. data).

Figure 1. Location of Ischigualasto Provincial Park (IPP) in San Juan province, Talampaya National Park (TNP) and the Monte desert biome (Argentina).

Density estimates

Guanaco population density was evaluated from a total of six 5-km transects during each of the late wet (March–April) and dry (August–September) seasons of 2005. The starting points and directions of transects were randomly chosen, with the proviso that they should not overlap. Transects were walked by two observers with binoculars and registered with a GPS. We recorded the distance (by laser telemeter) and bearing (by precision compass) from the transect line of different herds or individuals detected, as well as date and time, habitat and herd size. Density estimates were determined with the DISTANCE 5.0 programme (Thomas et al. 2005). To evaluate the accuracy of our population estimates with DISTANCE, we calculated the number of individuals per km^2 using all the sightings within a 500m strip to each side of the transect line, as recommended for large ungulates in open habitats (Caughley 1977). To achieve this purpose, we reprojected all the sightings and determined the 500 m buffer zone around the transect track with GIS software (ARCGIS 9.2).

Habitat use

To determine whether guanaco follow the hierarchical patterns of resources selection described for ungulates (Senft et al. 1987), habitat use was analysed at two different spatial scales: a mesoscale defined by plant communities and a landscape scale taken to be the different geological units found in the protected area. We have used geological units as a proxy for abiotic factors such as soil characteristics, topography, and particular microclimatic conditions or water availability, whereas plant communities represent food availability.

In addition to the transect data, we noted and georeferenced (using GPS), all records of guanaco herds (n=75 sightings) made during systematic daily surveys along the tourist route and along roads and secondary tracks within the park. The sampling effort was equivalent during wet and dry seasons and totalled 150 survey hours (approximately 40 km per day over 50 days). This sampling scheme was designed to address the low number of guanaco sightings made per day. Some groups may have been detected on more than one occasion. The plant communities given in Table 1 were noted when assigning guanaco sightings to habitat. These plant communities were used as a proxy for habitat on account of their variability in species composition, vegetation cover and structure.

Comparisons of the number of sightings in the different habitats employed the Monte Carlo CHITEST (Romesburg and Marshall 1985). To overcome problems arising from the assumption of minimum expected frequencies, this software generates random tables (n=9999) with the same distribution of rows and columns as the original data. Seasonal differences in herd sizes were evaluated with a Mann-Whitney U test (Zar 1998).

All guanaco observations were projected using GIS software into a Landsat 7 ETM+ satellite image (30 m resolution) previously classified by geological criteria (Chuvieco 2002) and then assigned to the geological units of the study area. The three geological units where guanaco observations were located varied in topography as well as in soil composition and structure: Ischigualasto unit is an open and relatively flat expanse of fine-textured Triassic silts where vegetation is scarce or absent; Los Rastros unit comprises rocky hillsides of consolidated Triassic sandstones with abrupt relief and, finally, Quaternary sediments are almost flat areas of coluvial deposits. Differences between seasons in guanaco sightings on these geological units were analysed with the Monte Carlo CHITEST.

RESULTS

Density estimates

Transect distances totalled 30 km in both seasons, with very few sightings. Density estimates using DISTANCE varied between seasons: Wet season: 0.60 individuals/km^2 (CV: 91.93%); dry season: 0.12 individuals/km^2 (CV: 0.0%); both seasons combined: 0.38 individuals/km^2 (CV: 134.23%). The alternative estimation method, i.e. the 1km-wide belt transect, gave similar results: 0.75 individuals/km^2 in the wet season and 0.10 individuals/km^2 in the dry season. The Park population is therefore estimated to range from 388 individuals in the wet season to 75 in the dry season.

Habitat use

On the systematic daily surveys we recorded 35 guanaco sightings in the wet season and 40 guanaco sightings in the dry season. Herd size differed significantly between the seasons (Mean±SD; wet 4.86±4.08, dry 6.70±3.56, Mann-Whitney U-test: U=456; p=0.009).

Habitat use at a landscape scale also differed between seasons (χ^2=20.645; df=2; P<0.0001). Most wet season guanaco observations were in the Quaternary sediments unit, while the Los Rastros unit was the most used by guanacos in the dry season (Figure 2).

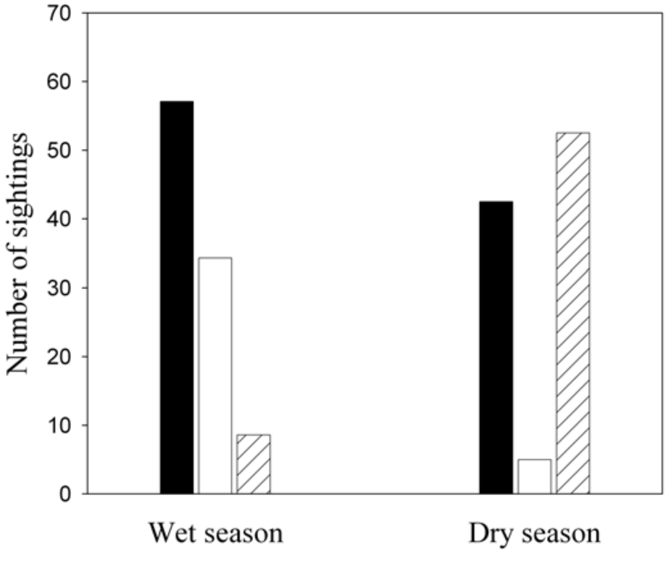

Figure 2. Guanaco habitat use at landscape scale between seasons. Black bars correspond to Quaternary sediments, white bars to Ischigualasto unit and striped bars to Los Rastros unit.

Guanaco habitat use at plant community scale also differed between the wet and the dry seasons (χ^2=38.915; df=9; P<0.0001). Mixed Creosote bushland and Saltbush were the most used in the wet season and Open and Mixed scrub and Columnar-cactus slopes were most used in the dry season (Figure 3).

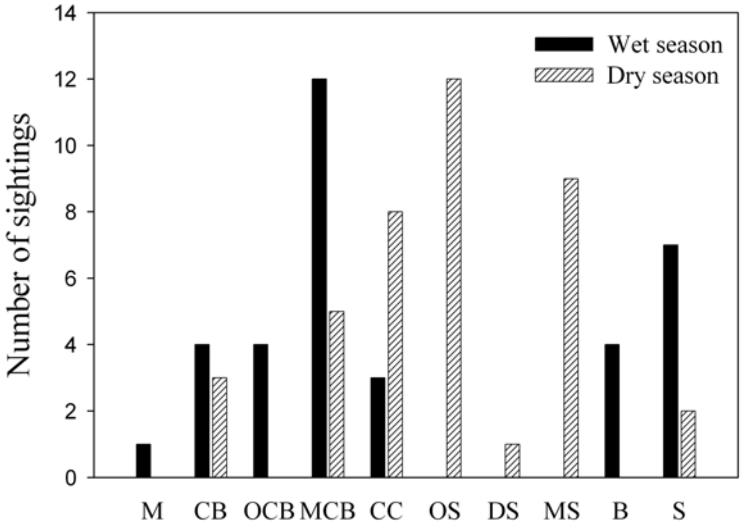

Figure 3. Number of guanaco sightings by plant communities: Mesquite woods (M), Creosote bushland (CB), Open Creosote bushland (OCB), Mixed Creosote bushland (MCB), Columnar-cactus slopes (CC), Open scrub (OS), Dense scrub (DS), Mixed scrub (MS), Barrens (B) and Saltbush (S).

DISCUSSION

These results show that the guanaco density in this protected area of the Monte desert is comparable to that of other important populations in Argentina (see below), despite its aridity and low plant cover. The low total numbers estimated makes the population potentially vulnerable to human pressure and other threats, especially in view of the seasonal displacement of the guanacos and their potential dependence on unprotected sites outside the reserve.

Density estimates

Density estimates obtained from DISTANCE and the transect method were very similar despite the number of guanaco observations being lower than that recommended to give robust results using DISTANCE (Buckland et al. 2001). The range of densities is lower than those encountered in the San Guillermo Biosphere Reserve in Argentina (1.46 ind./Km^2, Puig and Videla 2007), relatively close to Ischigualasto Provincial Park but within the Puna and High-Andean biome. In other parts of the country, such as the Valdés Peninsula (Chubut), densities are within the range of the protected sector in the Patagonian biome (0.59 ind./km^2) but lower than in the unprotected zones of the Monte biome (1.09 ind./km^2). Censuses by other authors (Amaya et al. 2001) yield guanaco densities similar to those in Ischigualasto Provincial Park (Chubut: 0.39 ind./km^2; Río Negro: 0.26 ind./km^2; Neuquén: 0.52 ind./km^2). The guanacos in the Patagonian steppe zones of Tierra del Fuego occur at lower densities (0.98 ind./km^2, Bonino and Fernández 1994; 0.52 ind./km^2, Montes et al. 2000) than those of the Woodland/Steppe ecotone (1.72 ind./km^2, Bonino and Fernández 1994; 2.13 ind./km^2, Montes et al. 2000) but always at higher densities than those in Ischigualasto Provincial Park. The density estimate for Ischigualasto Provincial Park falls within the range of other populations but seems relatively high for such a dry and unproductive area, which may be due to the refuge effect of this protected area relative to its surroundings (Malo et al. 2007). The estimated maximum of around 400 individuals is within the range of published minimum sizes for viable populations (Caughley and Sinclair 1994).

With respect to seasonal variation in herd size, our results accord with other studies that have found family herds to be larger in winter than in summer (Puig 1995). Herd sizes fall within the range described for other guanaco populations (6.6 individuals, Tierra del Fuego, Bonino and Fernández 1994), being larger than those in the Catamarca Andes (3.5 individuals, Lucherini 1996) and only slightly smaller than those in the San Juan Puna (8.36 individuals, Puig and Videla 2007), Argentine Patagonia (7.2 individuals, Gader and del Valle 1982) and the Chilean sector of Tierra del Fuego (7.5 individuals, Raedeke 1978). Differences in density estimates between seasons may result from short-distance movements during the dry season to the most productive zones, which comprise the western sector of the protected area and its surrounding mountains. Indeed, intra-annual variation in numbers is much less than that described for other populations (Ortega and Franklin 1995, Contreras et al. 2006) and very similar to that of the isolated populations in north-central Argentina (Sosa and Sarasola 2005).

Habitat use

Comparisons of sightings between plant communities/geological units were feasible since guanacos were readily detectable, so that their relative habitat preferences could be adequately described. The large size of guanacos assured their detectability and both the geological units and plant communities were sufficiently open to offer good visibility from the tourist route, roads and secondary tracks from where the surveys were made.

Large-scale movements of ungulates may be driven by the need to find new water sources or to avoid adverse climatic conditions. Microsite characteristics, such as the presence or absence of wind, affect where animals rest or graze (Bailey et al. 1996). During the wet season guanacos preferred geological units such as Ischigualasto and Quaternary sediments characterized by open and flat topography. Puig et al. (2008) found the same pattern of habitat use by guanacos in northern Patagonia. However during the dry season guanacos were mostly seen on the Rastros geological unit and secondarily on Quaternary sediments. The Rastros unit consists of stony hillsides full of gullies which generate their own microclimates and provide refuges for the guanacos, as has been described for the Patagonian populations (de Lamo et al. 1998). In contrast, the flatter areas with very low plant cover remain exposed to the strong cold winds of the area.

The mesoscale approach seemed to confirm the pattern described above. Habitats with low plant cover, such as saltbush and mixed creosote bushland located in the central and driest part of the study area, are generally flat and offer good visibility, and they were used by guanacos mainly during the wet season. Guanaco herds include newborns at this time and they probably favour open zones that allow potential predators to be detected more readily (Bank et al. 2003). Although sparse, plants are sprouting there at this season and are a source of food. Thus, during the wet season, guanacos probably face a trade-off between predation risk and trophic needs, as has been described for other ungulates (McCullough 1999, Creel et al. 2005). During the dry season, however, the guanaco mainly move to more peripheral areas with low to medium plant cover, such as open and mixed scrub, as well as the Columnar-cactus slopes. This may be because they seek green plants and water, the latter being a limiting resource during this period and found in very few locations in the park. This ability to modify their diet in response to trophic availability extends to eating cacti, as has been described from other hyperarid zones in South America, such as the Atacama desert (Raedeke and Simonetti 1988). Small patches of dense scrub were clearly avoided by guanacos in the wet season and occasionally used in the dry period. Predators such as puma (*Puma concolor*, Linnaeus 1771) could use these patches for concealment, as has been described in other ungulate studies (Kie 1999).

To conclude, these results also raise certain questions of great interest regarding the conservation of the guanaco population of the Monte desert biome. Population density was in the range of other populations but its small size makes it fundamental that there should be interconnectivity with some adjacent populations such as that of Talampaya National Park. However, in this latter protected area, data resulting from three randomly-chosen 5-km transects, which detected no guanacos, and from systematic surveys along the tourist routes and other roads of the park, which detected only two guanaco herds in distant locations, suggest a density and total number of guanacos considerably lower than in Ischigualasto Provincial Park. Therefore the survival of this interesting population, located at the arid extreme of the species' distribution within Argentina and in one of the most arid areas of South America, may not be guaranteed unless proper measures are carried out and such conservation efforts should be targeted at the full set of habitats used by the species during the course of the year.

REFERENCES

Amaya JN, Thüngen J and de Lamo DA. 2001. Densidad de guanacos (*Lama guanicoe*) en la Patagonia. INTA Bariloche, Argentina. pp. 1-14.

Bailey DB, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM and Sims PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49: 386-400.

Bank MS, Sarno RJ and Franklin WL. 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biological Conservation 112: 427-434.

Bonino N and Fernández E. 1994. Distribución general y abundancia relativa de guanacos (*Lama guanicoe*) en diferentes ambientes de Tierra del Fuego, Argentina. Ecología Austral 4: 79-85.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL and Thomas L. 2001. Introduction to Distance Sampling. Estimating abundance of biological populations. Oxford University Press, Oxford. pp. 416.

Caughley G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London. pp. 234.

Caughley G and Sinclair ARE. 1994. Wildlife ecology and management. Blackwell Scientific Publications, Massachusetts. pp. 334.

Chuvieco E. 2002. Teledetección ambiental: La observación de la Tierra desde el Espacio. Editorial Ariel, Barcelona. pp. 586.

Contreras M, González B and Novoa F. 2006. Patrón de migración altitudinal y rango de hogar de guanacos en un ambiente andino del centro norte de Chile. In: Camaño A, Castilla JC and JA Simonetti JA (eds). Minería y biodiversidad. Pp. 79-91. Publicación de Sonami, Chile.

Creel S, Winnie J, Maxwell B, Hamlin K and Creel M. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86: 3387-3397.

Cunazza C, Puig S and Villalba L. 1995. Situación actual del guanaco y su ambiente. In: Puig S (ed). Técnicas para el manejo del guanaco. Pp. 27-50. IUCN, Gland, Switzerland.

De Lamo DA, Sanborn AF, Carrasco CD and Scout DJ. 1998. Daily activity and behavioral thermoregulation of the guanaco (*Lama guanicoe*) in winter. Canadian Journal of Zoology 76: 1388-1393.

Gader R and del Valle A. 1982. Relevamiento aéreo de guanacos en el Dpto, Collón Curá. Neuquén (Argentina): Dirección General de Recursos Faunísticos. pp. 42.

Groom MJ, Meffe GK and Carroll. CR 2006. Principles of Conservation Biology. 3rd ed. Sinauer Associates, New York. pp. 699.

Kotliar NB and Wiens JA. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Kie JG. 1999. Optimal foraging and risk of predation: effects on behaviour and social structure in ungulates. Journal of Mammalogy 80: 1114-1129.

Lima SL. 2002. Putting predators back into predator–prey behavioral interactions. Trends in Ecology and Evolution 17: 70-75.

Lucherini M. 1996. Group size, spatial segregation and activity of wild sympatric vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe*. Small Ruminant Research 20: 193-198.

McCullough DR. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80: 1130-1146.

Malo JE, Acebes P, Giannoni SM, Borghi CE and Traba J. 2007. Do guanacos tolerate visitors in protected areas? Behavioural changes in response to tourists of a guanaco population in the Monte desert. Proceedings of the 41st International Congress of the International Society for Applied Ethology; Mérida, México.

Márquez J, Martínez Carretero E, Dalmasso A, Pastrán G and Ortiz S. 2005. Las áreas protegidas de la provincia de San Juan (Argentina) II. La vegetación del Parque Provincial de Ischigualasto. Multequina 14: 1-27.

Montes C, de Lamo DA and Zavatti J. 2000. Distribución de abundancias de guanaco (*Lama guanicoe*) en los distintos ambientes de Tierra del Fuego, Argentina. Mastozoología Neotropical 7: 23-31.

Ortega IM and Franklin WL. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural 68: 489-500.

Puig S. 1995. Abundancia y distribución de las poblaciones de guanacos. In: Puig S. (ed). Técnicas para el manejo del guanaco. Pp. 57-70. IUCN, Gland.

Puig S and Videla F. 2007. Distribución, densidades y estado de conservación de los camélidos. In: Martínez Carretero E. (ed). Línea de base de la Diversidad Biológica y Cultural en la Reserva de Biosfera San Guillermo (San Juan, Argentina). Pp. 199-223. UNSJ. Argentina.

Puig S, Videla F, Cona IM and Roig VG. 2008. Habitat use by guanacos (*Lama guanicoe*, Camelidae) in northern Patagonia (Mendoza, Argentina). Studies on Neotropical Fauna and Environment 43: 1-9.

Raedeke KJ. 1978. El guanaco en Magallanes, Chile. Su distribución y biología. - Corporación Nacional Forestal (Chile): Publicación Técnica 4. pp. 182.

Raedeke K and Simonetti J. 1988. Food habits of *Lama guanicoe* in Atacama desert of northern Chile. Journal of Mammalogy 69: 198-201.

Romesburg HC and Marshall K. 1985. CHITEST: A Monte-Carlo computer program for contingency table tests. Computional Geoscience-UK. 11: 69-78.

Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE and Swift DM. 1987. Large foraging and ecological hierarchies. Bioscience 37: 789-799.

Sosa RA and Sarasola JH. 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.

Thomas L, Laake JL, Strindberg S, Marques FFC, Buckland ST, Borchers DL, Anderson DR, Burnham KP, Hedley SL, Pollard JH, Bishop JRB and Marques TA. 2005. Distance 5.0. Release "x"1. - Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. pp. 308.

Turner MG, Pearson SM, Romme WH and Wallace LL. 1997. Landscape heterogeneity and ungulate dynamics: What spatial scales are important? In: Bissonette JA (ed). Wildlife and Landscape Ecology: Effects of Pattern and Scale. Pp. 331-348. Springer-Verlag, New York.

Zar JH 1998. Biostatistical Analysis. 4th ed. Upper Saddle River. Prentice-Hall, New York. pp. 929.

CAPÍTULO IV.

Uso del espacio del guanaco en simpatría con ungulados introducidos

Co-ocurrencia y competencia potencial entre grandes herbívoros silvestres y exóticos en un desierto sudamericano.

RESUMEN

La introducción de ungulados exóticos en zonas con presencia de ungulados silvestres puede conducir a procesos de competencia interespecífica, particularmente si las especies implicadas tienen un tamaño similar y comparten estrategias de forrajeo parecidas, debido a la escasez de recursos tróficos. Esta interacción no ha sido estudiada en desiertos sudamericanos en los que el guanaco (Lama guanicoe), el camélido silvestre sudamericano de mayor tamaño y más amplia distribución, co-ocurre con varias especies introducidas. En este trabajo estudiamos los patrones de ocurrencia y abundancia del guanaco, del burro y de la vaca en áreas desérticas de Argentina mediante el muestreo de excrementos. Los análisis de co-ocurrencia muestran cierto grado de segregación en el uso del espacio entre el guanaco y el ganado asilvestrado, el cual no es detectado, sin embargo, cuando se controla el efecto geográfico. Los modelos de abundancia y de ocupación del guanaco están fuertemente asociados a variables bióticas y abióticas, tales como escasa cobertura vegetal o la preferencia por sustratos rocosos, y a variables de influencia humana, apareciendo los guanacos en áreas alejadas de los núcleos habitados. Sin embargo, mientras que la distribución del guanaco está débilmente relacionada con la presencia del ganado asilvestrado, su abundancia está negativamente asociada con la presencia del burro. Por el contrario, las especies introducidas aparecen estrechamente asociadas, utilizando preferentemente áreas de vegetación más densa y más productivas. En conclusión (i) el guanaco no solapa con los herbívoros exóticos, aunque esta situación puede ser denso-dependiente, e incrementos en la abundancia de las especies exóticas puede tener impacto en la población de guanacos, (ii) la presencia y la abundancia del guanaco están negativamente relacionadas con la proximidad a los asentamientos rurales, y (iii) estos resultados son generalizables a otras zonas áridas de Sudamérica, en las que el guanaco co-ocurre con burros asilvestrados y los conflictos asociadas a la presencia humana son frecuentes.

Co-occurrence and potential for competition between wild and exotic large herbivores in a South American desert.

Acebes P, Traba J and Malo JE. Co-occurrence and potential for competition between wild and exotic large herbivores in a South American desert *(Manuscrito enviado)*.

ABSTRACT

Introduction of exotic ungulates may lead to interspecific competition with native herbivores, particularly if the species involved are in similar size and share similar foraging strategies due to scarcity of trophic resources. This interaction has not been investigated in South American deserts in which guanaco (*Lama guanicoe*), the larger South American wild camelid, and the most widely-distributed ungulate, co-occurs with several introduced species, standing out as a model species. We study occurrence and abundance patterns of guanaco, donkey and cattle in desert areas of Argentina by dung sampling. Analyses of co-occurrence show a certain degree of segregation in land use between guanaco and feral livestock, not detected when geographical effects are removed. Distribution and abundance models of guanaco are strongly associated with biotic and abiotic variables such as sparse plant cover, rocky substrata and human-influence variables, appearing in areas furthest from villages. Nevertheless, while guanaco distribution is weakly related to feral livestock presence, its abundance is negatively associated with donkey presence. In contrast, livestock species appear closely associated with each other, being centred on areas of densest and most productive vegetation. To conclude (i) guanaco does not overlap with alien herbivores, although this situation may be density-dependent, and increase in exotics abundance may impact on guanaco population, (ii) both guanaco occurrence and abundance are negatively related to rural settlements vicinity and, (iii) these results become widespread throughout other drylands of South America, where guanaco co-occurs with feral donkeys and conflicts with humans are frequent.

Key words: coexistence, Human impact, *Lama guanicoe,* Monte Desert, multimodel inference, protected areas, resource partitioning.

INTRODUCTION

Spatial occurrence patterns of species are an expression of multiscalar and multifactorial processes that act simultaneously. Such patterns are determined, at intermediate or finer scales, by evolutionary history of species, environmental factors such as distribution of trophic resources (Morris and Davidson 2000) and by biotic interactions (Rosenzweig 1981). Where herbivores are concerned, co-occurrence of native species may be due to evolutionary processes that have enabled coexistence through spatial or trophic resource partitioning (Voeten and Prins 1999), although they may have competed in the past (the 'ghost of competition past', Connell 1980). However, recent introduction of exotic ungulates into an assemblage of native species may culminate in interspecific competition, given that there has been insufficient time for resource partitioning (Putman 1996, Voeten and Prins 1999). Sympatric species of similar-sized ungulates that have similar foraging strategies may thus compete (Prins and Olff 1998, Owen-Smith 2002). However, for this to occur there must be a high overlap in their use of spatial and trophic resources, and such resources must be scarce (Putman 1996, Prins and Olff 1998, Hulbert and Andersen 2001). In addition, human presence modifies spatial exploitation by wild ungulates, as establishment of traditional pastoralism pushes wild ungulate populations away (Prins 2000, Bagchi et al. 2004, Mishra et al. 2004). Wild species are also often driven far from human settlements by poaching (Wilkie et al. 2000).

Arid lands world-wide are resource-limited environments. Large native herbivores and livestock in such biomes often compete for space and trophic resources (Young et al. 2005). Studies of competition between native and exotic herbivores in arid and semi-arid biomes are relatively numerous for African savannas (Fritz et al. 1996, Voeten and Prins 1999, Young et al. 2005 Sitters et al. 2009) or for Asian steppes (Bagchi et al. 2004, Shrestha and Wegge 2008, Suryawanshi et al. 2010). However, very few studies exist for similar biomes in South America, in which guanaco (*Lama guanicoe*, Müller), the largest and most widely-distributed ungulate, stands out as a model species to study this type of interactions.

Guanaco population prior to the Spanish conquest was between 30 and 50 million, occupying nearly all of Chile and Argentina, as well as parts of Bolivia, Peru and Paraguay (Raedeke 1979). Current estimate is that there are somewhat more than 600,000 guanacos, the pronounced decline being attributed to competition with livestock, habitat loss and poaching (Baldi et al. 2008). In many areas guanaco is sympatric with introduced herbivores, being the few existing studies on Patagonian steppes, where guanaco is abundant, and coexists with sheep since its introduction at the end of 19th century (Baldi et al. 2001, 2004, Puig et al. 2001). In extremely arid regions where guanaco maintains significant populations with high conservation value (Acebes et al. 2010) guanaco co-occurs with both feral donkeys (*Equus asinus*) and free-ranging cattle (*Bos taurus*). Donkey is native from arid zones of Africa and has colonized American and Australian deserts successfully (Grinder et al. 2006), but is still poorly studied, and no works on South American wild fauna impacts exist (Novillo and Ojeda

2008). Cattle has received more attention (see for instance Fritz el al 1996, Stewart et al. 2004), although studies about competition with South American herbivores are lacking.

The present study aimed to analyze use of space by 3 large herbivores, the native guanaco, exotic feral donkeys, and free ranging cattle, where trophic resources are limited. We hypothesized that there would be a high degree of spatial overlap among 3 species given their feeding styles (intermediate feeder-grazers), their digestive strategies (guanaco and cattle: ruminants; donkeys: hindgut fermenter), similar body weights (guanaco: 100–120kg; donkey: 140kg; cattle: 200kg), and scarcity of trophic resources. Particularly herbaceous layer is almost non-existent so herbivores should have browse-dominated diets. There would thus be potential competition among them that would have a negative impact on native species. The basic objectives were a) to determine co-occurrence patterns of 3 species from data on their presence and abundance, and b) to define their habitat selection requirements, evaluating effects of abiotic and biotic factors: including those related to human presence and the effect of potential competitor species.

MATERIALS AND METHODS

Study area

The study was carried out in the Ischigualasto-Talampaya World Heritage Site. This comprises 2 contiguous conservation units, Ischigualasto Provincial Park and Talampaya National Park, located in San Juan and La Rioja provinces respectively, in north-western Argentina (29º 55´ S, 68º 05´ W). 2 villages some 10-20 km from the protected areas are major sources of cattle and donkeys. Parks have a total area of 275,369 ha and extend along eastern foothills of Central Andes at a mean altitude of 1,300 m.a.s.l. Climate is typical of dry desert with a mean annual temperature below 18ºC (range -10º–45ºC) and a mean temperature in the hottest month above 22ºC. Mean annual precipitation ranges from 80 to 140 mm, concentrated in summer (November to February).

Monte Desert is the dominant biome (Marquez et al. 2005). Predominant vegetation is sparse shrubland, dominated by species of Zygophyllaceae (*Larrea* spp, *Zuccagnia punctata*, *Bulnesia retama* and *Plectrocarpa tetracantha*), Fabaceae (*Prosopis* spp, *Cercidium praecox*, *Geoffroea decorticans*, *Senna aphylla*, *Ramorinoa girolae*) and Chenopodiacae (*Atriplex* spp and *Suaeda divaricata*). Cacti (*Echinopsis* spp, *Tephrocactus* spp and *Opuntia sulphurea*) and Bromeliads (*Deuterocohnia longipetala* and *Tillandsia* spp) are also frequent but to a lesser extent. Total plant cover is less than 20%, with a very sparse and seasonal herbaceous layer (Acebes et al. in press).

Herbivore data

We employed the pellet-group count technique (Neff 1968) in order to estimate distribution and abundance of the different species. In particular, we used the ‘standing-crop method’, a count of pellet groups within sample plots in the first visit. This method is suitable for arid zones, where ungulate densities are low (Putman 1984). Bleached pellet groups were ignored, to ensure that counts reflected recent presence (Henley et al. 2007). There is ample evidence that dung counts are more reliable than aerial or ground counts when used to estimate relative habitat use (Young et al. 2005, Cromsigt et al. 2009), particularly in arid environments (Henley et al. 2007).

A total of 14 line transects 5 km long were established during 2005 and 2006 taking in the maximum possible environmental diversity. GPS-georeferenced circular plots of 15m radius were established at minimum intervals of 300m along each transect. The circular plots totalled 219 since the difficult terrain made sampling incomplete. Abundance of guanaco, donkey and cattle dung was recorded within each plot. Scattered pellets were scored as 1, dung heaps as 2 and guanaco latrines and accumulated dung heaps from donkeys or cattle scored 3. This scale amounts to an approximate logarithmic transformation of the number of pellets, given that individual pellet counts are impossible in medium-sized or large dung piles.

Explanatory variables

The following environmental variables were measured in each circular plot: gradient (º), plant cover (%) and extent of rock or bare ground (%). Mean and maximum vegetation heights (m) were estimated and principal plant species, second commonest species, and other plants present were recorded. Predictor variables were calculated using ArcGIS 9.2 software on existing maps. These were the Normalized Difference Vegetation Index (NDVI) using Landsat 7 ETM+ images for a buffer zone of 50m radius around each circular plot (named 'NDVI' hereafter), and minimum distance from each circular plot to a village ('distance from villages'), a small permanent spring ('distance from springs') and to a seasonal watercourse ('distance from swc'), where densest formations of *Prosopis chilensis* and *P. flexuosa* of the study area occurred. Distances to roads ('distance from roads'), which are used by tourists, village inhabitants and potential illegal hunters, and to tracks ('distance from tracks'), used by tourists and park wardens to visit and move around protected areas respectively, were also measured.

A prior analysis of cross-correlations was employed to reduce the number of original predictor variables and to avoid colinearity between them. The resulting redundant variables (i.e. extent of bare ground, mean vegetation height) were omitted from subsequent analyses.

Patterns of co-occurrence and abundance between species

Co-occurrence of species-pairs was analyzed by means of a C-score index (Stone and Roberts 1990), a measure of tendency for species not to coincide in the same plot. High values indicate low co-occurrence (greater segregation) between pairs of species. The significance of the observed C-scores was evaluated by means of null models in which the presence of 2 species was assigned randomly to the plots, keeping the total number of occurrences of each species constant. Statistically significant values ($p<0.05$) of observed C-scores higher than simulated C-scores indicate segregation, while lower ones indicate co-occurrence. Analysis employed Monte Carlo simulations (9,999 iterations) using EcoSIM 7.0 program (Gotelli and Entsminger 2001).

Correlation of occurrence and abundance for the 3 species was evaluated by means of partial Mantel test, in order to remove the spatial effect that may determine co-occurrence patterns between species (Manly 2007). Presence and abundance of each species in each circular plot were employed as response matrices and geographical location of each plot was taken as the control matrix. Analyses of occurrence used Jaccard distance matrices and those of abundance used Euclidean distance matrices. The said matrices represent the differences between pairs of occurrence/abundance observations of species-pairs and the geographical distance between their locations. Significance testing employed a randomisation approach with 9,999 permutations, via PASSaGE v.2 program (Rosenberg 2008).

Modelling species patterns

Generalized Linear Models were used to examine relationship between occurrence/abundance for each species and different predictor variables, assuming a binomial error distribution and a logit link function for presence/absence data and a Poisson error distribution and a log link function for abundance data (McCullagh and Nelder 1989). Presence/absence of potentially competing species was introduced as a categorical predictor, the other variables serving as continuous predictors. Occurrence models allow the area occupied by species to be evaluated whereas abundance models inform on their preferences in particular areas. These 2 analytic approaches were chosen given that the environmental factors that influence species abundance may differ from those that limit their distribution (Nielsen et al. 2005). Continuous predictor variables were square-root or log-transformed to fulfil the assumption of normality.

Floristic composition variables were reduced by means of a Principal Component Analysis intended to obtain independent components capable of straightforward interpretation, avoiding colinearity problems revealed by initial exploratory analyses. In them, principal species was assigned 50% of total plant cover for each circular plot, the second-dominant receiving 30% and the combined remaining species 10%. Differences in the predictor variables between guanaco, donkey, cattle and all plots together were examined by means of unifactorial ANOVAs. Tukey´s honest significant difference test for unequal samples was used, *a posteriori*, to compare pairs of means.

Approximation to model averaging described by Burnham and Anderson (2002) was employed in order to take such model uncertainty into account, allowing a final model to be constructed in which parameters for each variable are averaged across all candidate models. All possible models were thus ranked sequentially according to Akaike's second order information criterion (AIC_c). Selection of candidate models followed the rule proposed by Burnham and Anderson (2002), in which those where $\Delta_i \leq 2$ have substantial empirical support. See Gray et al. (2009), and McAlpine et al. (2008) for a similar approximation. The accuracy and fit of presence models were quantified in terms of the area under the ROC curve (AUC). AUC values greater than 0.7 indicate high model accuracy (Swets 1988).

RESULTS

The most widespread (most frequently encountered) of 3 herbivore species was guanaco (in 40.2% of plots), followed by cattle (36.5%) and donkey (27.9%). Table 1 gives values of predictor variables in those plots in which guanaco, donkey and cattle were recorded as well as for the whole set of sampled plots. In general, NDVI and plant cover values in plots where guanacos were present were similar to availability but lower than in those where domestic herbivores occurred. In contrast, rock surface cover and gradient were much greater in plots with guanacos than in those with a presence of donkeys and cattle. In addition, livestock species were more often detected near to watercourses and to roads.

Table 1. Untransformed values of the predictor variables (Means±SD) in plots where guanaco (n=88), donkey (n=61) and cattle (n=80) were present and in all the sampled plots combined (n=219). The plant cover variable has been included since it is simple to interpret, despite its elimination from model averaging on account of being strongly correlated with the NDVI. Swc=seasonal watercourses. The different superscripts indicate significant differences in Tukey post hoc comparisons between groups of observations.

Variable	Guanacos	Donkeys	Cattle	Total plots
NDVI	0.10 ± 0.02^{a}	0.11 ± 0.03^{b}	0.11 ± 0.02^{b}	0.10 ± 0.03^{a}
Plant cover	15.39 ± 14.43^{a}	25.11 ± 21.49^{b}	$22.86\pm18.87^{b,c}$	$17.32\pm17.05^{a,c}$
Maximum plant height	2.63 ± 1.08^{a}	2.89 ± 1.22^{a}	3.04 ± 1.21^{a}	2.69 ± 1.11^{a}
Rock cover	62.15 ± 32.58^{a}	33.95 ± 36.84^{b}	32.53 ± 35.61^{b}	46.71 ± 37.61^{b}
Gradient	8.81 ± 9.60^{a}	3.51 ± 4.61^{b}	3.18 ± 4.19^{b}	6.82 ± 9.08^{a}
Distance from swc	2.15 ± 2.82^{a}	0.48 ± 0.43^{b}	$0.82\pm0.81^{b,c}$	$1.55\pm2.41^{a,c}$
Distance from springs	5.81 ± 3.83^{a}	6.17 ± 4.95^{a}	8.75 ± 6.07^{b}	6.89 ± 4.98^{b}
Distance from tracks	3.24 ± 2.61^{a}	3.34 ± 2.51^{a}	3.76 ± 2.46^{a}	3.38 ± 2.51^{a}
Distance from roads	9.91 ± 6.72^{a}	4.38 ± 5.04^{b}	$5.84\pm5.77^{b,c}$	$7.87\pm6.23^{a,c}$
Distance from villages	27.25 ± 10.33^{a}	19.68 ± 9.24^{b}	$23.92\pm10.62^{a,b}$	24.53 ± 10.14^{a}

Patterns of co-occurrence and abundance among species

The C-score index results showed that number of coincidences between guanacos and both exotic species were significantly lower than expected from a null model ($p<0.05$). This indicates segregation between guanacos and exotic species, whereas donkeys and cattle co-occurred to a significant extent ($p<0.001$) (Table 2). However, partial Mantel test results showed that, after removing geographical effect, there was no correlation between guanacos and exotic species in either occurrence or abundance. In contrast, there was a significant positive correlation ($p<0.05$) between donkeys and cattle for both types of data.

Table 2. Correlation coefficients (r_M) and significance (*p*) of partial Mantel tests for paired observations of co-occurrence and abundance, controlling for geographical effects. Pairwise co-ocurrence patterns of large herbivores are compared using C-scores from null-model. High values indicate low co-occurrence in species-pairs. Superscripts indicate significant differences between observed and simulated C-scores. Negative superscripts indicate separation and positive superscripts indicate co-occurrence.

	Partial Mantel test				C-score index
	Occurrence		Abundance		
Guanacos – donkeys					
	r_M	- 0.039	r_M	- 0.027	1836^{-}
	p	0.083	*p*	0.449	
Guanacos – cattle					
	r_M	- 0.045	r_M	- 0.027	2144^{-}
	p	0.087	*p*	0.420	
Donkeys - cattle					
	r_M	0.283	r_M	0.102	684^{+}
	p	0.001	*p*	0.035	

Modelling species patterns

Single-best models received only limited support relative to alternative models of occurrence and abundance of guanaco, donkey and cattle, and Akaike weights differed slightly between single-best models and second-ranked models. Both circumstances indicate substantial uncertainty in choosing a single model and hence model averaging is appropriate (Burnham and Anderson 2002).

Guanacos

Model selection process for guanaco suggested that 13 occurrence models and 4 abundance models were regarded as plausible. Rock surface cover and distance from nearest village were given most weight in the process of selecting occurrence models for guanaco ($w_i=1$), having positive values. In short, areas occupied by guanacos are characterized by having rocky substrata and being far from villages. The greater presence of guanacos in plots furthest from seasonal watercourses was another robust finding (w_i>0.8) (Table 3).

Abundance models confirmed and complemented occurrence models, refining the occupation pattern. 3 types of variables greatly influenced guanaco abundance (Table 3). Guanacos were less abundant in plots where donkeys were present (w_i=1), in contrast to what was shown by occurrence models. Secondly, an array of variables (w_i=1 in all cases), both physical (rocky areas, of shallower gradient, close to springs but remote from seasonal watercourses) and biotic (zones with higher NDVI values, although avoiding tall vegetation), were of great significance to guanaco abundance. The latter seem to indicate selection with respect to trophic availability and predator avoidance. Finally, there was another important variable related to human activity: guanaco was most abundant far from villages (w_i>0.8). In contrast, cattle presence, and distance from roads and tracks, had no relevance both to models of occurrence or abundance (w_i<0.2). The 2 floristic composition PCA axes did not figure in the models.

Table 3. Results of model averaging inference for the probability of occurrence and abundance of guanaco. Model-averaged parameter estimates (*β*) and the unconditional standard errors (*SE*) of the variables obtained are given. Σw_i represents the weight of each variable across all the selected models.

Guanaco	**Occurrence**			**Abundance**		
Predictor	Σw_i	***β***	***SE***	Σw_i	***β***	***SE***
Intercept		-16.661	2.059		-4.349	3.048
Distance from villages	1.000	1.326	0.175	0.822	0.490	0.268
Rock cover	1.000	0.644	0.151	1.000	0.536	0.094
Distance from swc	0.840	0.218	0.130	1.000	0.19	0.087
Distance from tracks	0.236	-0.044	0.049			
Cattle presence	0.131	0.020	0.030	0.187	0.018	0.030
Distance from springs	0.075	-0.012	0.019	1.000	-0.261	0.116
Distance from roads	0.072	0.014	0.023	0.198	0.022	0.032
Maximum plant height	0.063	-0.019	0.037	1.000	-1.321	0.296
Donkey presence	0.060	0.006	0.013	1.000	-0.267	0.126
NDVI	0.056	0.109	0.374	1.000	7.621	3.813
Gradient	0.056	-0.008	0.029	1.000	-0.647	0.27

Feral donkeys

Seven occurrence models and 15 abundance models were selected as plausible for donkeys and both model types showed a high degree of coincidence. One group of variables was of great importance in both cases: presence of the other exotic species, proximity to springs and roads, avoidance of rocky substrata and attraction to areas of greater NDVI (w_i=1). In contrast, proximity to watercourses was important to donkey occurrence (w_i=1) but not to their abundance (Table 4). Similarly, avoidance of steep gradients was relevant to abundance models (w_i>0.55) but not to presence (Table 4).

Guanaco presence and distance from tracks or villages were unimportant to the averaged models (w_i<0.15). Once again, the 2 floristic composition PCA axes did not figure in the models.

Table 4. Results of model averaging inference for the probability of occurrence and abundance of donkey. Model-averaged parameter estimates (*β*) and the unconditional standard errors (*SE*) of the variables obtained are given Σw_i represents the weight of each variable across all the selected models.

Donkey	**Occurrence**			**Abundance**		
Predictor	Σw_i	***β***	***SE***	Σw_i	***β***	***SE***
Intercept		19.465	4.42		7.939	1.471
Distance from springs	1.000	-1.385	0.33	1.000	-0.628	0.115
NDVI	1.000	21.012	8.669	1.000	8.832	3.7
Rock cover	1.000	-0.526	0.16	1.000	-0.18	0.07
Cattle presence	1.000	0.95	0.233	1.000	0.457	0.11
Distance from roads	1.000	-0.843	0.218	1.000	-0.443	0.084
Distance from swc	1.000	-0.357	0.17	0.041	0.001	0.003
Gradient	0.130	-0.081	0.12	0.563	-0.344	0.254
Maximun plant height	0.124	-0.072	0.111	0.310	0.31	0.148
Guanaco presence	0.103	0.011	0.027	0.045	0.002	0.006
Distance from villages	0.102	-0.034	0.078	0.093	0.02	0.037
Distance from tracks	0.098	-0.008	0.021	0.149	0.02	0.024

Free ranging cattle

There were 55 plausible occurrence models and 9 for abundance. Avoidance of steep gradients, use of areas of high NDVI remote from villages and donkey presence (Table 5) were shared important variables in both model types. In addition, other variables of lesser importance that figured in occurrence models were choice of areas of taller vegetation (w_i>0.7) and proximity to seasonal watercourses (w_i>0.5). Variables that stood out in abundance models were preference for areas further from tracks (w_i=1), avoidance of rocky substrata, dependence on water sources and proximity to roads (Table 5). Guanaco presence had little weight in the 2 averaged models (w_i<0.1) and the 2 floristic composition PCA axes did not figure in the models.

DISCUSSION

This study analyses the role of biotic and abiotic interactions in determining the spatial occupation and abundance patterns of 3 ungulate species, one native and 2 exotics. We describe co-occurrence of the exotics and the apparent lack of interference to native species occupation, although guanaco abundance may be affected by feral donkey presence. Furthermore, the nature of interaction between guanaco and exotic species varies from no relationship (according to Mantel test) to segregation (according to null models), but always showing little overlap between them. In contrast, significant overlap between donkeys and cattle occur irrespective of the analytical tools employed. In addition, human influence determines occupation and abundance patterns of guanaco.

Table 5. Results of model averaging inference for the probability of occurrence and abundance of cattle. Model-averaged parameter estimates (*β*) and the unconditional standard errors (*SE*) of the variables obtained are given Σw_i represents the weight of each variable across all the selected models.

Cattle	**Occurrence**			**Abundance**		
Predictor	Σw_i	***β***	***SE***	Σw_i	***β***	***SE***
Intercept		-15.417	6.159		-10.210	3.051
Distance from villages	1.000	1.000	0.713	1.000	1.086	0.358
Gradient	0.981	-1.929	0.692	1.000	-1.347	0.370
NDVI	0.917	16.172	7.799	1.000	13.218	3.289
Maximum plant height	0.763	0.763	0.578	0.150	0.042	0.060
Donkey presence	0.731	0.818	0.205	1.000	0.265	0.101
Distance from swc	0.555	-0.156	0.114			
Distance from tracks	0.523	0.181	0.139	1.000	0.277	0.116
Rock cover	0.490	-0.106	0.085	0.690	-0.095	0.056
Distance from roads	0.436	-0.188	0.150	0.770	-0.180	0.106
Distance from springs	0.214	-0.075	0.081	0.525	-0.107	0.088
Guanaco presence	0.012	0.002	0	0.079	0.006	0.010

Species interactions

Our results reveal an important departure from our initial hypothesis. We predicted that, given their feeding styles (intermediate feeder-grazers) and body weights, and the scarcity of trophic resources, the 3 species would overlap spatially, and so would be potential competitors. However, analyses of spatial co-occurrence show that both presence and abundance of guanacos are not correlated with presence or abundance of the 2 introduced species. Ecological theory predicts that competition requires overlap between spatial and trophic resources and, furthermore, that the latter should be scarce (Putman 1996, Prins and Olff 1998, Voeten and Prins 1999, Hulbert and Andersen 2001). In the absence of spatial overlap, therefore, no potential competition occurs even if trophic resources are limited (Voeten and Prins 1999). Lack of overlap may be due to low density of guanacos (0.1–0.7 individuals/km^2, Acebes et al. 2010) and the even lower ones of donkeys and cattle (own unpublished data), but there may be other causes (see below). This finding also avoids problems arising from our methodology (counting pellet groups within sample plots in the first visit) since had there been spatial overlap we would have been unable to discriminate whether this was as a result of simultaneous or asynchronous co-occurrences. However, our methodology was unable to detect interference competition (i.e. one species denies resources to another by means of aggressive behaviour); nevertheless we have no evidence of such competition from personal observation, and is scarcely relevant in herbivores (Prins 2000, Hulbert and Andersen 2001).

In contrast to the situation regarding guanacos, exotic species overlapped spatially with each other, as other authors have found in cold-arid regions of Asia (Bagchi et al. 2004). Overlap in areas of occupation (occurrence models) is more marked than in areas of preferential use (abundance models). This may be due to asynchronous occupation, as noted above, but does not seem to be the case since donkeys and cattle were often seen together (pers. obs.). Differences between their occurrence and abundance patterns suggest slight differences in degrees of resource utilisation.

Modelling occurrence and abundance patterns

Employment of both occurrence and abundance models is informative and complementary (Nielsen et al. 2005). The most significant results of occurrence models were i) definition of distinct occupation patterns of guanaco and exotic species; ii) association between the 2 exotics in accordance with earlier findings; and iii) absence of any effect of exotics on the occurrence of native species. For their part, abundance models refined occupation patterns of the 3 species, maintaining association between the 2 exotics, but being guanaco abundance lower in the presence of donkey.

Guanaco occurrence patterns showed a tendency to avoid rural settlements as a response to human pressure, keeping guanacos inside parks, which enhances the relevance of protected areas in wildlife conservation. Evolutionary factors explain why guanaco keeps away from seasonal watercourses where strips of arboreal formations are found, due to its preference for open habitats (Bank et al. 2003). Their preference for rocky substrata over sandy sites may relate to locomotory needs linked to guanacos' cushion hoof soles, but no data exists to compare these results with.

Abundance model allowed ecological and evolutionary preferences of guanaco to be defined more precisely. Guanaco showed preferences for areas offering a trade-off between trophic resources availability and high visibility to detect their predator, the puma (*Puma concolor*) (Franklin 1983, Bank et al. 2003). As in other ungulates like elk *Cervus elaphus* **(**Clair and Forrest 2009**)** guanaco occurrence and abundance were unrelated to distance tourist circuit, suggesting that vehicular traffic does not change spatial patterns of guanaco. However, guanacos showed a tendency to keep away from roads, as is they were poached (Wilkie et al. 2000).

A lower abundance of guanacos in the presence of donkeys suggests these interpretations: (i) differences in habitat selection; (ii) competition resulting in the native species displaced by exotics and; (iii) a combination of both effects. Stewart et al. (2002) thus showed resource partitioning between cattle and 2 native herbivores, explained as competitive displacement of the natives by exotic species. In contrast, Sitters et al. (2009) recently found spatial redistribution between cattle and native herbivores without being any evidence of displacement; different ecological requirements explained as responsible. In other circumstances they found cattle and native herbivores coexisting at high densities without the latter being adversely affected. Guanaco occurs in nearly all habitats (Acebes et al. 2010), and prefers slightly different ones than donkey (Table 1), although the latter may force guanaco to make lesser use of certain habitats. Therefore, an increase in donkey density may increase likelihood of spatial overlap between species, leading to exploitation competition (Putman 1996, Owen-Smith 2002).

Differences between patterns of occurrence and abundance in guanacos are explained in terms of their social behaviour and reproductive strategies, which have implications on the use of spatial and trophic resources, as other polygyny ungulates (Clutton-brock et al. 1982). Guanaco shows a resource defence polygyny mating system (Franklin 1983) in which territorial males seek habitats favourable for attracting females (Emlen and Oring 1977). Territorial family harems are spatially stable, but guanaco social unit also includes non-breeding male groups and solitary males (Franklin 1983) which are more mobile than family groups. Family groups thus acquire more weight in abundance models since they concentrate higher densities of animals and have a large number of latrines within their territories. On the other hand, solitary males and male groups are highlighted in occurrence models since they show more scattered defecation patterns.

Factors defining occurrence and abundance of exotic species did not coincide with those of guanaco, revealing differences in their ecological requirements. Unlike guanaco, both exotic species were most abundant where plant productivity was greatest. Donkeys generally include springs in its territories (Saltz et al. 2000), as models showed. Tendency for cattle to appear far from springs matches what Sitters et al. (2009) have recently described and is related to livestock management as well as to lower trophic availability near springs due to overgrazing (Owen-Smith 2002, Sitters et al. 2009). Proximity to seasonal watercourses represents cattle greater dependency on trophic and water resources. Stewart et al. (2002) found that cattle choose areas near to water sources and riparian habitats, avoiding steep locations. Future studies should focus on potential for competition on springs, since they represent the scarcest resources in drylands. Finally, introduced herbivores are more closely linked to humans, as revealed by their closer proximity to rural settlements (donkeys) or to roads (donkeys and cattle), even using the latter for moving about their territories (P.A. pers. obs).

To conclude, our analyses of co-occurrence show no evidence of overlap between guanacos and exotic ungulates. Nevertheless, abundance models suggest that increases in the densities of feral donkeys alter this situation, having a negative impact on guanaco. Management policies for controlling exotic herbivores are thus recommended in locations with higher densities. In addition, human presence clearly influences guanaco distribution appearing in areas furthest from rural settlements. These results can be extrapolated to other drylands of Argentina, Chile and Peru, where guanaco co-occurs with feral donkeys close to human activities.

REFERENCES

Acebes P, Traba J, Malo JE, Ovejero R and CE Borghi. 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, Peco B, Reus L, Giannoni SM and Malo JE (in press). Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert. Revista Chilena de Historia Natural.

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

Baldi R, Albon S and Elston D. 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 B, Lichtenstein G, González B, Funes M, Cuéllar E, Villalba L, Hoces D and Puig S. 2008. Lama guanicoe. En: IUCN 2010. IUCN Red List of Threatened Species. <www.iucnredlist.org>

Bank MS, Sarno RJ and Franklin WL. 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biological Conservation 112: 427-434.

Burnham KP and Anderson DR. 2002. Model selection and multimodel inference: a practice information-theoretic approach. Spring Verlag, New York.

Clair CC and Farrest A. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, Cervus elaphus. Behaviour 146: 393-413.

Clutton-brock TH, Guinness FE and Albon SD. 1982. Red deer. Behavior and Ecology of Two Sexes. Edinburgh University Press, Edinburgh.

Connell JH. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138.

Cromsigt JPGM, Prins HHT and Olff H. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. Diversity and Distributions 15: 513-522.

Emlen ST and Oring LW. 1977. Ecology, Sexual Selection and the Evolution of Mating Systems. Science 197: 215-223.

Franklin WL. 1983. Contrasting socioecologies of South American's wild camelids: the vicuña and guanaco. En: Eisenberg JF y Kleiman DG (eds). Advances in the Study of Mammalian Behavior. Pp. 573-629. Special Publication No. 7. American Society of Mammalogists, Allen Press, Lawrence, Kansas.

Fritz H, de Garine-Wichatitsky M and Letessier G. 1996. Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. Journal of Applied Ecology 33: 589-598.

Gotelli NJ and Entsminger GL. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Incorporation and Kesey-Bear. URL: http://homepages.together.net/~gentsmin/ecosim.htm

Gray TNE, Borey R, Hout SK, Chamman H, Collar NJ and Dolman PM. 2009. Generality of models that predict the distribution of species: Conservation activity and reduction of model transferability for a threatened bustard. Conservation Biology 23: 433-439.

Grinder MI, Krausman PR and Hoffmann RS. 2006. Equus asinus. Mammalian Species 794: 1-9.

Henley SR, Ward D and Schmidt I. 2007. Habitat selection by two desert-adapted ungulates. Journal of Arid Environments 70: 39-48.

Hulbert IAR and Andersen R. 2001. Food competetion between a large ruminant and a small hindgut fermentor: the case of the roe deer and mountain hare. Oecologia 128: 499-508.

Márquez J, Martínez Carretero E, Dalmasso A, Pastrán G y Ortiz S. 2005. Las áreas protegidas de la provincia de San Juan (Argentina) II. La vegetación del Parque Provincial de Ischigualasto. Multequina 14: 1-27.

Manly BFJ. 2007. Randomization, Bootstrap and Monte Carlo Methods in Biology. 3rd ed. Chapman and Hall, London.

McAlpine CA, Rhodes JR, Bowen ME, Lunney D, Callaghan JG, Mitchell DL and Possingham HP. 2008. Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. Journal of Applied Ecology 45: 558-567.

McCullagh P and Nelder JA. 1989. Generalized Linear Models. Chapman and Hall, New York.

Mishra C, Van Wieren SE, Ketner P, Heitkönig IMA and Prins HHT. 2004. Competition between domestic livestock and wild bharal Pseudois nayaur in the Indian Trans-Himalaya. Journal of Applied Ecology 41: 344-354.

Morris DW and Davidson DL. 2000. Optimally foraging mice match patch use with habitat differences in fitness. Ecology 81: 2061-2066.

Neff DJ. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. Journal of Wildlife Management 32: 597-614.

Nielsen SE, Johnson CJ, Heard DC and Boyce MS. 2005. Can models of presence-absence be used to scaled abundance? Two case studies considering extremes in life history. Ecography 28: 1-12.

Novillo A and Ojeda RA. 2008. The exotic mammals of Argentina. Biological Invasions 10: 1333-1344.

Owen-Smith N. 2002. Adaptative herbivore ecology. From resources to populations in variable environments. Wits University Press, Johannesburg.

Prins HHT. 2000. Competition between wildlife and livestock in Africa. En: Prins HHT, Grootenhuis JG and Dolan TT (eds). Wildlife conservation by sustentable use. Pp. 51-80. Kluwer Academic Publishers, Boston.

Prins HHT and Olff H. 1998. Species richness of African grazer assemblages: towards a functional explanation. In: Newbery D, Prins HHT and Brown ND. Dynamics of tropical communities (eds). Pp. 448-490. Blackwell, Oxford.

Puig S, Videla F, Cona MI and Monge A. 2001. Use of food availability by guanacos (Lama guanicoe) and livestock in northern Patagonia (Mendoza, Argentina). Journal of Arid Environments 47: 291-308.

Putman R J. 1984. Facts from faeces. Mammalian Reviews 14: 79-97.

Putman RJ. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London.

Raedeke K. 1979. Population dynamics and socioecology of the guanaco (Lama guanicoe) of Magallanes, Chile. PhD dissertation, College of Forest Resources, University of Washington, Washington, USA.

Rosenzweig ML. 1981. A theory of habitat selection. Ecology 62: 327-335.

Saltz D, Rowen M and Rubenstein DI. 2000. The effect of space-use patterns of reintroduced asiatic wild ass on effective population size. Conservation Biology 14: 1852-1861.

Sarno RJ, Bank MS, Stern HA and Franklin WL. 2003. Forced dispersal of juvenile guanacos (Lama guanicoe): causes, variation, and fates of individuals dispersing at different times. Behavioral Ecology and Sociobiology 54: 22-29.

Shrestha R and Wegge P. 2008. Habitat relationships between wild and domestic ungulates in Nepalese trans-Himalaya. Journal of Arid Environments 72: 914-925.

Sitters J, Heitkönig IMA, Holmgren M and Ojwang GSO. 2009. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. Biological Conservation 142: 738-750.

Stewart KM, Bowyer RT, Kie JG, Cimon NJ, and Johnson BK. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83: 229-244.

Suryawanshi KR, Bhatnagar YV and Mishra C. 2010. Why should a grazer browse? Livestock impact on winter resource use by bharal Pseudois nayaur. Oecologia 162: 453-462.

Swets JA. 1988. Measuring the accuracy of diagnostic systems. Science 240: 1285-1293.

Voeten MM and Prins HHT. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120: 287-294.

Young TP, Palmer TM and Gadd ME. 2005. Competition and compensation among cattle, zebras and elephants in a semi-arid savanna in Laikipia, Kenya. Biological Conservation 122: 351-359.

Wilkie D, Shaw E, Rotberg F, Morelli G and Auzel P. 2000. Roads, development, and conservation in the Congo Basin. Conservation Biology 14: 1614-1622.

CAPÍTULO V.

Selección de hábitat del guanaco: abundancia de recursos *versus* riesgo de depredación

Desentrañando los factores principales involucrados en la selección de hábitat del guanaco: disponibilidad de alimento, comportamiento antidepredatorio, tamaño de grupo y estacionalidad.

RESUMEN

La selección de hábitat de los ungulados está determinada tanto por la cantidad, calidad y distribución de los recursos tróficos, como por los riesgos de depredación. Dicha selección puede también variar en función de las distintas estrategias reproductivas y de la organización social de las especies. El guanaco (Lama guanicoe) es un camélido sudamericano silvestre monomórfico típico de medios abiertos áridos y semiáridos, ideal para evaluar estas respuestas comportamentales, ya que la práctica totalidad de estudios se han realizado con ungulados dimórficos. Durante la estación húmeda-reproductiva (2005, 2006 y 2007) y seca (2005 y 2006) se realizaron recorridos en el Parque Provincial Ischigualasto y su entorno (San Juan, Argentina) anotando el tamaño de grupo y la estructura social de los avistamientos de guanaco realizados. Para cada observación de guanacos (N=114) y un número equivalente de controles aleatorios se calcularon 5 variables a partir de información procedente de imágenes de satélite que reflejaban productividad vegetal y morfología del terreno. El tamaño de los grupos no varió entre estaciones ni años (K-W test, $p>0.05$). No se encontraron diferencias en el uso de hábitat entre unidades sociales pero sí entre estaciones (MANOVA test, $p<0.05$), siendo preferidas durante la estación húmeda (reproductiva) las zonas menos productivas y con menor pendiente. El análisis específico para los grupos familiares mostró el mismo patrón, no viéndose modificado por la ratio crías/adultos, pero sí por el tamaño de grupo (MANCOVA test, $p<0.05$). Respecto a la totalidad del habitat disponible, los guanacos seleccionaron preferentemente zonas con escasa pendiente, no registrándose diferencias en la productividad vegetal. Estos resultados muestran la estabilidad en la organización social del guanaco, a diferencia de la mayoría de los ungulados con un marcado dimorfismo sexual. La ausencia de diferencias en el uso del hábitat entre las distintas unidades sociales, tratándose de una especie que exhibe un sistema de apareamiento basado en la defensa de recursos, sugiere que este pueda modificarse hacia un sistema de apareamiento basado en la defensa de hembras, dada la escasez de recursos tróficos y los elevados costes de defender territorios con poco alimento. Por último, nuestros resultados apuntan a que en el compromiso entre maximizar los beneficios de forrajeo y reducir el riesgo de depredación, los guanacos se inclinan por disminuir este último, aunque sea a costa de ocupar zonas minimamente productivas en las que satisfacer sus necesidades energéticas.

Disentangling the main factors involved in habitat selection of polygynous guanacos: food availability, antipredator behavior, group size and seasonality.

Acebes P, Traba J and Malo JE. Disentangling the main factors involved in habitat selection of polygynous guanacos: food availability, antipredator behavior, group size and seasonality *(Manuscrito enviado)*.

ABSTRACT

Habitat selection by ungulates is determined by the quantity, quality and distribution of trophic resources as well as by risks of predation. It may also vary in relation to species-specific reproductive strategies and social organization. The guanaco (*Lama guanicoe*), a monomorphic wild camelid typical of arid and semiarid open spaces, is ideal for evaluating behavioral responses of this type. Surveys were made during both the dry and wet seasons of 2005–2007 in and around Ischigualasto Provincial Park, San Juan, Argentina, during which the group size and social structure of guanaco groups sighted were recorded. Remote sensing data was used to calculate five variables that reflected trophic availability and terrain morphology for each guanaco group (N=114) and for an equivalent number of random controls. No differences in group size were detected either between seasons or years (K-W test, $p>0.05$). Habitat use did not differ between types of social groups but differed between seasons (MANOVA test, $p<0.05$). Guanacos use less productive but less steep areas during the wet (breeding) season, irrespective of juvenile:adult ratios in the case of family groups but smaller groups occupy more level areas (MANCOVA test, $p<0.05$). With respect to availability, guanacos preferred areas of limited gradient but no differences were noted relating to plant productivity. The results suggest that the usual mating system of the species, which is based on resource defence, is modified towards a female polygyny mating system due to the scarcity of trophic resources and the high cost of defending territories that offer little food. We also show that habitat selection in the guanaco prioritizes reducing the risks of predation to the extent that the animals occur in areas offering the minimum productivity capable of meeting their energy requirements.

Key words: antipredator behaviour, deserts, foraging niche, mating systems, NDVI, social organization, South America, ungulates.

INTRODUCTION

Populations of large herbivores are generally regulated via top-down mechanisms such as predation (Sinclair et al. 2003, Hopcraft et al. 2010) and by bottom-up constraints in primary production (McNaughton et al. 1989, Hopcraft et al. 2010). Large herbivores may face changes in resource availability or predation with behavioral responses (Sinclair and Arcese 1995, Kie 1999), which may affect demographic parameters (Creel et al. 2007). Such mechanisms operate differently within species according to their type of social organization (Jarman 1974).

Predation risk effects when a prey alter its behaviour in response to predators carry costs. In deed, risk effects can be larger thar direct effects of predation, even the direct rate of predation is zero (Creel and Christianson 2008). It is generally accepted that selection will favor individuals that optimally balance the benefits of risk reduction against its costs (Lima 2002). Behavioral responses to reduce predation risk (Lima 1998) include changes in habitat use (Creel et al. 2005) or in group size (Creel and Winnie 2005) given that perception of predation risk is lower in larger groups (Lima and Dill 1990). The response may also differ between sexes (Winnie and Creel 2007), males usually seeking habitats offering high trophic availability whereas females with offspring select habitats that firstly offer security agaist predators and secondly provide abundant forage (Main et al. 1996, McCullough 1999). Thus, habitat selection to maximize reproductive fitness represents a trade-off between maximizing foraging opportunities and minimizing predation risk (Kie 1999, McCullough 1999).

The guanaco (*Lama guanicoe* Müller), a highly social medium-sized South American ungulate, is sexually monomorphic in body size and exhibits a resource defense polygyny mating system (Franklin 1983). Three types of groups may be encountered during the breeding season (González et al. 2006): family groups (i.e. a territorial male with adult females and their offspring), groups of non-territorial males and solitary territorial males that are seeking or defending a territory without females. The guanaco inhabits arid and semi-arid zones thus making it an ideal species for analyzing the trade-off between resource availability and predation risk as a function of of its social organization, since most of studies have done in temperate ecosystems (Kunkel and Pletscher 2000, Pierce et al. 2004, Creel et al 2005, Theuerkauf and Rouys 2008). This is particularly so if it is borne in mind that most studies and hypotheses in this field have involved dimorphic ungulates, which show marked sexual segregation (Main et al. 1996, Ruckstuhl and Neuhaus 2000).

Remote sensing has become an invaluable tool for ecologists in this field, given that it allows plant abundance to be determined over extensive areas and helps understand herbivore dynamics (Kerr and Ostrovsky 2003) by informing on their distribution and movements patterns and performance (i.e. survival, reproduction or growth of their populations (Pettorelli et al. 2005, 2006). It is particularly useful where basic cartography is non-existent and fieldwork is difficult. The Normalized Difference Vegetation Index (NDVI) is especially useful due to the strong correlation between above-ground net primary productivity and absorbed photosynthetically active radiation (Kerr and Ostrovsky 2003). Digital elevation models allow topographical variables to be measured that serve as indicators of predation risk and of the escape terrain available to species (Sappington et al. 2007).

We here use field data and satellite-based methods: (i) to determine the guanaco social units in both the breeding and non-breeding seasons over three years in a hyperarid area of Argentina, where the main constraints are predation by pumas (*Puma concolor*) and food scarcity; (ii) to evaluate whether social units differ in habitat selection as a function of seasonal trophic availability and predation risk; and (iii) to determine whether any patterns depend on group size, the number of offspring and the yearling/adult ratio.

The hypotheses considered were: (H_1) The guanaco population will show year-long stability in its different social units due to its sedentary nature (Acebes et al. 2010). (H_2) There will be a different habitat selection between types of guanaco social organization: All-male groups and solitary males will occupy more productive zones than family groups, accepting a higher predation risk, given that they do not have calves (more vulnerable to predation), to maximize their body condition in order to gain access to reproduction (Main et al. 1996). (H_3) Habitat selection of family groups will be determine by the number of offspring and/or the higher the yearling/adult ratio, minimizing predation risk.

MATERIALS AND METHODS

Study area

The study was carried out in Ischigualasto Provincial Park, in San Juan province, north-western Argentina (29º 55´ S, 68º 05´ W), part of the Ischigualasto-Talampaya World Heritage Site together with Talampaya National Park (La Rioja province). The mean altitude is 1,300 m.a.s.l. The park comprises an area of 60,369 ha. The nearest village is 10 km from the park limit. The climate is dry desert with a mean annual temperature below 18ºC (range -10º–45ºC) and a mean temperature in the hottest month above 22ºC. Mean annual precipitation ranges from 80 to 140 mm, concentrated in summer (November to February). The puma (*Puma concolor*) is the sole predator of guanacos and occurs in low abundance in the park. During the studied period two pumas were sighted by park guards. There were also recorded several recent puma tracks and faeces, and two guanaco calves and one patagonian hare (*Dolichotis patagonum*) killed by pumas.

Monte Desert is the dominant biome (Marquez et al. 2005). The predominant vegetation is sparse shrubland, dominated by species of Zygophyllaceae (*Zuccagnia punctata*, *Larrea* spp. and *Bulnesia retama*), Fabaceae (*Prosopis* spp., *Geoffroea decorticans*, *Cercidium praecox*) and Chenopodiacae (*Atriplex* spp. and *Suaeda divaricata*). Cacti (*Tephrocactus* spp., *Opuntia sulphurea* and *Echinopsis* spp,) and Bromeliads (*Tillandsia* spp. and *Deuterocohnia longipetala*) are also frequent but to a lesser extent. Total plant cover is less than 20%, with a very sparse and seasonal herbaceous layer (Acebes et al. in press).

Guanaco data

The study was conducted during the wet seasons (February–March) of 2005, 2006 and 2007, when guanacos breed, and during the dry seasons (August) of 2005 and 2006. Two researchers with binoculars surveyed the protected area and its surroundings from roads, tourist routes and secondary tracks by vehicle, and secondarily on foot, covering 6700 km in total. The following were recorded when a solitary guanaco or a herd was sighted: (1) exact geographical location, using GPS, a laser telemeter and a precision compass; (2) group size; (3) social and age structure: the number of adult males and females, juveniles (yearlings > 1 and < 1.5 years old) and yearlings (up to one year old) and; (4) social unit: family group, male group, solitary male or mixed herds. Where animals were too distant for individuals to be identified they were approached on foot until this was possible. The local guanaco population is relatively small, fewer than 400 individuals (Acebes et al. 2010) so there was a chance that the same individual or group could be recorded more than once in the same season.

Habitat characteristics

Habitat variables that could be important to guanaco were obtained from a Landsat 7 ETM+ image, acquired on February 26 2002, and from an ASTER (Advanced Spaceborne Thermal Emission and Reflection Radiometer) digital elevation model (DEM). Both images had a resolution of 30×30 m. The NDVI was calculated from the red : near-infrared reflectance ratio (NDVI = [NIR - RED]/[NIR + RED]). We also used information derived from band 1 (0.45–0.52 mm) and band 5 (1.55–1.75 mm) of the same image. Band 1 discriminates between bare ground and vegetation (Kerr and Ostrovsky 2003): high values represent a high proportion of bare ground, giving additional information on forage abundance where ecosystem productivity is very low (Pettorelli et al. 2005). Band 5 is associated with soil moisture and vegetation (Kerr and Ostrovsky 2003): low values indicate high moisture, which may influence the quality of the plant forage available to herbivores (Olff et al. 2002).

Terrain gradient was obtained, and its ruggedness estimated, from the DEM. Ruggedness was determined by means of the ruggedness measure vector proposed by

Sappington et al. (2007). This is a more appropriate estimate than other indices since it is derived from aspect and not slope, allowing both to be independent variables in the analyses. The process employs a 3×3 pixel window moving over the terrain model. Index values range from 0 to 1, representing very smooth and very rough zones respectively. See Hansen et al. (2009) for a similar approach.

Habitat availability was analysed from two steps. In the first step, as many random points as there were guanaco sightings were established at random on the viewshed (obtained from the DEM) from all the roads and tracks prospected. In the second, given that 98% of guanaco observations fell within the protected zone, a new set of random points were established solely for the area that fell within the park. Habitat selection by guanaco is thus explained firstly in terms of availability within the entire prospected area and secondly within the park. The rationale is that the species' absence outside the protected area may be due to poaching and not to habitat characteristics. Five environmental variables (NDVI, band 1, band 5, slope and ruggedness) were determined in both estimates i.e. for each random point and guanaco observation. Spatial and remote sensing analyses employed ArcGIS 9.3 (ESRI, USA) and ERDAS IMAGINE 9.1 (Leica Geosystems) software.

Data analysis

The average value of each variable was calculated for all observations of the same individual or herd in the same season (min=1, max=5). The sample size of the 324 field sightings was thus reduced to 114, so avoiding pseudoreplication. Group size differences between seasons (breeding/non-breeding) and years (2005/2006/2007) were analysed via non parametric Mann-Whitney U and Kruskal-Wallis tests, respectively. Differences in the yearling/adult ratio between family groups were analysed by means of an ANOVA with season and year as factors.

A Principal Components Analysis (PCA) with the five environmental variables was carried out to obtain orthogonal variables (i.e. food availability and predation risk) that represent the bidimensional space in which guanaco habitat use occurs. A correlation matrix was chosen (based on variables standardized to zero mean and unit variance), which is necessary when variables are measured in very different units and the differences between variances are not the focus of the analysis (Quinn and Keough 2002). Multivariate analyses of variance (MANOVA) were employed to evaluate whether habitat use by different social units of guanaco varied as a function of season or year, using the first two components obtained from the PCA as response variables and the type of guanaco social unit, year and season as predictor variables. A MANCOVA was also undertaken to determine whether habitat use by family groups differed as a function of their group size and the number of calves, with year and season as categorical predictors, and group size and the yearling/adult ratio as continuous predictors. We tried substituting the yearling/adult ratio for the number of yearlings or the number of offspring (yearlings+juveniles) and results were unaltered. Tukey´s honestly significant difference test for unequal samples sizes was used *a posteriori* to compare pairs of means. Group size was square root-transformed and gradient log-transformed.

Analysis of habitat use with respect to availability was done in two stages, as outlined above. The first PCA employed values of the five variables for guanaco observations (n=114) and control sites (n=114). Differences between use and availability were analysed by a MANOVA, in which the first two components of the PCA were introduced as response variables and the factor guanaco observation *versus* control point was the categorical predictor. The second analysis repeated the process but this time using only availability data (n=114) from within the protected area. The Varimax rotation was used to allow a better interpretation of the components. All analyses were performed with STATISTICA 8.0 (StatSoft 2007).

RESULTS

Demography and social organization

No mixed groups were encountered during either the breeding season or the non-breeding season. The majority social unit throughout was the family group (63.2%), followed by solitary males (22.8%) and male-only groups (14%) (Table 1). Family group size did not differ between either seasons (Mann-Whitney U-test: U=597.49, p=0.995) or years (Kruskal-Wallis test: H=2.63, p=0.268). There were similarly no differences in the sizes of male-only groups between seasons (U=28.50, p=0.713) and years (H=1.09, p=0.581) (Table 1). Yearling/adult ratio varied between seasons (ANOVA, $F_{1,67}$=6.62; p=0.012) and years ($F_{2,67}$=3.79; p=0.027), being higher in the breeding season (mean±SD; 0.40±0.26) than in the non-breeding season (0.22±0.24) (Table 1).

Table 1. Guanaco social groups recorded during the breeding (BS) and non-breeding seasons (NBS) during the three study years. Mean group sizes are given with percentage occurrence of each social group per season given in parentheses. For family groups mean number of yearlings and juveniles and the yearling/adult ratio (Y/A) are given.

Social unit	2005		2006		2007	Total
	BS	NBS	BS	NBS	BS	
Family groups	6.29 (68.8)	7.14 (58.3)	8.27 (76.5)	8.18 (57.1)	8.21 (61.1)	7.72 (63.2)
Male groups	4.25 (12.5)	3.17 (25)	2.00 (5.9)	2.25 (9.5)	3.60 (13.9)	3.36 (14)
Solitary males	1 (18.8)	1 (16.7)	1 (17.6)	1 (33.3)	1 (25)	1 (22.8)
Total	4.89 (100)	5.12 (100)	6.62 (100)	5.22 (100)	5.77 (100)	5.54 (100)
Yearlings	1.82	1.00	1.62	1.50	2.32	1.72
Juveniles	2.64	2.07	2.15	2.08	3.14	2.5
Y/A Ratio	0.56	0.25	0.24	0.17	0.43	0.34

Habitat use by guanaco social units

The first two components of the PCA absorbed 73.7% of the variance. The first component (PCA 1) represents a plant productivity gradient: zones with a high proportion of bare ground and low soil moisture (-) *versus* zones with plant cover (+) (Table 2). The second component (PCA 2) comprises a topographic gradient: rugged, level zones (+) *versus* smooth, steep slopes (-). Habitat use by guanacos as defined by these two PCA components revealed no differences between types of social unit (MANOVA, $F_{4,214}$=1.01, p=0.405) (Fig 1a) nor between years ($F_{4,214}$=1.12, p=0.349), but there were significant differences between seasons ($F_{2,107}$=3.95, p=0.022) (Fig 1b). The ruggedness variable was the only one to give significant results in post hoc tests. During the breeding season guanacos occupied level areas of lower plant productivity but greater terrain ruggedness, the converse being the case during the non-breeding season (Fig 1b).

Table 2. Factor loadings of the first two components of the PCA obtained from NDVI, Band 1, Band 5, slope and ruggedness (VRM). Asterisks indicates significant values (p<0.05). Variable slope was log-transformed.

Variable	PCA 1	PCA 2
NDVI	0.875*	-0.019
Band 1 (barren ground)	-0.904*	0.268
Band 5 (dryness)	-0.855*	0.019
Logslope	0.193	-0.730*
VRM (ruggedness)	-0.064	0.851*
Explained Variance	2.353	1.329
Proportion of total (%)	47.1	26.6

The analysis centered on family groups showed the same pattern as for all guanacos combined, but with inter-seasonal differences in habitat use (MANCOVA, $F_{2,63}$=4.38, p=0.017) and as a function of group size ($F_{2,63}$=3.94, p=0.024). The plant productivity variable was the only one to give significant results in *a posteriori* tests on the effect of season, whereas larger groups occupied more level areas. There were no significant results for the effects of year ($F_{4,126}$=0.83, p=0.510), yearling/adult ratio ($F_{2,63}$=1.43, p=0.247), number of yearlings ($F_{2,63}$=1.21, p=0.310) or the total number of offspring ($F_{2,63}$=0.42, p=0.660).

Habitat selection

The first two components of the PCA for all guanaco observations and the random control points absorbed 71.3% of the variance. These two components explained trophic availability and predation risk. Habitat selection by guanacos was non-random (MANOVA, $F_{2,225}$=11.92, p<0.001) (Fig 2a). Post hoc tests showed significant differences only for plant productivity, this being greater in control points (Tabla 3). The variance absorbed by the second PCA, with the control points restricted to the protected zone, was 74.9%, with the same component configuration. The MANOVA once again showed differences ($F_{2,225}$=3.73, p=0.026) (Fig 2b), which were significant in post hoc tests, in this case between guanaco observation points and control points for the topography component. Habitat selection within the park thus seems to be determined by physical variables associated with predation risk.

Table 3. Values (mean±SD) of the five environmental variables calculated from the untransformed remote sensing data. Values are given for guanaco locations, control locations within the protected area and for the entire prospected zone (N=114 in all cases).

Variable	Guanacos	Control (park)	Control (total)
NDVI	0.098±0.023	0.105±0.027	0.128±0.032
Band 1 (barren ground)	113.118±21.937	112.294±22.966	103.339±21.135
Band 5 (dryness)	135.782±29.290	135.913±36.254	123.839±33.523
VRM (ruggedness)	0.497±0.164	0.516±0.192	0.515±0.176
Slope	2.146±2.317	3.539±3.372	4.085±5.195

DISCUSSION

Our results show year-long stability in types of guanaco social organization and that the different social units do not differ in habitat use in this hyperarid ecosystem. This suggests that the resource defense polygyny mating system described for this species may be converted into a female (harem) mating system where environmental conditions are extreme. Habitat use by guanacos nevertheless changed between seasons, the larger groups selecting areas of low forage abundance but with level, though rugged terrain, during the breeding season. This is due to guanacos perceive greater predation risk is in steeper areas where it is harder to flee.

Demography and social organization

Our results confirm our starting hypothesis (H_1) regarding the stability of different social units, showing no mixed groups at any time of year, and the relative high proportion of family groups throughout the year (63%, Table 1), compared to other guanaco populations (31%, Puig and Videla 2005). This seems to differ from what is expected in migratory populations of this species (Ortega and Franklin 1995). Here is probably due to the sedentary nature and low density of the study population (Acebes et al. 2010). The sizes of male-only and family groups was similar to populations in other less arid parts of the Monte Desert (3.77±1.09 and 8.07±4.05 respectively, Sosa and Sarasola 2005) and other populations located in more productive areas (Puig and Videla 1995) pointing at a conservative characteristic in the species.

The detected stability in the number and structure of guanaco social unit types throughout the study period may be influence by the monomorphic nature of the species. In general, polygynous ungulates display marked sexual dimorphism and males form leks and have temporary territories or harems during the breeding season, but they do not defend their females from rivals outside the reproductive period (Emlen and Oring 1977, Clutton-Brock 1989), when instead two sexes segregate (Main et al. 1996, Ruckstuhl and Neuhaus 2000). In the guanaco both sexes have the same risk of predation as well as similar trophic requirements (Ruckstuhl and Neuhaus 2000). The low density (0.38 individuals/km^2, Acebes et al. 2010) and the sedentary nature of the this population may also influence stability of guanaco social organization. Guanaco social behaviour in this harsh environment is similar to some equid species (*Equus burchelli, E. zebra, E. przewalskii, E. caballus),* non-ruminant ungulates that maintain large harems year-round (Linklater 2000, Neuhaus and Ruckstuhl 2002).

The year-long stability of social organization together with the scarcity of trophic resources not spatially clumped (Acebes et al. in press) suggests that resource defense polygyny mating system described for this species (Frankin 1983) may be modified into a female (harem) defense mating system. Previous studies in Patagonia have shown that breeding males monopolize territories around ephemeral wetlands that offer abundant forage and excellent visibility during the breeding season (Bank et al. 2003). However, where resources are scarce and not patchily distributed it is uneconomical defendable for a male that expends most of its time budget on such defense (Emlen and Oring 1977). Although not previously described in the guanaco, shifts in types of mating systems as a function of population density, availability of resources and females (Emlen and Oring 1977) have been documented in several ungulates, including elk *Cervus elaphus* (Carranza et al. 1996), fallow deer *Dama dama* (Apollonio et al. 1992), topi *Damaliscus lunatus* (Gosling 1991) and wild ass *Equus africanus* (Moehlman 1998). It would thus be interesting to have data from different regions that would reveal under which conditions such changes occur in the guanaco.

Despite the harsh environment, the yearling/adult ratio in the breeding season and the occurrence of small family groups suggest that all females succeed in being impregnated. The yearling/adult ratio in the breeding season estimated in the present study (0.41) is relatively high for a low density population when compared with other guanaco populations in Chilean Patagonia (0.32; own unpublished data) where the population density is higher (43 individuals/km^2, Sarno and Franklin 1999). This may indicate that adopting female defense polygyny is an effective strategy. Nevertheless, environmental rigor, in the forms of trophic scarcity and extreme climatic conditions, together with predation, may account for the sharp decline in this ratio during the non-breeding season (0.21) (Sarno and Franklin 1999, Sarno et al. 1999) as well as for its interannual variation.

Habitat selection

Foraging patterns, as defined by the quantity, quality and availability of food (Hansen et al. 2009), are limited by the conditions within the protected area, where forage is less abundant than in the surrounding areas (Table 3). Bearing in mind that desert ecosystems offer sparse plant cover of poor nutritional value (Noy-Meir 1973), it is the bottom-up processes led by forage scarcity that most often tend to limit herbivore abundance (McNaughton et al. 1989) rather than top-down constraints (Sinclair et al. 2003). Thus, the low guanaco densities (0.38 individuals/km^2, Acebes et al. 2010) would account for the low densities of their predators (Hopcraft et al. 2010). Nevertheless, although predation may have only a small regulatory effect on prey at a population level, behavioral responses of the latter when confronting predation risk may be significant (Byers 1997, Lima 2002, Creel and Christianson 2008).

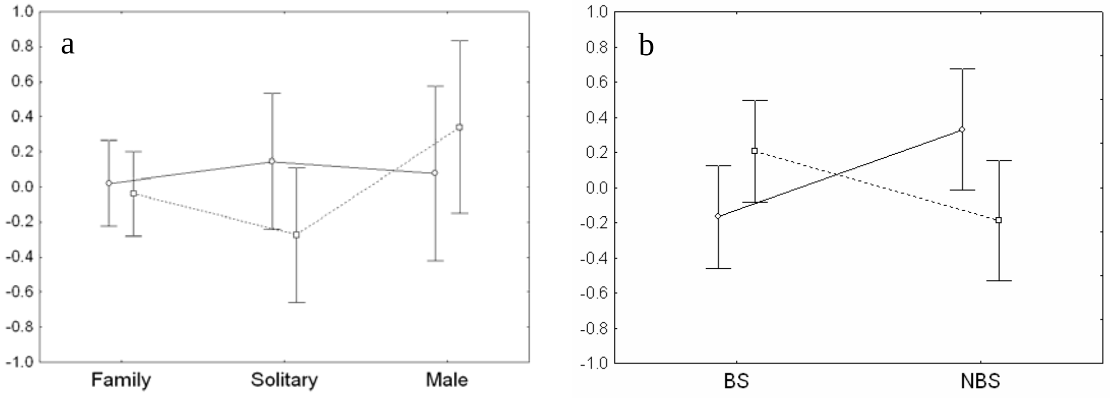

Figure 1. Means and standard deviations of factor scores of guanaco observations in the two resultant PCA axes (a) as a function of social group type, (b) for the breeding (BS) and non-breeding seasons (NBS). The continuous line represents axis 1: Vegetational gradient (high values) *vs* bare ground (low values). The broken line represents axis 2: level but rugged areas (high values) *vs* steep but smooth areas.

Second hypothesis (H_2) i.e. habitat selection differs between guanaco social units: male-only groups and solitary males selecting habitats offering high quality forage irrespective of a high predation risk (Main et al. 1996, Bank et al. 2003) and family groups occupying habitats that minimize predation risk (Bank et al. 2003) is not confirmed by our results. The explanation may rest in the scant variation in foraging niches in a desert area: resources are not clumped into high-quality patches but rather distributed along gradients of limited plant productivity, as commented above (Acebes et al. in press). Our results nevertheless suggest that, when compromising between maximising forage benefits and reducing predation risk, guanacos incline towards reducing the latter by occupying minimally productive areas that can meet their energy requirements although possibly at significant cost (Creel and Christianson 2008). Thus, during the breeding period, guanacos, especially the larger groups, occur in areas of low NDVI, i.e. with low forage abundance and a high proportion of bare ground. Selecting level areas rather than steep ones is related to the guanacos' perception of escape terrain, that is, guanaco flees easier from predator in level places, specially large groups with calves. With respect to forage abundance, vegetation in the study is typically shrubby (Acebes et al. in press), and the puma, an ambush and stealthy predator, conceals itself better in bushy vegetation (Bank and Franklin 1998). Guanacos of Chilean Patagonia (Bank et al. 2003) and guanacos and vicuñas (*Vicugna vicugna*) of the Argentine Puna (Cajal 1989) occur in open level areas with abundant grazing, and avoid areas associated with higher predator density, such as those with dense vegetation, steeper gradients or rocky terrain. However, our results show that the trade-off between low forage abundance but high visibility cannot be maintained in the dry season, when trophic resources are extremely scarce (Sinclair and Arcese 1995). Animals move to areas of greater plant cover despite the greater predation risk there.

The particular analysis of family groups reinforces the general pattern obtained from all guanaco observations, the larger groups occupying the more level areas. Nevertheless, we found no differences with respect to yearling/adult ratio, yearling numbers, or total offspring numbers (yearlings plus juveniles) as expected in hypothesis (H_3). Marino and Baldi (2008) have recently shown that the larger the guanaco family group the less time invested in vigilance and the longer spent foraging. They also suggest that predation risk is important in shaping social structure in the guanaco. Larger groups may thus occupy less productive habitats in the breeding season while minimizing predation risk. Other ungulates, such as the elk (*Cervus elaphus*), alter their habitat selection from forest areas to less favourable grasslands as a form of antipredator behavior (Creel et al. 2005).

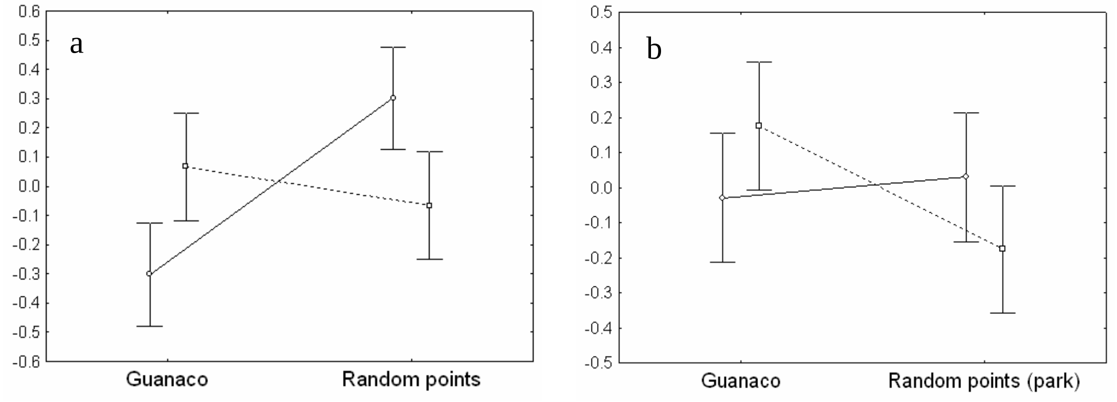

Figure 2. Means and standard deviations of factor scores for guanaco observation sites and for control areas in the two resulting axes of the PCA (a) in the total area prospected and (b) within the protected area only. The continuous line represents axis 1: Vegetational gradient (high values) *vs* bare ground (low values). The broken line represents axis 2: level but rugged areas (high values) *vs* steep but smooth areas.

Finally, it is important to highlight that barely 2% of guanaco sightings came from outside the protected area, despite the latter having similar topography but greater plant productivity. This finding may be indicative of how wild herbivore populations are becoming restricted to a few protected areas (Harris et al. 2009), in which populations are safe from poaching but have to occupy habitats with lower forage abundance, as our results have shown.

REFERENCES

Acebes P, Traba J, Malo JE, Ovejero R and Borghi CE. 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, Peco B, Reus L, Giannoni SM and Malo JE (in press). Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert. Revista Chilena de Historia Natural.

Apollonio M, Festa-Bianchet M, Mari F, Mattioli S and Sarno B. 1992. To lek or not to lek: mating strategies of male fallow deer. Behavioural Ecolology 3: 25-31.

Baldi B, Lichtenstein G, González B, Funes M, Cuéllar E, Villalba L, Hoces D and Puig S. 2008. *Lama guanicoe*. En: IUCN 2010. IUCN Red List of Threatened Species. <www.iucnredlist.org>

Bank MS and Franklin WL. 1998. Mountain lion (*Puma concolor patagonica*) feeding observations and attacks on guanacos (*Lama guanicoe*). Mammalia 62: 599-605.

Bank MS, Sarno RJ and Franklin WL. 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biological Conservation 112: 427-434.

Byers JA. 1997. American pronghorn. Social adaptations and the ghosts of predators past. University of Chicago Press, Chicago.

Cajal JL. 1989. Uso de habitat por vicunas y guanacos en la reserva San Guillermo, Argentina. Vida Silvestre Neotropical 2: 21-31.

Carranza J, Fernandez-Llario P and Gomendio M. 1996. Territoriality in rutting red deer. Ethology 102: 793-805.

Clutton-Brock TH, Guinness FE and Albon SD. 1982. Red deer. Behavior and Ecology of Two Sexes. Edinburgh University Press, Edinburgh.

Clutton-Brock TH. 1989. Mammalian mating systems. Proceedings of the Royal Society of London 236: 339-371.

Creel S and Winnie JA. 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.

Creel S, Winnie J, Maxwell B, Hamlin K and Creel M. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86: 3387-3397.

Creel S, Christianson D, Liley S and Winnie JA. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315: 960.

Creel S and Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23: 194-201.

Emlen ST and Oring LW. 1977. Ecology, Sexual Selection and the Evolution of Mating Systems. Science 197: 215-223.

Franklin WL. 1983. Contrasting socioecologies of South American's wild camelids: the vicuña and guanaco. In: Eisenberg JF y Kleiman DG (eds). Advances in the Study of Mammalian Behavior. Pp. 573-629. Special Publication No. 7. American Society of Mammalogists, Allen Press, Lawrence, Kansas.

González BA, Palma RE, Zapata B and Marín JC. 2006. Taxonomic and biogeographic status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae). Mammal Review 36: 157-178.

Gosling LM. 1991. The alternative mating strategies of male topi, *Damaliscus lunatus*. Applied Animal Behaviour Science 29: 107-119.

Hansen BB, Herfindal I, Aanes R, Saether B-E and Henriksen S. 2009. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. Oikos 118: 859-872.

Harris G, Thirgood S, Hopcraft JGC, Cromsigt JPGM and Berger J. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7: 55-76.

Hopcraft JGC, Olff H and Sinclair ARE. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology and Evolution 25: 119-128.

Jarman PJ. 1974. The social organisation of antelope in relation to their ecology. Behavior 48: 215-266.

Kerr JT and Ostrovsky M. 2003. From space to species: ecological applications for remote sensing. Trends in Ecology and Evolution 18: 299-305.

Kie JG. 1999. Optimal foraging risk of predation: effects on behavior and social structure in ungulates. Journal of Mammalogy 80: 1114-1129.

Kunkel KE and Pletscher DH. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology 78: 150-157.

Lima SL and Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lima SL. 2002. Putting predators back into behavioral predator–prey interactions.

Trends in Ecology and Evolution 17: 70-75.

Lima SL. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27: 215-290.

Linklater WL. 2000. Adaptive explanation in socio-ecology: lessons from the Equidae. Biological Reviews of the Cambridge Philosophical Society 75: 1-20.

Main MB, Weckerly FW and Bleich VC. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77: 449-461.

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.

McCullough DR. 1999. Density dependence and life-history strategies of ungulates. Journal Mammalogy 80: 1130-1146.

McNaughton SJ, Oesterheld M, Frank DA and Williams KJ. 1989. Ecosystem-level patterns of primary productiviy and herbivory in terrestrial habitats. Nature 341: 142-144.

Moehlman PD. 1998. Feral asses Equus africanus: intraspecific variation in social organization in arid and mesic habitats. Applied Animal Behaviour Science 60: 171-195.

Neuhaus P and Ruckstuhl KE. 2002. The link between sexual dimorphism, activity budgets, and group cohesion: the case of plain zebra (*Equus burchelli*). Canadian Journal of Zoology 80: 1437-1441.

Noy-Meir I. 1973. Desert ecosystems: environments and producers. Annual Review of Ecology and Systematics 4: 25-51.

Olff H, Ritchie ME and Prins HHT. 2002. Global environmental controls of diversity in large herbivores. Nature 415: 901-904.

Ortega IM and Franklin WL. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural 68: 489-500.

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ and Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20: 503-510.

Pettorelli N, Gaillard J-M, Mysterud A, Duncan P, Stenseth NC, Delorme D, Van Lare G, Toïgo C. and Klein F. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. Oikos 112: 565-572.

Pierce BM, Bowyer RT and Bleich VC. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68: 533-541.

Puig S and Videla F. 1995. Comportamiento y organización social del guanaco. In: Puig S (ed). Técnicas para el manejo del guanaco. Pp. 97-118. IUCN, Buenos Aires, Argentina.

Quinn GP and Keough MJ. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.

Ruckstuhl KE and Neuhaus P. 2000. Sexual segregation in ungulates: a new approach. Behaviour 137: 361-377.

Sappington JM, Longshore KM and Thompson, D.B. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71: 1419-1426.

Sarno RJ and Franklin WL. 1999. Population density and annual variation in birth mass of guanaco in southern Chile. Journal of Mammalogy 80: 1158-1162.

Sarno RJ, Clark WR, Bank MS, Prex WS, Behl MJ, Johnson WE and Franklin WL. 1999. Juvenile guanaco survival: management and conservation implications. Journal of Applied Ecology 36: 937-945.

Sinclair ARE and Arcese P. 1995. Population consequences of predation sensitive foraging: the Serengeti wildebeest. Ecology 76: 882-891.

Sinclair ARE, Mduma S and Brashares JS. 2003 Patterns of predation in a diverse predator prey system. Nature 425: 288-290.

Sosa RA and Sarasola JH. 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.

StatSoft Inc. 2007. STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

Theuerkauf J and Rouys S. 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowiez˙ a Forest, Poland. Forest Ecology and Management 256: 1325-1332.

Winnie J Jr and Creel S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behaviour 73: 215-225.

CAPÍTULO VI.

Efectos del turismo en el comportamiento del guanaco

Midiendo la tolerancia de ungulados al ser humano en áreas protegidas mediante la distancia de huida: ¿una herramienta fiable para la gestión del turismo?

RESUMEN

Los cambios comportamentales que sufren los grandes vertebrados en áreas protegidas visitadas por turistas deben ser motivo de preocupación para los gestores de las mismas: los grandes vertebrados atraen a turistas, pero estos pueden representar una fuente de perturbaciones que afecten a parámetros vitales de los animales, pudiendo además ser desplazados a zonas alejadas de las áreas visitadas. Así, el estudio del comportamiento animal frente al turismo puede ser utilizado como apoyo en la toma de decisiones de gestión. En este contexto, la respuesta del guanaco (Lama guanicoe) a turistas fue estudiada en un área protegida en la que habita una población de guanacos con un alto valor de conservación, debido a su situación en una zona extremadamente árida. Por una parte, los análisis de la distancia de huida del guanaco frente a vehículos (N=132) y peatones (N=77) muestran que los animales experimentan una gran tolerancia a la aproximación de seres humanos cerca del circuito turístico, reduciendo su distancia de huida a vehículos en aproximadamente 137 m (GLZ-test, p=0.0065) y en unos 40 m a peatones (GLM-test, p=0.0003), respecto de zonas fuera del espacio protegido. Un modelo exponencial ajustado muestra que ese efecto desaparece a distancias superiores a 500 m del área turística. Por otra parte, el número de observaciones de guanaco varió entre las campañas de campo realizadas en las estaciones húmeda y seca de 2005, 2006 y 2007, siendo significativamente menor los días con mayor afluencia de turistas (GLZ-test, p<0.0001), particularmente los días con más de 250 visitantes. Los análisis de distancia de huida indican que los guanacos muestran un apreciable acostumbramiento a los turistas dentro del área protegida, siendo diferente su reacción fuera de la misma, por lo que se podría concluir que la visita turística es sostenible. Sin embargo, la disminución en la frecuencia de observación de guanacos indica que los guanacos sufren molestias una vez superado un determinado umbral de visitantes. Nuestros resultados muestran la necesidad de utilizar métodos complementarios a la distancia de huida para evaluar las perturbaciones humanas sobre las poblaciones de especies bandera de áreas protegidas y permiten estimar niveles aceptables de perturbación.

Measuring ungulate tolerance to human in protected areas with flight distance: a reliable visitor management tool?

Malo JE, Acebes P and Traba J. Measuring ungulate tolerance to human in protected areas with flight response: a reliable visitor management tool? *(Manuscrito enviado).*

ABSTRACT

Tourist-induced behavioural changes in large vertebrates are an issue of concern for protected area management as they trigger a trade-off: large vertebrates attract visitors, but induced behavioral changes can reduce animal fitness and lead animals to avoid tourist-frequented zones. Animal behavioural response to tourists is often studied to ensure informed management decision-making. In this context, guanaco (*Lama guanicoe*) response to tourists was studied in a protected area where a high conservation priority population of the species thrives in an extremely arid environment. On the one hand, analysis of guanaco flight in the presence of vehicles (N=132) and pedestrians (N=77) shows that animals tolerate a significantly closer human approach when located near the tourist circuit, reducing their response distance to vehicles by approximately 137 m (GLZ-test, p=0.0065) and by approximately 40 m to pedestrians (GLM-test, p=0.0003). A fitted exponential model shows that this effect disappears at distances beyond 500 m from the tourist area. On the other hand, during five fieldwork campaigns in wet and dry seasons in 2005, 2006 and 2007 (N=107 days), the number of guanaco sightings showed differences among campaigns, and was significantly smaller on days with higher Park visitor numbers (GLZ-test, p<0.0001), particularly on days with over 250 visitors. Flight response analyses show that guanacos develop a considerable tolerance to visitors in tourist areas, a reaction that does not extend outside the protected area, potentially leading to the conclusion that tourist visits are sustainable. However, analysis of sighting frequencies suggests the potential risk of a lower probability of guanaco sightings if Park visitor numbers rise beyond current patterns. Results show that assessment of human disturbance to flagship species in protected areas requires further methods in addition to flight distance.

Key words: conservation, flight distance, guanaco, habituation, human disturbance, *Lama guanicoe*, protected area, tourism, wildlife management, flagship species

INTRODUCTION

Ecotourism has become a rapid growth industry, an important source of income and conservation funds, especially in areas with few economic alternatives (Giannecchini 1993). One of the most highly appreciated aspects of nature tourism is wildlife watching in protected areas, primarily large vertebrates (de Boer et al. 2004), although this can disturb the fauna (Nellemann et al. 2000, Taylor and Knight 2003, Stankowich 2008). The potential effects of tourism on vertebrate populations must therefore be assessed, especially in the case of small and endangered populations whose survival depends in many cases on the existence of protected areas (Caro 2007).

In the last decade, disciplines such as animal behaviour, behavioural ecology and conservation biology have striven to conjugate the demand for human activities in natural areas and the conservation requirements of endangered populations (Bucholz 2007, Caro 2007, Angeloni et al. 2008). This is the case of charismatic vertebrates with populations in danger of extinction, flagship species that fascinate the public attracted to protected areas where they still survive, in spite of the risks entailed for their conservation (Caro 2007, Angeloni et al. 2008). Despite efforts to date, this work is often theoretical, and further experimental studies are still required to resolve specific population management issues (Sutherland 1998, Caro 2007). This is particularly relevant bearing in mind that results are always somewhat context-dependent (Miller et al. 2006, Beale 2007), in spite of the constancy in each species' type of behaviour (Blumstein et al. 2003).

Behaviour studies should be accompanied by a careful interpretation of animal response in order to prevent the drafting of management proposals based on erroneous assumptions (Bejder et al. 2009). This is the case in the interpretation of the (apparent) adaptation to human presence by some populations in protected areas as a lack of negative repercussions, when in fact more subtle effects may emerge in the long-term (Nellemann et al. 2000, 2003, Gill et al. 2001). Relatively complex and/or costly measurements are available to assess tourist-caused disturbances to vertebrate populations (Tarlow and Blumstein 2007), such as stress estimates based on glucocorticoids (Fowler 1999, Múllner et al. 2004) and spatial usage analysis using telemetry (Preisler et al. 2006). Simpler techniques in use include estimates of flight distance, defined as the distance at which an animal flees from a person or some other stimulus (Stankowich 2008). This type of measurement is directly associated with the annoyance perceived by the animal and the costs incurred to change location whenever they are disturbed, and indirectly with disturbance to the spatial occupation pattern through the underutilisation of the most heavily visited areas (Gill et al. 1996). Another direct, simple-to-assess indicator rather uncommon in literature on the subject is animal sighting frequency in relation to tourist presence (Pelletier 2006).

There is little knowledge about the behavioural response by wild South American camelids to human activities (Stankowich 2008), despite their importance as flagship species in protected areas. The only published study showed large flight distances by guanaco (*Lama guanicoe* Müller) and vicuña (*Vicugna vicugna* Molina) due to poaching pressure (Donadio and Buskirk 2006), one of the causes for the decline of both species and for the reduction in their distribution range (Baldi et al. 2008, Lichtenstein et al. 2008). However, nothing is known about tourism effect, which in the documented area is anecdotal (Donadio and Buskirk 2006). The guanaco has a wider distribution area than the vicuña, occupying several protected and unprotected areas in Argentina, Chile, Perú, Paraguay and Bolivia (Baldi et al. 2008).

In this context, the present study analyses the effects of visitor presence on a guanaco population in an Argentinian protected area, where it is an important tourist attraction. For this purpose we used two complimentary procedures: measurement of flight distance in the presence of vehicles and pedestrians, and the analysis of guanaco sighting frequencies in relation to the number of visitors to the protected area. The results of these two procedures are used (i) to ascertain the point to which flight distance measurement (the most common procedure) is useful as an exclusive tool for management decision-making and (ii) to exemplify the effects of tourists on an animal species and how to extrapolate visitor management guidelines from them. We also present and discuss the basic data collated on the guanaco, a species with considerable tourist potential but little knowledge about its tolerance to human presence.

MATERIALS AND METHODS

Study Area

The study was conducted in the Ischigualasto Provincial Park (San Juan, Argentina), part of the Ischigualasto-Talampaya World Heritage Site. The area is inhabited by a small guanaco population (probably less than 400 individuals) of interest due to its location in the most arid part of the Monte Desert (Acebes et al. 2010). Ischigualasto PP (29º55’ S, 68º05’ W) covers 60,369 ha at an altitude of approximately 1300 m above sea level in an area with a desert climate and 80-140 mm annual summer rainfall, mean annual temperature below 18º C and a wide thermal regime (-10º to +45º C, Poblete and Minetti 1999). The predominant vegetation is sparse shrubland (less than 20% of plant cover), dominated by species of Zygophyllaceae (*Larrea* spp., *Zuccagnia punctata*), Fabaceae (*Prosopis spp., Cercidium praecox, Geoffroea decorticans*) and Chenopodiacae (*Atriplex* spp. and *Suaeda divaricata*) (Acebes et al. in press).

The Park receives around 50,000 visitors per year, with seasonal peaks during Easter and winter holiday periods (July). The main tourist attraction in the Park are the geomorphological formations on coloured sandstone and an extremely rich continental Triassic fossil record, which includes dinosaurs. For this reason, tourists can only visit the Park on guided tours in vehicles along a 40-km tourist circuit around the south-eastern sector (Figure 1). This route includes six tourist viewpoints where people leave the cars for short walks. Other tracks in the Park are off-limits to the public, some of which were used to access undisturbed areas (control zones) for the purposes of this study. Informal opinion surveys conducted with groups of visitors at the end of the guided tours show the tourists who observed guanacos getting more satisfied, indicating the value-added component of the species, even for visitors attracted by paleontological and landscape features of the Park.

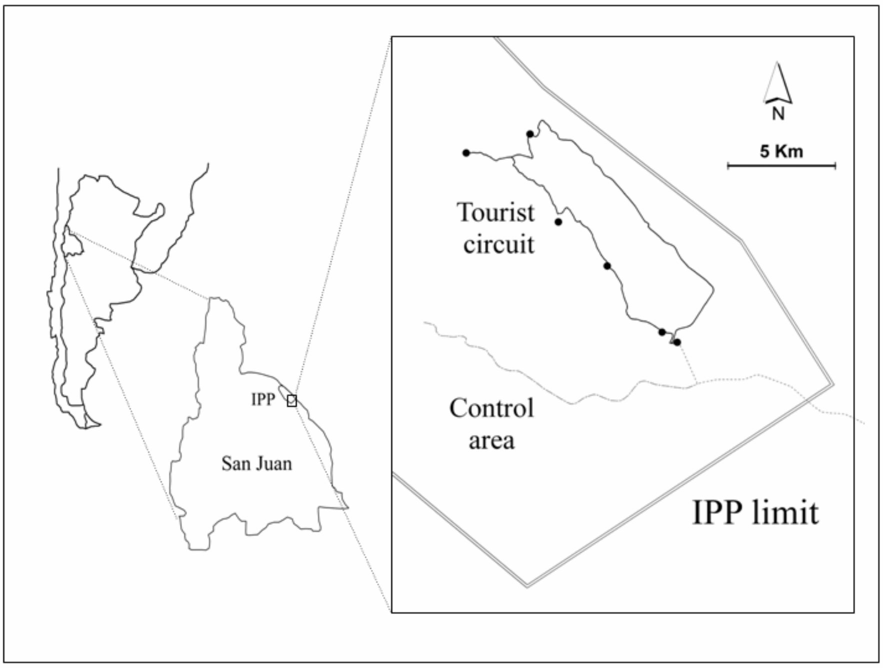

Figure 1. Location of Ischigualasto Provincial Park (IPP) in San Juan, Argentina. Tourist circuit, the six tourist viewpoints (dots) and control zones are represented.

Guanaco data

To evaluate the animal response to the presence of vehicles, two field surveys in July-August 2006 (winter) and January-February 2007 (summer) followed the tourist circuit and other tracks in the Park on a daily basis in search of guanaco herds. When a herd or an individual was sighted from the car (N=132), we recorded its reaction to the vehicle (alarm response and flight *vs.* no behavioural change), herd size and composition, distance from the car, measured by laser telemeter, and GPS location. A GIS was then used to calculate the animal distance from the tourist circuit and classify the sightings (inside or off the tourist circuit, defined as closer or further than 500 m from the track.

The guanaco response to tourists was also measured whenever possible (N=77) as the flight distance from an approaching pedestrian, i.e., the minimum distance allowed by guanaco to the researcher approaching in a non-threatening way, that led to the animal or the herd moving away (Stankowich 2008). As in the previous case, the sightings were GIS classified on the basis of their location inside or off the tourist circuit, measuring at the same time the minimum distance of the sighting point from the tourist track. ArcGIS 9.2 (ESRI, USA) software was used for the spatial analyses.

Finally, the guanaco response to tourists in the Park was measured in a supplementary way by crossing the daily number of detected guanaco herds with the number of visitors registered at the entrance gate. The daily number of guanaco sightings by researchers covers a total of 107 field days distributed across five sampling seasons in the summers of 2005, 2006 and 2007 (14, 25 and 20 days respectively) and the winters of 2005 and 2006 (28 and 20 days). This variable could potentially indicate the distancing of animals from the visited zones, and be used as an indirect measurement of the probability of guanaco sightings by tourists. Visitor figures were taken from the official entrance records held by the Ischigualasto Provincial Park.

Data analysis

The response by guanaco herds to the presence of a vehicle (0-1) was analysed with logit models using distance from the car and herd size as continuous explanatory variables, while the categorical factors were season, location inside/off the tourist circuit, and herd type. Three types of guanaco herds were defined in this analysis: families with offspring **(**from birth to < 1.5 years), herds without offspring, and solitary individuals. The best possible model was chosen on the basis of the minimum number of parameters and maximum information using Akaike ΔAIC corrected for overdispersion.

Guanaco flight distance from a pedestrian was analysed using General Linear Models, including the following categorical factors as explanatory variables: season, location inside/off the tourist circuit, and herd type, while the covariate was herd size. In this analysis, we only distinguished families with young versus the rest of the guanaco observations due to the small number of data from isolated individuals and herds without young. The response variable was log-transformed to meet homoscedasticity assumptions, and the selection of the best explanatory model was also based on the criteria of information and parsimony of the ΔAIC.

To supplement this information, the sightings were fitted to a logarithmic model of the flight distance (y) with respect to the distance from the circuit (x) expressed as::

$$y = a(1 - \ln(bx))$$

where a is the (asymptotic) expected flight distance away from the influence of the tourist circuit, and b is the coefficient that relates them on a logarithmic scale. This model was compared using ΔAIC to a simpler one based on the null hypothesis of no influence of the proximity to the touristic circuit on the animal behaviour, expressed as:

$$y=a$$

The number of guanaco herd sightings versus visitor numbers was analysed with a Generalized Linear Model for counts with Poisson errors, including the factor sampling season and the covariate visitor numbers. Due to the lack of parallelism in this covariate among sampling seasons, the model includes the effect of visitor numbers nested within the sampling season. Due to the possibility of the disturbance effect of tourists on guanacos extending over time, we compared models which included alternatively visitor numbers to the Park on the same day and the sum of visitors on that and the previous day.

Finally, the daily chance of a guanaco sighting on a workday in the Park, expressed as the percentage of guanaco herd sightings on one day as compared to the season average (expected value 100%), was modelled for visitor numbers with a linear regression. In this case, we compared the fit of a simple model and a piecewise linear regression with a breakpoint (StatSoft 2007), in order to test the possible definition of a visitor number threshold beyond which a reduction in guanaco sightings is detected.

STATISTICA 8.0 (StatSoft 2007) was used for all analyses.

RESULTS

On 39 occasions (30% of the total), vehicle encounters with guanacos led to a halt in their activity and the initiation of movement. Flight events occurred at a distance (mean±SE) of 141±44 m in contrast to sighted herds that did not flee from the vehicle (285±28 m). The fitted model that best explained the guanaco herd response to vehicle presence included the variables: distance from the car, herd size, group type, position relative to the touristic circuit and season; along with the following interactions: distance*position relative to circuit and season*position relative to circuit ($G^2=32.27$; 8 d.f.; $p<0.0001$; Table 1). The distances at which flight events took place showed that guanaco reaction to approaching vehicles was much shorter in the proximity to the circuit (seasonal averages 76-98 m on vs. 143-183 off). According to the model, this reduction is highly significant, estimated from the model parameters in Table 1 to be close to 60%. Significant effects linked to herd size, herd type and 'winter inside the tourist circuit' situation were detected. Each additional guanaco in the herd was equivalent to moving approximately 17 m away from the vehicle, while in winter, guanacos off the tourist circuit responded by fleeing 32 m further than expected with respect to those close to the circuit (Table 1). Additionally, the likelihood of a flight response to a vehicle followed a gradient among herd types as it was highest in family herds, intermediate in herds without young and lowest in individuals.

Table 1. Parameter estimates of the logit model fitted for the likelihood of flight response by guanaco herds to an approaching vehicle. Continuous variables in model are vehicle distance (m) and number of individuals in the herd. Reference class for categorical variables shown in brackets.

	Estimate ± SE	Wald-Statistic	p
Intercept	3.3265±0.9347	12.67	0.0004
Distance	-0.0198±0.0049	16.61	<0.0001
Herd size	-0.3514±0.0985	12.74	0.0003
Position (inside circuit)	0.7668±0.5763	1.77	0.1834
Season (winter)	0.2958±0.2331	1.61	0.2045
Group type (family)	1.9302±0.6038	10.22	0.0014
Group type (solitary)	-1.0558±0.5177	4.16	0.0414
Distance * Position (inside)	-0.0127±0.0047	7.40	0.0065
Position (inside) * Season (winter)	-0.6338±0.2447	6.71	0.0096

Guanacos showed an average flight distance from a pedestrian of 136±18 m (seasonal averages 89-102m in the Park and 154-184 m outside), with significant differences linked to location inside/off the tourist circuit, herd type and herd size (Table 2). According to the estimated parameters, other things being equal, guanaco flight distances were 21% shorter inside the tourist circuit than the expected distance off it, and increased by 44% in family herds. Flight distance decreased approximately 4% with each additional individual in the herd.

Table 2. Parameter estimates of linear model fitted for the effect of position (inside *vs.* outside the tourist circuit), group type (family *vs.* other) and number of individuals in the guanaco herd on guanaco flight distance from a pedestrian. Dependent variable (flight distance) log-transformed.

	Estimate ± SE	t	p
Intercept	4.9100±0.1184	41.45	<0.0001
Position (inside circuit)	-0.2305±0.0613	-3.76	0.0003
Group type (family)	0.3680±0.0961	3.83	0.0003
Herd size	-0.0518±0.0166	-3.11	0.0026

The fit of flight distance with respect to the guanaco distance from the circuit through an exponential model was highly significant ($F_{2,75}$=91.48, $p<0.0001$; Table 3) and more informative than the null linear model (ΔAIC=-3.29). This model (Figure 2) suggests that changes in flight distance occur in an area of approximately 500 m around the tourist circuit, where 67% of the cases in which guanacos with flight distances of ≤100 m were concentrated, despite the fact that the sightings <500 m from the circuit only comprised 43% of the total. According to this model, the expected guanaco flight distance away from visitor influence is 163 m.

During the 107 fieldwork days, there were 320 guanaco sightings, equivalent to 2.99±0.23 sightings per day. The use of predictors 'visitor numbers today' and 'visitor numbers today and yesterday' in models generated similar results. As the former was slightly more informative, (ΔLog-likelihood=1.20), only these results are presented.

The number of guanaco sightings varied significantly among sampling seasons (Chi-square 66.70; 4 d.f.; $p<0.0001$), ranging between 1.72±0.33 sightings per day in summer 2006, and 5.80±0.48 sightings per day in summer 2007. In each season, the daily number of sightings was significantly lower on days with larger visitor numbers (Chi-square 23.67; 5 d.f.; $p<0.0001$). The reduction was significant in two of the four seasons (summer 2005 and winter 2006), while no significant trends were detected in the other three (Table 4).

Table 3. Parameter estimates of exponential model fitted for the effect of distance (m) to the nearest point on the tourist circuit on guanaco flight distance from a pedestrian. *a* is expected flight distance (asymptotic) outside the influence of the tourist circuit, and *b* the coefficient relating them on a logarithmic scale.

	Estimate ± SE	t	p
a	163.16±13.41	12.17	<0.0001
b	0.0062±0.0021	2.87	0.0105

The linear regression fit shows that a simple regression is not significantly informative of the variation in the daily chance of guanaco sighting ($F_{2,105}=2.16$, $p=0.1201$), contrary to the piecewise regression with a breakpoint ($F_{4,103}=3.37$, $p=0.0123$). According to the latter, the daily chance of guanaco sighting shows no significant pattern for low park visitor numbers (constant and slope, $p>0.05$), but diminishes significantly (slope -0.4719±0.1658; $t=-2.85$; $p=0.0054$) beyond the breakpoint (247.4±68.6; $t=3.61$; $p=0.0005$).

Table 4. Parameter estimates of the Generalized Linear Model for the effect of visitor numbers on daily numbers of guanaco herds sighted by researchers. Average daily visitor numbers (±SE) for each season shown in brackets.

	Estimate ± SE	Wald-Statistic	p
Summer 2005 (210±92)	-0.0021±0.0004	30.26	<0.0001
Winter 2005 (214±32)	0.0000±0.0017	0.00	0.9791
Summer 2006 (122±7)	0.0123±0.0075	2.69	0.1011
Winter 2006 (336±56)	-0.0062±0.0011	34.13	<0.0001
Summer 2007 (124±7)	-0.0039±0.0187	0.04	0.8359

DISCUSSION

The results of the behavioural study show an appreciable habituation of guanacos to visitors, leading to attenuated flight response in the tourist area. Using these data, we can estimate the effect of tourists on guanaco spatial use, considered to be low, and also use the results as a scientific basis for management decision-making. However, the parallel study based on animals sighting frequency revealed more subtle effects on guanacos, highlighting the need to use complementary methods in addition to flight distance to accurately assess and manage the impact of tourists on ungulate populations in protected areas.

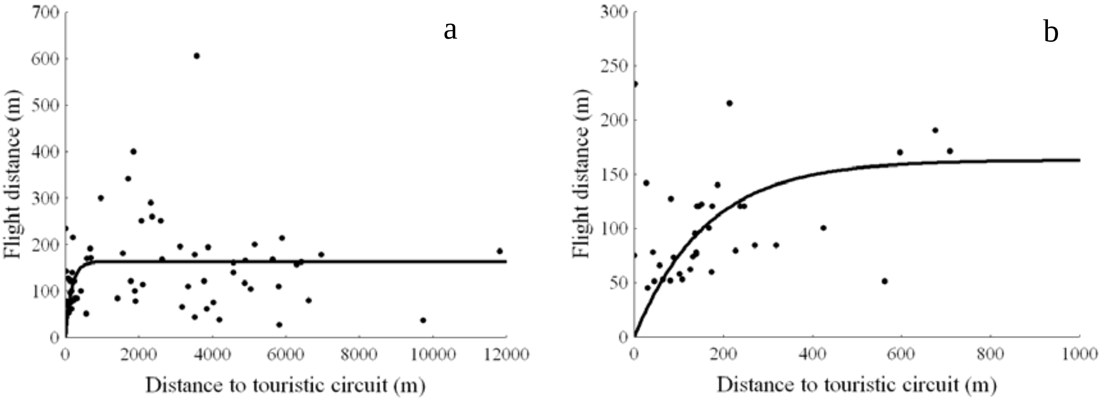

Figure 2. Logarithmic model linking guanaco flight distance in the presence of a researcher according to distance from tourist circuit. b) shows enlargement of the lower left area of Figure a).

Behavioural data suggest that although human presence often alters guanaco behaviour and makes them flee, there is probably little overall effect on the population in the form of habitat loss (Gill et al. 1996, Nellemann et al. 2003). In fact, guanaco flight distances in the tourist area lie within a range of 75-100 m for approaching vehicles and 90-100 m for pedestrians, confirming the same stronger reaction to the latter found in other ungulates (Stankowich 2008). On the basis of these data, we can estimate that tourist activity disturbs guanacos over an area of less than 900 ha, assuming a 100 m buffer zone around all the areas containing tourist activity (approximately 800 ha affected by the 40-km vehicle circuit plus less than 100 ha around the six viewpoints). In our case study, this area is small in absolute terms (approximately 1.5% of total protected area), considering additionally that the visitable zone is restricted to the south-eastern third of the protected area. In this situation, the protected area management authorities would probably conclude that the tourist exploitation of guanaco watching is appropriate (Blumstein et al. 2003, Reimers et al. 2006).

The apparent minor effects of tourists on guanacos is probably the result of these animals becoming accustomed to non-aggressive human presence, which leads to a reduction in their reaction to approaching vehicles and pedestrians. Flight distances found in this study were relatively short, explained by the population's protected status and perhaps also because it is not affected by poaching (Donadio and Buskirk 2006). The key factor is probably frequency of encounters with humans, as guanaco flight distances in the Ischigualasto PP are considerably shorter than those published for San Guillermo Nacional Park (median 390 m), a protected area 150 km of our study area which receives barely 1,000 visitors per year (Donadio and Buskirk 2006). In Torres del Paine National Park (Chile), with over 100,000 visitors per year, guanacos tolerate human approach down to a distance of scarcely a few metres (Bank et al 2003, Malo et al. 2009). In conclusion, guanacos seemed to display flexible behaviour that permits its adaptation to human frequentation, facilitating tourist-oriented use of the species. This is an important question for the management of natural protected natural areas in vast areas of South America, given its flagship effect as a visitor drawcard for the species' habitats.

On the other hand, the risk of death as a result of poaching may increase in areas where guanacos become more confident. Flight distance modelling shows that for guanacos, this effect spreads to approximately 500 m around the visited areas in the Park. Here, stringent measures must be taken to control potential poaching, as there is a very high hunting threat to docile animals, also bearing in mind the small population size of the species in this desert zone (Acebes et al. 2010).

Guanaco sensitivity to human presence varies among situations, which should also be taken into account by tourism planners. Guanacos tolerate humans more in situations where they are more familiarised, i.e., presence of humans in vehicles and in the zone with the heaviest traffic (Kucera 1976, Miller et al. 2001). This may be used to support the establishment of predictable tourist visiting patterns (e.g. fixed spotting sites), as the animals may react more to infrequent situations such as pedestrians walking in areas usually crossed by cars (Papouchis et al. 2001).

The effect of herd size is reflected in both a reduction in the likelihood of flight when a vehicle approaches and a reduction in the flight distance from a pedestrian, as the herd size increases. This effect has not been detected previously in guanaco (Donadio and Buskirk 2006) although it is relatively frequent amongst ungulates (Stankowich 2008). Given that the effect of herd size combines the likelihood of threat detection (higher for larger groups) and perception of risk, the sense of protection conveyed by the herd seems to be more relevant in the case of the guanaco (Fairbanks and Tullous 2002, Childress and Lung 2003, Reimers et al. 2006). It should also be noted that detection of vehicles and pedestrians by guanacos is not a limiting factor on their response, given the characteristically high visibility of the open landscapes preferred by this species (Franklin 1983, Donadio and Buskirk 2006, Acebes et al. 2010).

Differences in reaction associated to the presence/absence of young in the guanaco herd support the idea that the decision to flee when approaching humans are detected is associated with an assessment of the potential risk (Frid and Dill 2002, see however Gill et al. 2001). Thus, all else being equal, flight behaviour when a vehicle approaches is more likely in groups with young than without them, and the distance maintained between a herd and a pedestrian is also greater in groups with young. This more reclusive behaviour by the latter groups is relatively widespread amongst ungulates (Ciuti et al. 2008, see however Papouchis et al. 2001). In applied terms, this suggests minimising the approach by tourists to herds containing young, either by raising visitor awareness about this aspect or via seasonal restrictions on the use of zones occupied by guanaco family groups.

In summary, the results of flight distance analyses can be used to assess the suitability of tourists usage of protected areas and draft specific management measures such as those mentioned above. In the present case of the guanaco, we may conclude that the tourist usage model based on controlled vehicle and pedestrian routes circuits is not harmful for the guanaco population (Frid and Dill 2002, Beale 2007), provided that the areas visited by tourists do not coincide with certain indispensable spots for these animals.

However the complementary method based on sighting frequency in the Park suggests that the presence of tourists may have negative effects on the guanaco population, particularly when they pass a threshold, and that this tourist resource should be managed with caution. The study shows that the chance of guanaco sighting falls on days with high visitor numbers, possibly an indication that animals move away from the tourist circuit under these circumstances and seek areas that are undisturbed by the presence of tourists (Nellemann et al. 2000, Papouchis et al. 2001). This observation is similar to that of Pelletier (2006) in the Canadian Rocky Mountains, where the days of highest traffic coincided with a reduction in the frequency of sightings of three deer species as a result of the animals moving away towards less visible habitats. In our case, the guanaco sighting distance increased slightly with visitor numbers in the Park (beta 0.22; t=0.93; p=0.361), and no data are available to assess possible changes in habitat selection.

The use of linear regression with a breakpoint allowed us to detect a threshold in visitor numbers beyond which there was a significant decline in the daily chance of a guanaco sighting, facilitating the drafting of useful management guidelines (Caro 2007). In our case, the number of guanaco sightings began to fall beyond approximately 250 visitors per day, which only occurred on less than 17% of all the study days. This figure rised up to 43% and 25% of days in summer 2005 and winter 2006, the periods when significative coefficients were found. Thus, the guanacos in the study area seem to be unaccustomed to such high visitor numbers, and a higher disturbance intensity might lead either to greater tolerance or to their definitive movement out of the protected area with the ensuing long-term consequences for their conservation.

From an applied perspective, this finding suggests the advisability of caps on visitor numbers to the tourist area, and a gradual increase in this figure only after the animals are found to reduce the intensity of their reaction to visitors. This is, however, a somewhat unrealistic scenario given that a considerable part of the income in this region, as with many others that host protected areas, is increasingly dependent on tourism. The expected increase in tourist numbers should therefore be accompanied by educational programmes or activities aimed at raising the awareness of tourists with a view to minimising their impact on the wildlife. Along them monitoring studies with methods as those used in the present paper should be carried out to assess the way the guanaco population responds to the new scenarios (Griffin et al. 2006).

In conclusion, our results show on the one hand, the utility of behaviour-based methods for management decision-making in protected tourist areas that host vertebrate populations, and on the other hand, the need to employ approaches based on complimentary measurements to flight distance whenever possible. These results have emerged from the first field study of the effects of tourism on the guanaco, South America's most widely distributed ungulate and a key species in the ecosystems inhabited by it. Additionally, to the extent that flight distance can be viewed as a species-specific trait, managers need not necessarily collect site-specific data on a species if flight initiation distance data exist elsewhere (Blumstein et al. 2003). The main conclusions from this research can therefore be extrapolated to other protected areas in South America inhabited by the best preserved guanaco populations (Baldi et al. 2008), which act as flagship species and attracts large numbers of tourists.

REFERENCES

Acebes P, Traba J, Malo JE, Ovejero R and Borghi CE. 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, Peco B, Reus L, Giannoni SM and Malo JE (in press). Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert. Revista Chilena de Historia Natural.

Angeloni L, Schlaepfer MA, Lawler JJ and Crooks KR. 2008. A reassessment of the interface between conservation and behaviour. Animal Behavior 75: 731-737.

Baldi B, Lichtenstein G, González B, Funes M, Cuéllar E, Villalba L, Hoces D and Puig S. 2008. Lama guanicoe. In: IUCN 2010. IUCN Red List of Threatened Species. <www.iucnredlist.org>

Bank MS, Sarno RJ and Franklin WL. 2003. Spatial distribution of guanaco mating sites in southern Chile: conservation implications. Biological Conservation 112: 427-434.

Beale CM. 2007. The behavioral ecology of disturbance responses. International Journal of Comparative Psychology 20: 111-120.

Bejder L, Samuels A, Whitehead H, Finn H and Allen S. 2009 Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395: 177-185.

Blumstein DT, Anthony LL, Harcourt R and Ross G. 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? Biological Conservation 110: 97-100.

Buchholz R. 2007. Behavioural biology: an effective and relevant conservation tool. Trends in Ecology and Evolution 22: 401-407.

Caro T. 2007. Behavior and conservation: a bridge too far? Trends in Ecology and Evolution 22: 394-400.

Childress MJ and Lung MA. 2003.Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? Animal Behaviour 66: 389-398.

Ciuti S, Pipia A, Ghiandai F, Grignolio S and Apollonio M. 2008. The key role of lamb presence in affecting flight response in Sardinian mouflon (Ovis orientalis musimon). Behavioural Processes 77: 408-412.

de Boer H, Van Breukelen L, Hootsmans MJM and Van Wieren SE. 2004. Flight distance in roe deer Capreolus capreolus and fallow deer Dama dama as related to hunting and other factors. Wildlife Biology 10: 35-41.

Donadio E and Buskirk SW. 2006. Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. Biological Conservation 127: 139-145.

Fairbanks WS and Tullous R. 2002. Distribution o pronghorn (Antilocapra americana Ord) on Antelope Island State Park, Utah, USA, before and after establishment of recreational trails. Natural Areas Journal 22: 277-282.

Fowler GS. 1999. Behavioral and hormonal responses of Magellanic penguins (Spheniscus magellanicus) to tourism and nest site visitation. Biological Conservation 90: 143-149.

Franklin WL. 1983. Contrasting socioecologies of South American’s wild camelids: the vicuña and guanaco. In: Eisenberg JF and Kleiman DG (eds). Advances in the Study of Mammalian Behavior. Pp. 573-629. Special Publication No. 7. American Society of Mammalogists, Allen Press, Lawrence, Kansas.

Frid A and Dill LM. 2002. Human-caused disturbance stimuli as a form of predation risk.Conservation Ecology 6(1): 11. [online]

URL: http://www.consecol.org/vol6/iss1/art11

Giannecchini J. 1993. Ecotourism: new partners, new relationships. Conservation Biology 7: 429-432.

Gill JA, Sutherland WJ and Watkinson AR. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Appled Ecology 33: 786-792.

Gill JA, Norris K and Sutherland WJ. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:

265-268.

Griffin SC, Valois T, Taper ML and Mills LS. 2006. Effects of Tourists on Behavior and Demography of Olympic Marmots. Conservation Biology 2: 1070-1081.

Kucera E. 1976. Deer flushing distance as related to observers mode of travel. Wildlife Society Bulletin 4: 128-129.

Lichtenstein G, Baldi R, Villalba L, Hoces D, Baigún R and Laker J. 2008. *Vicugna vicugna*. In: IUCN 2010. IUCN Red List of Threatened Species. <www.iucnredlist.org>

Miller SG, Knight RL and Miller CK. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29: 124-132.

Miller KA, Garner JP and Mench JA. 2006. Is fearfulness a trait that can be measured with behavioural tests? A validation of four fear tests for Japanese quail. Animal Behaviour 71: 1323-1334.

Malo JE, González BA, Traba J, Estades CF, Acebes P, Galaz JL and Zapata OB. 2009. Modulation of guanaco (Lama guanicoe) flight behaviour by tourist use in Torres del Paine Region. 10th. International Mammalogical Congress, Mendoza (Argentina). pp: 134-135.

Müllner A, Linsenmair KE and Wikelski M. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (Opisthocomus hoazin). Biological Conservation 118: 549-558.

Nellemann C, Jordhøy P, Støen O and Strand O. 2000. Cumulative impacts of tourist resorts on wild reindeer (Rangifer tarandus tarandus) during winter. Arctic 53: 9-17.

Nellemann C, Vistnes I, Jordhøy P, Strand O and Newton A. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113: 307-317.

Papouchis CM, Singer FJ and Sloan WB. 2001. Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65: 573-582.

Pelletier F. 2006. Effects of tourist activities on ungulate behaviour in a mountain protected area. Journal of Mountain Ecology 8: 15-19.

Poblete AG and Minetti JL. 1999. Atlas Climatológico de San Juan. Instituto de Geografía Aplicada. Universidad Nacional de San Juan. San Juan (Argentina). CD-ROM Edition.

Preisler HK, Ager AA and Wisdom MJ. 2006. Statistical methods for analysing responses of wildlife to human disturbance. Journal of Applied Ecology 43: 164-172.

Reimers E, Miller FL, Eftestøl S, Colman JE and Dahle B. 2006. Flight by feral reindeer Rangifer tarandus tarandus in response to a directly approaching human on foot or on skis. Wildlife Biology 12:403-413.

Stankowich T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141: 2159-2173.

StatSoft Inc. 2007. STATISTICA (data analysis software system), version 8.0. www.statsoft.com.

Sutherland WJ. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56: 801-809.

Tarlow EM and Blumstein DT. 2007. Evaluating methods to quantify anthropogenic stressors on wild animals. Applied Animal Behaviour Science 102: 429-451.

Taylor AR and Knight RL. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological applications 13: 951-963.

CAPÍTULO VII.

Discusión general y conclusiones

DISCUSIÓN GENERAL

Las poblaciones de ungulados silvestres están reguladas mediante la productividad primaria y la depredación. Sin embargo, estos factores de regulación son alterados con frecuencia por la acción del hombre, cuyas actividades modifican el paisaje y alteran las áreas de distribución natural y los patrones de uso del espacio y selección de hábitat de los ungulados, a la vez que eliminan a sus depredadores naturales. Actividades como la ganadería o la caza furtiva entran en conflicto con las poblaciones de ungulados silvestres, quedando éstas relegadas en muchas ocasiones a unos pocos espacios naturales protegidos. Con frecuencia estas áreas albergan ecosistemas menos alterados que los de su entorno, pero los ungulados pueden sufrir otro tipo de perturbaciones derivadas de las actividades de recreo o del turismo de naturaleza.

Esta situación está muy extendida en Sudamérica y una especie afectada por este proceso es el guanaco *Lama guanicoe*, cuyas poblaciones se encuentran fragmentadas y aisladas a lo largo de su distribución continental, con excepción de aquéllas situadas en el sur de la Patagonia argentina y chilena. Desplazado de sus hábitats naturales a otros menos productivos por la ganadería y la agricultura e intensamente cazado, el guanaco mantiene poblaciones más o menos estables en espacios naturales protegidos (Baldi et al. 2008).

En la presente tesis doctoral se ha abordado el uso del espacio y la selección de hábitat de una población de guanacos en un espacio natural protegido situado en una zona hiperárida del Desierto de Monte (noroeste argentino), que reúne las características anteriormente mencionadas: población pequeña y aislada, recluida a un espacio protegido visitado por turistas, y que cuenta además con especies introducidas de ungulados. Los resultados de esta tesis han permitido avanzar en el conocimiento de diversos elementos clave de este problema. En primer lugar, se han analizado las comunidades vegetales de esta parte del Desierto del Monte, siendo esta información necesaria para poder explicar la selección de hábitat y el uso del espacio del guanaco (capítulo II). Además, se ha estimado el tamaño poblacional y la densidad de guanacos y se ha descrito el uso del hábitat del guanaco a diferentes escalas espaciales (capítulo III). Complementariamente, se han determinado los patrones de uso del espacio del guanaco y de las dos especies introducidas de ungulados, el burro y la vaca, a partir de variables de hábitat, de variables relacionadas con el hombre y de la presencia de las distintas especies de ungulados (capítulo IV). Una vez evaluado el pequeño efecto de la presencia de los ungulados introducidos sobre el guanaco, se ha estimado la selección de hábitat del guanaco a partir de la disponibilidad trófica y del riesgo de depredación, y en función del tipo de organización social, a la vez que se han aportado datos sobre la estructura social y demográfica de la población (capítulo V). Por último, se ha evaluado el efecto del turismo sobre la población de guanacos, a partir de dos medidas independientes: la distancia de huida de los guanacos, indicadora del grado de tolerancia y habituación a las perturbaciones, y la frecuencia de observación de animales (capítulo VI). Estos resultados aportan por tanto información sobre la ecología de la especie en una zona hiperárida, en tanto que ofrecen herramientas para los gestores de espacios naturales protegidos en los que el guanaco está presente. En los párrafos que siguen se discutirán los resultados más importantes de la presente tesis doctoral.

La vegetación típicamente xerofítica del Desierto del Monte se estructura en gradientes, por lo que resulta difícil definir comunidades vegetales discretas a pequeñas escalas. A partir de estos resultados se ha propuesto un modelo conceptual con los factores que estructuran la composición florística y fisonómica de las comunidades vegetales del Desierto del Monte en dos gradientes, a saber: factores edáficos y distancia a cauces o puntos de drenaje, es decir, zonas donde la capa freática está más próxima a la superficie (Acebes et al. en prensa). La cobertura media de la vegetación en el área de estudio es inferior al 20%, y las especies son fundamentalmente leñosas, estando las gramíneas y otras herbáceas escasamente representadas. Algunas de las especies dominantes como las *Larrea* spp. y la *Zuccagnia punctata* contienen gran cantidad de compuestos antiherbivoría, aunque este hecho no parece ser relevante para el guanaco ya que se alimenta de estas especies (observación personal). En los extremos del gradiente de humedad edáfica se sitúan los algarrobales (*Prosopis chilensis* y *P. flexuosa*), formaciones freatófitas discontinuas distribuidas a lo largo de los cauces secos, que sólo llevan agua después de intensas precipitaciones estivales, actuando a modo de torrenteras por las que se evacúa el agua del terreno. Son las formaciones vegetales con mayor cobertura de vegetación y las que aportan mayor sombra. En el extremo opuesto se encuentran los peladales, zonas de suelos arcillosos y salinos desprovistas de vegetación, con excepción de algunas plantas crasas (*Sclerophylax kurtzii* y *Halophytum ameghinoi*) y en zonas un poco más próximas a los cauces se encuentran los zampales (*Atriplex spegazzinii*). Sobre los suelos rocosos e inclinados aparecen un gran número de cactáceas de pequeño tamaño (por ejemplo *Tephrocactus* spp. y *Echinopsis leucantha*), y otras de gran porte como el cardón (*Trichocereus terscheckii*). Hay que destacar la presencia de varias especies de bromeliáceas epífitas (*Tillandsia* spp.). Todas las especies mencionadas forman parte de la dieta del guanaco (observación personal), con excepción del cardón, que se alimenta de sus frutos (Campos et al. 2008).

Una vez determinada la estructura y composición florística de las comunidades vegetales del Parque Provincial Ischigualasto, se ha podido inferir, por una parte, la escasa disponibilidad trófica del sistema, corroborada por los bajos valores del índice de vegetación (NDVI) obtenidos a partir de imágenes de satélite. Por otra, que la dieta del guanaco deberá diferir respecto de las poblaciones patagónicas, en las que el componente principal son las gramíneas (Puig et al. 2001, Baldi et al. 2004). Tendrá previsiblemente una mayor similitud con aquéllas de los desiertos costeros de Chile, que incluyen en su dieta líquenes, arbustos y cactáceas (Raedeke y Simonetti 1988). El estudio sistemático de la dieta del guanaco, sin duda relevante para explicar de forma más precisa las decisiones de forrajeo y la selección de hábitat del guanaco, no ha sido abordado en la presente tesis doctoral, por tratarse de uno de los objetivos de una tesis llevada a cabo por una doctoranda del equipo argentino del proyecto en el que se enmarca el presente trabajo de investigación. Por último, la dificultad para diferenciar *de visu* las comunidades de plantas como consecuencia de una ausencia de cambios fuertes de la composición-estructura de la vegetación, pone de manifiesto la dificultad para interpretar la selección de hábitat del guanaco en esos términos.

El uso del hábitat del guanaco a escala de unidad geológica, que se puede interpretar como determinante de factores abióticos tales como la topografía (pendiente, rugosidad), exposición al viento o distancia a puntos de agua (Bailey et al. 1996), han mostrado la preferencia del guanaco por zonas abiertas y topográficamente horizontales durante la estación húmeda (Hoyada de Ischigualasto y coberteras cuaternarias). Sin embargo, en la estación seca los guanacos se desplazan a zonas con más pendiente y mayor número de quebradas (formación Los Rastros) donde el riesgo de depredación es mayor. El análisis a escala de comunidades vegetales ha mostrado la preferencia por comunidades con menor cobertura de vegetación en la estación húmeda que en la seca, mostrando probablemente un compromiso entre forrajeo y riesgo de depredación. La identificación de 10 comunidades vegetales representa un esfuerzo por definir de forma más precisa el uso del hábitat del guanaco. Sin embargo, los resultados de los análisis de comunidades, obtenidos con posterioridad, desaconsejan la utilización de tantas clases, dada la dificultad para diferencias *de visu* las comunidades, como se ha comentado más arriba. Asímismo, en un trabajo preliminar, Acebes et al. (2007) determinaron la selección de hábitat estacional (estación húmeda y seca) e interanual (2005-2006) del guanaco utilizando las 6 comunidades vegetales descritas como *proxy* de los hábitats. La ausencia de patrón claro de selección estacional e interanual sino, por el contrario, la detección de un patrón de evitación poco esclarecedor, sugirió la posibilidad de utilizar variables obtenidas a partir de imágenes de satélite para explicar la selección de hábitat del guanaco.

La selección de hábitat del guanaco, estimada a partir de datos procedentes de teledetección y con cinco campañas de trabajo de campo (2005-2007) corcuerda con el análisis de uso del hábitat con datos del primer año de trabajo (2005), con una salvedad: lo que se identificaba como laderas con multitud de quebradas y por tanto más abruptas (formación Los Rastros), con el índice de rugosidad calculado a partir del modelo digital de elevación, son definidas como poco rugosas (pero con pendiente). Por el contrario, las zonas utilizadas por los guanacos durante la estación húmeda se caracterizaban por ser topográficamente llanas y abiertas (Formación Ischigualasto y coberteras cuaternarias) y ahora se indentifican como rugosas (aunque sin pendiente). Esto se debe a las características topográficas del terreno y al procedimiento empleado para el cálculo del índice de rugosidad: una ventana móvil de 3×3, a partir de un tamaño de píxel de 30 m. Sería recomendable trabajar a escalas más grandes para generar modelos de rugosidad más precisos, pero lamentablemente no hay imágenes disponibles de mayor resolución espacial. En cualquier caso, muestra la consistencia de ambos resultados y pone de manifiesto la relevancia de utilizar métodos “asépticos” frente a otros visuales o intuititvos.

La ausencia de diferencias en la selección de hábitat entre los distintos tipos de organización social (grupos familiares, grupos de machos y machos solitarios) puede deberse a la escasa variabilidad de los nichos de forrajeo en este área desértica. A pesar de la baja productividad vegetal, los resultados sin embargo apuntan a que en el compromiso entre maximizar los beneficios de forrajeo y reducir el riesgo de depredación, los guanacos se inclinan por esto último, hasta el punto de ocupar zonas mínimamente productivas en las que satisfacer sus necesidades energéticas, aunque ello les pueda acarrear importantes costes (Creel y Christianson 2008). Así, los guanacos en la estación reproductora (estación húmeda) ocupan zonas menos productivas y de escasa pendiente, especialmente los grupos más grandes. Sin embargo, el compromiso entre baja abundancia de forraje y alta visibilidad no puede ser mantenido en la estación seca, ya que los recursos tróficos son extremadamente escasos (Sinclair y Arcese 1995), lo que obliga a los animales a desplazarse a zonas con mayor cobertura de vegetación, pese al mayor riesgo de depredación. Estos resultados apuntan a que el riesgo de depredación percibido por el guanaco es importante en su selección de hábitat, a pesar de que la densidad del único depredador natural, el puma, es baja en el área de estudio.

El efecto directo de la depredación explica, en parte, la disminución en la ratio chulengo/adulto registrada en la estación seca respecto de la húmeda, mientras que las fluctuaciones interanuales en la ratio podrían deberse a las oscilaciones climáticas entre años. 2005 fue un año especialmente seco, lo que explicaría la reducción en un 55% en la ratio (de 0,56 en la estación húmeda a 0,25 en la seca), afectando también a la condición corporal de los adultos, que se refleja en una menor ratio en la estación reproductora del año siguiente. 2006 fue por el contrario un año húmedo, que se tradujo en una mayor disponibilidad trófica y, por tanto, en una mejor condición corporal de los guanacos, registrándose un decremento del 29% en la ratio chulengo/adulto (de 0,24 en la estación húmeda a 0,17 en la seca), y una recuperación en la estación reproductora del año 2007 (0,43).

Algunos autores comparan la respuesta comportamental de las presas frente al riesgo de depredación al comportamiento que experimentan frente a perturbaciones asociadas a las actividades humanas (Frid y Dill 2002). La respuesta comportamental para minimizar el riesgo de depredación lleva al guanaco a ocupar hábitats minimamente productivos, aun cuando el efecto directo de la depredación sea pequeño (Creel y Christianson 2008). Sin embargo, los resultados de la presente tesis doctoral han mostrado un apreciable acostumbramiento de los guanacos a los turistas que visitan el área protegida, que se traduce en una distancia de huida atenuada en la misma, especialmente hacia los vehículos, que constituyen la perturbación antrópica a la que están más familiarizados los guanacos (Kucera 1976, Miller et al. 2001). El circuito turístico discurre principalmente por la hoyada de Ischigualasto, que constituye la unidad geológica más árida del área protegida. En esta formación es más difícil encontrar rastros de puma, ya que es una zona con escasa vegetación o quebradas donde pueda ocultarse, dado que se trata de un depredador que caza al acecho. Así, la selección de hábitat del guanaco puede ser consecuencia de un efecto combinado. El guanaco quizá podría seleccionar zonas poco productivas y de gran visibilidad para reducir el riesgo de depredación, que son precisamente las zonas por las que discurre el circuito turístico, a la vez que el efecto del turismo puede disuadir al puma, más sensible a la perturbación humana que el guanaco. En otras zonas dentro del área protegida no frecuentadas por turistas hay liebre, que probablemente forme parte de la dieta del puma, junto con la mara y los chulengos.

Un efecto interesante es la mayor tolerancia a la perturbación cuanto mayor sea el tamaño del grupo, o dicho en otras palabras, la disminución de la probabilidad de huida ante un vehículo o peatón cuanto mayor sea el grupo, situación descrita para otros ungulados (Stankowich 2008). En la selección de hábitat del guanaco, también se detecta un efecto en los grupos familiares cuanto mayor es el tamaño del grupo. Por el contrario, sí que se aprecian diferencias en la respuesta comportamental del guanaco en los grupos con crías, que no son detectados en la selección del hábitat.

Otro factor que puede afectar a la población de guanacos estudiada es la presencia de dos especies introducidas, burros asilvestrados y ganado vacuno. Sin embargo, -y al igual que el turismo- los patrones de uso del espacio del guanaco, burro y vaca apuntan a una ausencia de efecto de las especies introducidas sobre la autóctona, al menos en las densidades actuales, probablemente debido a las diferencias en sus requerimientos ecológicos. Así, aunque los análisis de co-ocurrencia a partir de modelos nulos (Gotelli y Entsminger 2001) mostraron segregación entre el guanaco y las especies introducidas y solapamiento entre estas últimas, los resultados de ocurrencia y abundancia, controlando el efecto de la posición geográfica (test de Mantel), no mostraron relación entre el guanaco y las exóticas, mientras que burro y vaca aparecían fuertemente correlacionados. Este solapamiento espacial entre especies exóticas ha sido descrito en otros sistemas fríos y áridos asiáticos (Bagchi et al 2004) y concuerda con el patrón esperable de selección para ambas especies.

Estos patrones se han podido entender mejor mediante los modelos de ocurrencia y abundancia. Así, los modelos de ocurrencia identificaron los patrones de ocupación del guanaco y de las especies exóticas, remarcaron la asociación de las dos especies exóticas y, en consonancia con los anteriores resultados, apuntaron a una ausencia de efecto de las exóticas sobre la presencia de la especie autóctona. Sin embargo, los modelos de abundancia detectaron una abundancia menor de guanaco en presencia del burro. Este efecto podría explicarse como consecuencia de una competencia por interferencia, en el que la especie introducida desplazase a la nativa, aunque es rara entre herbívoros (Prins 2000, Owen-Smith 2002, Ritchie 2002). Así, Stewart et al. (2002) mostraron un reparto de recursos entre la vaca y dos herbívoros silvestres y lo explicaron en base a un desplazamiento espacial de la especie introducida sobre las nativas por competencia. Por el contrario, Sitters et al. (2009) encontraron, un reparto espacial entre la vaca y los herbívoros silvestres sin tener evidencias de que se debiese a un desplazamiento espacial, sino a los distintos requerimientos ecológicos. En otras circunstancias, los mismos autores registraron altas densidades de vacas y herbívoros silvestres sin que éstos se viesen afectados Así, el efecto de la presencia de burro sobre los modelos de abundancia de guanaco debe ser atribuible a diferencias en la selección de hábitat, aunque no son descartables otro tipo de efectos que se manifiesten con un incremento en la densidad de burros. Incrementos en la densidad de población de las tres especies de ungulados que actualmente coexisten podría a obligarles a ocupar hábitats sub-óptimos, especialmente las especies introducidas, aumentando el solapamiento espacial con la especie silvestre.

Otros dos trabajos desarrollados en el área de estudio apuntan en la misma dirección: segregación espacial a pequeña escala y ausencia de interferencia en el uso del hábitat. Así, uno de los estudidos que ha evaluado los daños a cactáceas columnares de gran porte (cardones) ha detectado, a partir de datos de excrementos, una segregación espacial entre burros y guanacos en una misma zona (Malo et al. enviado). El otro, también realizado con excrementos pero con un diseño de muestreo diferente, analizando otras variables ambientales y con aproximaciones analíticas distintas, ha mostrado una ausencia de interferencia de las especies introducidas sobre el guanaco y la asociación del burro y la vaca (Ovejero et al. enviado).

El carácter sedentario de la población de guanacos estudiada, la escasez de recursos tróficos del área de estudio y la estabilidad en los distintos tipos de organización social del guanaco parecen indicar que el sistema de apareamiento basado en la defensa de recursos descrita para la especie (Frankin 1983), puede modificarse hacia un sistema de apareamiento basado en la defensa de las hembras. La reversibilidad entre unas formas y otras de de sistemas de apareamiento ha sido previamente descrita en otros ungulados (Gosling 1991, Apollonio et al. 1992, Carranza et al. 1996, Moehlman 1998), y también podría darse en poblaciones de guanaco que reúnan las mencionadas condiciones. La defensa de hembras a lo largo del año ha sido también descrita para algunos équidos (Linklater 2000, Neuhaus y Ruckstuhl 2002). En general, en ungulados poligínicos que presentan un marcado dimorfismo sexual, los machos forman leks, tienen territorios temporales o harenes en la estación reproductora, pero no defienden a las hembras frente a rivales fuera del periodo reproductivo (Emlen y Oring 1977, Clutton-Brock 1989), sino que los dos sexos se segregan (Main et al. 1996, Ruckstuhl y Neuhaus 2000).

Los escasos trabajos en los que se ha analizado el comportamiento territorial de guanaco se han realizado en sistemas más productivos, sujetos a fuertes oscilaciones climáticas interestacionales, en los que los animales realizan migraciones de corta distancia y forman grupos mixtos fuera del periodo reproductivo (Ortega y Franklin 1995, Young y Franklin 2004). Por el contrario, la población de guanacos del área de estudio no comparte ninguna de esas características, siendo más parecida a otras poblaciones fragmentadas y aisladas del Desierto del Monte (Sosa y Sarasola 2005). Hay otro dato que apoya la idea de un sistema de apareamiento basado en la defensa de las hembras: en otras poblaciones se ha estimado que el porcentaje de grupos familiares entre las distintas estructuras sociales es del 31% (Puig y Videla, 1995), mientras que el que se ha registrado en este trabajo es del 63%, lo que apunta a la estabilidad de los grupos familiares a lo largo del año. Hay, sin embargo, un rasgo que parece bastante conservativo en la especie: el tamaño de los grupos familiares y los grupos de machos (Puig y Videla 1995, Sosa y Sarasola 2005).

Por último, la estimación de la población en menos de 400 guanacos alerta del riesgo de desaparición, por estar en el rango de tamaños mínimos viables (Caughley y Sinclair 1994). Sin embargo, la densidad estimada (0,1-0,7 indiv./Km^2) es similar a la de otras poblaciones de guanacos en áreas de Argentina fuera de la Patagonia (<1 indiv./Km^2, Baigún et al. 2008). En cualquier caso, los sistemas desérticos como el área de estudio tienen escasa disponibilidad de forraje, tal y como han mostrado el ánalisis de comunidades y el bajo índice de vegetación registrado (NDVI=0,1), lo que limita la densidad de guanacos (Hopcraft et al. 2010). Esta situación obliga al guanaco a tener áreas de campeo más amplias para satisfaces sus requerimientos tróficos en la estación seca, realizando desplazamientos de corta distancia a otras zonas periféricas más productivas (Acebes et al. 2007). Algunas de estas zonas quedan fuera de la influencia turística y por tanto los guanacos son más vulnerables frente a la caza furtiva.

En definitiva, el problema de conservación de esta población de guanacos es su pequeño tamaño poblacional y su confinamiento por presiones antrópicas, ya que la ratio chulengo/adulto registrada y la densidad estimada están dentro del rango de otras poblaciones, y el efecto de las especies de ungulados introducidos es pequeño.

Aportaciones a la conservación y gestión de la especie

Con excepción de las poblaciones del sur de la Patagonia, el resto de poblaciones de guanaco se encuentran fragmentadas y aisladas, como la población que ha sido objeto de estudio en la presente tesis doctoral. Una de sus mayores amenazadas sigue siendo la caza furtiva, especialmente en el centro y norte de Argentina, quedando las poblaciones de guanaco confinadas a unos cuantos espacios protegidos. Sería por tanto necesaria la creación de nuevas áreas protegidas que alberguen poblaciones de guanaco, especialmente en el Desierto del Monte, donde la superficie protegida es menor del 4% (Pol et al. 2006) y representa el segundo bioma en abundancia del guanaco, después del patagónico (Baldi et al. 2008). En estas áreas el guanaco puede sufrir nuevas perturbaciones derivadas de la presencia de turistas, por lo que es necesario evaluar el posible impacto. En esta tesis se han empleado dos medidas complementarias y sencillas para evaluar el efecto de las actividades turísticas. El guanaco es una especie que ha mostrado cierta tolerancia al turismo, aunque superados determinados umbrales (más de 250 turistas al día) se ha mostrado sensible, por lo que sería recomendable llevar a cabo nuevos estudios en escenarios futuros de incremento de turistas. La habituación del guanaco puede tener consecuencias negativas para la especie, ya que de desplazarse a zonas fuera de los espacios protegidos sería más vulnerable a la caza furtiva que, como ya se ha comentado, constituye una de las principales amenazas de la especie, aunque las ventajas de declarar nuevos espacios protegidos que atraigan a turistas es si duda beneficioso para la conservación de la especie.

Por otra parte, los resultados de esta tesis apuntan a una aparente coexistencia del guanaco con especies ganaderas siempre que se encuentren en bajas densidades. Esto es importante porque en estas zonas muchas de las tierras son comunales, y la ganadería vacuna y caprina constituye en ocasiones la principal fuente de ingresos de las familias del campo, mientras que el burro sigue siendo el animal de trabajo. Por el contrario, en la Patagonia las tierras pertenecen a grandes terratenientes y la ganadería ovina es el principal motor económico de la región. Si se produjese un incremento en la densidad de especies introducidas debería ir acompañado de nuevos trabajos y si fuera necesario, de medidas activas de gestión sobre dichas especies.

Unas breves notas a modo de cierre

Con los antecedentes existentes antes del inicio de presente trabajo de investigación y ante la necesidad de realizar nuevas aportaciones en la ecología del guanaco en zonas extremadamente áridas, nace esta tesis doctoral. Hay además una motivación adicional: los ecólogos y zoólogos europeos y norteamericanos han estudiado profusamente los ungulados de distribución holártica y los ungulados africanos. En el caso de los primeros la razón puede estar en la proximidad geográfica y en el interés que sin duda suscitan las especies que habitan en nuestro entorno. En cuanto a los ungulados africanos, las motivaciones pueden ser múltiples; desde factores históricos relacionados con la colonización de África (en el caso de los europeos), a otros meramente científicos. Y no es de extrañar, dado el fascinante ensamblaje de ungulados de este continente que ha dado lugar a buena parte de las teorías sobre la ecología de ungulados que se conocen hoy en día, algunas de las cuales quedaron expuestas sucintamente en la introducción y constituyen el eje que vertebra la presente tesis doctoral.

Como quiera que sea, lo cierto es que los científicos norteamericanos y europeos (especialmente estos últimos) han prestado escasa atención a los camélidos del Nuevo Mundo, pese a contar con estimulantes testimonios, algunos de índole naturalista. Así, el mismísimo Charles Darwin en su *Diario de un naturalista alrededor del mundo* se refería al guanaco como “un animal elegante, de cuello largo y esbelto y finas patas”, mientras que el prestigioso zoólogo y paleontólogo español, Ángel Cabrera, lo describía como un “animal airoso y gallardo” (1935). Y contamos también con testimonios de la antropología socio-cultural. E. Lucas Bridges en su fabuloso libro *El último confín de la Tierra* (2008) relata cómo los *onas*, los extintos y temidos habitantes de Tierra de Fuego por los *yaganes* y *alacalufes*, se vestían con las pieles de los guanacos que ellos mismos cazaban. Y parece atribuírsele a la cultura precolombina Diaguita, distribuida por el noroeste argentino y el Norte Chico (Chile), la existencia de un ser mitológico, *Coquena*, que velaba por la seguridad de guanacos y vicuñas en la Puna, castigando a aquellos hombres que los cazaban irresponsablemente y premiando con ofrendas a aquellos pastores que los protegían.

Así, la presente tesis tiene una clara vocación científica, queriendo contribuir al conocimiento de la ecología del guanaco, pero constituye, sin duda, un guiño a la actualmente denostada Historia Natural (por determinados círculos y editoriales científicos). Espero que, a lo largo de estas páginas, se haya aportado conocimiento valioso de este ‘elegante, gallardo y airoso animal’, como dijeran C. Darwin y A. Cabrera, y que además contribuya a una mejor gestión y conservación de la especie, para perpetuar el legado de *Coquena*.

CONCLUSIONES

1. La vegetación del Monte hiperárido argentino, como la de otros desiertos templados, se estructura en gradientes, por lo que resulta difícil diferenciar comunidades discretas de plantas dada la gran heterogeneidad dentro y entre dichas comunidades.
2. Los dos principales factores que determinan la estructuración en gradientes de las comunidades vegetales son la disponibilidad hídrica y las características edáficas.
3. La disponibilidad trófica del área de estudio es escasa, siendo en su mayoría vegetación leñosa de porte arbustivo y cactáceas, por lo que es esperable que los ungulados se comporten fundamentalmente como ramoneadores y, excepcionalmente, durante el periodo de lluvias estival como pastadores-ramoneadores, momento en el que crecer algunas herbáceas, poco importantes en términos de biomasa vegetal total.
4. La población de guanacos del área de estudio, estimada en menos de 400 individuos, es pequeña y está probablemente aislada, como las otras poblaciones del centro y norte de Argentina.
5. La densidad poblacional, sin embargo, se encuentra dentro del rango descrito para la especie en poblaciones no patagónicas, a pesar de encontrarse en una zona extremadamente árida.
6. El uso del hábitat de la especie está determinado tanto por factores abióticos, definidos por las características topográficas del terreno, como por la disponibilidad de forraje.
7. La presencia de especies introducidas en el espacio protegido no parece influir en los patrones de uso del espacio del guanaco, probablemente debido a las diferencias en los requerimientos ecológicos de las especies, aunque esta situación puede cambiar si se produce un incremento en la densidad de las especies introducidas, especialmente en la del burro.
8. Los patrones de uso del espacio del guanaco están fuertemente asociados a variables bióticas y abióticas, tales como escasa cobertura vegetal, sustrato rocoso y variables de influencia humana, apareciendo en áreas alejadas de los pueblos. Por el contrario, los patrones de uso del espacio de las especies introducidas, que aparecen estrechamente asociadas, están determinados por zonas con mayor densidad de vegetación y más productivas y más próximas al hombre.

9. La selección de hábitat del guanaco dentro del espacio protegido está determinada por la disponibilidad de forraje y el riesgo de depredación. En la estación reproductora los guanacos seleccionan hábitats mínimamente productivos, probablemente para reducir el riesgo de depredación, aunque en la estación seca la escasez de recursos tróficos les obliga a desplazarse a zonas más productivas y con mayor riesgo de depredación. Este efecto es más acusado en grupos familiares, no detectándose, sin embargo, diferencias en función del número de crías.

10. La estabilidad en los distintos tipos de organización social del guanaco y la escasez de recursos da pie a pensar el sistema de apareamiento basado en la defensa de recursos descrita para la especie pueda modificarse hacia una defensa de las hembras, ya que no existen recursos abundantes económicamente defendibles por los machos.

11. Los datos demográficos apuntan a unas tasas de natalidad bastante altas, aunque las duras condiciones ambientales y el efecto de la depredación provocan un descenso de la crías en un 50 % en el mismo año.

12. El tamaño de los grupos familiares se encuentra dentro del rango descrito para la especie, lo que parece apuntar a que se trata de un rasgo bastante conservativo en el guanaco, modificándose con densidades muy altas.

13. El guanaco muestra una tolerancia al uso turístico del espacio protegido, que se manifiesta en una habituación a la perturbación generada por los visitantes, siendo más tolerantes a la aproximación de vehículos que a peatones.

14. La probabilidad de huida es menor cuanto más grande es el tamaño del grupo, lo que parece indicar que la percepción del riesgo disminuye como consecuencia del sentimiento de protección que confiere el grupo. En los grupos con crías las distancias de huida se incrementan probablemente porque la valoración del riesgo es mayor al ser las crías más vulnerables.

15. A partir de un determinado umbral en el número de visitantes, estimado en 250, los guanacos parecen reaccionar negativamente, manifestándose en una reducción en la frecuencia de observación de animales.

REFERENCIAS BIBLIOGRÁFICAS

Acebes P, Malo JE, Suárez F, Borghi CE, Giannoni SM y Traba, J. 2007. Space use in desert areas by guanaco (*Lama guanicoe*) and its seasonal dependence on the most productive patches. En: Bunce RGH, Jongman RHG, Hojas L y Weel S (eds). 25 years Landscape Ecology: Scientific Principles in Practice. Proceedings of the 7th IALE World Congress. Pp. 371-372. Wageningen, The Netherlands.

Apollonio M, Festa-Bianchet M, Mari F, Mattioli S y Sarno B. 1992. To lek or not to lek: mating strategies of male fallow deer. Behavioural Ecolology 3: 25-31.

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

Baigún RJ, Bolkovic ML, Aued MB, Li Puma MC y Scandalo RP. 2008. Manejo de fauna silvestre en la Argentina, primer censo nacional de camélidos silvestres al norte del río Colorado. Dirección de Fauna Silvestre, Secretaría de Ambiente y Desarrollo Sustentable. Buenos Aires, Argentina.

Bailey DB, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM y Sims PL. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49: 386-400.

Baldi R, Albon S y Elston D. 2001. Guanacos and sheep: evidence for continuing competition in arid Patagonia. Oecologia 129: 561-570.

Baldi B, Lichtenstein G, González B, Funes M, Cuéllar E, Villalba L, Hoces D y Puig S. 2008. Lama guanicoe. En: IUCN 2010. IUCN Red List of Threatened Species. <www.iucnredlist.org>

Bridges EL. 2008. El último confín de la Tierra. Editorial Sudamericana, Argentina.

Cabrera A. 1935. Historial Natural. Vida de los animales, de las plantas y de la tierra. Instituto Gallach de librería y ediciones. Barcelona.

Campos CM, Peco B, Campos VE, Malo JE, Giannoni SM and Suárez F. 2008. Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of *Prosopis* seeds. Seed Science Research 18: 91-100.

Carranza J, Fernandez-Llario P y Gomendio M. 1996. Territoriality in rutting red deer. Ethology 102: 793-805.

Clutton-Brock TH. 1989. Mammalian mating systems. Proceedings of the Royal Society of London 236: 339-371.

Creel S y Christianson D. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23: 194-201.

Emlen ST y Oring LW. 1977. Ecology, Sexual Selection and the Evolution of Mating Systems. Science 197: 215-223.

Frid A y Dill LM. 2002. Human-caused disturbance stimuli as a form of predation risk.Conservation Ecology 6(1): 11. [online] URL: http://www.consecol.org/vol6/iss1/art11

Gotelli NJ y Entsminger GL. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Incorporation and Kesey-Bear. URL: http://homepages.together.net/~gentsmin/ecosim.htm

Caughley G y Sinclair ARE. 1994. Wildlife ecology and management. Blackwell Scientific Publications, Massachusetts. pp. 334.

Franklin WL. 1983. Contrasting socioecologies of South American's wild camelids: the vicuña and guanaco. En: Eisenberg JF y Kleiman DG (eds). Advances in the Study of Mammalian Behavior. Pp. 573-629. Special Publication No. 7. American Society of Mammalogists, Allen Press, Lawrence, Kansas.

Gosling LM. 1991. The alternative mating strategies of male topi, *Damaliscus lunatus*. Applied Animal Behaviour Science 29: 107-119.

Hopcraft JGC, Olff H y Sinclair ARE. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology and Evolution 25: 119-128.

Kucera E. 1976. Deer flushing distance as related to observers mode of travel. Wildlife Society Bulletin 4: 128-129.

Linklater WL. 2000. Adaptive explanation in socio-ecology: lessons from the Equidae. Biological Reviews of the Cambridge Philosophical Society 75: 1-20.

Main MB, Weckerly FW y Bleich VC. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77: 449-461.

Miller SG, Knight RL y Miller CK. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29: 124-132.

Moehlman PD. 1998. Feral asses Equus africanus: intraspecific variation in social organization in arid and mesic habitats. Applied Animal Behaviour Science 60: 171-195.

Neuhaus P y Ruckstuhl KE. 2002. The link between sexual dimorphism, activity budgets, and group cohesion: the case of plain zebra (*Equus burchelli*). Canadian Journal of Zoology 80: 1437-1441.

Ortega IM and Franklin WL. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural 68: 489-500.

Owen-Smith N. 2002. Adaptative herbivore ecology. From resources to populations in variable environments. Wits University Press, Johannesburg, South Africa.

Pol RG, Camín SR y Astié AA. 2006. La situación ambiental de la Ecorregión del Monte. En: Brown A, Martinez Ortiz U, Acerbi M and Corcuera J (eds). La situación Ambiental Argentina. Pp. 227-239. Fundación Vida Silvestre Argentina, Argentina.

Prins HHT y Olff H. 1998. Species richness of African grazer assemblages: towards a functional explanation. En: Newbery D, Prins HHT y ND Brown (eds). Dynamics of tropical communities. Pp. 448-490. Blackwell, Oxford.

Prins HHT. 2000. Competition between wildlife and livestock in Africa. En: Prins HHT, Grootenhuis JG y Dolan TT (eds). Wildlife conservation by sustentable use. Pp. 51-80. Kluwer Academic Publishers, Boston.

Puig S and Videla F. 1995. Comportamiento y organización social del guanaco. In: Puig S (ed). Técnicas para el manejo del guanaco. Pp. 97-118. IUCN, Buenos Aires, Argentina.

Puig S, Videla F, Cona MI y Monge A. 2001. Use of food availability by guanacos (*Lama guanicoe*) and livestock in northern Patagonia (Mendoza, Argentina). Journal of Arid Environments 47: 291-308.

Putman RJ. 1996. Competition and resource partitioning in temperate ungulate assemblies. Chapman and Hall, London.

Raedeke K y Simonetti J. 1988. Food habits of *Lama guanicoe* in Atacama desert of northern Chile. Journal of Mammalogy 69: 198-201.

Ritchie ME. 2002. Competition and coexistence in mobile animals. En: Sommer U y Worm B (eds). Competition and coexistence. Pp. 127-141. Springer, Berlin.

Sinclair ARE y Arcese P. 1995. Population consequences of predation sensitive foraging: the Serengeti wildebeest. Ecology 76: 882-891.

Sinclair ARE, Mduma S y Brashares JS. 2003. Patterns of predation in a diverse predator prey system. Nature 425: 288-290.

Sitters J, Heitkönig IMA, Holmgren M y Ojwang GSO. 2009. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. Biological Conservation 142: 738-750.

Sosa RA y Sarasola JH. 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.

Stankowich T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141: 2159-2173.

Stewart KM, Bowyer RT, Kie JG, Cimon NJ y Johnson BK. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83: 229-244.

Voeten MM y Prins HHT. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120: 287-294.

Young JK y Franklin WL. 2004. Territorial fidelity of males guanacos in the Patagonia of southern Chile. Journal of Mammalogy 85: 72-78.