

Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators?

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Machicote, M., Branch, L. C. and Villarreal, D. 2004. Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? – *Oikos* 106: 527–535.

Terrestrial vertebrates exhibit dynamic, positive interactions that form and dissolve under different circumstances, usually with multiple species as participants. Ecosystem engineers are important facilitators of other species because they cause physical changes in the environment that alter resource availability. Although a species can be associated with more than one partner, facilitators may not be interchangeable if they differ in abundance, behavioral characteristics, or interactions with other factors in ways that condition the outcome of the association. We examined interactions between burrowing owls (*Athene cunicularia*) and two burrowing mammals, hairy armadillos (*Chaetophractus villosus*) and plains vizcachas (*Lagostomus maximus*), and determined whether these ecosystem engineers are interchangeable for owls. We examined reproductive success for owls nesting in these mammal burrows, constructed a logistic regression model to identify habitat characteristics associated with owl nests, and examined the engineering activities of the mammals. Data on reproduction and habitat indicate that armadillos and vizcachas are not interchangeable for owls. Thirty-five percent of the nests in vizcacha burrows produced fledglings; no fledglings were produced from nests outside vizcachas colonies, even though owls nest successfully in armadillo burrows in other parts of Argentina. Vizcachas facilitate burrowing owls by construction of burrows and by producing open understory vegetation through herbivory. In contrast, armadillos do not alter vegetation, and their burrows are suitable for nest sites only when they occur in recently burned areas or areas maintained by anthropogenic disturbance. Our habitat model also suggests that fire plays a key role in maintaining owl populations because fire is the only natural process that reduces shrubs to the level required by owls. Current management practices of eradication of vizcachas and fire suppression in shrublands could have strong negative consequences for burrowing owls.

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Recent theoretical and empirical work in ecology suggests that positive interactions among organisms are at least as important as negative interactions (e.g. competition and predation) in determining species distributions and abundances (Bertness and Callaway 1994, Hacker and Bertness 1999, Levine 2000, Bruno et al. 2003). Moreover, positive and negative interactions

are recognized as the ends of a gradient of possible outcomes of interactions between species (Bronstein 1994a, Stachowicz 2001), but empirical evidence of mechanisms that shift the balance between positive and negative interactions is limited for most systems (Tielbörger and Kadmon 2000). Conditional outcomes may be caused by such factors as changes in abundance, size

Accepted 30 January 2004

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ISSN 0030-1299

or age of participants, species composition of communities, and abiotic conditions (Bronstein 1994a).

Positive and negative interactions among terrestrial vertebrates are important in structuring communities (Dickman 1992, Mönkkönen et al. 1997, van der Wal et al. 2000). Negative interactions among vertebrates have been examined in many ecosystems (Gustafsson 1987, Heske et al. 1994, Hanski et al. 2001); however, most research on facilitation has focused on plant communities, plant–animal interactions, or intertidal communities (Bronstein 1994b, Bertness and Leonard 1997, Underwood 2000). Terrestrial vertebrates facilitate other species by two major mechanisms: a) behaviors that increase feeding efficiency and/or decrease predation risk (Dickman 1992, Chapman and Chapman 2000), and b) physical modification of the environment (i.e. ecosystem engineering, Jones et al. 1994, Lawton 1994).

Most positive interactions among terrestrial vertebrates appear to be commensalism (+/0 interaction), where one species provides a benefit to a partner without being negatively affected (Dickman 1992). However, interactions among vertebrates often are dynamic; interactions usually involve multiple species as participants and outcomes are likely to shift over time and space (Dickman 1992, Bronstein 1994a). Although a species can be associated with more than one partner, facilitator species (i.e. species that provide goods or services to other species) may not be interchangeable (Callaway 1998). For example, two ecosystem engineers may differ in the mechanisms through which they affect another species and the outcome of these interactions (i.e. fitness consequences for species dependent upon engineering activities) may be conditional upon population characteristics (e.g. abundance) and behavior of the partners or abiotic factors (Jones et al. 1997, Gutiérrez et al. 2003). The degree to which species are interchangeable as facilitators is unknown for most systems and more empirical work on conditional outcomes of interactions is needed as a foundation for incorporating these factors into models of community dynamics (Bertness and Callaway 1994).

In this paper, we examine interactions between burrowing owls (*Athene cunicularia*, Strigidae) and burrowing mammals in the semiarid shrublands of central Argentina. This system allows us to examine two broad questions: if ecosystem engineers create similar habitats (in this case, burrows), how similar are their effects on species that use these habitats? What factors condition the outcomes of these interactions? These questions are important both from theoretical and applied perspectives. Throughout most of their distribution from Canada to the southern tip of South America, burrowing owls nest in burrows constructed by mammals (Haug et al. 1993). Decline of prairie dogs (*Cynomys* spp., Sciuridae) and other burrowing mam-

mals has been proposed to play a major role in a dramatic decline of these owls in North America (Clayton and Schmutz 1999, Desmond et al. 2000). The status of burrowing owls and the relationships between owls and mammals are largely unknown for South America. The interchangeability of burrowing mammals as facilitators of burrowing owls has not been examined in detail in North or South America and may be critical to long-term survival of this species.

In central Argentina, the range of burrowing owls coincides with two common, medium-size burrowing mammals: plains vizcachas (*Lagostomus maximus*, Chinchillidae) and hairy armadillos (*Chaetophraactus villosus*, Dasypodidae). Both of these species construct burrows that are used by owls for nests, but their biology differs leading us to hypothesize that they are not interchangeable as hosts for owls. Vizcachas are large colonial rodents native to the pampas and semiarid shrublands of Argentina, Paraguay, and Bolivia (Jackson et al. 1996). These rodents occupy the same communal burrow system for many years and, through herbivory, reduce the biomass of understory vegetation in large patches (1–2 ha) around their burrows (Branch et al. 1996). Hairy armadillos also are found in grasslands and shrublands and range from Paraguay to southern Argentina and Chile (Redford and Eisenberg 1992). In contrast to vizcachas, these armadillos are solitary and occupy individual burrows for short periods of time (Carlini, pers. comm.). Hairy armadillos are omnivorous and only alter vegetation structure locally by digging and soil deposition at the burrow entrance. Owls nest in armadillo burrows in some parts of their range where vizcachas are absent. The degree to which these mammals are interchangeable as partners for owls has significant conservation implications because vizcachas, which are considered an agricultural pest, have declined severely and continue to decline as a result of intense eradication programs (Jackson et al. 1996).

In this study, we examine the roles of vizcachas and armadillos as facilitators for burrowing owls and evaluate whether these species are interchangeable. First, we focus on the outcomes of species interactions and compare reproductive success of owls nesting in vizcacha colonies and armadillo burrows. Then we construct a logistic regression model to identify habitat characteristics associated with burrowing owl nests and compare these characteristics to habitat modifications induced by vizcachas versus armadillos. Finally, we identify other environmental factors that may be critical in maintaining burrowing owls in the landscape and suggest how these factors interact with the activities of vizcachas and armadillos to produce conditional outcomes in owl–mammal interactions.

Methods

Study area

The study was conducted from May 2000 to February 2001 on Los Valles Ranch (7500 ha, 39°11' S, 63°42' W), a typical cattle ranch in the semiarid scrub of La Pampa Province, Argentina. The study area covered approximately 3000 ha. Annual precipitation in this area is low (mean \pm SE, 480 \pm 23 mm, 1971–1998, Río Colorado Meteorological Station located 60 km W of Los Valles, unpubl.). Vegetation is dominated by creosote bush (*Larrea divaricata*) with mixed shrub patches (e.g. *Condalia microphylla*, *Cercidium praecox* and *Prosopis flexuosa*) and an understory of bunch grasses (e.g. *Stipa* spp.) and forbs (Cano et al. 1980).

Survey for burrowing owl nests and assessment of reproductive success

The study area was searched for owls by traversing the area on foot and horseback during September–November. Monitoring of burrowing owls in the study area over the previous four years indicated that owls are highly visible and present on territories throughout the year (Romero and Machicote, unpubl.). Nests are easily identified by presence of feathers, droppings, owl pellets and owl castings with eggshell fragments (Haug et al. 1993). Sites where owls were observed were classified as nest sites only when a pair was seen at least five times and a burrow showed signs that a breeding attempt occurred (Millsap and Bear 2000).

All nests encountered in the study area ($n = 26$) were examined once a week from mid-November, when nesting was initiated, to mid-February to evaluate reproductive success. A nest was considered successful if at least one fledgling survived to 42 days of age (Millsap and Bear 2000). The number of fledglings per nest that survived to this age was taken as an estimate of fledging success (Desmond et al. 2000). Nest and fledging success were compared for nest sites located in vizcacha colonies and outside vizcacha colonies using a resampling procedure that allows for comparison of means when samples sizes are small (Resampling Stats 1995). The procedure uses simulations based on random sampling of the data to generate a probability distribution of differences in two means.

Habitat assessment

In order to identify characteristics of nesting habitat of burrowing owls, we assessed habitat structure and landscape variables at all nest sites ($n = 26$) and at non-nest sites ($n = 99$). Nest sites included active vizcacha colonies ($n = 14$), extinct vizcacha colonies ($n = 3$), armadillo

burrows ($n = 6$), and unknown burrows ($n = 3$). Non-nest sites included active vizcacha colonies ($n = 24$), extinct vizcacha colonies ($n = 25$), a random sample of armadillo burrows ($n = 25$), and random points on the landscape ($n = 25$). All active and extinct vizcacha colonies in the study area were surveyed. Burrows of armadillos, which were widespread throughout the ranch, were located by walking random transects. On each transect, the first burrow encountered was used as the sample plot. Random transects for armadillo burrows and random points in the landscape were selected by overlaying a dot grid on the study area and then randomly selecting points for sampling. At each point, we examined burrows for signs of owls and searched an area of approximately 4–5 ha to avoid misclassification of the site as occupied or unoccupied by owls. Each area was surveyed at least twice.

Vegetation was sampled using the circular sample-plot method (James and Shugart 1970, below) with one 0.04-ha plot per site. At nest sites, plots were centered on the nest. In vizcacha colonies, burrowing owls nest in satellite burrow systems constructed by vizcachas within 5–50 m of the principal burrow system (Jackson et al. 1996). One satellite burrow was chosen at random for the center of the plot in colonies (active or extinct) without owls. Sample plots were large enough to incorporate the entire satellite burrow system. At armadillo sites, the armadillo burrow was used as the center of the plot.

In each survey plot, 17 habitat characteristics were measured (Table 1). Following the circular sample-plot method (James and Shugart 1970), we placed two 22.5-m transects in random directions within the plot, and estimated cover of understory vegetation by component and maximum height of the understory every 2 m along the transects (James and Shugart 1970). For each variable, means of all measures on both transects were used as plot values. We also counted all shrubs with at least one stem inside a 1.8-m strip along each transect, averaged counts for the two transects, and calculated shrub density (James and Shugart 1970). Mean shrub height for each plot was determined from measurements of heights of 20 shrubs chosen randomly in each 0.04-ha plot. The number of trees in the 0.04-ha plot and the number of perches (dead shrubs or trees) in a 0.12-ha plot also were recorded. In order to estimate habitat heterogeneity, habitat surrounding each plot was classified as one of 15 categories based on dominant vegetation, and then we measured the distance from the center of the plot to the nearest different vegetation type (distance to edge, Clark and Shuter 1999). We also recorded type of burrow used for each nest and number of vizcacha and armadillo burrows in each plot.

To examine whether availability of either armadillo or vizcacha burrows could limit nest sites, we estimated the number of burrows of each type in the 3000-ha study area. The total number of armadillo burrows in the study

area was estimated from the number of armadillo burrows encountered per hectare in random plots established for habitat assessment. Because owls nest in satellite vizcacha burrows, we only estimated the number of vizcacha burrows in satellite systems. These estimates were obtained by multiplying the number of vizcacha colonies (active and extinct) in the study area by published estimates of the mean number of satellites per colony for La Pampa Province (9.0 ± 0.9 SE; Branch et al. 1994a) and then by the mean number of burrows recorded for satellite burrow systems in habitat plots in this study (burrows in satellite systems in active colonies, 5.0 ± 0.4 ; extinct colonies, 7.3 ± 1.4).

In order to examine the importance of patch isolation as a potential factor limiting occupancy of active vizcacha colonies by burrowing owls, we mapped all owl nests and vizcacha colonies using a GPS. We then calculated the distance between each unoccupied vizcacha colony and the nearest owl nest and the distance between each nest and the nearest neighboring nest.

Habitat model for nest sites

A univariate logistic regression model was constructed for each habitat variable to test whether the variable was associated with nest site selection by burrowing owls (Neter et al. 1989). Prior to analysis, data were tested for normality using Kolmogorov–Smirnov and Shapiro–Wilk tests, and transformations were made when appropriate (Zar 1984). We used arcsine transformations for percent cover of soil and understory vegetation, and square-root transformations for variables related to vegetation height, counts, and density. Correlations between variables were calculated using Pearson's correlation coefficient. Total understory cover and height of understory were highly correlated with other understory variables, and number of perches was highly correlated with shrub density and shrub height ($r \geq 0.7$ in all cases). These variables were eliminated resulting in a set of 14 characteristics for analyses (Table 1). The Wald statistic (Z^2), which has a χ^2 distribution, was used to test significance of coefficients of univariate regressions (Agresti 1996). Then we constructed a multi-factor logistic regression model using those variables found to be significantly associated with owl nests (Table 1). The full model was compared with alternative reduced models using Akaike's information criterion (AIC, Akaike 1985, Burnham and Anderson 1992). Using the parsimony principle, the multiple regression model that statistically fit the data with fewest parameters was chosen as the final habitat model (Goodman 1984, Neter et al. 1989). A likelihood ratio test was performed to compare the full model with this reduced model (Hosmer and Lemeshow 1989, Trexler and Travis 1993).

Once the model was selected, components of vegetation structure shown to be relevant for owl nests were compared for nest sites and non-nest sites at active and extinct vizcacha colonies and armadillo burrows, and these sites were compared to random sites, using t-tests adjusted for inequality of variances when necessary. Throughout this paper, data are presented as means ± 1 SE without transformation, and P values ≤ 0.05 are considered significant in all tests. All statistical analyses were performed using SPSS (SPSS 1999), except the analysis of reproductive success conducted with resampling statistics (Resampling Stats 1995).

Results

Burrow occupancy and reproductive success

Burrowing owls nested in 14 of 38 active vizcacha colonies (36.8%) and three of the 28 extinct colonies (10.7%). Only one pair occupied each colony. Armadillo burrows were abundant throughout the study area. Forty percent of the random plots contained armadillo burrows (1.4 ± 0.4 burrows per plot). No owls were located in armadillo burrows during the habitat survey, but six pairs were found nesting in armadillo burrows and three pairs in unknown burrows in the extensive search of the study area. Owls occupied a very small proportion of the total number of the burrows in the study area (estimated number of burrows – burrows in satellite vizcacha colonies, 3561; armadillo burrows, 105 000). All owls nesting outside of active vizcacha colonies were in sites recently burned, plowed, and/or heavily used by cattle. In contrast, only one active vizcacha colony occupied by burrowing owls had been subjected to anthropogenic modification.

All vizcacha colonies with owl nests were occupied by owls when the study began in May 2000 and had been occupied continuously by owls for at least four years prior to this study (Romero and Machicote, pers. obs.). In contrast, of the nine pairs that nested outside vizcacha colonies, at least five arrived at their territories in late October 2000. The first signs of nesting occurred in early November and the first young emerged from burrows in late December. Three of the nine pairs that nested outside vizcacha colonies disappeared in November and December before the emergence of young. All vizcacha colonies with nests were occupied by owls when this study terminated in late February.

Twenty three percent of the owl nests were successful, and the mean number of fledglings per nest was 0.62 ± 0.24 . All nests outside vizcacha colonies failed. In contrast, 35.3% of the nests in vizcacha colonies (active and extinct) fledged chicks with an average of 0.95 ± 0.13 fledglings per nest and 2.67 ± 0.33 fledglings per successful nest. Even with small sample sizes outside vizcacha colonies, nest success and fledging success were

significantly higher in vizcachas colonies than at other nest sites ($P = 0.03$, $P = 0.04$, respectively).

Habitat model for nest sites

Four understory parameters and two shrub parameters were significantly (negatively) associated with the presence of owl nests, and therefore were used to build the multivariate logistic model (Table 1). We compared the full model with six variables plus an intercept term to reduced models with 2–5 variables using AIC (Table 2). The model that included percent cover and height of perennial grasses, and height and density of shrubs resulted in the model with the lowest AIC, indicating that a model with four parameters adequately fit the data using the fewest parameters ($\chi^2 = 68.4$, $df = 4$, $P < 0.0001$). Further reduction in parameters always increased the AIC. The likelihood ratio test confirmed that this model and the full model containing all parameters were not significantly different ($\chi^2 = 0.8$, $df = 7$, $P = 0.10$). Therefore, the final model based on transformed data was as follows:

$$P_i = \exp(41.79 - 19.15 \text{ Pgrass} - 0.08 \text{ Hgrass} - 2.68 \text{ Hshrub} - 0.26 \text{ Dshrub}) \div [1 + \exp(41.79 - 19.15 \text{ Pgrass} - 0.08 \text{ Hgrass} - 2.68 \text{ Hshrub} - 0.26 \text{ Dshrub})]$$

where, P_i is the probability that site i contains a burrowing owl nest, P_{grass} is percentage of soil covered by perennial grasses at site i , H_{grass} is height of perennial grasses at site i , H_{shrub} is height of shrubs at site i , and D_{shrub} is density of shrubs at site i . The model correctly classified 97.6% of the plots with respect to presence or absence of owl nests, including 98.6% of the non-nest sites and 93.3% of the nest sites.

Table 2. Comparison of alternative habitat models for burrowing owl nest sites using Akaike's information criterion (AIC). The five models with the lowest AIC are shown.

Habitat model	np	-2 LF	AIC
Pgrass + Hgrass + Hshrub + Dshrub + Bsoil + Ann	7	11.39	25.39
Pgrass + Hgrass + Hshrub + Dshrub + Bsoil	6	10.27	22.27
Pgrass + Hgrass + Hshrub + Dshrub	5	10.86	20.86
Pgrass + Hgrass + Hshrub	4	15.14	23.14
Hgrass + Hshrub + Dshrub	4	19.25	27.25

$AIC = -2LF + 2np$, where LF is the estimate of the minimum negative value log-likelihood function, and np is number of parameters including an intercept term (Akaike 1985, Burnham and Anderson 1992). See Table 1 for full names of habitat variables.

Comparisons of characteristics of nest sites and non-nest sites

Burrowing owl nest sites are characterized by short shrubs, low shrub density, and low perennial grass cover (Fig. 1). Shrub height and density were significantly lower at nest sites than non-nest sites at all types of sites surveyed (Table 3). Grass cover was lower on nest sites (all types combined) than in random plots. In all active vizcacha colonies, grazing by vizcachas resulted in low grass cover and there were no significant differences in areas with and without owls (Table 3). Similarly, perennial grass cover was not different between nest sites and non-nest sites in extinct vizcacha colonies, but the height of perennial grasses was significantly lower at nest sites because these sites had been plowed (Table 3). Areas around armadillo burrows with owl nests had lower grass cover than armadillo burrow sites without nests as a result of fires and plowing at these

Table 1. Results of single factor logistic regression models for effects of individual habitat characteristics on nest site selection by burrowing owls. For each model, the value of the coefficient and SE for the parameter, Wald's statistic (Z^2), and associated P value are shown.

Variable ¹	Coefficient	SE	Z^2	P
Cover of perennial grasses (Pgrass)	-2.50	0.88	8.02	0.005*
Cover of perennial herbs (Pherb)	2.73	1.42	3.70	0.06
Cover of annual grasses and herbs (Ann)	-1.84	0.71	6.71	0.01*
Cover of bare soil (Bsoil)	7.29	1.47	24.61	< 0.0001*
Cover of litter (Litter)	-2.23	1.68	1.76	0.18
Height of perennial grasses (Hgrass)	-0.37	0.16	5.38	0.02*
Height of annual grasses and herbs (Hann)	-0.38	0.31	1.51	0.22
Number of trees (Tree)	-0.44	0.61	0.53	0.46
Density of shrubs (Dshrub)	-0.20	0.04	27.43	< 0.0001*
Height of shrubs (Hshrub)	-0.80	0.18	19.33	< 0.0001*
Number of vizcacha burrows (Vizbur)	-0.01	0.21	0.01	0.93
Number of armadillo burrows (Armbur)	-0.09	0.25	0.12	0.72
Total number of burrows (Burr)	-0.07	0.22	0.10	0.75
Distance to the edge (Edge)	-1.06	0.85	1.57	0.21

¹Total understory cover, height of understory, and number of perches were highly correlated ($r \geq 0.7$) with other variables (see Methods) and were eliminated from the analysis.

*Variables used in multifactor logistic regression model.

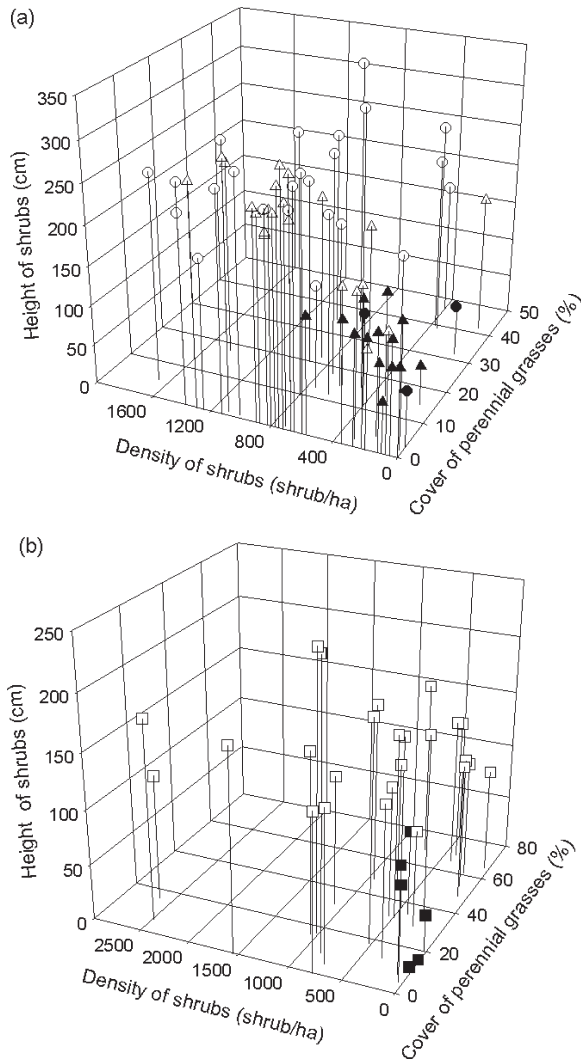


Fig. 1. Vegetation structure at (a) active vizcacha colonies with burrowing owl nests (▲), active colonies without nests (△), extinct colonies with nests (●), extinct colonies without nests (○), and (b) armadillo burrows with (■) and without owl nests (□).

sites (Table 3). Areas around armadillo burrows without anthropogenic impacts did not differ from random plots ($t = 1.1$, $df = 47$, $P = 0.30$). Cover of perennial grasses was lower on active vizcacha colonies (nest sites and non-nest sites combined) than extinct colonies ($t = 3.4$, $df = 48$, $P = 0.001$), random plots ($t = 6.2$, $df = 58$, $P < 0.0001$), and armadillo burrow sites ($t = 7.1$, $df = 52$, $P < 0.0001$).

At the scale of this study, occupation of vizcacha colonies by owls was not limited by colony isolation. The mean distance between colonies without owls and the nearest owl nest (241.9 ± 31.5 m) was lower than the mean distance between neighboring nests (787.4 ± 139.3 m, $t = 3.3$, $df = 42$, $P = 0.002$).

Discussion

Burrowing owls nested in burrows dug by vizcachas and armadillos, but these mammals clearly are not interchangeable as partners for owls. The interactions of owls with vizcachas and armadillos had different fitness consequences for owls and the mammals differed in their effects on owl habitat. During this study, no fledglings were produced from owl nests outside vizcacha colonies. Overall, nest success was low (23%) when compared with values commonly reported for burrowing owls in North America (50–70%; Green and Anthony 1989, Lutz and Plumpton 1999, Millsap and Bear 2000), but similar to values reported for other agroecosystems in Argentina (Bellocq 1997). The continual occupancy of vizcacha colonies by owls, as compared to the more temporary inhabitation of other sites, indicates that site fidelity is higher for owls nesting in vizcacha colonies and/or that vacancies are filled rapidly.

The lack of successful nesting in armadillo burrows suggests that these sites may act as ecological traps for owls (i.e. areas that appear to be suitable habitat based on physical characteristics but, due to some other factor such as predation, result in lowered reproductive success, Dwrnychuk and Boag 1972). However, burrowing owls nest successfully in armadillo burrows in other parts of Argentina (Harris 1998) and fledge young from armadillo burrows at our site during some years (Machicote, pers. obs.). Environmental conditions, particularly rainfall, are highly stochastic in semiarid areas and influence reproduction in burrowing owls (Botelho and Arrowood 1998, Millsap and Bear 2000). The ecological trap hypothesis, including the environmental conditions under which armadillo burrows act as ecological traps, merits further evaluation as owls may depend increasingly on armadillo burrows as vizcachas are eradicated.

In our study area only a small percentage of the mammal burrows were occupied by owls indicating that, although burrows are important, they are not limiting for owls. In contrast, vegetation structure, which is modified by vizcachas but not by armadillos, strongly influenced the location of burrowing owl nests. Even if nest success of owls were similar in vizcacha and armadillo burrows, interchangeability of vizcachas and armadillos as partners for owls would be conditional upon fire or other processes that decrease vegetation cover and height around armadillo burrows. In addition, the time period over which habitat is suitable differs for owls that nest in vizcacha versus armadillo burrows.

As in North America, owl nests were associated with habitat patches characterized by little grass cover and shorter grasses (Green and Anthony 1989, Clayton and Schmutz 1999). Owls were absent from all areas with greater than 40% cover of perennial grasses. Three types of disturbance can create or maintain open understory required by owls in semiarid scrub of central Argentina:

Table 3. Comparison of vegetation structure between nest sites and non-nest sites. Values are means (SE). Within pairs of columns representing nest and non-nest sites, variables marked with * are significantly different.

Variable	All nests		Random		Active vizcacha colonies		Extinct vizcacha colonies		Armadillo burrows	
	Nest (n = 26)	No nest (n = 25)	Nest (n = 14)	No nest (n = 24)	Nest (n = 3)	No nest (n = 25)	Nest (n = 6)	No nest (n = 25)		
Cover of perennial grasses (%)	7.21 (1.93)	27.49*** (4.21)	2.61 (1.45)	6.40 (2.32)	15.08 (8.59)	15.61 (3.18)	15.79 (4.40)	33.80* (4.62)		
Height of perennial grasses (cm)	24.88 (3.36)	35.70 (5.08)	26.83 (7.31)	35.22 (6.41)	15.13 (2.77)	47.74* (5.11)	30.99 (5.61)	44.65 (4.27)		
Density of shrubs (shrub/ha)	155.77 (29.88)	994.00*** (111.09)	185.71 (42.15)	683.33*** (73.58)	175.00 (118.15)	819.00** (80.30)	108.33 (59.39)	765.00** (130.69)		
Height of shrubs (cm)	91.90 (10.41)	176.21*** (10.64)	124.84 (9.32)	228.74*** (11.92)	84.83 (16.67)	251.13*** (10.19)	48.38 (17.61)	146.59* (8.70)		

*P < 0.05, **P < 0.001, ***P < 0.0001.

1) vizcachas, 2) fire, and 3) anthropogenic activities (e.g. trampling by livestock or agriculture). Spatial and temporal dynamics of these disturbances differ greatly. Vizcachas preferentially forage on grasses, which significantly reduces perennial grass cover and biomass on colony sites and results in a shift in dominant understory vegetation from grasses to low growing herbs (Branch et al. 1996). Because vizcacha colonies are occupied for multiple generations, these colonies can provide the low understory required for owls for many years (Jackson et al. 1996). In contrast, armadillo burrows are suitable for nest sites only when they occur in burned areas or open areas created by anthropogenic disturbance. Cover of perennial grasses can return to pre-burn levels within two-four years after a fire (Llorens and Frank 1999), rapidly making these areas unsuitable for owls in the absence of vizcacha grazing or other disturbance. Similarly, local extinction of vizcacha colonies results in unsuitable habitat for owls unless open vegetation is maintained by anthropogenic disturbances. Studies from nearby areas show that grass cover can increase from less than 5% on active vizcacha colonies to greater than 50% within two years following local extinction of vizcachas, although recovery of grasses is slower in low rainfall years (Branch et al. 1996).

Because the semiarid landscape of central Argentina is dominated by shrubs, habitat modifications by mammals in the form of burrows and open understory are not sufficient to maintain burrowing owls in the landscape. Owls did not nest in areas where mean shrub height exceeded 150 cm or shrub density exceeded 575 shrubs ha⁻¹. Neither vizcachas nor armadillos significantly decrease woody vegetation. We hypothesize that, in the absence of extensive anthropogenic disturbance, the persistence of owls in this landscape and the association of owls with both armadillos and vizcachas is conditional upon fire. Fire is the only natural process that reduces shrub cover over large areas and retards woody plant succession in this system (Boó et al. 1997). Also, fire interacts with the activities of vizcachas in complex

ways. Fire facilitates expansion of vizcacha colonies (Branch et al. 1994b) and this may have an indirect positive effect on owls. However, vizcacha grazing reduces fine fuel loads and prevents penetration of fire into colonies once colonies are well established (Hierro 1999). We hypothesize that vizcachas facilitate owls by removing understory vegetation but over time inhibit owls by preventing the spread of fires and removal of shrubs. Return of fire to colony sites is conditional upon local extinction of vizcachas, or at least a large reduction in animal numbers, so that fine fuel accumulates. Such extinctions occur naturally at irregular intervals in the semiarid scrub of central Argentina, but these dynamics are poorly understood (Branch et al. 1994b, 1996).

Ecosystem engineers modulate availability of resources to other species by causing physical changes in the environment (Jones et al. 1994). Some species, including vizcachas, have far reaching effects because they alter key abiotic processes (Chapin et al. 1997, Hierro 1999). For example, beaver dams change stream hydrology, biogeochemical processes, and composition of aquatic communities (Pollock et al. 1995, Wright et al. 2002); grazers modify ecosystem structure and function by altering fire regimes (Laws 1970, Savage and Swetnam 1990, Hierro 1999, Knapp et al. 1999); and oyster reefs control water flow and sediment deposition (Gutiérrez et al. 2003). As demonstrated by armadillos in our study, other ecosystem engineers do not influence abiotic processes but modulate availability of resources for other taxa only when their effects occur in conjunction with abiotic or biotic forces. When ecosystem engineers plus other processes create and maintain habitat for other species, temporal availability of habitat is limited by the effect or process with the shortest duration and longest return interval. For example, in large wetlands American alligators (*Alligator mississippiensis*) create wallows that retain water during drought and serve as refuges for vertebrates and invertebrates when wetlands dry out (Finlayson and Moser 1991). These wallows can persist for decades, but their function

as refuges for other species is limited by the duration and frequency of droughts. Similarly, the availability of suitable habitat for burrowing owls nesting in armadillo burrows is limited by the length of time vegetation remains open following fire and return interval of fire, not by burrows, which persist for long periods of time and are created continually.

Conclusion

Understanding the mechanisms and conditionalities underlying species interactions is a key challenge for ecosystem conservation (Stachowicz 2001). Our study system demonstrates complex conditional outcomes that involve positive and negative interactions between burrowing owls, their mammalian partners, and abiotic factors. The dynamics of owls, vizcachas, and fire are linked, and the outcome of these interactions changes through time and space. Current management practices of eradication of vizcachas throughout Argentina and fire suppression in shrub-dominated ecosystems could have strong negative consequences for burrowing owls.

Interactions with conditional outcomes are likely to be common in many systems (Bronstein 1994a, Stachowicz 2001). Our study suggests that assessment of activities of ecosystem engineers and development of habitat models for associated species in conjunction with identification of other key processes that drive the study system can provide insight into these complex interactions. In general, linkages among population dynamics of ecosystem engineers, dynamics of species that depend on these engineers, and processes that condition their interactions are poorly known (Gurney and Lawton 1996), even though such information is of fundamental importance because humans influence both the abundance and distribution of ecosystem engineers and the critical range of natural processes in many ecosystems (Gutiérrez et al. 2003).

Acknowledgements – We are indebted to H. Bernabé for access to Los Valles Ranch. We thank E. Bontti, J. L. Cuartero, M. E. Estanga-Mollica, and volunteers from the National University of La Pampa (UNLPam) for field assistance. J.L. Hierro generously shared ideas and data. We thank K. Sieving, K. Clark and M. Sunquist for helpful comments. Research was funded by the Fulbright – Laspau Program, Disney Conservation Award, UNLPam, and University of Florida. This is Florida Agricultural Series No. R-10018.

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