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Source: Wildlife Biology, 14(2) : 228-236

Published By: Nordic Board for Wildlife Research

URL: [https://doi.org/10.2981/0909-6396\(2008\)14\[228:EFICBF\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2008)14[228:EFICBF]2.0.CO;2)

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Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment

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Marshal, J.P., Bleich, V.C. & Andrew, N.G. 2008: Evidence for interspecific competition between feral ass *Equus asinus* and mountain sheep *Ovis canadensis* in a desert environment. - Wildl. Biol. 14: 228-236.

Different ungulate species that co-occur over evolutionary time have been hypothesized to develop mechanisms to limit the degree to which they directly compete for the same limited resources (i.e. resource partitioning). In situations where an exotic ungulate has been recently introduced to a system, resource partitioning has not likely developed; this appears to be the situation between introduced feral ass *Equus asinus* and indigenous mountain sheep *Ovis canadensis* in the Sonoran Desert of southeastern California, USA. We analysed data from aerial surveys conducted during 1993-2003 to look for evidence of an effect of feral ass abundance on mountain sheep demography. After controlling for the influence of forage availability via rainfall, we found no evidence of relationship between an index of feral ass abundance and indices of reproduction or recruitment in mountain sheep ($P \geq 0.360$). However, we found strong evidence for an effect on indices of sheep abundance and population rate of change. There was an interactive effect of rainfall and feral ass, such that a negative relationship between abundances of mountain sheep and feral ass was strongest during the driest years ($P = 0.014$). There was a negative relationship between rate of change for sheep populations and feral ass abundance ($P = 0.016$), which was not affected by rainfall. These results indicated a competitive effect of feral ass on mountain sheep populations, but the mechanism of competition remains unclear. Further research should use manipulations in feral ass abundance to clarify interactions between these species.

Key words: California, *Equus asinus*, exotic large herbivore, interspecific competition, invasive species, *Ovis canadensis*, Sonoran Desert

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Mountain sheep *Ovis canadensis* in the deserts of southeastern California have exhibited decreasing populations in recent years (Epps et al. 2003). As with populations of wild large herbivores in many arid regions, loss of sheep habitat caused by human activity (Bleich et al. 1996), changes in forage conditions in response to climate (Bleich et al. 1990), and competition from exotic large herbivores (Bleich 2005) have all contributed to an ongoing conservation problem. Mountain sheep occur widely over much of southern California (Bleich et al. 1990). They exhibit specialized habitat use, occupying mountainous regions having escape terrain provided by steep, rugged slopes (Krausman et al. 1989, Bleich et al. 1997). They avoid areas of low visibility containing dense vegetation that can hide ambush predators, while requiring adequate forage in the form of forbs and browse (Valdez & Krausman 1999). This creates a naturally fragmented sheep distribution where persistence of populations requires both favourable patches of habitat and corridors between patches and mountain ranges across the larger landscape (Bleich et al. 1990, 1996, Singer et al. 2000). This specialized habitat use has made mountain sheep populations particularly vulnerable to anthropogenic disturbances, and competition with exotic feral ass *Equus asinus* is suspected to exacerbate those influences (Bleich & Andrew 2000, Bleich 2005).

Interspecific competition is believed to play an important role in shaping animal communities, including those of ungulates (Sinclair & Norton-Griffiths 1982, Arsenault & Owen-Smith 2002). Where different species of ungulates have been sympatric through evolutionary time, mechanisms are hypothesized to have evolved that allow for coexistence between extant species (Putman 1996). In the systems where habitat partitioning is not facilitated by behavioural influences (i.e. interference competition), other mechanisms allow maintenance of sympatry. Through resource partitioning, the potential for exploitative competition is lessened: different ungulate species maintain sympatry by specializing on different forage species or different parts of the same forage species in the same environment.

The type of resources used by a species, particularly forage resources, has been related to body size (Bell 1970, Jarman 1974). Among ruminants, species-specific body size has led to selection of different foraging strategies, from highly selective browsers with small body sizes and delicate mouths that select high-quality browse and forbs to large-bodied grazers that consume low-quality grasses (Hofmann 1989). Based on these patterns, one would expect two ungulate species of similar size in the same community to show similar foraging strategies with a greater potential for competition.

When a novel ungulate species is introduced into an existing natural community, interspecific competition might become an issue for one or more native species because selection for coexistence via resource partitioning has not had the opportunity to occur (Douglas & Leslie 1996). Introduced exotic species can exhibit foraging strategies or body forms that overlap those of the native ungulates. Thus, depending on densities of exotic and native species and, hence, resultant pressure on resources used in common, potential for competition and exclusion of one of the species is enhanced. This situation has been hypothesized to exist between mountain sheep and introduced feral ass in the arid southwestern United States (Douglas & Leslie 1996).

Feral equids have increased throughout the western United States since they were afforded federal protection in 1971; that protection likely has resulted in detrimental effects on native herbivores with which those feral equids are sympatric (Bleich 2005). Indeed, concerns about impacts to arid systems by non-native ungulates have grown among ecologists. Mountain sheep and feral ass are widely recognized to use similar habitat (Dunn & Douglas 1982), and many plant species are common to the diets of both (Ginnett & Douglas 1982). For example, in Death Valley National Monument, California, both species concentrate habitat use in sage-brush (60-70%) and shade-scale (30-40%) vegetation associations (Dunn 1984), and they exhibit common use of 67% of the forage species that occur in the collective diets of both species (Ginnett 1982). Based on overlaps in distributions and diets, feral ass might exclude mountain sheep from their

preferred habitats (Douglas & Leslie 1996). Nonetheless, one cannot conclude that overlap in diet and range indicates competition between these species. Interspecific competition can occur only if common use of limited resources affects the demography of one or both species (Wiens 1989, Putman 1996).

Based on differences in body sizes and foraging strategies, one might not expect substantial overlap in resource use between mountain sheep and feral ass. Adult body size of feral ass (147-158 kg at Death Valley, California) is considerably larger than that of mountain sheep (34-68 kg at Lake Mead, Nevada; Douglas & Leslie 1996). As a result, resource partitioning based on body size alone might occur despite the recent introduction of feral ass to North America. Nonetheless, both species fall into the body size category defined by Jarman (1974) as having intermediate selectivity associated with intermediate body mass, and differing foraging strategies (generalist vs specialist) and digestive morphology (caecal vs ruminant) are apt to result in diets of feral ass that overlap with those of mountain sheep. That two species have very different body sizes and digestive morphologies, however, does not exclude them from the possibility of interspecific competition (Belovsky 1984).

We used demographic data for sympatric mountain sheep and feral ass occupying the Sonoran Desert to evaluate the hypothesis that feral ass were having demographic impacts on mountain sheep because of interspecific competition. We predicted that there would be a negative relationship between abundance of feral ass and reproduction, recruitment, population rate of change, and population size of mountain sheep. Our analysis provided evidence for a competitive effect of feral ass on this population of mountain sheep; there were negative relationships between abundance of feral ass and abundance and rate of change of mountain sheep.

Material and methods

Study area

Our study area was located in the East Chocolate Mountains, Imperial County, California, USA, where we investigated the demography of mountain sheep during 1993-2003. This is a highly arid region of the Sonoran Desert, located near the juncture of the Colorado River and the international border with Mexico (Fig. 1; Andrew et al. 1999). Average

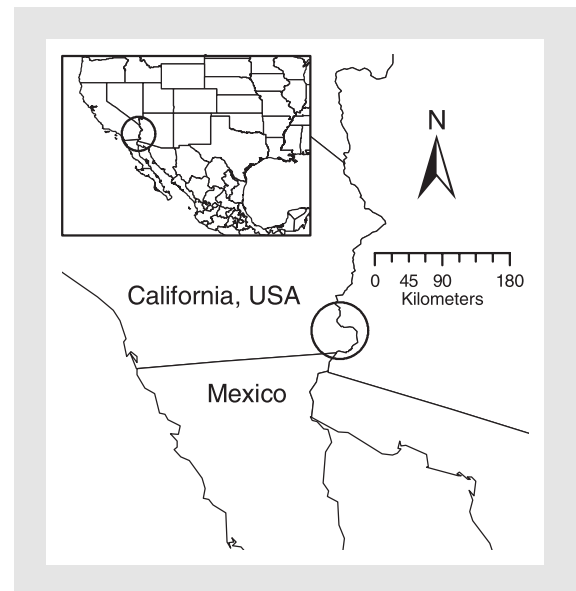


Figure 1. Location of our study area in the East Chocolate Mountains, California, USA.

rainfall was approximately 70 mm per year, and summer high temperatures were regularly $>45^{\circ}\text{C}$ (Imperial Irrigation District, Imperial, California, unpubl. data). The size of our study area was approximately 1,400 km².

The East Chocolate Mountains lie within the Lower Colorado River subdivision of the Sonoran Desert, and support vegetation common to that region (Andrew 1994, Turner 1994). Mountainous regions contained creosote bush *Larrea tridentata*, brittle-bush *Encelia farinosa*, burro-weed *Ambrosia dumosa*, and ocotillo *Fouquieria splendens*. In addition to these, riparian species, including salt cedar *Tamarix* spp., cattails *Typha domingensis*, and arrowweed *Pluchea sericea*, were common near the Colorado River.

Within the study area, $>90\%$ of plant biomass away from the river occurred in xeroriparian associations along dry desert washes (Marshall et al. 2005). Common species in these associations were desert ironwood *Olneya tesota*, palo verde *Parkinsonia florida*, mesquite *Prosopis glandulosa*, and catclaw *Acacia greggii* (Andrew et al. 1999). Other large- and medium-sized herbivores in the area included mule deer *Odocoileus hemionus*, black-tailed jackrabbit *Lepus californicus*, desert cottontail *Sylvilagus audubonii*, and desert tortoise *Gopherus agassizii*. Removals of some feral ass occurred periodically during our study, either by the United States Bureau of Land Management (BLM) personnel or by illegal

activity. Variation in observed feral ass abundance might have been a result of either of those activities.

Data collection

We used readily identifiable ground features to divide the study area into seven survey polygons (Norton-Griffiths 1978). The total area was 295 km², with polygons ranging in size within 22-56 km² (\bar{x} = 42 km²). We completely surveyed each polygon by flying contour lines separated by approximately 150 m elevation, at an average rate of 2.5 minutes/km² (Bleich et al. 1997). Annual survey flights (\bar{x} = 9.0 hours; range: 8.0-10.2 hours) occurred over two consecutive days in late September or early October. Three observers and an experienced pilot conducted the surveys using a Bell 206 B-III Jet Ranger helicopter. The pilot and the senior observer were the same for all the surveys. The other two observers varied from year to year, but all were experienced with aerial surveys, with the terrain where the surveys occurred, and with the species being counted. All observations of mountain sheep and feral ass encountered during the surveys were recorded. Individual mountain sheep were classified (Geist 1968) as adult males (i.e. horn classes II-IV), yearling males (i.e. horn class I), adult females, yearling females or young-of-the-year.

Analysis

From the data collected during the aerial surveys, we calculated indices of abundance, population rate of change, reproduction and recruitment for use in our analyses. For abundance, we calculated mountain sheep observed per hour (sheep/hour) and feral ass observed per hour (ass/hour) from the total number of each species observed during each annual

survey divided by the amount of time flown for that survey. We calculated an index of population exponential rate of change (r) by taking the natural logarithm of sheep/hour, and estimating successive differences between each year. Because data were unavailable for 2000, r for 2001 was the average rate of change over two years. We used two indices of reproduction: the number of young-of-the-year (both sexes) observed per 100 adult females, and the proportion of young-of-the-year (both sexes) out of all observed sheep. We used two indices of juvenile recruitment: the number of yearlings (both sexes) observed per 100 adult females, and the proportion of yearlings (both sexes) out of all observed sheep.

With these indices, we investigated relationships between mountain sheep demography and feral ass abundance using linear regression. We evaluated six models where the explanatory variables for all models were rainfall over the year preceding the survey (an index to forage availability), ass/hour on surveys, and the interaction of these two variables. We checked for collinearity between ass/hour and rainfall, and found no evidence of a correlation (Pearson's $R=0.24$, two-sided $P=0.50$). Use of rainfall in this manner did not account for the forage that might have been consumed by feral ass. Thus, including both factors in our analysis was necessary to investigate overall forage effects, and then those effects specific to feral ass. Use of rainfall as an index to forage availability was supported by past research in our study area (Marshal et al. 2005), which demonstrated an association between amount of precipitation and forage biomass ($\log_e(\text{forage biomass (g/m}^2)) = 2.269 + 0.017 (\text{previous six months' rainfall (mm)}) - 0.017 (\text{temperature (}^\circ\text{C)})$; $R^2=0.44$, $P<0.001$). We did not account for the influence of other

Table 1. Mountain sheep survey results from the East Chocolate Mountains, California, USA, during 1993-2003. The exponential rate of change (r) was calculated as $\log_e(\text{Sheep/hour (at } t) / \text{Sheep/hour (at } t-1))$. No data were available for 2000, so the r -value for 2001 is the average annual exponential rate of change over two years.

Year	Sheep/hour	r	Lambs/ 100 ewes	Yearlings/ 100 ewes	Proportion of		Precipitation (mm)	Feral ass/hour
					Lambs	Yearlings		
1993	11.1	-	43.5	13.0	0.19	0.06	160	7.4
1994	5.8	-0.65	11.4	0.0	0.05	0.00	72	7.2
1995	6.1	0.05	5.9	2.9	0.03	0.02	80	4.7
1996	3.2	-0.64	54.5	9.1	0.19	0.03	21	7.5
1997	4.4	0.32	20.0	26.7	0.08	0.11	17	4.4
1998	5.9	0.29	77.3	4.5	0.33	0.02	128	3.6
1999	3.6	-0.51	41.2	35.3	0.21	0.18	73	5.0
2001	4.6	0.13	55.6	5.6	0.24	0.02	57	2.6
2002	3.9	-0.18	37.5	0.0	0.19	0.00	11	3.0
2003	5.1	0.29	56.3	12.5	0.22	0.05	72	3.5

Table 2. Relationships between bighorn sheep demographic measures and the influence of rainfall and abundance of feral ass in the East Chocolate Mountains, California, USA, during 1993-2003. For calculation of the exponential rate of change (r), see the legend of Table 1.

Response	Explanatory variable	Coefficient	SE	t	P	df	R ²
Sheep/hour	Precipitation	-0.0218	0.0183	-1.191	0.279	6	0.91
	Feral ass/hour	-0.4901	0.2596	-1.888	0.108		
	Precipitation \times feral ass/hour	0.0106	0.0031	3.404	0.014		
	Feral ass/hour	-0.1805	0.0571	-3.159	0.016	7	

herbivores in the system, choosing to treat their influences as background noise that would occur regardless of the influence of feral ass. Overlap in habitat use between mountain sheep and the only other large herbivore (mule deer) was small, with sheep occurring in the more rugged terrain and higher elevations of mountainous areas (Andrew et al. 1999) and deer occurring in flatter areas near the larger washes (Marshall et al. 2006). Further, mule deer were not commonly observed during surveys; thus, influence on interactions between mountain sheep and feral ass likely were minimal. We did not address in the models the specific influence of feral ass removals, assuming that their effects on feral ass abundance would be reflected in the index ass/hour. The response variables for each of the six models were 1) sheep/hour, 2) r , 3) young/100 females, 4) log-odds transformed proportion of young, 5) yearlings/100 females, and 6) log-odds transformed proportion of yearlings. We used log-odds transformations to meet assumptions of linearity and homogeneity of variances required for proportion data (Ramsey & Schafer 2002).

Results

The aerial surveys performed during 1993-1999 and 2001-2003, yielded 10 years of demographic information (Table 1). Sheep/hour ranged from 11.1 in 1993 to 3.2 in 1996, but generally fluctuated between approximately four and six sheep/hour from 1997 to 2003. Similarly, ass/hour fluctuated from year to year, showing a decreasing trend from 7.5 in 1996 to 3.0 in 2002.

We did not detect an effect of forage availability or abundance of feral ass on our indices of reproduction in mountain sheep. There was no evidence of a relationship between rainfall or feral ass abundance and young/100 females ($F_{3,6}=0.90$, $P=0.493$). Similarly, we detected no relationship between rainfall or feral ass abundance and log-odds (proportion of young) ($F_{3,6}=0.43$, $P=0.741$). Moreover, we did not detect an influence of either forage availability or abundance of feral ass on recruitment. Indeed, there was no evidence for an effect of rainfall or feral ass abundance on either yearlings/100 females ($F_{3,6}=0.02$, $P=0.997$) or log-odds (proportion of yearlings) ($F_{3,6}=0.14$, $P=0.930$).

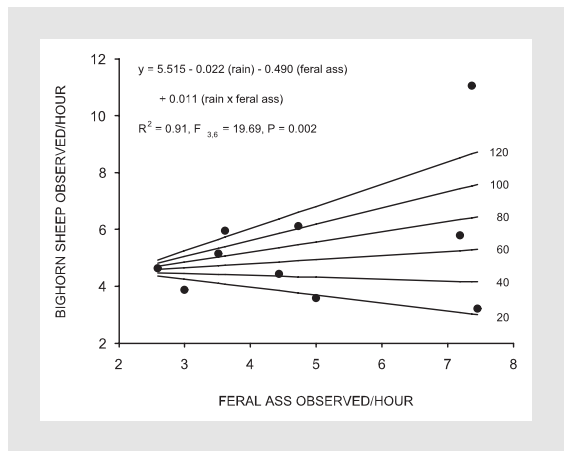


Figure 2. Relationships between feral ass observed per hour and mountain sheep observed per hour, based on surveys conducted in the East Chocolate Mountains, California, USA, during 1993-2003. Lines indicate predicted effects of feral ass on abundance of mountain sheep at different levels of annual rainfall (in mm).

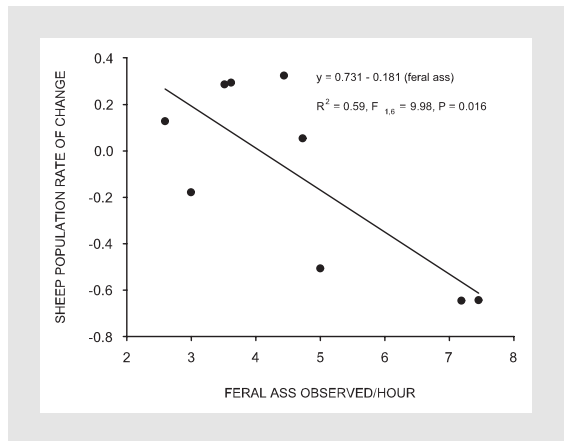


Figure 3. Relationship between feral ass observed per hour and rate of change in the mountain sheep population, based on aerial surveys conducted in the East Chocolate Mountains, California, USA, during 1993-2003.

Although reproduction and juvenile recruitment did not appear to be influenced by either forage availability (as indexed by rainfall) or abundance of feral ass, there was strong evidence that those factors influenced abundance and r of the mountain sheep population (Table 2). There was an interactive effect of rainfall and feral ass abundance on mountain sheep abundance, such that there was a negative association between ass/hour and sheep/hour when rainfall was low, but the association became positive with increasing rainfall (Fig. 2). Rate of change in sheep was negatively related to ass/hour (Fig. 3), such that the rate decreased by 0.18 (SE=0.06) for each increment of one ass/hour.

Discussion

Our results for abundance and r of mountain sheep are consistent with the hypothesis that feral ass have a competitive impact on the mountain sheep population in the East Chocolate Mountains. Such competition likely is greatest during years of low rainfall (see Fig. 2), but additional survey data will be necessary to strengthen this conclusion. Under low-rainfall conditions, resource use by feral ass would exacerbate the effects of competition on limited forage and, consequently, on mountain sheep. During years of high rainfall, both species appeared to benefit from greater forage, which would have substantially reduced competitive effects between feral ass and mountain sheep; consequently, the association between abundances of mountain sheep and feral ass was positive during wet years. A competitive effect of feral ass on mountain sheep was also demonstrated in the rate-of-change data (see Table 2), where there was strong evidence for a negative relationship between abundance of feral ass and change in abundance of mountain sheep, even in the absence of an influence of forage availability.

Further research is necessary to understand the mechanism by which competition between feral ass and mountain sheep occurs. If exploitative competition were the mechanism, we would have expected relationships between abundance of feral ass and reproduction or recruitment of mountain sheep, but such relationships were not evident. Our data set might have been too small to detect these influences, a possibility supported by the failure to detect relationships involving forage availability. That there was no evidence for an association between r and

rainfall is counter-intuitive, considering the importance of rainfall in driving the population dynamics of arid-land wildlife species (Wehausen et al. 1987, Caughley 1987, Marshal et al. 2002).

It also is possible that the mechanism for competition between feral ass and mountain sheep was behavioural; that is, mountain sheep were averse to the presence of feral ass, but feral ass did not consume available sheep forage. For example, mountain sheep have been known to avoid drinking from water sources being used by feral ass; some male sheep waited hours for feral ass to leave a water source before approaching to drink, and female sheep generally would not drink at a source if >3 feral asses were present (Dunn & Douglas 1982). These examples involve interactions at water sources, but they suggest a larger tendency for mountain sheep to avoid areas containing large numbers of feral ass. As a result, behavioural avoidance could have contributed to the negative relationships between sheep and ass abundance that we observed. During years of below-average rainfall, feral ass might concentrate near a smaller number of wildlife water developments and force sheep away from those areas, such that where large numbers of feral ass were observed during surveys, small numbers of mountain sheep also were observed. Whether mountain sheep abandoned localized areas (e.g. in the vicinity of water sources) is uncertain; nevertheless, the existence of a clearly negative relationship between indices of abundance of the two species suggests that some interaction existed.

The traditional view is that if competition occurs between feral ass and mountain sheep, it happens via overlap in habitat and, subsequently, diet (Douglas & Leslie 1996). Dunn (1984) reported substantial similarities in all seasons in the use of vegetation associations in the Cottonwood Mountains of Death Valley National Monument, California. Further, Ginnett (1982) reported that of 55 forage taxa used collectively by both species, 67% were used in common. The degree of similarity between diets of feral ass and mountain sheep varied between 20 and 61% in the Grand Canyon, Arizona (Walters & Hanson 1978), and diets of feral ass and mountain sheep demonstrated 40% similarity in spring and 50% during summer in western Arizona (Seegmiller & Ohmart 1981, Ginnett 1982).

Based on diet similarity, many investigators have recognized that the potential for competition could exist between feral ass and mountain sheep (Douglas

& Leslie 1996). Nevertheless, simple niche overlap is not sufficient to conclude the existence of competition, and Welles (1962) questioned the notion that feral ass directly impact mountain sheep populations. Resources must be limiting to at least one of the species, with resultant demographic consequences for at least one of the species. Our data suggest competitive influences on population abundance and rate of change, but not on reproduction or recruitment.

Deserts are resource-limited environments, where population dynamics of large herbivores are driven primarily by fluctuations in precipitation and resultant forage availability (Noy-Meir 1973, Caughley 1987, Marshal et al. 2002). Except during brief periods at the end of a drought, when populations are at low densities and forage is growing rapidly, ungulate populations are likely to be resource-limited (sheep/hour in our study area had a positive correlation with rainfall alone (Pearson's $R=0.84$, two-sided $P=0.003$), consistent with this pattern). In such an environment, feral ass might have an advantage over mountain sheep because of their generalist foraging strategy and monogastric digestive system (Janis 1976). This combination of traits could make feral ass better able to persist on forage of lower nutritional quality (i.e. with higher fibre content) during times of scarcity by increasing intake rate and having a shorter digestive retention time. Mountain sheep, as ruminants, would be less able to follow this strategy: a minimum nutritional quality of forage is required to provide nutrients at a rate sufficient to sustain those herbivores, plus faster through-put of poor-quality forage would allow less time for fermentation and subsequent nutrient absorption (Demment & Van Soest 1985). Under conditions of sympatry and when forage production is low, feral ass might be more likely to meet minimum forage requirements than mountain sheep (Douglas & Leslie 1996).

Evidence available to us suggests that competition between feral ass and mountain sheep is most apt to occur when resources are limited in the environment (see Fig. 2). Whether the mechanism for competition is behavioural or food niche-related, this finding is consistent with other studies that have reported variation in diet overlap, and where the greatest degree of overlap occurs during the most limiting environmental conditions. For example, guanaco *Lama guanicoe* and domestic sheep *Ovis aries* in Patagonia, Argentina, demonstrated a greater degree of diet overlap in summer

than in spring, when forage resources were less scarce (Baldi et al. 2004). Similar results have been reported for marsupial herbivores and domestic livestock occupying arid ecosystems in Australia (Dawson & Ellis 1994), and between pronghorn *Antilocapra americana* and domestic sheep in North America during winter, when forage availability was most limited (Schwartz & Ellis 1981).

Manipulative experiments could be used to test relationships between competing ungulate species in the region containing the East Chocolate Mountains; however, such experiments are rare. Hobbs et al. (1996a,b) manipulated density of wapiti *Cervus elaphus* on grazing pastures during winter to estimate the effect of forage removal by wapiti on pasture plant biomass and, subsequently, on cattle *Bos taurus* growth and reproduction the following spring. Those authors reported a substantial influence of wapiti density on pasture biomass. Furthermore, they reported that forage consumption by wapiti beyond a threshold level caused a decrease in cattle production (Hobbs et al. 1996b). Stewart et al. (2002) manipulated cattle density on an enclosed experimental range to study niche overlap and resource partitioning among cattle, mule deer and wapiti. In their system, presence of cattle influenced how the two native ungulates used space and habitat, with mule deer and wapiti avoiding areas used by cattle. Stewart et al. (2002) concluded that competition between cattle, deer and wapiti likely resulted in spatial displacement of native cervids.

The region encompassing our study area contains several feral ass management zones, where BLM personnel periodically remove feral ass in an attempt to limit impacts of feral ass on the desert ecosystem. In a framework of adaptive management, such removals provide an opportunity to more thoroughly test for an influence of feral ass abundance on the demographics of mountain sheep. Any such experiment would necessarily occur over a long period of time and, ideally, would involve a treatment area where removals occur and a control area where density of feral ass remain unmanipulated. Such a design would be useful for separating the effects of feral ass abundance from that of fluctuating forage availability. Over time, comparisons between physiological condition, survival, reproduction, juvenile recruitment, population rate of change, or population abundance among mountain sheep in treatment and control areas would demonstrate whether there is an effect of

abundance on feral ass. If feral ass do have a competitive effect on mountain sheep, one or more of those parameters should be higher in the treatment area, indicating the presence of interspecific competition and more clearly demonstrating the mechanism for that competition.

Acknowledgements - we are grateful to P. Duncan and an anonymous reviewer for comments that substantially improved the manuscript. We thank J. Brana, J. Davis, S. DeJesus, B. Gonzales, P. Kane, M. Kimberlin, L. Lesicka, G. Mulcahy, A. Pauli, R. Rister, T. Rutherford, M. Santee, S. Torres, G. Verbrugge, J. Wehausen, and the late G. Weise for assistance in the field. Funding for helicopter surveys was provided by the California Department of Fish and Game Mountain Sheep Conservation Program, the Imperial County Fish and Game Commission, Desert Wildlife Unlimited, and the United States Department of the Interior Bureau of Reclamation. This is professional paper 051 from the Eastern Sierra Center for Applied Population Ecology.

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