

## Decline in the endemic Mexican prairie dog *Cynomys mexicanus*: what do we know about extinction risk?

Laura M. Scott-Morales, Eckhard Gottschalk and Michael Mühlenberg

**Abstract** The Mexican prairie dog *Cynomys mexicanus* is an endemic burrowing rodent with a restricted distribution. Up to 1996 the species experienced a loss of c. 60% of its historical range, and in the last few years a further loss of habitat has occurred, with the current range now covering only 36% of the historical range. In this study we examined the population dynamics of the Mexican prairie dog to determine the relative effects of habitat loss, isolation of remaining colonies, and decreasing habitat quality. We used data on prairie dog numbers in all colonies and demographic data for two colonies to carry out a stochastic population viability analysis. We found differing vital rates, which are presumed to result from differing habitat quality, at two colonies. As small

variations of vital rates in the model strongly influenced the extinction risk for small populations, we conclude that habitat quality is important for the small populations. In the model the Los Angeles complex of colonies experienced a low risk of local extinction whereas at the Manantial complex local extinctions were frequent. Scenarios with changes in population sizes had the largest effect on extinction risk. Differing migration scenarios had little impact on extinction risk.

**Keywords** *Cynomys mexicanus*, decline, endemic species, Mexican Plateau, Mexican prairie dog, mortality, population viability analysis, reproduction.

### Introduction

The Mexican prairie dog *Cynomys mexicanus* is one of five species of the genus *Cynomys* in North America. Endemic to north-east Mexico, *C. mexicanus* has a restricted distribution on the Mexican Plateau of the Chihuahuan Desert between the states of Zacatecas, San Luis, Coahuila and Nuevo León (Hall, 1981). *C. mexicanus* is a medium-sized diurnal burrowing rodent, inhabiting prairie with short grasses typical of calcareous soils. *C. mexicanus* is active throughout the year and lives in territorial family groups known as coterie; a group of coterie living in an area is called a colony. Each coterie typically includes one adult male, several adult females and their offspring. Male juveniles leave the coterie shortly before the beginning of the breeding season, which is from the end of January to April (Rioja, 2003).

Because of a drastic decline in the range of *C. mexicanus* it is now considered to be threatened in the wild (Diario

Oficial de la Federación, 2002) and is categorized as Endangered on the IUCN Red List (IUCN, 2004). By 1996 its historical range of c. 1,255 km<sup>2</sup> had been reduced to 477 km<sup>2</sup> (Treviño-Villareal & Grant, 1998) because of habitat loss to agriculture, overgrazing and human settlement (Treviño-Villarreal, 1990). More recently, however, habitat loss has intensified and new monitoring of the distribution of *C. mexicanus* has confirmed a further decrease, and 74% of its historical range has now been lost or is fragmented (Scott-Morales *et al.*, 2004). However, although the species' ecology has been studied (Treviño-Villarreal, 1990; Navarro, 2003; Rioja, 2003), information is not available on demographic threats, population dynamics or the colony size needed to maintain a viable population.

Population viability analysis (PVA) has been proposed as a tool for conservation strategies and management planning for threatened species (Boyce, 1992; Kelly & Durant, 1999; Lopez & Pfister, 2001; Goodman, 2002; Shaffer *et al.*, 2002, but see Beissinger & Westphal, 1998, for a discussion). The most important aims of PVA are to evaluate factors threatening a species, to categorize the vulnerability of threatened species, and to make decisions between management options (Brook *et al.*, 2000; Possingham *et al.*, 2002). Because there is generally a lack of reliable knowledge of a particular species and of the myriad of factors that can affect them, PVA is inherently stochastic and therefore speculative (Shaffer, 1990). Nevertheless, some authors have shown that PVA can be accurate and reliable (Brook *et al.*, 2000; Beissinger &

Laura M. Scott-Morales (Corresponding author) Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, México Carretera Nacional Km. 145, 67700 Linares, N.L., Mexico. E-mail lscott@fci.uanl.mx

Eckhard Gottschalk and Michael Mühlenberg Centre for Nature Conservation, University of Goettingen, Von Sieboldstr. 2, D-37075 Goettingen, Germany.

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McCullough, 2002; McCarthy *et al.*, 2002). Here we carry out the first population viability analysis for *C. mexicanus*, use this to make comparisons between management options, and discuss the relative impact of factors threatening the species' survival. The analyses will help to evaluate management options and give direction to future research on the ecology and demography of, and threats to, *C. mexicanus*.

### Study area

The area under study include portions of the states of Nuevo León, Coahuila and San Luis Potosí in the north-eastern portion of the Central Highland of the Chihuahuan Desert (Fig. 1), at 1,600–2,100 m altitude. The plant community is dominated by associations of *Muhlenbergia villiflora*-*Scleropogon brevifolius*, *Buchloe dactyloides*-*Scleropogon brevifolius* and *Muhlenbergia*-*Scleropogon*-*Dasyochloa*. Total annual precipitation is 200–500 mm (González-Saldivar, 1990; Mellink and Madrigal, 1993).

### Methods

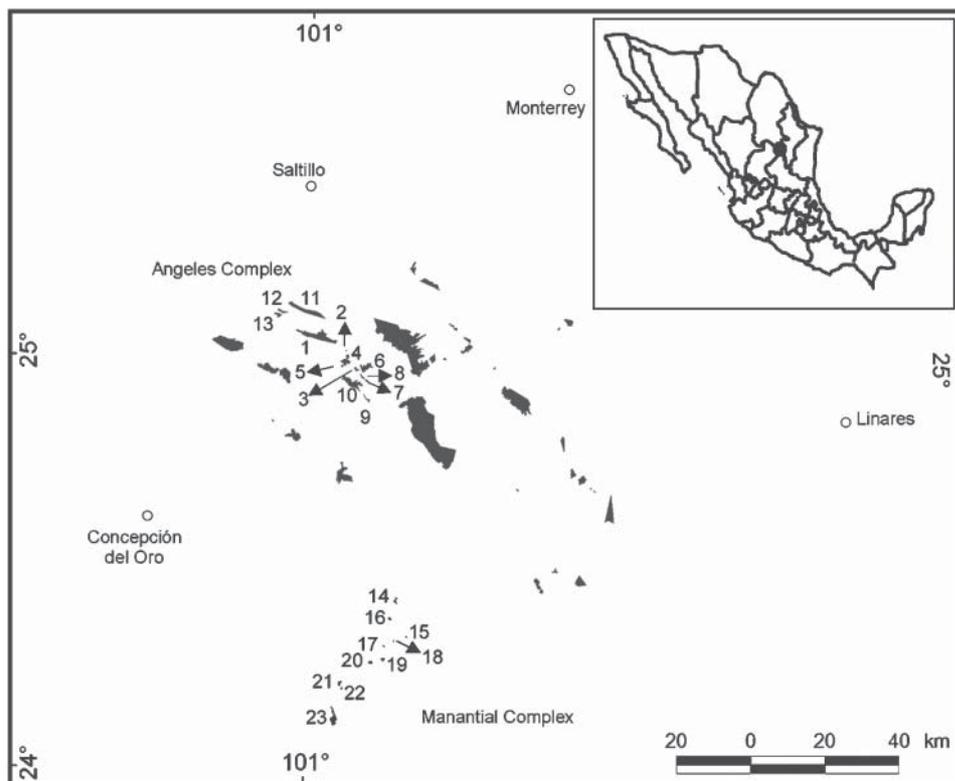
Here we present data from 22 of the 54 prairie dog colonies (we selected only those colonies that were close enough to each other to simulate a metapopulation structure) occurring in the study area (Appendix). They

are in two complexes: Los Angeles and El Manantial. Two data sets were used in the PVA model. For estimated colony sizes we used data collected in summer 1999 in a study on prairie dog density across its geographic range (Scott-Morales & Estrada, 1999) and, for demographic parameters, data collected from a study in the colonies Los Angeles and La Perforadora, both in the Los Angeles Complex, in 2002 and 2003 (Rioja, 2003).

### Estimation of density

We used indexes of activity to estimate the density of prairie dogs by sampling with the quadrant method (Wilson *et al.*, 1996; Southwood & Henderson, 2000). Because activity depends on external conditions that regulate the behaviour of the species (Southwood & Henderson, 2000), we conducted all counts during the hours of greatest activity at the colonies (08.00–13.00 and 16.00–20.00; Treviño-Villarreal, 1990) and during good weather. We also assumed that activity patterns were the same in all colonies.

Two-ha square plots were located randomly along the centerline through a colony, and each plot was separated from others by at least 500 m. The number of plots per colony varied according to colony size, but at least 5% of a colony area was censused. During 10 minutes of observation all individuals seen simultaneously in each plot were counted. To estimate the number of prairie dogs



**Fig. 1** Distribution of *Cynomys mexicanus* colonies on the Mexican Plateau. Colonies are in black. The colony numbers refer to the numbers in the Appendix. The whole distribution range of *C. mexicanus* is illustrated. Dot on inset indicates location of the main figure in Mexico.

per colony (Appendix) we multiplied the mean number of prairie dogs per ha by colony area. The estimated number of prairie dogs per hectare used in our metapopulation model are listed in the Appendix.

### Estimation of demographic parameters

#### Reproduction

The colonies of Los Angeles and La Perforadora have the same climate and altitude and >50% of their plant species are in common. Because of different silviculture management, they differ in vegetation cover (36% at Los Angeles and 28% at La Perforadora) and vegetation biomass (75 kg ha<sup>-1</sup> at Los Angeles and 52 kg ha<sup>-1</sup> at La Perforadora) (Scott-Morales & Estrada, 1999; Rioja, 2003).

Five circular plots of 100 m radius were randomly located at each colony. Each plot had 3–4 coterie, with a total of 18 coterie in each colony (Table 1). We considered a member of a coterie to be each individual that left, entered or remained in the same burrow and showed no aggressive behaviour to other members. Once the territory of each coterie was identified, we determined the size of the coterie by counting, using binoculars or a telescope, all active individuals inside the territory during 08.00–13.00 and 14.00–19.00. Every day we rotated observations such that each plot was observed at different hours of the day. Each site was monitored at least twice per month from February to August in 2002 and 2003.

Breeding success (the number of young that emerged during the observation period) were obtained by directly observing families in the reproductive season (March–May). Once all young were outside the burrow we began the daily monitoring; this was daily for 1 month, and then 5 days every 20 days for 4 months.

#### Survival rate

All individuals were aged. We distinguished three age classes: pups (all individuals born in the year up to the age of 6 months), yearlings (individuals of 6–12 months of age, distinguished from adults by size and behaviour) and adults (reproductively mature individuals). We estimated survival rate during the first year of life by comparing the number of yearlings in 2003 to the number of pups observed the year before in the same coterie (Table 1).

#### PVA model

For modelling extinction risk and detecting further data requirements we used the software Ramas Metapop (Akçakaya, 1994), which is a stochastic matrix-based model. The model uses data on initial population size, reproduction and mortality of different age classes to calculate population size after a series of time steps. The vital rates are changed for each year stochastically according to the standard deviation of the time series of mortality and reproduction. Other data included in the

**Table 1** Coterie composition and demographic parameters for *C. mexicanus* in Los Angeles and La Perforadora colonies in 2002 and 2003. Census of adults and pups was in April/May and that of yearlings in February/March.

Colony & plot	No. of coterie	2002				2003			
		Adult males	Adult females	Yearlings	Pups	Adult males	Adult females	Yearlings	Pups
<b>Los Angeles<sup>1</sup></b>									
1	3	4	7	10	17	4	7	13	31
2	4	6	10	13	36	6	10	22	36
3	3	5	8	10	18	5	8	10	21
4	4	6	9	18	28	6	9	21	24
5	4	7	10	13	36	7	10	22	28
Mean		5.6	8.8	12.6	27.0	5.6	8.8	17.6	28.0
Total	18	28	44	63	135	28	44	88	140
<b>La Perforadora<sup>2</sup></b>									
1	3	4	4	6	6	3	3	1	3
2	4	5	9	11	23	5	8	8	19
3	4	7	8	14	22	7	9	14	19
4	3	4	5	7	7	4	5	6	11
5	4	7	9	18	21	7	9	11	16
Mean	3.6	5.4	7.2	11.4	15.8	5.2	6.8	8.0	13.6
Total	18	27	35	57	79	26	34	40	68

<sup>1</sup>Reproductive rate (female pups per adult female) was 1.50 in 2002 and 1.67 in 2003 (mean = 1.58). Survival rate during the first year (yearling 2003/ pups 2002) was 0.63.

<sup>2</sup>Reproductive rate (female pups per adult female) was 1.12 in 2002 and 1.00 in 2003 (mean = 1.06). Survival rate during the first year (yearling 2003/ pups 2002) was 0.49.

model are carrying capacity, age structure, and exchange rates between local populations.

Only females were modelled. We used discrete time steps of 1 year and ran 1,000 replicates of 100 years duration for each scenario. During each simulation the carrying capacity of the habitat was not changed. Carrying capacities are assumed to equal the population size measured in the field. We modelled population dynamics using the mean and standard deviations of reproductive and survival rates, and defined two stages: young of the year concerned, and adults. The population census used in the model takes place once a year in April after the emergence of pups. In our field study we did not distinguish the age of females when they reproduce, but because Treviño-Villarreal (1990) found reproductive yearling female *C. mexicanus*, we considered yearling females (1 year old) as adults in our reproduction matrix. Reproduction and survival were different in the two complexes, with a higher rate of reproduction and survival in Los Angeles because of better range-management strategies (Rioja, 2003). We modelled the population dynamics of all colonies (excluding Los Angeles for which we have other data) using the survival and reproduction of colony La Perforadora. The survival rate of pups during their first year of life was estimated by dividing the number of yearlings (before leaving their coteries) in 2003 by the number of pups in the same coteries in 2002 (Table 1), giving a rate of 0.49. This was used as the survival rate for Stage 1 in our matrix model. Because we lacked good quality data to estimate adult survival, we used the survival rate from a long-term study on *C. ludovicianus* (Hoogland, 1995, p. 377), which was 0.72.

We calculated reproduction rate as the number of female pups (assuming a sex ratio of pups of 1:1, Hoogland, 1995; Table 1) divided by the number of all adult females. For 2002 and 2003 we calculated 1.13 and 0.97 female pups per adult female respectively, resulting in an average of 1.05. For use in the stage matrix we multiplied the reproduction rate by the survival rate of adults. This is because fecundity in the matrix model is the number of pups (counted in this census) per adult (counted in the previous census) and therefore adults first have to survive mortality within the model.

At the colony Los Angeles the first-year survival rate was 0.63 and reproduction rate 1.58 (Table 1). For adult survival, we also used the data from *C. ludovicianus*. Because Ramas Metapop uses only a single stage matrix, we transformed the data into an individual growth rate (1.5) of the Los Angeles colony.

Because survival and reproduction data in time series are missing for *C. mexicanus*, we estimated variance in survival and reproduction from a 15-year study of

*C. ludovicianus* (Hoogland, 1995), obtaining standard deviations of 0.1 for adult female survival, 0.12 for survival during the first year and 0.2 for reproduction rate.

As *C. mexicanus* is a territorial species, we used a form of asymmetric competition (ceiling competition) in the model, which means that growth rate of the population reaches 1.0 at maximum, when the capacity of the local population is attained. We did not incorporate catastrophes in our model. Other species of prairie dogs suffer from diseases, but until now *C. mexicanus* is considered to be isolated from any epidemic threat (Treviño *et al.*, 1998).

The model requires assumptions on the degree of correlation of the stochastically changing vital rates between local populations. Annual variation in populations is assumed to be highly correlated between all local populations of the metapopulation complex. We therefore used highly correlated changes in vital rates of local populations in the model. The reason for expecting synchronous dynamics is that vital rates are presumed to be dependent on vegetation cover, which changes with the amount of rainfall. We also ran a scenario without correlation to test the effect of different assumptions.

There is no dispersal data for *C. mexicanus*, but other studies have reported dispersal of >5 km in *C. ludovicianus* (Koford, 1958; Hoogland, 1995; List, 1997; Roach *et al.*, 2001). We assumed the same dispersal distance to assess exchanges between colonies of *C. mexicanus*. Distances between colonies were considered, with exchange rates depending on distance. Ramas describes the relative number of migrating individuals with a distance-dependence function, but nothing is known about the proportions of migrating prairie dogs. We tested the effect of two different assumptions about exchange rates: without migration (used in one scenario only), and including migration. The scenario with migration assumes maximum exchange rates of 3%, and 2% between colonies 2 km apart.

The carrying capacities of colonies in the two complexes were modelled using the census data (Appendix). Because only females are modelled, we multiplied the abundances by the proportion of females in the Los Angeles colony (0.61). The initial population sizes had the same values, assuming that populations are at their carrying capacity. Initial stage abundances were given by the proportion of age classes counted in the Los Angeles colony (Table 1): female adults/female pups = 44/67.5.

A sensitivity analysis was performed for different values of reproduction, pup and adult survival and standard deviations of vital rates. We used a hypothetical single population of 20 females (corresponding to a total population size of 34 animals). Extinction risk for population sizes of *c.* 20 females is particularly sensitive to changes in scenarios and we therefore changed each

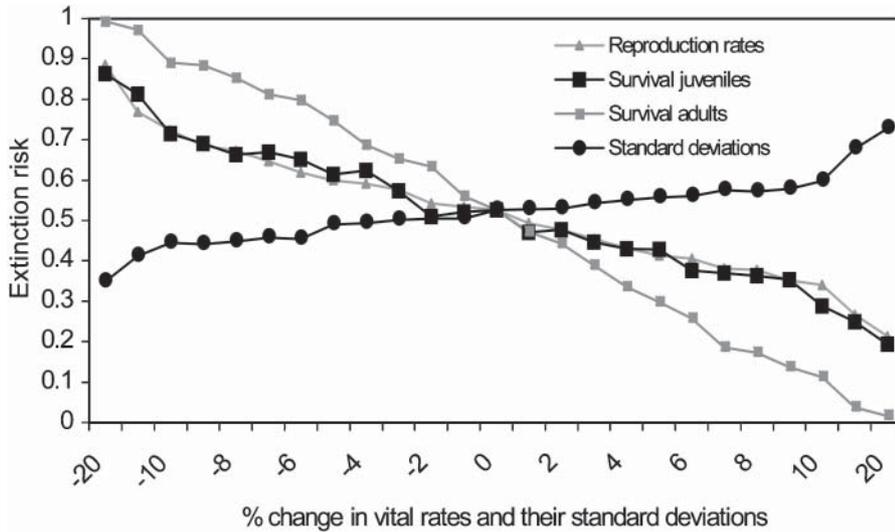


Fig. 2 Variation in modelled extinction risk as a consequence of modified vital rates and standard deviations, with 100 time steps (years) per run and 1,000 runs. Changes were made by steps of 1% up to 10%, and thereafter by 15 and 20%. Each parameter was modified separately whilst holding other parameters constant.

parameter by steps of 1% up to 10%, and then 15 and 20%. For all changes we calculated the extinction risk. We did not run scenarios with combinations of changed parameters.

As the main threat to *C. mexicanus* in most of its geographic range is habitat loss (Scott-Morales *et al.*, 2004), we simulated the viability of the El Manantial complex with population sizes reduced to 50% of their original sizes.

## Results

### Densities and demographic parameters

Estimations of density and numbers per colony are given in the Appendix. There were markedly different densities for the two complexes, with 1.3–15 per ha (mean 6.9) in the colonies of Los Angeles and 0.6–2.6 (mean 1.6) in those of El Manantial. A total of 135 and 79 offspring for the year 2002 and 140 and 68 offspring for the year 2003 were observed in 18 coterries in Los Angeles and La Perforadora respectively. The mean litter size per coterrie in La Perforadora and Los Angeles was significantly

different (4 and 8 respectively;  $t = 4.30$ ,  $P < 0.01$ ). Offspring survival rates over 12 months were significantly different ( $t = 75.89$ ,  $P < 0.01$ ; Table 1) at 63 (86/135) and 49% (39/79) in Los Angeles and La Perforadora respectively.

### Sensitivity analysis of vital rates

The sensitivity of the model to changes in vital rates and standard deviations of vital rates is given in Fig. 2. For all modelled parameters we found that changes in adult survival have the greatest impact on population survival because they result in high variations in extinction risk.

### Metapopulation dynamics

Figs 3–4 give the average number of time steps local populations occupied during the simulations. At Los Angeles complex the whole metapopulation did not become extinct (Fig. 3), but extinctions occurred in 8 of the 13 colonies, and in the colonies Cercado 1 and 2 and Las Hormigas 3, extinctions occurred frequently.

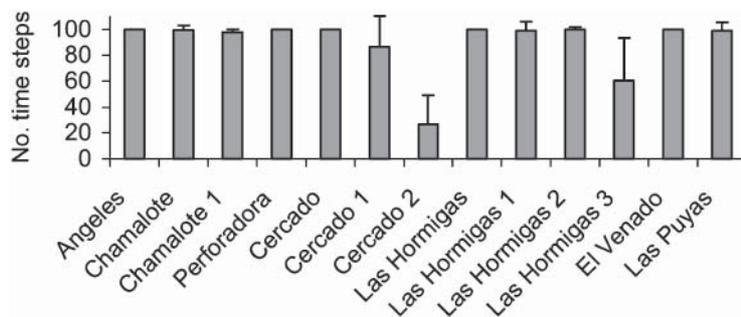
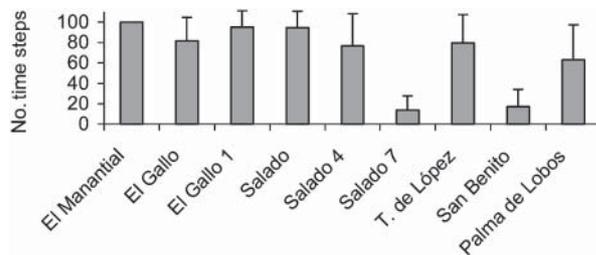


Fig. 3 Modelled occupancy structure of Los Angeles complex (average number of time steps the colonies were occupied during a 100-year run), with 100 time steps (years) per run and 1,000 runs. In El Cercado 2 and Las Hormigas 3 extinctions occurred frequently, whereas in the other colonies only El Cercado 1 has an occupancy of  $< 90\%$ .

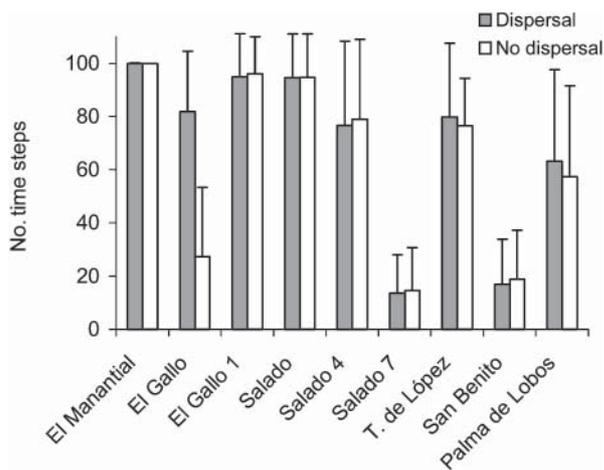
Similarly El Manantial complex did not go extinct, but 6 of 9 colonies were occupied for <80% of the years modeled (Fig. 4). The persistence of the whole metapopulation is a consequence of the survival of the largest colony, El Manantial.

Correlations of the variation in vital rates of local populations as well as exchange rates may also influence metapopulation dynamics. When we compared the occupancy of local populations using independent versus correlated variance in vital rates between colonies in our model, our results were nearly identical for both scenarios and both complexes.

In testing different migration scenarios we found that only El Gallo colony of El Manantial complex is highly dependent on migration (Fig. 5). The rest are independent of the exchange of individuals because they are out of range of other colonies, or they are large enough to survive on their own. In Los Angeles complex, which has



**Fig. 4** Modelled occupancy structure of El Manantial complex (average number of time steps the colonies were occupied during a 100-year run), with 100 time steps (years) per run and 1,000 runs. Extinctions occurred in 8 colonies, and six colonies were empty for  $\geq 20\%$  of all years.



**Fig. 5** Modelled occupancy structure of El Manantial complex (average number of time steps the colonies were occupied during a 100-year run), with and without dispersal. Dispersal is particularly important for the persistence of the El Gallo colony.

larger local populations, differing migration scenarios had no effect on the survival of any colonies.

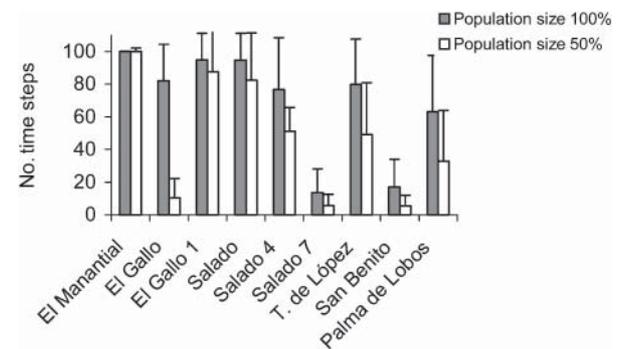
With population sizes of El Manantial colonies reduced to 50% of their original sizes, the whole metapopulation experienced lower occupancy, and El Manantial colony faced the probability of not being populated in some years (Fig. 6). Six of the 9 colonies were not populated for >50% of the years modelled.

## Discussion

There are high variations in density between the two complexes and individual colonies because of differing colony conditions. This variation seems to be a function of plant cover, with 45–50% vegetation cover being associated with higher densities such as those in the Los Angeles and El Cercado colonies (15 and 11 prairie dogs per ha, respectively; Scott-Morales & Estrada, 1999). Colonies with vegetation cover <5% have much lower population densities (Scott-Morales & Estrada, 1999).

We found differences in the reproduction and survival of offspring in both colonies under study. Rioja (2003) suggested that differences in management strategies for the colonies of Los Angeles and La Perforadora could have an impact on reproduction. The effect of vegetation cover on body mass and reproduction has been reported for *C. ludovicuanus* and *C. gunnisoni* (Garret *et al.*, 1982; Cully, 1997), where sites providing more food contributed to faster growth of juveniles and improved reproduction.

Absolute predictions from our simulations, such as the size of a minimum viable population, may be strongly influenced by uncertainties in parameter estimation, and therefore we focus here on comparative statements between the complexes. Our sensitivity analysis demonstrates that all vital rates have an influence on population



**Fig. 6** Modelled occupancy structure of El Manantial complex (average number of time steps the colonies were occupied during a 100-year run), with and without a reduction in the colony's carrying capacities to 50%. All colonies experience extinction within 100 years.

persistence but that adult survival is the critical parameter. Because our sensitivity analysis was made with a small population (20 adult females), these results indicate the importance of management strategies for *C. mexicanus*. In small colonies, such as those at the periphery of the species' range (Fig. 1), population survival and expansion of the colonies could be increased by reduction in the grazing pressure of cattle and sheep and thus habitat improvement.

Our metapopulation modelling indicates that the largest local populations will be able to persist, and that those of smaller size may survive if they are close enough to larger populations to allow dispersal. If the reduction in the size of El Manantial complex continues (Scott-Morales *et al.*, 2004), its future is uncertain. Because of the low abundance and small size of most of the colonies in the marginal southern parts of its distribution range the future of *C. mexicanus* there is not assured.

Some studies on the Mexican Plateau have described habitat loss as the main factor affecting the geographic range of *C. mexicanus* (Trevino-Villareal & Grant, 1998; Scott-Morales *et al.*, 2004). Fig. 6 reveals that a severe decline in the colony size (50%) of the local populations (as a result of habitat loss) could result in a decline in colony occupancy. This scenario seems realistic, considering the rate of habitat loss in recent years.

Fragmentation of habitat has two main effects: reduction in population sizes and isolation of remaining habitats. Isolated populations experience a high extinction risk (Hanski, 1999; Lomolino & Smith, 2001). Modelling scenarios without migration and with reduction of population size (Figs 5 & 6) indicate the relative importance of the latter, and there was not a strong effect of migration on extinction risk. This may be interpreted in two ways: stability of single colonies is most important, and/or isolation is already too high to provide the necessary exchange, even when including migration in the model. Based on our modelling we suggest that conservation actions should focus on increasing the carrying capacities of colonies through habitat management, including the control of invading plant species (Yeaton, 2001) and management of secondary vegetation.

We conclude that population size and adult survival are the main factors influencing the persistence of Mexican prairie dog colonies. Collection of long-term data on the relationship between habitat quality and vital rates, including the marking of animals, is required to improve our knowledge of the demography and life history of this species. Protection of the colonies of Los Angeles complex and El Manantial colony in El Manantial complex is particularly important because the metapopulation model indicates that survival will depend mainly on the size of the largest colonies. Continued habitat loss (Scott-Morales *et al.*, 2004) could cause the extinction of this endemic species.

Action is required to conserve remaining habitat fragments for this species and also to restore lost habitat. These matters are being pursued by local government, the NGO PRONATURA Noreste and the University of Nuevo León, with three protected areas recently declared in the state of Nuevo León. Studies are underway to examine genetic flow between populations and colonies to improve management and conservation decisions (M. Coterá, pers comm.). However, poverty in the region and the economic interests of private farming are hindering the implementation of conservation strategies for the remaining colonies. The efforts and interests of NGOs, landowners, government, scientists and public opinion need to be integrated for the successful conservation of this Endangered endemic species.

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### Biographical sketches

Laura Scott is interested in biodiversity and ecosystem degradation in arid regions. Her research focuses on population ecology and conservation of grassland vertebrates.

Eckhard Gottschalk is interested in connecting population biology and conservation. His research covers area requirements of threatened insect populations and factors determining vertebrate population dynamics.

Michael Mühlenberg's research and teaching activities cover many aspects of wildlife conservation, with an emphasis on natural landscapes, monitoring programmes and ecological field methodology.

## Appendix

Colonies in the Los Angeles and El Manantial complexes (numbers identify locations in Fig. 1), with latitude and longitude of each colony, density of prairie dogs per ha, area of the colony, and estimated number of prairie dogs in each colony.

	Colony name	Latitude	Longitude	Density (per ha)	Colony area (ha)	Estimated colony size
<b>Los Angeles Complex</b>						
1	Perforadora	25°03'57"	100°59'10"	6.8	1,124	7,643
2	Cercado 2	25°01'19"	100°54'12"	5.0	2	10
3	Hormigas 1.	24°58'38"	100°52'14"	5.0	43	215
4	Cercado	25°00'27"	100°53'53"	11.0	248	2,728
5	Cercado 1	25°00'11"	100°54'04"	4.0	14	56
6	Las Hormigas	24°58'16"	100°51'23"	10.0	310	3,100
7	Hormigas 2	24°57'59"	100°51'42"	6.5	27	176
8	Hormigas 3	24°56'48"	100°50'25"	1.3	28	36
9	Las Puyas	24°54'08"	100°50'12"	6.7	33	221
10	El Venado	24°56'44"	100°52'12"	4.3	637	739
11	Los Ángeles.	25°06'00"	100°57'32"	15.0	776	11,640
12	Chamalote	25°07'15"	101°05'06"	6.0	63	378
13	Chamalote 1	25°06'41"	101°05'30"	8.0	89	712
	<i>Mean</i>			6.9	260.0	
<b>El Manantial Complex</b>						
14	Palma de Lobos	24°24'54"	100°46'01"	0.6	46	28
15	San Benito	24°19'38"	100°43'49"	1.8	5	9
16	Salado 4	24°16'17"	100°47'34"	1.6	27	43
17	Salado 7	24°18'23"	100°47'36"	1.0	7	7
19	Salado	24°22'25"	100°46'49"	2.6	38	99
20	Tanque de López	24°16'05"	100°40'23"	1.0	40	40
21	El Gallo 1	24°12'34"	100°54'38"	2.4	50	120
22	El Gallo	24°11'55"	100°54'15"	1.1	10	11
23	Manantial	24°09'19"	100°55'42"	2.5	325	813
	<i>Mean</i>			1.6	55.0	