



## Mule deer (*Odocoileus hemionus*) density in a landscape element of the Chihuahuan Desert, Mexico

Gerardo Sánchez-Rojas\*† & Sonia Gallina\*

\**Departamento de Ecología y Comportamiento Animal, Instituto de Ecología A.C., A.P. 63, Xalapa, Ver. 91000, México*

†*Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, A.P. 69 Plaza Juárez, Pachuca, Hidalgo 42001, México*

(Received 1 March 1999, accepted 6 October 1999)

The densities of two subpopulations of mule deer were estimated in two patches of the same landscape element in the Chihuahuan Desert. Each patch was characterized by 12 variables. Deer density was different between patches. According to univariate comparison, both patches may be considered as pertaining to the same landscape element. However, principal components analysis indicated that patches were different. Furthermore, certain patch variables corresponded with subpopulation densities of mule deer. Specifically, unevenness of terrain and distance to water were significantly associated with differences in population density between patches. The utility of patch-based studies in developing conservation strategies is discussed.

© 2000 Academic Press

**Keywords:** mule deer; *Odocoileus hemionus*; density; patches; Mexico; Chihuahuan Desert; pellet-group counts; landscape

### Introduction

Population area can be conceptualized as an array of patches of varying habitat quality that are occupied by all or part of an animal population. Patch arrays create spatial heterogeneity which is considered to affect biological phenomena such as population distribution and density (Levin, 1992). Many factors such as resource availability, predation risk and physiological stress can vary from patch to patch (Wiens, 1996), therefore, it is unlikely that all patches within an area are equally suitable to the population (McCullough, 1996a). For this reason, it is considered advisable to measure all relevant heterogeneity, both between and within patches, when studying population phenomena.

The landscape is an heterogeneous land unit composed of a cluster of interacting ecosystems called landscape elements. These elements represent ecological subunits within the landscape whose structural and functional integrity is generally repeated throughout the area (Forman & Godron, 1986). The landscape elements may be of natural or human origin, and are distributed in patches (Forman & Godron, 1986). The spatial arrangement and quality of these patches are factors that can influence and modify the behaviour of species, populations, and communities (Farina, 1998). Thus,

\*E-mail: [gsanchez@uaeh.reduaeh.mx](mailto:gsanchez@uaeh.reduaeh.mx)

from the population perspective the patch is the fundamental unit within a landscape (Hanski & Gilpin, 1991).

The utility of landscape ecology to population biology research has been limited by common constraints found in studies at large spatial scales (Bowers & Matter, 1997). For example, theoretical studies relevant to entire landscapes often incorporate assumptions about patch distribution that are untested in the field. On the other hand, field studies which have focused on patches frequently ignore higher structural and functional levels of organization. Nevertheless, certain field studies have identified 'meso-scale' patterns that appear to subsets of patches. However, it is unclear whether these represent natural landscape units.

The ability to link patch dynamics with landscape-level processes is clearly important, but much depends on the development of conceptual frameworks and appropriate methodologies for extrapolation. One approach is to ask how population processes acting within and between patches might be related, and how variation in the composite performance of various local populations might drive regional population dynamics (e.g. see Bowers & Dooley, 1991). To explore this approach and investigate these questions, we have chosen as our study group certain mule deer subpopulations within the Chihuahuan Desert, Mexico.

The Chihuahuan Desert is the largest hot desert in North America. Three subdivisions are recognized within its boundaries: the Trans-Pecos (52% of the area), the Mapimian (35%), and the Saladian (13%). The Mapimian subdivision, located in the central region of the Chihuahuan Desert (Morafka, 1977), shows vegetational variation strongly related to environmental gradient and soil form (Montaña & Breimer, 1988).

In order to conserve a representative portion of the Mapimian subdivision, the Mapimi Biosphere Reserve was created (MBR) as part of the Man and Biosphere Program of UNESCO (Montaña, 1988). The MBR has 172,000 hectares within which seven landscape elements have been identified: bajadas and hills of igneous and sedimentary origin (37% of the area); bajadas and sierras of calcareous origin (17%); Southern Playa (18%); Northern Playa (6%); dunes (13%); transition between eolian and fluvial landscape (8%); and basaltic lava flows (1%) (Montaña & Breimer, 1988). These elements are geomorphological and vegetational subunits of the Chihuahuan Desert landscape.

While studying mule deer distribution within MBR using permanent sampling plots and intensive surveys in the different landscape elements over a period of 6 months, it was found that populations were restricted to bajadas and hills of igneous and sedimentary origin, and bajadas and sierras of calcareous origin. Thus, we assumed that bajadas were selected by mule deer over the other elements available.

Bajadas are piedmont plains; weakly sloping plains connecting mountains and hills with floodplains and non-inundated bottomlands at lower elevations. Operationally, we consider patches to be fragments of these elements, recognized as isolated hills with well-defined borders. This distinction is important because in this study we attempt to associate patch quality of a landscape element selected by mule deer.

The objectives of this study were: (1) to compare the densities of two mule deer subpopulations at different sites but located within the same preferred landscape element, the bajadas and hills of igneous and sedimentary origin; (2) to contrast habitat quality at these two sites; (3) to determine if differences in habitat quality at these sites are associated with differences in deer subpopulation densities, and if so; (4) to discuss the possibility that these sites may represent habitat patches that are selected by mule deer by their quality.

### Study site

This study was carried out in the MBR, located in the north-western part of the state of Durango, Mexico, bordering the states of Chihuahua and Coahuila. The polygonal



**Figure 1.** Location of the Mapimí Biosphere Reserve showing the position of the patches of the bajadas of igneous and sedimentary origin units at the outskirts of the San Ignacio Hill and Corona Hill. Dotted lines show the position of the streams which flow through the interior of the reserve.

boundaries are located between  $26^{\circ}48'$ ,  $26^{\circ}31'$  N, and  $104^{\circ}03'$ ,  $103^{\circ}32'$  W (Fig. 1). The area is dry, with semi-arid weather patterns and summer rains. Precipitation consists of heavy rains of short duration; average annual precipitation is 271 mm (based on 25 years of data), with rains occurring mainly in summer. The average annual temperature is approximately  $20^{\circ}\text{C}$  with a seasonal variation of  $16^{\circ}\text{C}$  and daily variation of  $20^{\circ}\text{C}$  (Montaña, 1990).

MBR form part of a closed basin-like depression, consisting of a wide plain with a few scattered, interspersed mountains. During and after the rainy season a few ephemeral rivers and streams flow into the region. Maximum elevation of the basin is 1480 m at San Ignacio Hill and the average elevation of the basin floor is 1150 m.

The landscape element of bajadas and hills of igneous and sedimentary origin are located in the central and western parts of MBR. The dominant plant species are *Larrea tridentata* and *Fouquieria splendens* (and less frequently, *L. tridentata* and *Yucca rigida*). In some cases, succulent species such as *Opuntia microdasys*, *O. rastrera*, *Agave asper-rima*, and *A. lechugilla* are co-dominant with *L. tridentata*. All soils in the region are shallow, and may sometimes be rocky (Montaña & Breimer, 1988).

Within the reserve, the most important economic activity is livestock (Kaus, 1992). The main grazing sites are located in the lower grassland zones (playa landscape elements), although in very dry years the bajadas are used to graze cattle (Barral, 1988).

### Methods

San Ignacio Hill and Coronas Hill were selected to carry out this study. Both sites are separated by a plain approximately 17 km wide, which consists mainly of playa areas dominated by low grass and shrubs. Little protective cover is available for the deer and it is used to graze cattle (Fig. 1). We assume that this plain may act as a barrier, preventing exchange between individuals of both subpopulations. The history of land use in both sites is unknown to us, although local opinions suggest that both areas have been managed in a similar way for pasturing cattle.

In our study, mule deer subpopulation densities were evaluated using the pellet group-count method. We selected this method because direct observations are very rare and soil characteristics do not allow the detection of tracks in all the areas. Pellet groups were collected at the same time in both sites. Sampling was carried out in June and September of 1996; March, June, September and December of 1997; and March and June of 1998. Pellet depositing time between surveys was from 90 to 120 days. Fourteen permanent transects were established, eight at San Ignacio Hill and six at Coronas Hill. Transects were 780 m in length, consisting of 40 circular plots (28.27 m<sup>2</sup> each) spaced at intervals of 20 m.

Population density was determined by the following formula (Eberhardt & Van Etten, 1956):

$$\text{deer km}^{-2} = \frac{\text{Number of plots ha}^{-1} (353.7) \times \text{Pellet groups average plot}^{-1}}{\text{Number of deposit days} \times 21 \text{ pellet groups animal day}^{-1}}$$

This method has been used in many deer studies in Mexico (Ezcurra & Gallina, 1981; Gallina, 1994; Gallina *et al.*, 1991; Mandujano & Gallina, 1995). The daily defecation rate used to calculate population density was 21 pellet groups per animal per day (Urness, 1981). We did not base the calculation on 12.7 pellet groups per animal per day (Eberhardt & Van Etten, 1956), a rate frequently used in deer population density studies. Instead, we chose the higher rate, suggested by Urness, to conservatively estimate rather than overestimate population density.

An appropriate model for understanding pellet group distribution is essential for the calculation of reliable density estimates for deer populations. To set these population parameters, we used the negative binomial distribution (Ezcurra & Gallina, 1981). Using two-factor analysis of variance without replications, density differences were estimated between patches and among the eight census (Zar, 1996).

We characterized each patch considering only the woody and succulent plants because we assumed that these are the most important plants used by mule deer at these

sites for food and cover. We used the 'point-centred quarter method' (Muller-Dombois & Ellenberg, 1974) to describe vegetation along each transect. Four quarters are established at the sampling point by a cross formed by two lines. One line was in the direction of the transect and the second was a virtual line running perpendicular through the sampling point. The distance to the mid-point of the nearest plant was measured in each quarter and the major and minor diameter of plant crown and plant height was registered. A total of 160 plants were characterized along each of the 14 transects.

Plant density was calculated using the formula  $DT = 100 d^{-2}$ ; where  $d$  is the average distance to plant in the transect, and  $DT$  is total density of plants. Crown area was obtained using the ellipse formula  $C = (\pi \times 0.25 \times D_1 \times D_2)$ ; where  $D_1$  stands for the major diameter of the crown,  $D_2$  is the perpendicular diameter, and  $C$  is crown area. Volume was obtained using the inverse cone formula  $V = 1/3B \times h$ ; where  $B$  is the crown area,  $h$  is height, and  $V$  is plant volume in  $\text{cm}^3$ .

Diversity was calculated from cover and frequency values, using the Shannon index. We used both frequency and cover values in this calculation because previous studies on vegetation demonstrated that each of these values contribute with different information on vegetation in the same area (Valverde *et al.*, 1996).

In order to separate the volumes of potential mule deer forage plants from those plants that are not eaten, we used the available information on mule deer diets in the Chihuahuan Desert (Guth, 1987; Krausman *et al.*, 1997). We reported the total volume of each group of plants. We consider that, although this was a gross approximation, this volume of forage plants may be an estimate of the availability of food for the deer.

Hidden cover was estimated according to the method suggested by Griffith & Youtie (1988), using a 2 m  $\times$  5 cm bar alternately painted with black and white stripes, each measuring 10 cm in length. The bar was placed at a distance of 15 m perpendicularly from the centre point of the sample plot on either side of the transect. From the centre point of each plot, the percent area of stripes that were visible to an observer on one knee was estimated. This height of observation was judged to be similar to the visual height of the deer. We used the inverse of this percentage as an index of visibility.

The co-ordinates of the transect locations, and water sources found around San Ignacio Hill and Coronas Hill (approximate radius of 7 km), were determined with a Garmin 45° geopositioning device. With this information, the distance from water sources to the mid-point of each transect was calculated. Two values were obtained: the average distance from the transect to all sources of water in each locality, and the minimum distance. In this case, both of these distances were considered as a measure of water availability because the actual amount of water stored at each water source was not estimated. During the study period, water was always present at these sites.

For each transect we used a clinometer Suunto® to estimate the degree of slope along the 20 m intervals separating each sampling plot. These data were used to calculate the average slope and its variance for each transect. Both values were taken to represent measurements of the unevenness of the terrain.

From the raw transect data, the following 12 variables were derived and used to characterize the San Ignacio and Coronas sites: (1) plant density per 100  $\text{m}^2$ ; (2) average crown area of plant; (3) average height of plant; (4) index of visibility; (5) total volume of potential mule deer forage plants; (6) total plant volume not eaten by mule deer; (7) average distance to water sources; (8) minimum distance to water source; (9) average slope; (10) variance of slope; (11) Shannon diversity index using plant cover values; and (12) Shannon diversity index based on plant frequency values.

The two sites were compared, variable by variable, using the univariate Student's *t*-test (Zar, 1996). Also, a principal components analysis (PCA) was undertaken to compare sites in multivariate space (Randerson, 1996). Because some variables differed in value by orders of magnitude (e.g.  $\text{cm}^3$ ,  $\text{m}^2$ , m), principal components analysis was carried out on transformed or standardized values (Randerson, 1996), rather than on raw data.

## Results

The density of mule deer between census periods varied from 0.70 to 4.21 deer km<sup>-2</sup> at the San Ignacio site, whereas density varied from 0.77 to 2.73 deer km<sup>-2</sup> at the Coronas site (Table 1). According to the two factor analyses of variance without replications, there was a significant difference ( $F = 5.731$ ;  $df. = 1, 1$ ;  $p < 0.05$ ) in the factor site, with the density at the San Ignacio site ( $\bar{x} = 2.64$  deer km<sup>-2</sup>) being greater than that at the Coronas site ( $\bar{x} = 1.7$  deer km<sup>-2</sup>). However, over the entire factor census no significant differences in density among census were detected ( $F = 1.62$ ;  $df. = 1, 7$ ;  $p = 0.252$ ).

The values of the  $k$  parameter for the negative binomial distribution varied at the San Ignacio site between 0.027 and 0.34 ( $\bar{x} = 0.234$ ), whereas at the Coronas site these values ranged from 0.041 to 0.81 ( $\bar{x} = 0.21$ ) (Table 1). Chi-square tests ( $\chi^2$ ) confirm that the pellet group distribution for each census period within patches fitted a negative binomial distribution, since no value larger than the critical value was noted (see Table 1). Values of  $k$  suggest a clumping of pellet groups at both sites (zero value for  $k$  indicates maximum clumping and values greater than eight indicate a random, or Poisson distribution).

Based on Student's  $t$ -test, five of the variables (average crown area, average height of plants, index of visibility, average distance to water source, and minimum distance to water source) were significantly different between the two sites (Table 2).

In the PCA, we found that the first two components summarized 66% of the original variability (Table 3). Considering only those variables whose scores were significantly correlated with either component, the following results were obtained. Six variables were positively associated with component I: plant density, index of visibility, average slope, variance of slope, and diversity of plants based on cover and frequency. Five variables

**Table 1.** Density and aggregation pattern of two mule deer subpopulations in patches of the bajadas of igneous and sedimentary origin units in the Mapimí Biosphere Reserve, during 2 years. The values of  $\chi^2$  show that the pellet-group distribution is adjusted to a negative binomial distribution, because no value was higher than 7.815, which is the value expected for 3  $df.$ , and a 0.05 probability

Patch	Census	Density (deer km <sup>-2</sup> )	Confidence intervals 95%	$k$ value	$\chi^2$
San Ignacio	June 1996	3.56	1.07	0.16	6.87
	November 1996	1.66	0.69	0.34	2.06
	March 1997	2.92	0.98	0.26	2.68
	June 1997	0.7	0.58	0.02	0.13
	September 1997	2.81	0.95	0.31	1.60
	December 1997	3.16	1.20	0.16	1.9
	March 1998	4.21	1.28	0.31	2.74
	June 1998	2.10	0.80	0.29	4.19
Coronas	June 1996	2.73	1.11	0.19	3.06
	November 1996	1.99	0.96	0.13	2.07
	March 1997	1.64	1.14	0.05	5.35
	June 1997	1.23	0.93	0.04	1.04
	September 1997	1.79	1.29	0.04	6.39
	December 1997	2.33	0.99	0.31	0.005
	March 1998	1.12	0.61	0.81	0.08
	June 1998	0.77	0.57	0.08	0.0007

**Table 2.** Variables obtained from the San Ignacio and Coronas patches at the bajadas of igneous and sedimentary origin element, showing the average value in each site, standard deviation, and the *p* value of a Student's *t*-test

Variable	San Ignacio	Coronas	<i>p</i>
Shrub density per 100 m <sup>2</sup>	28.24 ± 11.32	21.12 ± 5.02	0.180
Average crown area (m <sup>2</sup> )	5.51 ± 0.41	6.54 ± 0.75	0.006
Average height of plants (m)	0.84 ± 0.08	0.99 ± 0.06	0.002
Index of visibility	1.94 ± 0.23	1.17 ± 0.19	0.015
Total volume of potential mule deer forage plants (m <sup>3</sup> )	513.65 ± 105.48	539.48 ± 90.41	0.639
Total plants volume not eaten by mule deer (m <sup>3</sup> )	368.31 ± 140.94	507.30 ± 149.09	0.099
Average distance to water source (m)	3219 ± 239	5547 ± 109	<0.001
Minimum distance to water source (m)	1448 ± 869	2879 ± 675	0.006
Average of the slope in degrees	1.80 ± 2.22	1.65 ± 1.53	0.908
Variance of the slope	18.46 ± 19.67	6.80 ± 9.80	0.210
Shannon diversity index using plants' cover values	1.98 ± 0.29	1.87 ± 0.21	0.464
Shannon diversity index value using frequency values	2.05 ± 0.24	2.11 ± 0.15	0.628

were negatively associated with component I: average crown area, average height of plants, total plant volume not eaten by mule deer, average distance to water source, and minimum distance to water source. Only five variables were positively associated with component II: total volume of potential mule deer forage plants, average distance to water source, minimum distance to water source, and diversity of plants based on cover and frequency (Table 3).

A visual exploration of the scatter plot of variables along the first two component axes showed that the transects from both patches do not overlap. The transects of Coronas Hill are clearly separated, whereas the distribution of the transects from San Ignacio Hill is more heterogeneous (Fig. 2).

Along component I, transects of the San Ignacio patch had high values, whereas transects of the Coronas patch had low values. This means that transects in the San Ignacio patch tended to present high values of plant density, index of visibility, slope, slope variance, and plant diversity. Correspondingly, transects in the Coronas patch tended to present high values of shrub crown, average height of plants, plant volume not eaten by mule deer, average distance to water source, and minimum distance to water source. Along component II, transects at the San Ignacio site generally showed lower values, whereas transects at the Coronas site were higher. Specifically, the following variables showed higher values at the Coronas site when compared to the San Ignacio site: volume of potential mule deer forage plant, average distance to water source, minimum distance to water source, and diversity of plants based on cover and frequency.

## Discussion

Our data indicate that mule deer density was significantly greater at the San Ignacio site than at the Coronas site. Furthermore, both univariate and multivariate analysis indicate that there were significant quantitative and qualitative differences between these

**Table 3.** Results of the arrangement of the variables of two patches of the bajadas and hills of igneous and sedimentary origin units using a principal component analysis; correlation values between the value of component one with the real value of the variable were estimated with the Pearson's correlation coefficient (\* $p < 0.05$  and \*\* $p < 0.001$ )

Component	I	II
Variation explained	44.43%	21.13%
Cumulative variation	44.43%	65.74%
Variable	Correlations with original variable	
Shrub density per 100 m <sup>2</sup>	0.788**	-0.230
Average crown area (m <sup>2</sup> )	-0.728*	0.309
Average height of plants (m)	-0.823**	0.268
Index of visibility	0.729*	-0.106
Total volume of potential mule deer forage plants (m <sup>3</sup> )	0.410	0.690*
Total plants volume not eaten by mule deer (m <sup>3</sup> )	-0.596*	-0.192
Average distance to water source (m)	-0.674*	0.592*
Minimum distance to water source (m)	-0.534*	0.692*
Average of the slope in degrees	0.836**	0.128
Variance of the slope	0.613*	0.347
Shannon diversity index, using plants' cover values	0.702*	0.558*
Shannon diversity index value using frequency values	0.550*	0.768*

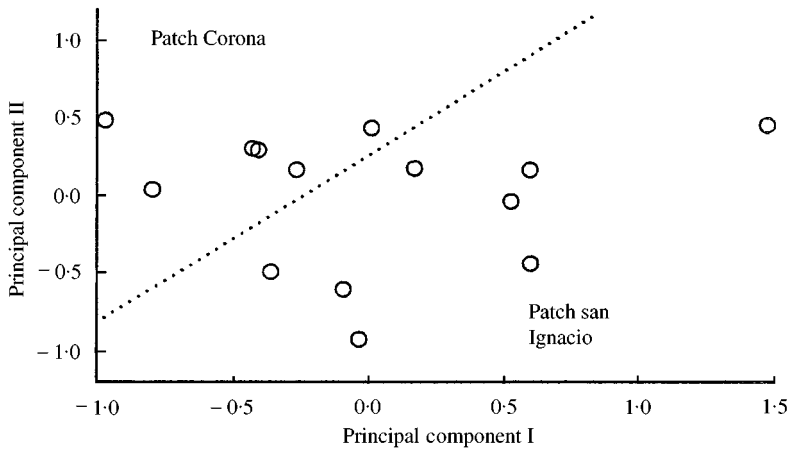
sites. These results strongly suggest that mule deer density at MBR depends on such differences between sites.

Although deer density is clearly different in both patches, it is important to note that mule deer in the Chihuahuan Desert normally occur in low density populations (Wallmo, 1981; Galindo-Leal, 1993), which is a fact to consider in conservation and management decisions. Furthermore, mule deer subpopulations at the MBR are discontinuously distributed, occupying patches of landscape elements that have a very heterogeneous topography, such as the bajadas of igneous and sedimentary origin and the bajadas of calcareous origin. For these reasons, we could say that MBR deer populations behave like a metapopulation (McCullough, 1996b).

According to this scenario, small subpopulations scattered about the landscape might be expected, in theory, to have a greater probability of local extinction due to natural and anthropogenic disturbances (McCullough, 1996b). Our data indicate that mule deer density was significantly greater at the San Ignacio site than at the Coronas site, suggesting that mule deer abundance is not independent of the patch and the population.

Using univariate comparison of individual variables we did not detect significant differences in those variables that are supposed to define the patches as pertaining to some landscape element, such as terrain heterogeneity and plant diversity. However, those variables that potentially affect the selection of habitat patches by mule deer, such as plant size and visibility, were significantly different between patches. There is also a significant difference in distance to water source between patches, maybe because some artificial water sources have been framed in the area surrounding San Ignacio Hill.





**Figure 2.** Location of the transects of both patches of the bajadas of igneous and sedimentary origin unit, in the plain formed by components 1 and 2 of the principal component analysis. The dotted line separates the transects corresponding to each patch.

The results of ordination are the arrangement of transects and variables in a low-dimensional space, such that similar entities are close by and dissimilar entities far apart (Grauch, 1985). In our analysis, transects from the same patch are more similar. This supports the idea that there are important qualitative differences between the patches. These differences may be described as follows. The San Ignacio patch had a higher plant density, but plants were smaller in size. In addition, there was better visibility, higher water availability, rougher terrain, and higher plant diversity based on cover at the San Ignacio site. The Coronas site was characterized by larger shrubs, less visibility, less available water, less rough terrain, and greater plant diversity based on frequency.

Feeding efficiency and predation risk are two factors that influence habitat selection by ungulates (Bowyer *et al.*, 1998). Individuals attempt to resolve the conflict between foraging and predation by selecting patches that minimize the ratio between predation risk and foraging efficiency (Pulliam & Danielson, 1991). In other words, animals tend to avoid patches where the risk of predation is high and the quantity and quality of food is low.

In relation to resource availability in the two patches, the amount of available food did not differ between sites. Therefore, we suggest that this factor did not influence patch selection by deer or affect subpopulation densities. However, water resources were distributed differently between patches. Average and minimum distances to water sources were lesser at the San Ignacio site when compared with the Coronas site, indicating that water was more available to deer at the former site. This greater availability of water at San Ignacio corresponded to a greater deer population density. This suggests that decisions made by individual deer to choose patches was influenced by water availability (Hervert & Krausman, 1986; Leopold & Krausman, 1991; Boroski & Mossman, 1998).

Univariate comparisons of the unevenness of the terrain using the average and variance of the slope showed no significant differences between patches. Nevertheless, PCA showed that unevenness loaded heavily on the component axes and contributed, in an important way, to distinguishing between the sites. In this study, the San Ignacio site was more uneven than the Coronas site.

It is acknowledged that one of the anti-predator strategies of mule deer is to use rough terrain as escape routes because it is more difficult for predators to follow them

(Geist, 1981). We suggest that mule deer preferred the San Ignacio site for its steeper slopes, and therefore, its greater refuge from predators (Ordway & Krausman, 1986; Carson & Peek, 1987; Gallina *et al.*, 1991).

Our results have shown that two patches within a single landscape element, the bajada of igneous and calcareous origin, differ in their suitability for deer populations, and that differences in population densities at these two sites may reflect preferences for the San Ignacio site over the Coronas site. The latter suggests that patches at MBR could be hierarchically classified according to population density and/or patch quality criteria. This would have important implications for the management and conservation of mule deer on the reserve.

The fact that patches with different characteristics at MBR support deer populations with correspondingly different densities suggests that mule deer populations may be following a source/sink dynamic (Pulliman & Danielson, 1991). Under such a scenario, a local population with a high density (the source) would donate individuals to a nearby population having a low density (the receiving population or sink) (Wiens, 1996). This model assumes that the greater density of the source population is due to greater productivity (i.e. annual recruitment exceeds annual mortality) and that the excess of individuals must disperse away from their natal patch in order to establish themselves and breed (Maffe & Carroll, 1994).

For these reasons, we believe it is necessary to continue research at MBR in order to determine if the reserve contains a source adequate to prevent the local extinction of mule deer, or if it only contains receptor populations (sinks). In the latter case, it would be important to identify a population source outside the reserve and consider habitat corridors between them.

From the management point of view, it is important to point out that certain patch components, such as water availability, can be modified artificially. Such manipulations can have positive effects on local population densities (Hervert & Krausman, 1986; Leopold & Krausman, 1991; Boroski & Mossman, 1998). Using the patch as the management unit, such manipulations could be initiated with the intention of improving the area for local deer populations. Results could be evaluated in terms of changes in population density. In conclusion, we suggest that patches located within the bajadas and sierras of MBR be utilized as the primary management and conservation units by mule deer in the reserve area.

The authors wish to thank C. Montaña, L. Hernandez, V. Sanchez-Cordero, S. Mandujano, J. Bello, J. Heffelfinger and A. Gonzalez for comments, suggestions and ideas on earlier drafts of the manuscript. D. Bennack provided comments on a later version and translated portions from Spanish to English. This study was supported from funds awarded to S. Gallina by the Consejo Nacional de Ciencia y Tecnologia de Mexico (CONACYT), as part of project 22560-5-2480PB, and by a scholarship (CONACYT; No. 95013) and a grant (Fondo Mexicano para la Conservación de la Naturaleza; No. D-0-97/019) awarded to G. Sánchez-Rojas.

## References

- Barral, H. (1988). El hombre y su impacto en los ecosistemas a través del ganado. In: Montaña, C. (Ed.), *Estudio integrado de los recursos vegetación, suelo y agua en la reserva de la biosfera de Mapimí*, pp. 241–268. México D. F.: Instituto de Ecología. 290 pp.
- Boroski, B.B. & Mossman, A. (1998). Water use pattern of mule deer (*Odocoileus hemionus*) and the effects of human disturbance. *Journal of Arid Environments*, **38**: 561–569.
- Bowers, M.A. & Dooley, J.L.J. (1991). Role of habitat mosaic on the outcome of two-species competition. *Oikos*, **60**: 180–186.
- Bowers, M.A. & Matter, S.F. (1997). Landscape ecology of mammals: Relationships between density and patch size. *Journal of Mammalogy*, **78**: 999–1013.
- Bowyer, R.T., Kie, J.G. & Bellenberghé, V.V. (1998). Habitat selection by neonatal black-tailed deer: Climate, forage, or risk of predation. *Journal of Mammalogy*, **79**: 415–425.

- Carson, R.G. & Peek, J.M. (1987). Mule deer habitat selection patterns in northcentral Washington. *Journal of Wildlife Management*, **51**: 46–51.
- Eberhardt, L.L. & Van Etten, R.C. (1956). Evaluation of the pellet group count as deer census method. *Journal of Wildlife Management*, **20**: 70–74.
- Ezcurra, E. & Gallina, G. (1981). Biology and population dynamics of white-tailed deer in northwestern Mexico. In: Ffolliott, P.F. & Gallina, S. (Eds), *Deer Biology, Habitat Requirements, and Management in Western North America*, pp. 78–108. México, D. F.: Instituto de Ecología. 238 pp.
- Farina, A. (1998). *Principles and Methods in Landscape Ecology*. London: Chapman & Hall. 235 pp.
- Forman, R.T.T. & Godron, M. (1986). *Landscape Ecology*. New York: Wiley and Son. 619 pp.
- Galindo-Leal, C. (1993). Densidades poblacionales de los venados cola blanca, cola negra y bura en Norteamérica. In: Medellín, R.A. & Ceballos, G. (Eds), *Avances en el Estudio de los Mamíferos de México*, pp. 371–391. México, D. F.: Publicaciones Especiales Vol. I, Asociación Mexicana de Mastozoología. 464 pp.
- Gallina, S. (1994). Dinámica poblacional del venado cola blanca en la reserva de la biosfera La Michilia, Durango, México. In: Vaughan, C. & Rodríguez, M.A. (Eds), *Ecología y Manejo del Venado Cola Blanca en México y Costa Rica*, pp. 207–234. Heredia, Costa Rica: EUNA. 455 pp.
- Gallina, S., Galina-Tessaró, P. & Álvarez-Cárdenas, S. (1991). Mule deer density and pattern distribution in the pine-oak forest at the Sierra de La Laguna in Baja California Sur, Mexico. *Ethology Ecology and Evolution*, **3**: 27–33.
- Gauch, H.G.J. (1985). *Multivariate Analysis in Community Ecology*. New York: Cambridge University Press. 278 pp.
- Geist, V. (1981). Behavior: Adaptative strategies in mule deer. In: Wallmo, O. C. (Ed.), *Mule and Black-Tailed Deer of North America*, pp. 157–223. Nebraska: University of Nebraska Press. 605 pp.
- Griffith, B. & Youtie, B.A. (1988). Two devices for estimating foliage density and deer hiding cover. *Wildlife Society Bulletin*, **16**: 206–210.
- Guth, A.M. (1987). Hábitos alimenticios del venado bura (*Odocoileus hemionus* Rafinesque 1817) en la Reserva de la Biosfera de Mapimi Durango. Bachelor Thesis México, D. F., University of Mexico. 86 pp.
- Hanski, I. & Gilpin, M. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society*, **42**: 3–16.
- Hervert, J.J. & Krausman, P.R. (1986). Desert Mule deer use of water development in Arizona. *Journal of Wildlife Management*, **50**: 670–676.
- Kaus, A. (1992). Common ground: Ranchers and researchers in the Mapimi Biosphere Reserve. Unpublished Doctoral Thesis, Riverside, University of California. 433 pp.
- Krausman, P.R., Kuenzi, A.J., Etchberger, R.C., Rautenstrauch, K.R., Ordway, L.L. & Hervert, J.J. (1997). Diets of desert mule deer. *Journal of Range Management*, **50**: 513–522.
- Leopold, B.D. & Krausman, P.R. (1991). Factors influencing desert mule deer distribution and productivity in southwestern Texas. *The Southwestern Naturalist*, **36**: 67–74.
- Levin, S. (1992). The problem of pattern and scale in ecology. *Ecology*, **73**: 1943–1967.
- Meffe, G.K. & Carroll, C.R. (1994). *Principles of Conservation Biology*. Massachusetts: Sinauer Associates. 600 pp.
- Mandujano, S. & Gallina, S. (1995) Comparison of deer censusing methods in tropical dry forest. *Wildlife Society Bulletin*, **23**: 180–186.
- McCullough, D.R. (1996a). Spatially structured populations and harvest theory. *Journal of Wildlife Management*, **60**: 1–9.
- McCullough, D.R. (1996b). Introduction. In: McCullough, D. R. (Ed.), *Metapopulations and Wildlife Conservation*, pp. 1–10. Washington: Island Press. 429 pp.
- Montaña, C. (1988). Presentación. In: Montaña, C. (Ed.), *Estudio integrado de los recursos vegetación, suelo y agua en la reserva de la biosfera de Mapimi*, pp. 15–18. México D. F.: Instituto de Ecología. 290 pp.
- Montaña, C. (1990). A floristic-structural gradient related to land forms in the southern Chihuahuan Desert. *Journal of Vegetation Sciences*, **1**: 669–674.
- Montaña, C. & Breimer, R.F. (1988). Major vegetation and environment units. In: Montaña, C. (Ed.), *Estudio integrado de los recursos vegetación, suelo y agua en la reserva de la biosfera de Mapimi*, pp. 99–114. México D. F.: Instituto de Ecología. 290 pp.

- Morafka, D. J. (1977). *A Biogeographical Analysis of the Chihuahuan Desert Through its Herpeto Fauna*. The Hague: Dr. W. Junk B.V. 343 pp.
- Mueller-Dombois, D. & Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. New York: John Wiley and Sons. 547 pp.
- Ordway, L.L. & Krausman, P.R. (1986). Habitat use by desert mule deer. *Journal of Wildlife Management*, **32**: 334–349.
- Pulliam, H.R. & Danielson, B.J. (1991). Sources sink and habitat selection: A landscape perspectives on population dynamics. *The American Naturalist*, **137**: S50–S66.
- Randerson, P.F. (1996). Ordination. In: Fry, J.C. (Ed.), *Biological Data Analysis A Practical Approach*, pp. 173–219. Oxford: Oxford University Press. 418 pp.
- Urness, P.J. (1981). Food habits and nutrition. In: Wallmo, O. C. (Ed.), *Mule and Black- Tailed Deer of North America*, pp. 347–386. Nebraska: University of Nebraska press.
- Valverde, P.L., Zavala-Hurtado, J.A., Montaña, C. & Ezcurra, E. 1996 Numerical Analyses of vegetation based on environmental relationship in the southern Chihuahuan Desert. *The Southwestern Naturalist*, **41**: 424–433.
- Wallmo, O.C. (1981). Mule and black-tailed deer distribution and habitats. In: Wallmo, O.C. (Ed.), *Mule and Black- Tailed Deer of North America*, pp. 366–386. Nebraska: University of Nebraska press. 605 pp.
- Wiens, J.A. (1996). Wildlife in patchy environments: Metapopulations, mosaics and management. In: McCullough, D.R. (Ed.), *Metapopulation and Wildlife Conservation*, pp. 53–84. Washington, D. C.: Island Press. 429 pp.
- Zar, J.H. (1996). *Biostatistical Analysis*. New Jersey: Prentice-Hall. 662 pp.