



# Influence of grazing management on resource selection by a small mammal in a temperate desert of South America

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Drylands occupy almost 50% of the Earth's surface and are increasingly affected by extensive land uses such as grazing. These practices affect multiple biotic and abiotic interactions mainly through loss of habitat and resources available for native wildlife. We examined the effects of local vegetation conditions on resource selection by a small mammal species in drylands with different resource availability. The study was conducted in a semi-arid woodland that included an area protected from livestock grazing and human settlement for more than 50 years, the Man and the Biosphere Ñacunán Reserve, and an adjoining area that has experienced long-term cattle grazing. We tracked radio-collared individuals of Graomys griseoflavus, the most abundant small mammal in the Nacunán region, and calculated resource selection functions (RSFs) to evaluate habitat selection. We modeled resource selection using a suite of habitat variables measured in both areas. We hypothesized that long-term changes in vegetation associated with livestock grazing would substantially influence habitat selection. G. griseoflavus selected vegetation patches with relatively greater cover of forage species (i.e., taxa commonly consumed) and avoided open spaces; they also selected sites with greater species richness and cover of grasses and trees. Although resource selection patterns were generally similar under both management conditions (i.e., under passive restoration and grazing), the strength of selection was greater in the grazed area. The final RSF model validated well with k-fold cross-validation ( $R^2 = 0.61$ ). Because of the importance of rodents in ecosystem function, management to meet their resource requirements could be an important tool for habitat restoration in degraded drylands.

Las tierras secas ocupan casi el 50% de la superficie de la tierra y están sujetas a un creciente avance de usos extensivos como el pastoreo por ganado. Estas prácticas afectan múltiples interacciones bióticas y abióticas y la disponibilidad de recursos para especies nativas. En este trabajo se examinaron los efectos de los cambios generados por el pastoreo en estructura del hábitat a escala local sobre la selección y disponibilidad de recursos por parte de un pequeño mamífero nativo. El estudio se realizó en un ecosistema de bosque seco sujeto a diferentes manejos (un área con restauración pasiva, Reserva del Hombre y la Biosfera de Ñacuñán; y un área con pastoreo vacuno continuo). Mediante la técnica de radio-telemetría se realizó el seguimiento de individuos de *Graomys griseoflavus*, y se calcularon las funciones de selección de recursos para evaluar uso del hábitat. Los modelos de selección de recursos se crearon a partir del uso de variables de hábitat medidas en ambas áreas. Se planteó la hipótesis que los cambios de largo plazo en la vegetación debido al pastoreo vacuno influenciaron el uso del hábitat del pequeño mamífero. *G. griseoflavus* seleccionó parches de vegetación que contienen una alta cobertura de especies presentes en su dieta, alta riqueza de especies y una gran cobertura de hierbas y árboles, evitando los espacios inter-parches. Si bien los patrones de selección de recursos fueron similares en ambas condiciones de manejo (es decir, bajo restauración pasiva y pastoreo), la fuerza de la selección fue mayor en el área pastoreada. El modelo final de selección de recursos fue validado a través del método

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de validación cruzada, obteniendo un alto ajuste para el mismo ( $R^2 = 0.61$ ). Debido a la importancia funcional de los pequeños mamíferos en ecosistemas áridos, la gestión dirigida a preservar sus requerimientos ecológicos de hábitat constituye una herramienta importante para la conservación y recuperación de zonas áridas degradadas.

Key words: Graomys griseoflavus, livestock grazing, Monte Desert, passive restoration, resource selection functions, small mammals

Livestock grazing in drylands can alter the spatial heterogeneity of vegetation, influencing ecosystem processes and biodiversity (Asner et al. 2004; Hanke et al. 2014). Overgrazing is among the main causes of desertification in arid systems because it diminishes vegetation cover and disrupts important ecological processes such as grass recruitment and nutrient cycling (Reynolds et al. 2007). Livestock grazing also changes the landscape configuration of vegetation, including changes in the number of resource patches, their sizes, and potential isolation (Fischer and Lindenmayer 2007; Okin et al. 2015). Therefore, understanding how native wildlife respond and acquire resources in a grazing matrix is a central challenge to maintaining or recovering ecosystem functions and biodiversity of lands modified by human activities (Plieninger and Gaertner 2011; Martensen et al. 2012).

Resource availability denotes the quantity or quality of resources (e.g., food or nesting habitat) an animal can access in the landscape and is influenced by habitat structure and permeability (i.e., the degree to which the landscape facilitates or impedes animal movement; Burel and Baudry 2003; Bissonette and Adair 2008). Here, we define habitat based on concepts of the niche; it includes the resources and environmental conditions that support a given level of animal or population performance (Hall et al. 1997; Gaillard et al. 2010). For instance, large but isolated resource patches might not be reached by-and thus will be unavailable for-individuals inhabiting other areas (Awade et al. 2012; Decout et al. 2012). Changes in availability and distribution of resources across landscapes shape the way in which animals use the resources (Fischer and Schröder 2014). If animals require a particular amount or quality of a given resource, they may show strong selection (relative use greater than expected from random use) for it when scarce but not when abundant (Mauritzen et al. 2003; McLoughlin et al. 2010). Mysterud and Ims (1998) define this behavior as a functional response in resource selection studies, demonstrating how resource selection might differ according to its availability. Functional responses may result from tradeoffs between habitat that fulfills different life-history requirements, such as forage and safety (Mauritzen et al. 2003; Godvik et al. 2009), forage quantity and quality (Bremset Hansen et al. 2009), or prey density and human disturbance (Hebblewhite and Merrill 2008).

The persistence of wildlife in highly modified landscapes generally depends on the species' ability to use habitat patches and move across heterogeneous landscapes to find essential resources (Fahrig 2003; Cushman et al. 2006). Small mammals are considered a key component of biodiversity in drylands (Meserve et al. 2011; Ojeda et al. 2011). These species tend to be opportunistic consumers, varying their diet according to local availability and seasons (Fox 2011), and taking advantage of abundant food resources when they are available, principally during the wet season (Noy-Meir 1973; Rossi 2004). At fine-grained scales, small mammals usually select densely vegetated patches, because these areas are associated with a lower predation risk compared to open areas (Morris 2005; Corbalán 2006). Moreover, distance and connectivity between dense vegetation patches can alter small rodents' behavior. When distances are short, animals may readily cross non-habitat, treating the whole area as part of their home range (Zollner and Lima 1997). As distances increase, a threshold is reached at which small mammals no longer risk traveling through unfavorable environmental conditions (Gillis and Nams 1998; Nams 2012; Zeller et al. 2012). This behavioral change can result in substantially diminished ecosystem functions and reduced biodiversity (Kelt 2011).

Small mammals, particularly rodents, fulfill a number of ecological roles, such as habitat modification by digging and burrowing in soil, foraging on plants and seeds, and hoarding food (Campos et al. 2007; Roth et al. 2009; Yoshihara et al. 2009). Their foraging pits trap litter and seeds under vegetation, thus forming nutrient-rich germination sites that enhance species diversity and influence ecosystem processes from the microhabitat to the landscape scale (Martin 2003). Because of the importance of small rodents in ecosystem function, they can serve as focal species for habitat restoration, and their requirements could help guide restoration (Hobbs 2007). However, the precise relationship between particular management actions and changes in habitat quality and associated resource availability often are difficult to quantify, especially for small rodents.

In arid landscapes, animals constantly balance resource availability and risk avoidance (Dickman et al. 2011; Tabeni et al. 2012). Thus, examining their functional response to differing environmental conditions could provide new information on ecosystem function not available from species composition and richness estimates derived from the documentation of species presence and absence (Lindell 2008). To explore these functional responses, we evaluated the effect of a combination of passive restoration and grazed treatments in the central Monte Desert (Argentina) on resource selection of a small rodent species. Specifically, we explored how fine-scaled differences in resource availability related to predation risk and foraging influence resource selection by small mammals. In the absence of other major constraints beyond forage, we hypothesized that:

- 1) Small rodents select habitat in response to a combination of factors related to forage species cover and vegetation cover for protection, while avoiding open spaces where predation risk is high.
- Selection of certain habitat variables, such as cover of forage species, increases as resources become less available, specifically as influenced by effects of chronic livestock grazing on vegetation structure.

# MATERIALS AND METHODS

Study area.-We conducted our study in the Man and the Biosphere Ñacunán Reserve, Mendoza Province, Argentina (34°02' S, 67°58' W; 12,300 ha), and in an adjoining unprotected area of ~10,000 ha under continuous cattle grazing (Guevara et al. 2009). The stocking rate outside the reserve, expressed as animal units per hectare (AU/ha), was between 0.03 and 0.08 AU/ha (F. Spirito, pers. obs.). The study area lies in the central Monte Desert biome (Morello 1958). The climate is semiarid, with marked seasonality of warm, humid summers (mean temperature >  $20^{\circ}$ C) and cool, dry winters (mean temperature < 10°C). Average annual rainfall is ~324 mm (Estrella et al. 2001). The region has a diverse mosaic of habitats that includes Prosopis flexuosa woodland and shrubland dominated by Larrea spp. and Bulnesia sp. (Zygophyllaceae). The Ñacuñán Reserve was created in 1961 to protect native woodland and its biota, and has been protected through fencing from livestock grazing since its inception. In 1986, the Nacuñán Reserve was included in the world network of Man and Biosphere Reserves (UNESCO; Boshoven et al. 2001), and is the most important reference site in Argentina for monitoring the ecological health of the Monte Desert. This long-term grazing exclusion site exhibits a remarkable passive restoration of native vascular vegetation (Rossi 2004). Small and medium-sized native mammal species associated with dense vegetation cover were mainly found inside the Nacuñán Reserve, and surrounding areas were occupied by mammals adapted to open habitats. For example, the presence of the endangered Dolichotis patagonum in rangelands outside the Reserve demonstrates that unprotected areas surrounding Ñacuñán Reserve also may play a major role in conserving species diversity (Tabeni et al. 2013).

*Captures and data collection.*—We evaluated resource selection by *Graomys griseoflavus* (mean total length = 262 mm; mean weight = 62.4 g; Rosi 1983), the most abundant small mammal in the Ñacuñán region (Tabeni and Ojeda 2005). This species is widely distributed in Argentina, Bolivia, Paraguay, and southwestern Brazil (Eisenberg and Redford 1992), and is herbivorous, feeding mainly on leaves of *Prosopis* spp. and *Lycium* spp. (Campos et al. 2001).

We conducted 2 trapping sessions, first in the dry season (June-July 2012), and second during the wet season (February-March 2013). The sampling during the wet season did not overlap with the peak breeding activity of G. griseoflavus (Corbalán et al. 2006) to avoid captures of pregnant or lactating females. We established trapping grids, in a 10 by 13 configuration, in Prosopis woodland in both passive restoration and grazed areas (~1.5 ha each). We placed Sherman live traps (H. B. Sherman Co., Tallahassee, Florida) 10 m apart, baited with rolled oats and vegetable oil. We trapped for 5 consecutive nights during each season and checked traps each morning. Captured animals were weighed and sex was recorded to ensure that we only fit transmitters to adults. We conducted all handling methods in accordance with Purdue Animal Care and Use Committee guidelines and guidelines of the American Society of Mammalogists on the use of wild mammals in research (Sikes et al. 2016).

We fitted very high frequency (VHF) telemetry transmitters to captured adults of G. griseoflavus weighing > 45 g, to minimize variability in resource selection due to different developmental stages of the species. We attached the transmitters in the field just before release of captured individuals. To reduce the influence of trapping on the rodents' use of space, we recorded telemetry locations only after traps were closed (i.e., after all trapping in a site was completed; Webster and Brooks 1981). The VHF transmitters were the 2 g-TXB-004C type with a magnetic on-off switch (Telenax Wildlife Telemetry, Playa del Carmen, Mexico). Weights of the transmitters did not exceed 5% of the average body mass for this species (most were 3-5%; Johannesen et al. 1997). We released all animals at the point of capture, previously recorded with a global positioning system (GPS-62s-Garmin; Garmin Ltd., Olathe, Kansas) with approximately 2-m accuracy. The collared animals were located with a RX-TLNX receiver equipped with a 3-element Yagi antenna (Telenax Wildlife Telemetry). We followed each animal for 10 consecutive days, nearly the full battery life of the transmitters, and collected locations every 2 h throughout each day and night.

We defined a used location as the place where the VHF signal was strongest, and recorded this location before the animal moved and the intensity of the signal declined. Once located, we recorded the position of each animal to the nearest meter using the GPS. Transmitters that could not be detected were searched for on foot within a 1-km radius of the last known location. To estimate the location error of the telemetry equipment, we placed 2 transmitters in known stationary positions and located them from 10 different positions, 7 times each. We calculated the error with LOAS 3.0.3 (Ecological Software Solutions, Urnasch, Switzerland) and compared our recorded locations to the real transmitter locations (Millspaugh and Marzluff 2001). Estimated location error was  $8.04 \pm 2.47$  m (mean  $\pm$  SD, n = 14). We recaptured experimental animals at the conclusion of the tracking period for removal of transmitters by saturating the area with traps around the last documented location of each animal.

Resource selection functions.-We used 792 telemetry locations from 13 radio-tagged adults to develop resource selection functions (RSFs) to characterize resource use by G. griseoflavus. Manly et al. (2002) defined a RSF as any function that is proportional to the probability of selection of a resource unit by an organism. A RSF estimates the probability of an animal selecting a given area or resource, given a combination of covariates and coefficients, by fitting a logistic regression model that estimates the coefficients of an exponential model (Johnson et al. 2006). It does this by comparing used to available resources or habitat units (Manly et al. 2002). Resource units are tangible items that are distributed over space and time as discrete units, such as eggs that are available for consumption by a fox, or grass seeds for a small granivore. Available units are those units that could potentially be encountered by the animal. Used units are those resource units that are encountered and selected and are part of a set of resource units that have received some investment by an animal (i.e., used set) during a sampling period (Lele et al. 2013).

Development of RSFs by comparing used to available resource units (McDonald et al. 2006) is appropriate when resource units used by animals can be estimated with high certainty but unused units cannot be identified well because of limited sampling intensity (Johnson et al. 2006). The used resource units were a subset of what was available to the animal; when resources are used at a higher or lower proportion than available, the animal is said to be selecting or avoiding that resource, respectively (Manly et al. 2002). We defined used units as locations of G. griseoflavus recorded with radio-tracking. We evaluated selection using RSFs with a design II approach, following individuals to identify a set of used resources, but assessing availability at the population level (Erickson et al. 2001). RSF modeling of used versus available resources under a design II approach is a commonly accepted method with the type of data and objectives of our study and is robust to lower intensity of animal sampling (Johnson et al. 2006; Manly et al. 2002).

Selecting data for construction of models.—Due to the limited number of locations recorded per animal (see Results), it was not possible to build a RSF for each individual. Instead, we estimated a population-level model by pooling location data across individuals and seasons, contrasting the used and available resource units from the data of 2012–2013. We then tested for significant interactions between each variable and treatment (i.e., grazing versus passive restoration) to determine if management condition affected resource selection, i.e., if patterns of selection differed between the passive restoration and grazed areas.

We defined the available area for our sample of telemetered animals using minimum convex polygons (MCP; Harris et al. 1990), creating 1 polygon for locations of animals captured in the passive restoration area and 1 for animals from the grazed area. We then sampled available locations within each of our 2 study areas by randomly selecting approximately 400 available locations within each MCP and a 1,000-m buffer around those locations (Fig. 1). We used ~400 available locations as a way of equalizing the total number of used and available locations (Supplementary Data SD1). The buffer area of 1,000-m was consistent with the recommendation of McClean et al. (1998) that the study-area level of habitat availability be based on the distribution of radio-collared animals.

We checked normality of the distribution of each habitat variable defined in Table 1 (see *Habitat variables* below). Because some variables were not normally distributed, we used Spearman's rank correlation coefficient (Zar 2010) to identify potential multicollinearities and to determine whether any variable should be excluded from the modeling ( $|r| \ge 0.6$ ). To reliably assess the relationship between resource selection and habitat variables, only non-correlated variables were used to build a model.

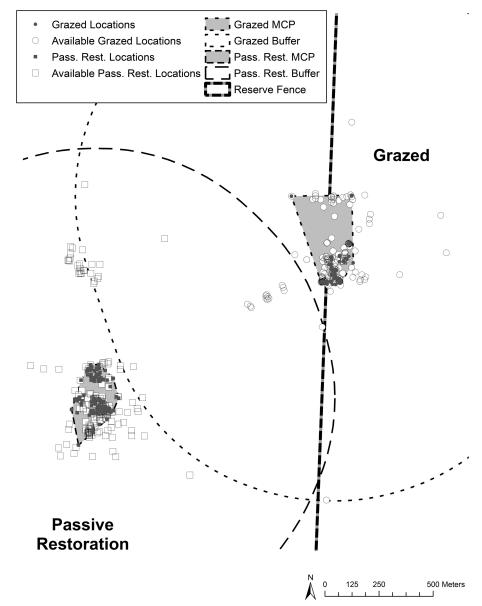
For the non-correlated variables, we constructed univariate exponential models for each environmental variable to determine which ones were related to resource selection by *G. griseoflavus* (Silva et al. 2007). We used 90% confidence intervals (*CIs*) to test for statistical significance of the regressions to reduce the probability of type II errors (conclusion of no statistical difference when in fact a difference exists) that are more

probable with small sample sizes and low precision as with our data (Zar 2010). To determine which variables should include a treatment interaction term (i.e., management condition), we compared the estimated coefficients for each univariate model for the passive restoration versus grazed areas using a 2-sample *t*-test (Zar 2010). If the difference between coefficients for the areas was statistically significant, we included the interaction term for that variable in our modeling. If not, we estimated a single coefficient for that variable to represent habitat use in both areas.

Habitat variables and analysis.—We identified 9 variables as potential environmental predictors of resource selection based on prior research and knowledge about the ecology of G. griseoflavus (Table 1). We sampled vegetation following each period of release of captured animals at documented (i.e., used) locations of G. griseoflavus and in available locations in the passive restoration and grazed areas. We measured vegetation at each location (i.e., used and available) with the line intercept method using two 5-m transects in a cross configuration (Canfield 1941). The center point of each transect was the georeferenced site previously documented as a location used by G. griseoflavus or as one of the available locations. From this point we ran a transect 2.5 m in each of the 4 cardinal directions (i.e., N-S-W-E). On each transect, we recorded the length (cm) of the line covered continuously by individual species, by litter, and by bare ground. The plant species were then grouped into different categories to estimate the percentage of cover within each; categories corresponded to different vegetation life forms, i.e., grasses, forbs, shrubs, and trees, as well as forage species consumed by G. griseoflavus, cover of bare ground and litter, and species richness. Forage species were those previously identified by Giannoni et al. (2005) as being important items in diets of G. griseoflavus; they included P. flexuosa (mainly leaves), Lycium spp. (leaves and seeds), Capparis atamisquea (stems), and Larrea spp. (seeds). We also created a separate habitat variable for P. flexuosa because it is considered a key desert species that also provides food and shelter to small mammals (Campos et al. 2001; Albanese et al. 2011). We calculated the relative percent cover for each habitat variable along the total transect length (i.e., 10 m).

We used Kruskal-Wallis tests (Zar 2010) to compare mean values of habitat variables between treatments (i.e., passive restoration and grazed areas) during each season. We used the H statistic in the Kruskal-Wallis test (Zar 2010) to first evaluate overall significance between treatments before proceeding with multiple tests between mean values among treatments. We considered differences in mean values to be statistically significant when P < 0.05; this level of significance provided a balance between protection against type I versus type II errors, given the more moderate precision of the vegetation data collected in our study versus the less precise telemetry data where 90% *CIs* on RSF coefficients were more appropriate. This analysis differs from the resource analysis in that it simply compares habitat characteristics between the 2 treatment areas.

*Model fitting and selection.*—Although a variety of statistical models are available to compute a RSF, the most common



**Fig. 1.**—Used and available locations for all radio-collared *Graomys griseoflavus* under passive restoration and grazed management in the central Monte Desert, Argentina and their associated minimum convex polygons (MCPs). The available locations were randomly drawn from an area including the used locations and a 1,000-m buffer around them. Portions of the buffered MCPs are not displayed.

Table 1.—Habitat variables used to estimate resource selection functions for *Graomys griseoflavus* in passive restoration and grazed areas in the central Monte Desert, Argentina.

Habitat variables	Name De				
% cover of grasses	Grasses	Relative percent cover of grasses			
% cover of shrubs	Shrubs	Relative percent cover of shrubs			
% cover of forbs	Forbs	Relative percent cover of forbs			
% cover of trees	Trees	Relative percent cover of trees			
% cover of forage species	Forage	Relative percent cover of species consumed by G. griseoflavi			
% cover of Prosopis flexuosa	Prosopis	Relative percent cover of <i>P. flexuosa</i>			
% cover of litter	Litter	Relative percent cover of litter			
% cover of bare ground	Bare ground	Relative percent cover of bare ground			
Species richness	Sprichness	Number of plant species present at each location			

analysis is to apply a binomial generalized linear model (GLM; Nielson and Sawyer 2013) to estimate the exponential RSF (McDonald 2013). To construct a multivariate RSF, we used variables with significant coefficients derived from the univariate models of association with the presence of G. griseoflavus. Using a forward stepwise modeling approach, variable entry was determined by considering the collective direction (i.e., positive or negative) and strength of the variable (Sawyer et al. 2006). We first created singlevariable models for all habitat variables brought forward for analysis that did not demonstrate a potential treatment effect; for those that did, we created models with treatment interactions (i.e., a variable and treatment). We then used the smallsample version of the Akaike Information Criterion (AICc; Akaike 1987) to select the single-variable model best supported by the data, i.e., the model with the lowest AICc value, and created a new model set by combining this model with all other possible variables to create new sets of 2-variable models. We repeated this process until the AICc value of the next set of models was greater than that of the prior step, indicating no improvement in information content compared to the previous best-fitting model (Burnham et al. 2011). We selected the model with the lowest number of parameters and best fit to the data (parsimony principle); i.e., the model with the lowest AIC<sub>c</sub>.

Due to our small sample sizes (Supplementary Data SD1) it was not possible to build independent models for the passive restoration and grazed areas. Thus, we constructed a single model with all location data pooled and used interaction terms to identify variables for which selection differed by management condition. To simplify the presentation of results for the final models, we re-fit the final habitat model separately for each management condition without interaction terms. To address the small sample sizes, we estimated standard errors and CIs for each variable in the final model using the bootstrap method, repeatedly selecting (500 iterations) individual G. griseoflavus locations with replacement (Efron and Tibshirani 1985). The primary advantage of bootstrapping is its treatment of the animal as the primary sampling unit (Erickson et al. 2001) without the complication of attempting to fit a generalized linear mixedmodel with the animal as a random effect. We also calculated marginal plots for each variable in the final RSF model, to visualize how predictions of G. griseoflavus use changed across the range of observed values for a single covariate while values of other covariates remained constant.

*Model validation.*—Following identification of the top model, we used the validation technique described by Johnson et al. (2006) to assess the predictive power of our RSF model. We validated the model following a traditional k-fold cross-validation (Boyce et al. 2002), in which we temporarily dropped a random sample of 25% of the used locations and 25% of the available locations from the data set. We re-estimated the final model using data from the remaining used and available locations (i.e., 75% of the data) and repeated this process 4 times. For each re-fitted model, we used the reserved locations (25% of the used and available locations) to validate the model as

follows. We ran the model and then sorted predicted values of use from lowest to highest and grouped the values into 10 equal-sized categories, or bins, and calculated the median value of each bin. We calculated expected counts of animals by multiplying the proportional use in each bin by the total observed animals for the model run. Next, we counted numbers of observed animal locations within each of these bins and compared observed versus expected counts with linear regression. We evaluated model performance using the coefficient of determination and the *CI*s about the fitted line, and by testing whether the slope was different from 0 and different from 1, and that the intercept differed from 0. An average slope of 1.0 and intercept of 0 would indicate excellent model performance (i.e., estimated relative probabilities of use were proportional to the true probabilities of use).

We performed statistical analyses in R language and environment for statistical computing (version 2.15.2, R Development Core Team 2013) with the following packages: "vegan" (Kruskal-Wallis and NMDS; Oksanen et al. 2013), "Hmisc" (RSF; Harrell 2008), and "adehabitatHR" (minimum convex polygon; Calenge 2011).

#### RESULTS

Habitat variables.-The available resources, as indexed by habitat variables, differed in several instances by management condition (passive restoration versus grazed), but less so by season (dry versus wet; Table 2). Differences between the grazed and passive restoration areas were generally more pronounced in the dry season (Table 2). In the dry season, cover of grasses, shrubs, forage species, and litter were significantly lower in the grazed area compared with the passive restoration area (Table 2). By contrast, forb and bare ground cover were higher under grazing. Percentage cover of trees and Prosopis did not differ by treatment in the dry season (Table 2). Only differences in shrub cover and litter were significant between treatments in the wet season; both were higher under passive restoration (Table 2). Species richness was similar between management conditions (Table 2). Within treatment type, few differences were found by season. Grass cover was lower in the dry season in the grazed area, and forb cover was lower in the dry season under both management conditions (Table 2). Lastly, tree cover was lower in the wet season versus the dry in the passive restoration area.

*Resource selection.*—We tracked 13 individuals during the dry (6 males and 3 females) and wet (2 males and 2 females) seasons. We attempted to fit transmitters to an equal number of males and females during each session, but this was not possible because too few females were caught (8 males versus 5 females). We used a total of 792 locations in our analysis: 197 used locations and 267 available in the passive restoration area, and 199 used locations and 129 available in the grazed area (Supplementary Data SD1). The smaller sample size for the available locations in the grazed area was due to some of the random (i.e., available) locations associated with the grazed area falling into the passive restoration area when mapped with

**Table 2.**—Evaluation of mean values of each habitat variable using Kruskal-Wallis (*H*-value) between the passive restoration and grazed areas in the central Monte Desert, Argentina (see Table 1 for descriptions of variables). Values are means with *SE* in parentheses (dry season:  $n_{\text{grazed area}} = 98$  and  $n_{\text{passive restoration area}} = 173$ ; wet season:  $n_{\text{grazed area}} = 31$  and  $n_{\text{passive restoration area}} = 94$ ). Different superscript letters indicate significant differences (*P* < 0.05) between mean values of each variable for a given treatment evaluation.

Habitat variables	Dry		Wet			
	Grazed	Passive restoration	Grazed	Passive restoration	<i>H</i> -value	P-value
Grasses (%)	15.83 (1.14) <sup>a</sup>	22.95 (1.29) <sup>b</sup>	23.21 (2.43) <sup>b</sup>	29.17 (2.21) <sup>b</sup>	36.61	< 0.0001
Forbs (%)	8.68 (0.82) <sup>b</sup>	4.23 (0.54) <sup>a</sup>	11.18 (1.47) <sup>c</sup>	9.04 (0.93) <sup>bc</sup>	50.43	< 0.0001
Shrubs (%)	53.39 (1.66) <sup>a</sup>	65.23 (1.56) <sup>b</sup>	56.78 (2.43) <sup>a</sup>	66.44 (2.14) <sup>b</sup>	34.52	< 0.0001
Trees (%)	29.87 (2.36) <sup>b</sup>	23.1 (2.47) <sup>b</sup>	20.55 (3.28) <sup>ab</sup>	16.14 (2.51) <sup>a</sup>	13.47	0.0031
Forage (%)	68.36 (1.42) <sup>a</sup>	74.6 (1.49) <sup>b</sup>	66.22 (2.35) <sup>a</sup>	71.61 (2.16) <sup>ab</sup>	13.80	0.0032
Prosopis (%)	22.6 (2.41)	15.47 (2.33)	12.46 (3.06)	12.82 (2.40)	4.23	0.1903
Litter (%)	64.63 (2.28) <sup>a</sup>	80.74 (1.45) <sup>b</sup>	68.01 (4.01) <sup>a</sup>	76.88 (1.79) <sup>b</sup>	43.71	< 0.0001
Bare ground (%)	35.37 (1.86) <sup>c</sup>	19.26 (1.79) <sup>a</sup>	31.99 (3.16)bc	23.12 (2.01) <sup>ab</sup>	40.89	< 0.0001
Sprichness	10.30 (2.31)	11.07 (1.45)	11.48 (1.15)	10.31 (2.12)	41.24	0.123

the MCP and buffer. Thus, they were considered instead as available locations for animals in the passive restoration area (Supplementary Data SD1).

We developed the RSF model by a forward stepwise process (Supplementary Data SD2). The top-ranked model included percent cover of bare ground, grass, forage, and trees, as well as species richness (Table 3; Supplementary Data SD2). All variables in this model except tree cover had a significant treatment interaction (passive restoration versus grazing), which indicates the relationship between those variables and resource selection depended on the management regime (Table 3). For example, G. griseoflavus selected greater cover of grass in the passive restoration area, but less grass cover in the grazed area. To better interpret results of the final model (Table 3), we re-fit the model separately for each management condition (Table 4). Based on the standardized coefficients, bare ground cover was the resource most avoided by G. griseoflavus under both management conditions, although this avoidance was not statistically significant in the grazed area (i.e., the CI included 0; Table 4). Under passive restoration, small mammals strongly avoided patches with >20% bare ground cover (Fig. 2). With grazing, however, predicted use was still moderate ( $\sim 0.40$ ) with 60% bare ground cover (Fig. 2). After bare ground, species richness was the second most selected resource in the grazed area (Table 4). This high selection also was reflected in the marginal plot, where the probability of selection increased with higher values of species richness (Fig. 2). By contrast, under passive restoration, selection did not change in response to species richness (Fig. 2). Grass cover was the second most important resource selected in the passive restoration area, and was positively associated with the probability of use by G. griseoflavus (Table 4; Fig. 2). Tree cover was highly selected in the grazed area compared with passive restoration (Table 4), with selection increasing exponentially there in contrast to the passive restoration condition (Fig. 2). Higher cover of forage species also was used more than expected based on availability under both management conditions, but selection was not statistically significant (Table 4; Fig. 2). Our k-fold validation confirmed good fit between observed and predicted counts of G. griseoflavus for the final model (Fig. 3), with an  $R^2$  value of 0.61 ( $CI_{lower} = 0.45$ ;  $CI_{upper} = 0.76$ ). Moreover, the slope was different from 0 and 1. **Table 3.**—Parameter estimates ( $\beta_i$ ), *SE*, and 90% *CIs* for each coefficient of the model covariates included in the final resource selection function model for *Graomys griseoflavus* in the central Monte Desert, Argentina (Supplementary Data SD2). Negative association by *G. griseoflavus* with a given variable is indicated by (–). The interaction term (\*) reflects the grazed management condition (G). See Table 1 for descriptions of model variables.

Model variable	$\beta_i$	SE	CI <sub>lower</sub>	CIupper
Intercept	0.437	_	_	_
Bare ground	-0.034	0.007	-0.046	-0.021
Bare ground + Bare ground * G	-0.049	0.009	-0.086	0.065
Sprichness	-0.037	0.05	-0.119	0.045
Sprichness+ Sprichness * G	0.251	0.074	0.129	0.372
Grasses	0.016	0.006	0.005	0.025
Grasses + Grasses * G	-0.038	0.011	-0.056	-0.020
Forage	0.001	0.007	-0.013	0.011
Forage + Forage * G	0.012	0.009	-0.004	0.028
Trees	0.005	0.003	0.0004	0.011
Treatment (G)	-3.933	1.171	-5.86	-2.006

## DISCUSSION

Reduction in native vegetation cover is generally considered the most deleterious consequence of land degradation on biodiversity (Fischer and Lindenmayer 2007; Pardini et al. 2010). Results from our study supported this global pattern by showing far greater bare ground cover in the grazed area compared with passive restoration. The Nacuñán Reserve, where grazing has been prohibited for more than 50 years, had greater connectivity among plant patches as reflected by lower bare ground cover and greater litter and forage species cover compared to the grazed area. In our study, G. griseoflavus apparently perceived these differences and selected resources in response to a combination of factors related to vegetation cover and foraging conditions. Contrary to our first hypothesis, bare ground was not uniformly avoided under both management conditions. However, it was significantly avoided in the passive restoration area: its coefficient was negative in all cases, and this variable had the largest standardized coefficients among all model variables in both management conditions.

Most resource selection studies of small mammals show that these species select resources to minimize predation risk

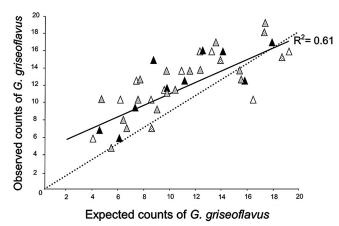
**Table 4.**—Parameter estimates ( $\beta_i$ ), standard errors (*SE*), and 90% confidence intervals (*CIs*) for each coefficient of the model covariates included in the final resource selection function model, re-fit for each management condition (grazed versus passive restoration) for *Graomys* griseoflavus in the central Monte Desert. Standardized parameter estimates (Std  $\beta_i$ ) also are reported so that effect size of model variables can be compared. Negative association by *G. griseoflavus* with a given variable is indicated by (–). See Table 1 for descriptions of model variables.

Grazed Passive restoration	Intercept Bare ground Sprichness Grasses Forage Trees Intercept Bare ground	-3.508 -0.016 0.224 -0.024 0.007 0.010 0.272	0.005 0.054 0.009 0.007 0.004	-0.024 0.134 -0.039 -0.005	0.026 0.313 -0.009 0.020	-1.708 1.009 -0.682
Passive restoration	Bare ground Sprichness Grasses Forage Trees Intercept Bare ground	0.224 -0.024 0.007 0.010 0.272	0.054 0.009 0.007	0.134 -0.039 -0.005	0.313 -0.009	1.009 -0.682
Passive restoration	Grasses Forage Trees Intercept Bare ground	-0.024 0.007 0.010 0.272	0.009 0.007	-0.039 -0.005	-0.009	-0.682
Passive restoration	Grasses Forage Trees Intercept Bare ground	0.007 0.010 0.272	0.007	-0.005		
Passive restoration	Trees Intercept Bare ground	0.010 0.272			0.020	
Passive restoration	Trees Intercept Bare ground	0.272	0.004		0.0-0	0.245
Passive restoration	Bare ground			0.003	0.018	0.577
	Bare ground		_	_	_	
		-0.034	0.007	-0.047	-0.022	-1.176
	Sprichness	-0.029	0.05	-0.112	0.053	-0.128
	Grasses	0.014	0.006	0.004	0.024	0.539
	Forage	0.001	0.007	-0.010	0.014	0.067
	Trees	< 0.001	0.004	-0.006	0.008	0.04
Relative probability of selection	20 40 60 80 bare ground (%)		10 12 14 16 18 sprichness	gras	 55 (%)	

**Fig. 2.**—Marginal plots showing relative probability of resource selection by *Graomys griseoflavus* in the central Monte Desert, Argentina, for the habitat variables in the final Resource Selection Function Model (Table 3). For variables with an interaction term for management condition, black lines represent the passive restoration area and dashed lines represent the grazed area. For variables without interaction effect, i.e., tree cover, the probability of selection is represented by a single line.

and secure food access (Yunger et al. 2002; Corbalán 2006; Milstead et al. 2007). Predation risk is often implicated as the most important factor determining differential fine-scale habitat use by small mammals (Bhattacharyya et al. 2015). A higher predation risk is associated with open spaces because common predators of small mammals, like birds and snakes, generally benefit from open spaces for detecting prey (Taraborelli et al. 2003; Borowski and Owadowska 2010; Tabeni et al. 2012). In our study, *G. griseoflavus* avoided open spaces under both management conditions, but this was not significant in the grazed area, where on average open spaces represented almost 35% of the total cover. Use of open spaces may reflect the grazed area conditions in our study area, which are perhaps not as degraded as other grazing areas in the Monte Desert (Torres et al. 2015). Our findings also support prior studies suggesting that animal populations and resource use patterns may not be strongly affected by degradation until a relatively high proportion of habitat is lost (e.g., > 70%; Flather and Bevers 2002).

In relation to food provision, under livestock grazing *G. gris-eoflavus* selected patches with higher plant species richness. In some cases, grazing can lead to a reduction of heterogeneity at the fine scale (Chillo 2013), which could lead *G. griseoflavus* to select patches of vegetation that contain a relatively high number of species to meet their requirements. Space use by small mammals in deserts usually has been considered only along the horizontal dimension; however, vertical structure could be an important variable for habitat segregation among small mammal species, especially for food (Albanese et al. 2011). In the



**Fig. 3.**—Expected versus observed counts of *Graomys griseoflavus* based on *k*-fold cross-validation of the final model predicting resource selection by this species in the central Monte Desert, Argentina. Different colors represent results of the 4 folds, partitioned into 10 bins of predicted use for each re-fitting of the model. The fit regression is shown as a solid line with the coefficient of determination ( $R^2$ ) for the final model, and the dotted line represents perfect correspondence of observed and predicted, i.e., y = x.

passive restoration area, *G. griseoflavus* selected higher cover of grass species, presumably to avoid predators (Simonetti 1989; Bowers and Dooley 1993), which can be explained principally because the vegetation in the Monte Deserts is distributed in patches of *Prosopis* with a dense understory of grasses (Rossi 2004).

Our results indicated that vegetation cover and, conversely, open spaces affected habitat use of G. griseoflavus, even under passive restoration with a relatively high cover of available resources. G. griseoflavus is a generalist species that perceived the differences in resources at a fine-grained scale under the 2 management conditions. These patterns of resource selection by animals can be altered by changes in availability (Osko et al. 2004; Morellet et al. 2011). In terms of habitat variables, strength of selection by G. griseoflavus was greater in the grazed area than under passive restoration (as explained by the coefficient values). Because G. griseo*flavus* is able to choose the same resources (habitat variables) under both conditions, the strength of selection depends on their availability. Selection was less pronounced in the area under passive restoration, which was characterized by a greater abundance of vegetation and litter and lower cover of bare ground. Where resources are more abundant and thus available, selection may be less apparent (Wright and Jones 2004).

Considering that most drylands worldwide are degraded and that most reserves are too small to ensure the conservation of many wildlife species, it is critical for conservation to better understand the role of the landscape mosaic and management of private lands adjacent to public reserves. The persistence of animals in highly modified landscapes generally depends on the species' ability to use fragments of natural habitat and move along the landscape to find essential resources. Studies of resource selection by animals can guide restoration efforts, identifying how habitat composition influence critical behaviors for survival and reproductive success.

#### **ACKNOWLEDGMENTS**

We thank B. Bender and the people that collaborated in the field sampling and the rangers at Nacuñán Reserve for logistic support. Special thanks to B. K. Johnson, and the Discussion manuscript group-Gualeguaychú 2015 at IFEVA for invaluable discussions and comments on previous versions of the manuscript. Many thanks to B. Naylor and J. Hafer for their help with GIS analyses. Thanks to L. Ebensperger and the group at the Pontificia Universidad Católica de Chile for training in telemetry techniques. Financial support was provided by Agencia Nacional de Promoción Científica y Tecnológica (BID PICT 2010-0185), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP - 0325) and a CONICET doctoral fellowship.

### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Total number of locations obtained from radio-tracking of *Graomys griseoflavus* in the passive restoration and grazed conditions in the central Monte Desert of Argentina for 2 sampling seasons.

**Supplementary Data SD2.**—Results from model building to predict resource selection by *Graomys griseoflavus* in the central Monte Desert, Argentina, using a forward stepwise approach based on Akaike Information Criterion corrected for small samples (AIC<sub>c</sub>). The interaction term (\*) reflects management condition: passive restoration or grazed. Model variables are described in Table 1.

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Submitted 4 January 2017. Accepted 7 July 2017.

Associate Editor was Ricardo Ojeda.