

Pablo Acebes*, Juan E. Malo, Ramiro Ovejero and Juan Traba

Sympatric guanacos and livestock share water resources in drylands of Argentina

DOI 10.1515/mammalia-2014-0074

Received May 21, 2014; accepted October 13, 2015

Abstract: There is growing concern about the effect of livestock on wild ungulate populations, particularly in arid ecosystems, where waterholes are an extremely scarce resource, around which animals tend to gather, primarily in the dry season. This situation is worrying in South American deserts, where guanaco is the native species that often shares trophic and water resources with livestock from local communities, even inside protected areas. We assess through general linear modeling (GLM) the use of waterholes by guanaco and two introduced species, free-ranging cattle and feral donkeys, during the summer-wet and winter-dry seasons, in an arid, water-limited region in northwestern Argentina. Waterholes were more intensively used in the dry than the wet season by all three herbivores. However, introduced ungulates did not use all of the waterholes, whereas guanaco used them all with equal intensity, which points to an apparent absence of interference probably due to the low density of the introduced species. Nevertheless these results could mask negative effects regarding the risk of parasite transmission, the under-use of one of the waterholes, and the risk related to increasing livestock density in a near future. Therefore, it would be advisable to make long-term monitoring to prevent potentially negative effects on guanacos.

Keywords: cattle; coexistence; feral donkeys; ungulates; waterholes.

Introduction

Growing concern about the effects of free-ranging livestock on wildlife has arisen in various ecosystems around the world (Voeten and Prins 1999, Bagchi et al. 2004; Mishra

et al. 2004, Young et al. 2005, Yoshihara et al. 2008, Sitters et al. 2009). This concern is particularly evident in arid ecosystems, where waterholes are limited resources linked to biodiversity conservation (Leeuw et al. 2001, Attum et al. 2009, Sitters et al. 2009) and are often used by low density populations found at their extreme of the species' distribution. In these ecosystems, wildlife distribution is thus related to surface-water availability, especially during the dry season, when animals drink more frequently to meet their body requirements (Western 1975). These waterholes are often used by livestock of the surrounding human communities as well, with potential negative consequences on wildlife populations (Western 1975, Leeuw et al. 2001, Sitters et al. 2009). Several authors have shown that cattle (*Bos taurus* Linnaeus), horses (*Equus ferus caballus* Linnaeus) and feral donkeys (*Equus asinus* Linnaeus) can compete with wild ungulates for water resources in arid and semiarid ecosystems, mostly in dry periods, by gathering around the remaining waterholes, apparently displacing wild ungulates and reducing availability of the resource (Leeuw et al. 2001, Ostermann-Kelm et al. 2008, Attum et al. 2009).

In drylands of South America, it is frequent to find the guanaco (*Lama guanicoe* Müller), the largest and most widely distributed wild herbivore (Franklin 1983), in sympatry with livestock, mainly sheep (*Ovis aries* Linnaeus), and to a lesser extent with cattle and feral donkeys (pack animals abandoned by herders). Various authors have shown the existence of competitive processes of sheep on the native species (Baldi et al. 2001, Puig et al. 2001), regarding such competition as one of the major causes of its continental population decline (Baldi et al. 2008). Ovejero et al. (2011) and Acebes et al. (2012) have demonstrated that habitat overlap among guanacos, feral donkeys and free-ranging cattle in the Argentinean Monte Desert is relatively low, with differences being found in habitat selection and space use between the wild and the introduced species. While livestock species tended to appear together, these authors have shown that the guanaco had a wider niche breadth and its distribution was independent from the former species, so potential for competition was low (Ovejero et al. 2011, Acebes et al. 2012), although a recent study in the same area has shown that guanacos and donkeys overlap in trophic resources, specially in the dry season, when food resources are less

*Corresponding author: Pablo Acebes, Terrestrial Ecology Group-TEG. Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, C/. Darwin, 2, E-28049 Madrid, Spain, e-mail: pablo.acebes@uam.es

Juan E. Malo and Juan Traba: Terrestrial Ecology Group-TEG. Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, C/. Darwin, 2, E-28049 Madrid, Spain

Ramiro Ovejero: Biodiversity Research Group (GIB), IADIZA, CCT MENDOZA, CONICET, CC 507, 5500 Mendoza, Argentina

abundant (Reus et al. 2014). However, little is known about the possible interference on the use of waterholes in the wet and dry seasons, especially in the last one, when the water resource is extremely scarce and can be a limiting factor for the survival of wildlife species. These ungulates differ in their water requirement: guanacos and donkeys are well adapted to low-quality arid environments and to the shortage of water resources (Franklin 2011, Rubenstein 2011), while cattle show higher dependence on water sources for subsistence (Groves et al. 2011). In addition, the donkey is a species that is expanding in arid ecosystems of South America, and given that territorial males can make an active defense of waterholes (Moehlman 1998), this could affect the guanaco's use of waterholes.

In the present study, we assess the use of perennial water sources by three ungulate species that occur in sympatry: guanacos, feral donkeys and free-ranging cattle, in the wet and dry seasons, in an arid, water-limited region of Northwestern Argentina (Monte Desert biome), with the aim to evaluate (i) if the three species overlap in the use of waterholes and/or (ii) if the use of waterholes by livestock provokes the under-use or even the avoidance of waterholes by guanacos. The guanaco population in this region is small (probably <400 individuals), and of interest due to its location in the most arid part of the Monte Desert (Acebes et al. 2010a), where guanaco seems to select the driest areas to reduce the risk of predation by puma (Acebes et al. 2013). The two introduced species show low densities and, overall, lower than the native one (Acebes et al. 2012), estimated to be 0.38 guanacos/km² (Acebes et al. 2010a).

We expect that (i) during the dry season, cattle and donkeys will do a more intense use of permanent waterholes, which represent the only and small watering points in the study area, and guanacos will remain away from these waterholes as a result of, or to avoid livestock, which will be therefore reflected in a lesser use of waterholes by guanacos; (ii) during the wet season, as a consequence of a higher availability of drinking points in the landscape (permanent+ephemeral waterholes), cattle and donkeys will not gather in the surroundings of permanent waterholes, so their use by guanacos will not be constrained by the presence of the introduced ungulates.

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. Ischigualasto PP (29°55'S, 68°05'W) covers 60,369 ha at an altitude of approximately 1300 m above sea level, with a desert climate of 80–140 mm annual summer rainfall (November to February), mean annual temperature below 18°C and a wide thermal regime (-10°C to 45°C, Poblete and Minetti 1999). The predominant vegetation is sparse xeric shrubland (<20% of plant cover), dominated by species of Zygophyllaceae (*Larrea* spp., *Zuccagnia punctata*), Fabaceae (*Prosopis* spp., *Cercidium praecox*, *Geoffroea decorticans*) and Chenopodiaceae (*Atriplex* spp. and *Suaeda divaricata*). Cactaceae (*Echinopsis* spp., *Tephrocactus* spp. and *Opuntia sulphurea*) and Bromeliaceae (*Deuterocohnia longipetala* and *Tillandsia* spp.) are also frequent but to a lesser extent (see Acebes et al. 2010b for a description of plant communities in the area).

The main land use in the surroundings is extensive livestock ranching of cattle and goats although in low numbers. Inside the protected area, three ungulate species move freely: one wild species, guanaco, and two introduced species, feral donkeys and free-ranging cattle. One village about 20 km SE from the protected area is the major source of cattle and donkeys. Feral donkeys are a mixture of old animals abandoned by herders and/or their offspring, while cattle range throughout the territory without herders. Only once a year herders get into the park to mark newborn calves, therefore herder's presence do not alter the use of waterholes by guanacos.

In this protected area there are three permanent natural waterholes (named WHA, WHB and WHC) from 4 to 15 m² in size, on silt or rocky substrates. These small waterholes represent the only source of water in the area during the dry season. They are placed along a distance and aridity gradient to the nearest village: WHA is at 17 km (least arid area), WHB at 25 km and WHC at 32 km (most arid area), although all three of them are potentially usable by the three ungulate species. Cacti, some grasses and shrubs are found around WHA, while there are only scant shrubs in the surroundings of WHB. In WHC no plant cover occurs. In contrast, in the wet season, temporary waterholes can be found along rivers and creeks after rainfall events. No ranches are found between the village and waterholes.

Use of waterholes

The study was conducted in the 2006 summer-wet (February) and winter-dry seasons (August). To determine the use of waterholes by all three ungulates, in both seasons we set up 10 plots of 50×20 m (sampling units) within a

100 m radius around each of the three waterholes, thus completing a total of 60 plots (60,000 m²). At each season ten plots were surveyed in each waterhole within a radius of 100 m around waterholes. Four plots were located at the four cardinal points at a distance of 2 m from the waterholes. The rest of them were randomly placed at least 5 m separated each other within the 100 m radius. The use of waterholes by guanaco, donkey and cattle was recorded from fecal pellets within each plot: scattered pellets were scored as 1, dung heaps as 2 and accumulated dung heaps were scored as 3. These data were used to obtain a use index (UI) per transect aimed at having an estimate of local frequentation by herbivores, which was determined as follows:

$$UI = a + 2b + 3c$$

where a is the number of scattered deposits, b is the number of dung piles or pellet groups, and c the number of dung aggregations. This index was formulated to measure dung abundance in a (approximately) logarithmic scale since counting the actual number of depositions in areas of animal concentration (e.g. latrines, resting areas) would be an unfeasible task. Bleached pellets were ignored, to ensure that counts reflected recent presence (Acebes et al. 2012). Fecal counting has been broadly used in ecology as an indirect indicator of abundance, habitat use and spatial segregation in medium to large-sized herbivores, especially when species densities are low and it is difficult to determine relative abundances from animals observed by transect or fixed-point counts (Bailey and Putman 1981, Putman 1984).

Statistical analyses

In order to assess the use of waterholes (WHA, WHB and WHC) by the species within and between seasons (dry and wet season), several models were built and compared. As dung types and defecation rates vary among the species, three models were performed, one for each of the species. The response variable was the use index, and the predictor variables were season, waterhole, and the interaction season×waterhole. All model comparisons were made using Akaike information criterion (AIC) (Zuur et al. 2009). We first built a generalized mixed model (GLMM) in which plots were nested within waterhole, which was a random factor, and assuming a negative binomial distribution of residuals (NB). Then, we built a similar generalized linear model (GLM, i.e. without the random effect) and compared the fit of this model to the previous one. Finally, after selecting the model that best fitted the data,

we used maximum likelihood estimator (logLik) and AIC to simplify the model. Prior to these analyses, Negative binomial, Poisson and zero inflated Poisson distribution models were compared, being NB the best models. All analyses were performed using R 3.1.1 (R Development Core Team 2014) and the MASS, lme4 and lmerTest packages (Zeileis and Hothorn 2002, Zeileis et al. 2008, Bates et al. 2014).

Results

Comparison between GLMM and GLM showed the last one as a better model for the three species: guanaco (GLMM, AIC=220.2; GLM, AIC=218.2), donkey (GLMM, AIC=95.4; GLM, AIC=94.3) and cattle (GLMM, AIC=114.0; GLM, AIC=102.2). After simplification, the best model to predict the use of waterholes by guanacos (logLik=-102.1, AIC=210.2) included season (Table 1). Guanacos only showed different use of waterholes between seasons, being much more intensive in the dry than in the wet season (Figure 1A). The best model to predict the use of waterholes by donkeys after simplification (logLik=-56.1, AIC=112.1) included season and waterhole (Table 1), indicating differences in waterholes use between seasons, with a much more intense use in the dry season (Figure 1B). In addition, donkeys used exclusively WHA in both the dry and the wet seasons (Figure 1B). In relation to cattle, after simplification the best model to predict the use of waterholes (logLik=-44.3, AIC=98.5) included season and waterhole (Table 1), as cattle used waterholes differently between seasons, being more intense in the dry period (Figure 1C). All waterholes were used in the dry season, being WHA the most intensively used, whereas

Table 1: Results of the simplified GLM negative binomial models to explain the use of waterholes by guanacos, donkeys and cattle in the Ischigualasto Provincial Park (San Juan, Argentina).

Species	Variable	Estimate	SE	Z	p-Value
Guanaco	Intercept	1.214	0.225	5.406	<0.001
	Season [wet]	-1.725	0.383	-4.506	<0.001
Donkey	Intercept	2.190	0.175	12.501	<0.001
	Season [wet]	-2.423	0.409	-5.912	<0.001
	Waterhole [WHB]	-3.871	0.734	-5.283	<0.001
	Waterhole [WHC]	-3.871	0.734	-5.283	<0.001
Cattle	Intercept	1.833	0.435	4.215	<0.001
	Season [wet]	-3.102	0.816	-3.795	<0.001
	Waterhole [WHB]	-3.499	0.916	-3.822	<0.001
	Waterhole [WHC]	-4.186	1.158	-3.614	<0.001

SE, Standard error; Z, statistical value; p, significance of each term.

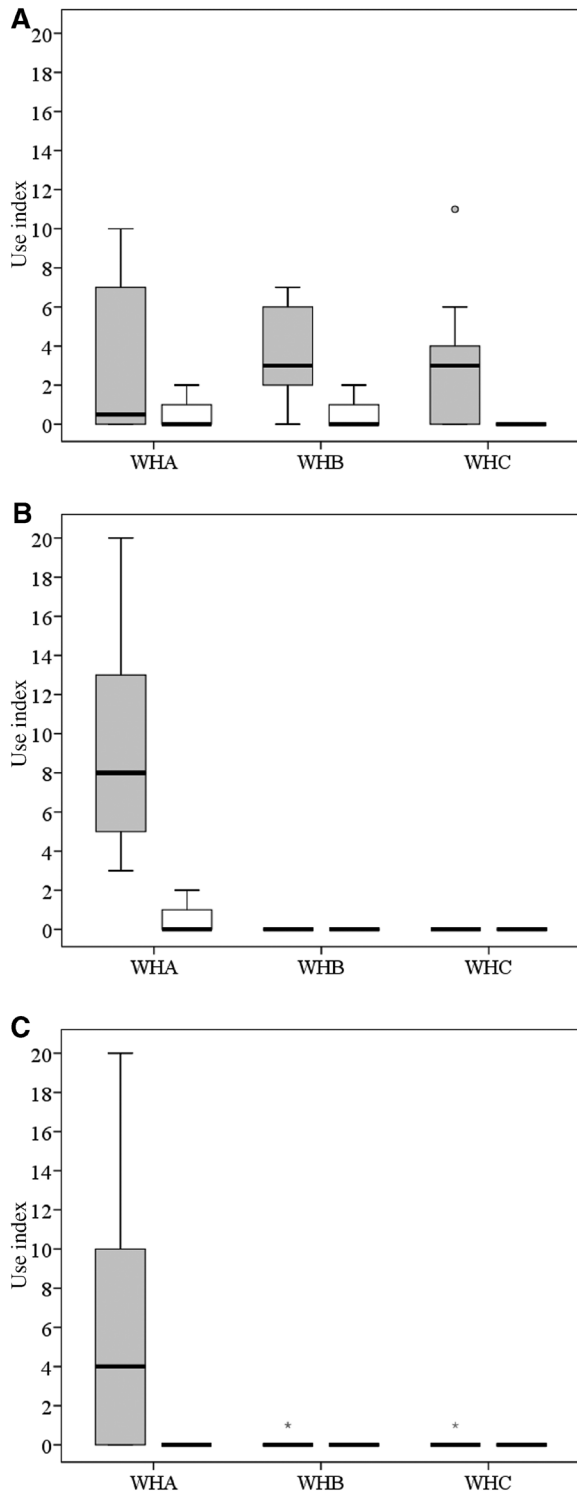


Figure 1: Box-plots indicating the use of waterholes (WHA, WHB, WHC) by guanacos (A), feral donkeys (B) and free ranging cattle (C) in the dry (gray boxes) and wet (white boxes) seasons through dung sampling in the Ischigualasto Provincial Park (San Juan, Argentina). Black lines within the boxes represent the median, while the upper and lower hinges of boxes indicate 75th and 25th percentiles, respectively. The whiskers above and below the boxes indicate the minimum and maximum values.

the use of the other two waterholes was completely anecdotal (Figure 1C). In the wet season, cattle only used WHA, though sparsely (Figure 1C).

Discussion

According to our results, guanaco used the waterholes without apparently being affected by the use of livestock. Because of the shortage of natural waterholes in arid areas, and their importance to wildlife, knowing the likely effect of their use by livestock has major implications for management and conservation. On the whole, the three ungulates made a much more intensive use of waterholes in the dry season. Moreover, the guanaco maintained a similar use of all three waterholes in both seasons, although to a lesser extent during the wet season. Conversely, the introduced species used almost exclusively, and with great intensity, one of the waterholes in the dry season (WHA), whereas the remaining waterholes were barely used. This pattern was replicated in the wet season, albeit much less markedly, and may apparently be explained in both seasons by the shorter distance of WHA to the nearest village, but also due to the aridity, where WHA and its surroundings had sparse plant cover, while the other two waterholes had almost no vegetation, particularly WHC, where no plant cover occurred.

Overall, habitat and diet overlap between wildlife and livestock is often acknowledged as the primary mechanism whereby exploitation competition occurs when these resources are limited, and affects negatively the performance of either or both species (Voeten and Prins 1999, Mishra et al. 2004, Young et al. 2005, Georgiadis et al. 2007). However, some authors also interpret the absence of overlap as a consequence of spatial displacement (i.e. avoidance), and therefore it is also used as evidence of competitive exclusion (Stewart et al. 2002, Hibert et al. 2010). Unlike what was described by other authors for African savannas (Leeuw et al. 2001), the use of waterholes by free-ranging cattle and feral donkeys appears not to affect their use by the native species in this hyper-arid area of Argentina. Thus, because guanacos are distributed over the entire protected area (Acebes et al. 2012), a likely response from them would be under-using the waterhole intensively used by the introduced species, while concomitantly making higher use of the other waterholes, as was reported for the desert bighorn sheep (*Ovis canadensis nelsoni* Merriam) in the presence of feral horses (Ostermann-Kelm et al. 2008). Still, this response did not occur in the area. During the dry season, where the permanent waterholes are the only and scarce water sources, the guanaco made

a relatively intensive use of WHA (the one highly used by cattle and donkeys) as well as the waterholes from which the livestock were absent or where their presence was anecdotal. Moreover, the waterhole intensively used by donkeys and cattle (WHA) showed large accumulations of feces in the dry season, but even under these circumstances guanacos still used it in the same way as they used the other waterholes. Nonetheless, the risk of disease transmission cannot be ruled out (Beldomenico et al. 2003). In the wet season, where other temporary (ephemeral) sources of surface water can be found, the use of the three permanent waterholes dropped considerably in all three species. Consequently, our study provides no evidence of spatial displacement of guanacos by free-ranging cattle and feral donkeys for any of the two seasons. Nevertheless, it could be hypothesized that guanacos under-used WHA, the one with greater plant cover, as a consequence of the intensive use of both donkeys and cattle. Unfortunately, to test this hypothesis an experiment is needed.

Some authors argue that effects on wild ungulates are partly due to the pressure exerted by herders on wildlife and not only by the influence of livestock (Leeuw et al. 2001, Sitters et al. 2009, Burt and Turner 2012), which could account for the detected pattern. However both donkeys and cattle moved freely without being led by herders. In addition, the fact that there were waterholes not used by the introduced ungulates, but indeed used by the native species, which would operate as natural controls in an experimental design, facilitates interpretation of these interspecific relationships.

Our sampling protocol however does not allow us to determine whether some behavioral interference exists, that is, if guanacos avoided waterholes at moments when feral donkeys or free-ranging cattle were present nearby. Other authors have reported temporal partitioning of water resources for desert bighorn sheep and feral horses in North America (Ostermann-Kelm et al. 2008), although we found no agonistic behaviors when the introduced ungulates were near the guanaco (pers. obs.). It is likely, however, that the guanaco increases its rate of vigilance in the presence of livestock, to the detriment of foraging or drinking water.

To conclude, despite these results point to an apparent lack of interference in the use of waterholes, several points with conservation implications can be raised: First, although no evidence of displacement was detected, it could be speculated that guanacos were under-using WHA as a response of its over-use by livestock. Second, an increase in livestock density could have negative effects on the wild population. Third, the potential deleterious effects from the risk of parasite transmission, so that

health studies are needed; hence measures for monitoring and control of the introduced species should be taken, always seeking to involve local communities, with the aim to prevent conflicts between wildlife conservation and sustainable resource use. Getting local people involved in conservation is the only viable option to reduce conflict with livestock and for an effective human stewardship in the vast areas inhabited by the species (Lichtenstein and Carmanchahi 2012).

Acknowledgments: This research was funded by a Biological Conservation project from the BBVA Foundation (INTERMARG Project). Partial support for UAM researchers is provided by the REMEDINAL 3-CM research network (S-2013/MAE-2719). We thank the staff at the Ischigualasto Provincial Park for their collaboration and help, and Nelly Horak for helping us with the English. C. Jaime helped us with statistical analyses with R. This work is dedicated to the memory of Francisco “Quico” Suárez, who helped us in the field work.

References

- Acebes, P., J. Traba, J.E. Malo, R. Ovejero and C.E. Borghi. 2010a. 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., J. Traba, B. Peco, M.L. Reus, S.M. Giannoni and J.E. Malo. 2010b. Abiotic gradients drive floristic composition and structure of plant communities in the Monte Desert. *Rev. Chil. Hist. Nat.* 83: 395–407.
- Acebes, P., J. Traba and J.E. Malo. 2012. Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *J. Arid Environ.* 77: 39–44.
- Acebes, P., J.E. Malo and J. Traba. 2013. Trade-offs between food availability and predation risk in desert environments: the case of polygynous monomorphic guanaco (*Lama guanicoe*). *J. Arid Environ.* 97: 136–142.
- Attum, O., S.K. El Noby and I.N. Hassan. 2009. The influence of landscape characteristics and anthropogenic factors on waterhole use by vulnerable Nubian ibex *Capra nubiana*. *Oryx* 43: 564–567.
- Bagchi, S., C. Mishra and Y.V. Bhatnagar. 2004. Conflicts between traditional pastoralism and conservation of Himalayan ibex (*Capra sibirica*) in the Trans-Himalayan mountains. *Anim. Conserv.* 7: 121–128.
- Bailey, R.E. and R.J. Putman. 1981. Estimation of fallow deer (*Dama dama*) populations from faecal accumulation. *J. Appl. Ecol.* 18: 697–702.
- Baldi, R., S. Albon and D. Elston. 2001. Guanacos and sheep: evidence for continuing competition in arid Patagonia. *Oecologia* 129: 561–570.
- Baldi, B., G. Lichtenstein, B. González, M. Funes, E. Cuéllar, L. Villalba, D. Hoces and S. Puig. 2008. *Lama guanicoe*.

- In: IUCN 2013. IUCN Red List of Threatened Species Version 2013.2 <www.iucnredlist.org>. Downloaded on 23 February 2014.
- Bates, D., M. Maechler, B. Bolker and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- Beldomenico, P.M., M. Uhart, M.F. Bonoa, C. Marull, R. Baldi and J.L. Peralta. 2003. Internal parasites of free-ranging guanacos from Patagonia. *Vet. Parasitol.* 118: 71–77.
- Burt, B. and M.D. Turner. 2012. Clarifying competition: the case of wildlife and pastoral livestock in East Africa. *Pastoralism: Research, Policy and Practice* 2: 9.
- Franklin, W.L. 1983. Contrasting socioecologies of South American wild camelids: the vicuña and the guanaco. In: (J.F. Eisenberg and D.G. Kleiman, eds.) *Advances in the study of mammalian behavior*. Spec. Publ. Am. Soc. Mammal. 7: 573–629.
- Franklin, W.L. 2011. Family Camelidae (Camels). In: (D.E. Wilson and R.A. Mittermeier, eds.) *Handbook of the mammals of the World*, Vol. 2 – Hoofed mammals. Lynx Edicions, Barcelona, Spain. pp. 206–246.
- Georgiadis, N.J., J.G.N. Olwero, G. Ojwang' and S.S. Romañach. 2007. Savanna herbivore dynamics in a livestock-dominated landscape: dependence on land use, rainfall, density, and time. *Biol. Conserv.* 137: 461–472.
- Groves, C., D. Leslie, B. Huffman, R. Valdez, K. Habibi, P. Weinberg, J. Burton, P. Jarman, S. Hedges and W. Robichaud. 2011. Family Bovidae (Hollow-horned Ruminants). In: (D.E. Wilson and R.A. Mittermeier, eds.) *Handbook of the mammals of the World*, Vol. 2 – Hoofed mammals. Lynx Edicions, Barcelona, Spain. pp. 444–779.
- Hibert, F., C. Calenge, H. Fritz, D. Maillard, P. Bouché, A. Ipavec, A. Convers, D. Ombredane and M.-N. de Visscher. 2010. Spatial avoidance of invading pastoral cattle by wild ungulates: insights from using point process statistics. *Biodivers. Conserv.* 19: 2003–2024.
- Leeuw, J., M.N. Waweru, O.O. Okello, M. Maloba, P. Nguru, M.Y. Said, H.M. Aligula, I.M.A. Heitkönig and R.S. Reid. 2001. Distribution and diversity of wildlife in northern Kenya in relation to livestock and permanent water points. *Biol. Conserv.* 100: 297–306.
- Lichtenstein, G. and P. Carmanchahi. 2012. Guanaco management by pastoralists in the Southern Andes. *Pastoralism: Research, Policy and Practice* 2: 16.
- Mishra, C., S.E. Van Wieren, P. Ketner, I.M.A. Heitkönig and H.H.T. Prins. 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *J. Appl. Ecol.* 41: 344–354.
- Moehlan, P.D. 1998. Feral asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. *Appl. Anim. Behav. Sci.* 60: 171–195.
- Ostermann-Kelm, S., E.R. Atwill, E.S. Rubin, M.C. Jorgensen and W.M. Boyce. 2008. Interactions between feral horses and desert bighorn sheep at water. *J. Mammal.* 89: 459–466.
- Ovejero, R.J.A., P. Acebes, J.E. Malo, J. Traba, M.E. Mosca Torres and C.E. Borghi. 2011. Lack of feral livestock interference on native guanaco during the dry season in a South American desert. *Eur. J. Wildl. Res.* 57: 1007–1015.
- Poblete, A.G. and J.L. Minetti. 1999. Atlas climatológico de San Juan. Instituto de Geografía Aplicada, UNSJ. CD-ROM Edition. INGENO, San Juan. Argentina.
- Puig, S., F. Videla, M.I. Cona and S.A. Monge. 2001. Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patagonia (Mendoza, Argentina). *J. Arid Environ.* 47: 291–308.
- Putman, R.J. 1984. Facts from faeces. *Mammal Rev.* 14: 79–97.
- R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Reus, M.L., F.M. Cappa, N. Andino, V.E. Campos, C. de los Ríos and C.M. Campos. 2014. Trophic interactions between the native guanaco (*Lama guanicoe*) and the exotic donkey (*Equus asinus*) in the hyper-arid Monte desert (Ischigualasto Park, Argentina). *Stud. Neotrop. Fauna Environ.* 49: 159–168.
- Rubenstein, D.I. 2011. Family Equidae (Horses and relatives). In: (D.E. Wilson and R.A. Mittermeier, eds.) *Handbook of the mammals of the World*, Vol. 2 – Hoofed mammals. Lynx Edicions, Barcelona, Spain. pp. 106–143.
- Sitters, J., I.M.A. Heitkönig, M. Holmgren and G.S.O. Ojwang. 2009. Herded cattle and wild grazers partition water but share forage resources during dry years in East African savannas. *Biol. Conserv.* 142: 738–750.
- Stewart, K.M., R.T. Bowyer, J.G. Kie, N.J. Cimon and B.K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J. Mammal.* 83: 229–244.
- Voeten, M.M. and H.H.T. Prins. 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120: 287–294.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *Afr. J. Ecol.* 13: 265–286.
- Yoshihara, Y., T.Y. Ito, B. Lhagvasuren, and S. Takatsuki. 2008. A comparison of food resources used by Mongolian gazelles and sympatric livestock in three areas in Mongolia. *J. Arid Environ.* 72: 48–55.
- Young, T.P., T.M. Palmer and M.E. Gadd. 2005. Competition and compensation among cattle, zebras and elephants in a semi-arid savanna in Laikipia, Kenya. *Biol. Conserv.* 122: 351–359.
- Zeileis, A. and T. Hothorn. 2002. Diagnostic checking in regression relationships. *R News* 2: 7–10.
- Zeileis, A., C. Kleiber and S. Jackman. 2008. Regression Models for Count Data in R. *J. Stat. Softw.* 27: 8–29.
- Zuur, F., E.N. Ieno, A.A. Saveliev and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Zero-Truncated and Zero-Inflated Models for Count Data. Springer, New York, NY. pp. 574.