

Original Research Article

Tracking native small mammals to measure fine-scale space use in grazed and restored dry woodlands

Florecia Spirito ^{a,1,*}, Mary Rowland ^b, Michael Wisdom ^b, Solana Tabeni ^a^a Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA), CCT CONICET-Mendoza. Av. A. Ruiz Leal s/n, Parque General San Martín, Mendoza, Argentina, C.C. 507, C.P. 5500^b U.S. Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR, 97850, USA

ARTICLE INFO

Article history:

Received 12 May 2020

Received in revised form 12 October 2020

Accepted 29 October 2020

Keywords:

Desert mammals

Graomys griseoflavus

Grazing

Land degradation

Movement

ABSTRACT

The degradation of dry woodlands in South America by agricultural activities affects wildlife through a decrease in available habitat and fine-scale changes in habitat structure. The impact of land use can be perceived by small, mobile organisms as preventing or facilitating their movement through and among habitats, consequently altering ecosystem functions. By tracking with radiotelemetry we describe for the first time the pattern of movement of a small mammal (*Graomys griseoflavus*) that inhabits dry woodland ecosystems in South America and its relationship with environmental features that affect movement. We measured environmental variables linked to the ecological requirements of the species (e.g., plant cover and patches of forage species consumed) in restored and grazed woodlands and compared movements between seasons (dry and wet). We found that the fine-scale differences in the vegetation cover associated with livestock grazing changed the mobility and use of space of this small mammal. The step-lengths and used area for *G. griseoflavus* were greater under passive restoration compared to the area grazed by livestock. Small rodents moved between patches of similar mean size of forage species, avoiding large inter-patches of bare ground. Although both management conditions showed seasonal variations in plant cover, the step-lengths decreased significantly in the grazed woodland during the wet season, while step-lengths in the restored area were unaffected by season. The fine-scale spatial arrangement of plants in restored woodlands elucidated notable changes in animal movement on grazed lands, suggesting that space use by small mammals may be an important tool to identify habitat structures that facilitate the movement of animals in restoration of degraded systems.

Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

The processes of degradation of dry woodlands around the planet are mainly due to the removal of vegetation by agricultural activities (Bastin et al., 2017). Although the quantification of the loss of habitat on a large scale is necessary for making decisions at a regional or global level, the fine-scale alteration in the organization of plant patches can affect habitat

* Corresponding author.

E-mail addresses: florspirito@gmail.com, florecia.spirito@ufrontera.cl (F. Spirito).¹ Laboratory of Agroecology and Food Systems Sustainability, Universidad de La Frontera, Casilla 54 D, Temuco, Chile.

connectivity, altering the movement of organisms and availability of the resources they procure through the landscape. In arid woodlands of Argentina, the conservation of plant communities and their historical fine-scale distribution are key considerations for survival of desert mammals, given their influence on the availability of food and shelter necessary to withstand rigorous climatic extremes and high predation risk present in arid ecosystems (Taraborelli et al., 2003). Passive ecosystem restoration is an appropriate strategy to recover many components of biodiversity in degraded lands.

(Hobbs and Cramer, 2008). One approach, the removal of livestock, can trigger changes in plant communities, including the increase of perennial grass cover and subsequently lead to a significant spatial rearrangement of plant patches and modification of soil stability and nutrient cycling (Ruecker et al., 1998; Valone and Sauter, 2005; Arnaez et al., 2010). The occurrence and magnitude of these changes, however, will depend on disturbance intensity and duration and site-specific properties.

The fine-scale spatial arrangement of plants influences ecological processes mediated by the movement of animals (e.g., seed dispersal), which may even affect the trajectory of woodland ecosystems under restoration (McCallum et al., 2018). For example, seed dispersal of *Prosopis* trees by mammals through protected and grazed woodland networks is remarkably conditioned to the spatial organization of plants in the landscape (Miguel et al., 2018b). Previous research also found that the loss of connection between patches of plants in cattle-grazed habitats lowered richness in the mammal assemblage and thus reduced habitat quality (Spirito and Tabeni, 2016).

Animal movement plays an important role by shaping fine-scale processes, such as habitat patch choice, which ultimately influence biological processes at broader spatial scales and higher levels of organization (Nams, 2005). Desert small mammals (<100 g) have been widely recognized to be mobile link species (i.e., organisms that actively move in the landscape and connect habitats in space and time, Lundberg and Moberg, 2003) with significant effects on ecosystem processes across the landscape (Kelt, 2011). One of the best characteristics of small mammals for understanding landscape degradation is their fine-grained perception of environmental changes (Tabeni et al., 2007). For example, small mammals use physical cover to reduce their risk of predation and may move slower where there is more protection from predators (Gehring and Swihart, 2004). Knowledge of this type of behavioral response, combined with a relatively large body of research on the natural history of rodents (e.g., Ojeda and Tabeni, 2009), can be used to explore the utility of small mammals as indicators of changes in landscape structure due to degradation (Lindenmayer et al., 2000; Shanley et al., 2013).

We present a case study analyzing the movement patterns among resource patches by a small mammal species, comparing woodland habitats under continuous livestock grazing and under passive restoration for more than 50 years in the Monte Desert, the largest arid region of southern South America (Roig et al., 2009). Over the last two centuries, this biome has been subjected to deforestation, woodland degradation, and wildlife habitat fragmentation principally due to intensive, continuous grazing by livestock (Fernández and Busso, 1999). In particular the Nacuñán region has shown, after 50 years of grazing exclusion, an increase in plant diversity and richness, particularly among the primary grasses and shrubs of high palatability to livestock (Rossi, 2004). These changes in vegetation patterns led to spatial homogenization compared with surrounding grazed fields (Tabeni and Ojeda, 2005). By contrast, the areas that continued to be subjected to continuous grazing showed reductions in total plant cover and grass strata and increases in unpalatable species and bare ground cover (Villagra et al., 2009). Continuous livestock grazing also produced a habitat structure with more gaps in plant distribution and greater spatial heterogeneity (Spirito et al., 2017). In addition, differences between wet and dry seasons, characteristic of drylands in this region, lead to seasonal differences in plant communities. The total annual precipitation ranges between 100 and 350 mm in most of the Monte Desert (Labraga and Villalba, 2009). In the central region of the Monte, the distribution of rainfall produces two seasonal periods, the wet season, where 75% of the rains are concentrated (November–March), and coincides with the thermal summer (mean monthly temperature of 22.4 °C), and the dry season (April–October) with a mean monthly temperature of 7 °C (Estrella et al., 2001; Rossi, 2004). These dissimilarities are accentuated under grazing. Previous studies in the central Monte Desert found that in the dry season the cover of grasses, shrubs, plant litter, and forage plant species for small mammals were significantly reduced in grazed lands compared with the passive restoration area (Spirito et al., 2017).

Generalist species of small mammals can exploit a broad spectrum of environmental characteristics, such as forage species or vegetation structure, as habitat, and thus can serve as model species to investigate previously unexplored aspects of habitat change caused by land use change (Wells et al., 2006). Use of animal telemetry data extends the spectrum of knowledge on small mammal ecology, complementing traditional approaches based on capture and recapture techniques typically used for small mammals (Wilson et al., 2015).

We evaluated space use, specifically movements and area used, in *Graomys griseoflavus*, a habitat generalist and the most abundant small mammal in the Nacuñán region and the Monte Desert (Tabeni and Ojeda, 2005) and widely distributed in Argentina, Bolivia, Paraguay and southwestern Brazil (Redford and Eisenberg, 1992; Yahnke, 2006; Udrizar Sauthier et al., 2011). In the Monte, *G. griseoflavus* can occupy a wide variety of habitats (i.e., shrublands, grasslands, steppes and cultivated and grazed fields). It has the ability to climb and probably uses the arboreal strata for foraging purposes. Its diet is omnivorous with a tendency to folivore and with a significant consumption of fruits and leaves of *Prosopis flexuosa*. *G. griseoflavus* remove, transport and hoard pods, and behaves as *Prosopis* seed predator (Albanese et al., 2011; Giannoni et al., 2013; Miguel et al., 2018a).

In this study we evaluate the influence of landscape modification on native fauna and document the movement patterns of a desert mammal, *G. griseoflavus*, in dry woodlands. We had two objectives: (i) to characterize the pattern of movement and space use (step-lengths and area used) of a desert small mammal in protected and grazed woodlands through seasonal

variations (wet vs. dry seasons), and (ii) to analyze the influence of habitat structure in woodlands under different management regimes on the movement patterns of *G. griseoflavus*. We predicted that movement patterns (based on step-lengths) and used areas of small mammals within passive restoration conditions would be greater than under grazed management because the restored area offered less open space and shorter distances between resource patches. That is, animals would freely move over a larger area because of more numerous and interconnected patches of habitats under restored conditions.

2. Methods

2.1. Study site

We conducted our study in the Man and the Biosphere Reserve of Ñacuñán, Mendoza Province, Argentina (34°02' S, 67°58' W; 12,300 ha), which has been protected from grazing by livestock for >50 yrs, and in an adjoining unprotected area under continuous livestock grazing. Grazing in this area, predominantly by cattle, is intensive, with an average stocking density of 27 ha per animal unit (Guevara et al., 2009). There are no other large herbivores in the area, and the only medium-sized grazer, the Patagonian mara (*Dolichotis patagonum*) is rare. The study area is part of the central Monte Desert biome. Climate is semiarid, with a marked seasonality of humid summers (mean temperature > 20 °C) and dry winters (mean temperature < 10 °C). Average annual rainfall is 324 mm, largely occurring during the wet season (Estrella et al., 2001). This region supports a diverse mosaic of habitats that includes *Prosopis flexuosa* (Fabaceae) woodlands mixed with grasses, and shrublands dominated by the evergreens *Larrea* spp. and *Bulnesia* spp. (Zygophyllaceae). The Ñacuñán Reserve was established in 1961 to protect native woodland and its biota, initiating the exclusion of livestock and the passive restoration process. In 1986, the Reserve was included in the world network of Man and Biosphere Reserves (UNESCO) (Boshoven et al., 2001). As one of the oldest protected areas in the Monte Desert biome, Ñacuñán Reserve is currently the most important reference site in Argentina for monitoring the ecological health of the Monte. Long-term grazing exclusion (>50 years) with livestock fencing has resulted in compelling evidence of passive restoration of native vascular vegetation in the absence of livestock grazing (Rossi, 2004).

2.2. Live-trapping and radio-telemetry

We carried out two trapping sessions, June–July 2012 (dry season) and February–March 2013 (wet season). We intentionally avoided sampling during the peak breeding activity of *G. griseoflavus* (Corbalán et al., 2006), when females were frequently pregnant or lactating. During each trapping session, we established two trapping grids (10 × 13 configuration, 10 m between traps) in *Prosopis* woodlands, one each in the passive restoration and grazed areas (~1.5 ha for each grid). The trapping grids were separated by > 2 km and thus considered independent sampling areas. In each grid, we placed Sherman live traps 10 m apart, baited with rolled oats and vegetable oil. We trapped for five consecutive nights during each season and checked traps each morning. We conducted all handling methods in accordance with Purdue Animal Care and Use Committee guidelines and American Society of Mammalogists animal care and use guidelines (Sikes, 2016).

We fitted telemetric transmitters to captured adults of *G. griseoflavus* weighing >45 g to reduce variability in movement patterns due to development stages (Fig. S1). We attached the transmitters in the field just before release of the captured individuals. To reduce the influence of trapping on the rodents' use of space, we recorded telemetry locations only after all traps were closed at a site (Webster and Brooks, 1981). The transmitters were a radiocollar 2-grTXB-004C with an on-off magnet switch (Telenax Wildlife Telemetry, Mexico). We tracked each animal with a RX-TLNX receiver equipped with a three-element Yagi antenna (Telenax Wildlife Telemetry, Mexico) for 6–10 days during each season (wet and dry), given the limited transmitter battery life of ~15 days). We collected telemetry data by locating each radio-collared animal by foot with a minimum time between sampling for each individual of two hours during the nighttime. Small mammals in drylands are most active during the night (Lockard and Owings, 1974); therefore, tracking was focused on nighttime (from dusk to dawn). However, we also recorded some locations during the daytime and corroborated that *G. griseoflavus* was not moving then but stayed underground. Once located, we recorded the position of each animal to the nearest meter using a hand-held global positioning system (GPS) unit. For additional details on radio-tracking technique and data acquisition, see Spirito et al. (2017).

2.3. Characterization of environmental variables

To analyze the influence of habitat structure on the movements of *G. griseoflavus* we selected 6 environmental variables, representing finer-scale habitat conditions. Four of the variables were significant predictors of resource selection by *G. griseoflavus* in the Monte Desert, as reported in previous work (Spirito et al., 2017), and included the relative percent cover of bare ground, grasses, trees and forage species consumed by *G. griseoflavus* (Campos et al., 2001). We also created 2 structural variables: size of inter-patches of bare ground and size of patches of forage species consumed by *G. griseoflavus*. For these, we considered vegetation as a patch when its cover was continuous for ≥5 cm along the transect; if the intercepted vegetation cover was <5 cm, we recorded it as an inter-patch of bare ground (Tongway and Hindley, 2004). We considered the fine-grain scale of 5 cm based on a previous measurement of landscape perception (*sensu* Zollner and Lima, 1997) by *G. griseoflavus* at Ñacuñán (Tabeni et al., 2007). The mean inter-patch size of bare ground and mean patch size of forage species were calculated by summing the length of patches and dividing by the number of patches for each of these variables.

Data for environmental variables were collected at ~400 random available locations, with 129 in the grazed area and 267 in the restored area (Spirito et al., 2017) immediately after telemetry data collection ended. Available locations were selected by first creating a minimum convex polygon (MCP) around the pooled (used) locations of *G. griseoflavus* in each of the two management areas and drawing a 1000-m buffer around each. We then randomly selected available locations within each of the 2 polygons. Sample size was greater for the restored area because some of the random available locations associated with grazed animals fell in the restored area when the buffered MCP was drawn (Spirito et al., 2017). Vegetation was sampled at each location along 4 2.5-m transects, and data were tallied along the total transect length (i.e., 10 m) for each location. See Spirito et al. (2017) for more details on site selection and sampling methods.

Because exploration of the environmental variable data revealed that they were not normally distributed, we used the Kruskal-Wallis test (Zar, 2019) to compare mean values of the variables between the passive restoration and grazed areas during each season, using the package “dplyr” in R (Wickham et al., 2015). We first used the H statistic of the Kruskal-Wallis test to check for overall significance between the two treatment types before comparing mean values of variables among the treatments and seasons.

2.4. Data analysis

2.4.1. Movement patterns: step-length

We defined step-length as the straight-line distance linking successive animal locations taken at regular time intervals (Turchin, 1998). We assigned each nighttime location for each animal to a 2-hr sampling period. If it was not possible to collect consecutive measures (e.g., the transmitter could not be found) we censored those locations from analysis, that is we only considered consecutive locations in calculating step-lengths. For the dry season, the sampling period started at 1800 h and concluded at 0800 h; and for the wet season (summertime in Southern Hemisphere), the sampling period was from 2000 h to 0800 h. We calculated step-lengths using the software *Geospatial Modeling Environment-Spatial Ecology* (Beyer, 2012).

We first generated frequency distributions of nighttime step-lengths by 25-m intervals for grazed and passive restoration areas to evaluate the potential differences in step-length patterns by *G. griseoflavus* under the two different treatments. Because we were interested in the overall pattern of step-length distributions by treatment type for this visualization, we pooled all locations among animals and season.

We then compared mean step-lengths of animals between each season within the two management conditions (i.e., passive restoration vs. grazed) with a *t*-test (Zar, 2019) using the “Hmisc” package in R (Harrell, 2016). We considered each individual as an experimental unit to avoid pseudo-replication (Otis and White, 1999) for these tests of statistical significance. Thus, we used locations for each animal as correlated subsamples that, when summarized for each animal, represented the sample or observation unit for statistical tests, as typically done for most animal-based studies (Otis and White, 1999). Further, we plotted step-lengths against environmental variables blocked by season (i.e., wet vs. dry) to offer visual comparisons of differences between the 2 management conditions.

2.4.2. Used area estimation

To estimate the area used by *G. griseoflavus* under the two management conditions, we calculated for each tracked individual the area (m²) of habitat used per hour over the total number of nights tracked (Bentley, 2008). We first calculated the area of the MCP (Harris et al., 1990; based on 95% of all locations recorded for an individual over all days that it was tracked) and then divided this area by the total number of tracking hours. We were unable to estimate home range sizes (i.e., the area that an animal uses regularly and for which it stores information in a “cognitive map”; Spencer, 2012), due to the short sampling period (≤ 10 days). Before we created the individual MCPs for animals in the 2 management conditions, we first

Table 1

Telemetry data obtained by radio-tracking *Graomys griseoflavus* ($n = 13$) in the passive restored and the grazed conditions during two sampling seasons (dry and wet), 2012–2013, in dry woodlands of the Monte Desert, Argentina.

	Season	Animal number	Sex (Male/Female)	Total locations	Night-time locations	Daytime locations	Total days of radio-tracking
Grazed	Dry	#1	F	23	13	10	8
		#2	M	20	14	6	8
		#3	F	32	22	10	7
		#4	M	39	33	6	9
		#5	M	35	21	14	8
	Wet	#6	M	22	15	7	7
		#7	M	28	22	6	10
Passive restoration	Dry	#8	M	37	23	14	8
		#9	M	40	21	19	8
		#10	F	35	21	14	10
		#11 ^a	M	10	8	2	6
	Wet	#12	F	40	25	15	9
		#13	F	35	22	13	8

^a Animal 11 was omitted from used area calculations due to the small number of locations.

evaluated differences in total area used as influenced by number of locations, to standardize this analysis across animals with different numbers of locations. We randomly selected 20 locations for each animal, which was the smallest number of total locations for any one animal used in this analysis, and created 10 new “used areas” for each animal by bootstrapping. We then compared these new MCPs with the original ones and found no difference in MCP size between using the minimum and maximum number of locations. Therefore, we used all locations documented for each individual to calculate its used area. We also compared MCPs created for each radio-collared animal from all its nighttime vs daytime locations. Because day locations were nested within the areas used at night, we pooled day and night locations for the used area analysis. We estimated MCPs with the “move” package and *HR bootstrap* function (Kranstauber and Smolla, 2016).

Due to the small sample sizes and non-normality of the data, we compared used areas (i.e., m²/hour) for *G. griseoflavus* in the passive restoration vs. grazed areas, but not by season, using the Mann-Whitney-Wilcoxon test (also referred to as Mann-Whitney U; Zar, 2019). We performed all statistical analyses in R language and environment for statistical computing (version 3.5.1, R Development Core Team, 2018). We considered *p* values < 0.05 to be statistically significant for analysis of the environmental variables. For analysis related to telemetry data, we used *p* values < 0.10 as a general guide in identifying significant differences, to reduce the probability of committing Type II errors (i.e., concluding no difference when in fact an ecological difference existed), which was more likely given our small sample sizes (Zar, 2019).

3. Results

3.1. Small mammal capture and telemetry locations

Thirteen mature individuals of *G. griseoflavus* (8 males and 5 females) were tracked, 7 in the grazed area and 6 in the passive restoration (Table 1). We attempted to fit transmitters to an equal number of males and females during each session, but this was not achieved because few large adult males were caught (Table 1; see Spirito et al., 2017 for more details on capture and tracking methods). Total locations per individual ranged from 10 to 40, with animals tracked from 6 to 10 days. Total nighttime locations varied from a low of 8 to a maximum of 33 locations.

3.2. Environmental characterization

Environmental variables at locations available to *G. griseoflavus* differed between management conditions depending on the season (Table 2). During the dry season, the contrast between management regimes was characterized by significantly lower grass and forage cover and greater bare ground cover and larger inter-patches of bare ground in the grazed areas compared to the restored area (Table 2). During the wet season, we observed more similarities in environmental variables between management conditions. As was true for the dry season, both grass and forage species cover were higher in the passive restoration sites and the grazed area had greater bare ground cover and larger patches of bare ground compared to passive restoration. These differences, however, were not significant (Table 2). Importantly, differences in forage patch size were significant during the wet season, and patches were much larger in the passive restoration area ($\bar{x}$ = 227 cm) than in the grazed sites ($\bar{x}$ = 175 cm), in contrast to forage patches in the dry season (Table 2).

3.3. Movement patterns: step-length

The frequency distribution of nighttime step-lengths showed a distinctive pattern of more frequent longer movements in the passive restoration area compared to the grazed area, using all locations pooled among animals and seasons (Fig. 1). The preponderance of short (0–25 m) steps occurred in the grazed area, and >90% of step-lengths were in the 2 shortest distance intervals (≤ 50 m) in the grazed area (Fig. 1). By contrast, step-lengths for the passive restoration area had a more extended tail of infrequent but longer movements (Fig. 1).

Step-lengths of *G. griseoflavus* were significantly longer under passive restoration vs. grazed management during both seasons, although the pattern was strongest during the wet season ($t = -3.18$, $p = 0.001$; Fig. 2) compared to the dry season ($t = -1.67$; $p = 0.096$). Mean step-length was ~1.5–2.5 times greater in the restored area (Fig. 2), which reflected like patterns in frequency distributions of step-lengths between restored and grazed areas (Fig. 1).

In the dry season, nighttime step-lengths were notably greater in the restored area during early evening (1800–2000 h) and early morning (0600–0800 h; Fig. S2). Forage cover and forage patch size used were similar to what was available in both areas (Fig. S2; Table 2). On the other hand, values of bare ground cover and patches used were at the low range of what was available (Fig. S2). During the wet season, marked differences in nighttime step lengths between the 2 management regimes were observed during key foraging hours (~2200–0200 h; Fig. S3). Animals in the passive restoration area moved between relatively small patches of bare ground cover and higher values of grass cover (Fig. S3; Table 2). During most hours, grass cover was much greater at used sites in the passive restoration, and bare ground cover greater in the grazed area during the wet season (Fig. S3); these differences were less pronounced in the dry season (Fig. S2). Other differences also emerged in the wet season, forage cover and patch size in used sites were consistently greater in restored areas across all nighttime hours, and inter-patches of bare ground were consistently larger in used sites in the grazed area (Fig. S3).

Table 2

Comparisons of mean values of environmental variables between the passive restoration and grazed areas in the Monte Desert, Argentina, using Kruskal-Wallis (H -value). Values are means with standard errors in parentheses. Different superscript letters indicate significant differences ($p < 0.05$) between mean values of each variable for a given evaluation. * Forage-MPS = mean patch size of forage species; bare ground-MiPS = mean inter-patch size of bare ground. Portions of the data were previously published in Table 2, Spirito et al. (2017).

Environmental variables	Dry season		Wet season		H-value	p-value
	Grazed	Passive restoration	Grazed	Passive restoration		
Grass cover (%)	15.83 (1.14) ^a	22.95 (1.29) ^b	23.21 (2.43) ^b	29.17 (2.21) ^b	36.61	<0.0001
Tree cover (%)	29.87 (2.36) ^b	23.1 (2.47) ^b	20.55 (3.28) ^{ab}	16.14 (2.51) ^a	13.47	0.0031
Forage cover (%)	68.36 (1.42) ^a	74.6 (1.49) ^b	66.22 (2.35) ^a	71.61 (2.16) ^{ab}	13.80	0.0032
Bare ground cover (%)	35.37 (1.86) ^c	19.26 (1.79) ^a	31.99 (3.16) ^{bc}	23.12 (2.01) ^{ab}	40.89	<0.0001
Forage-MPS (cm)*	220.75 (9.92) ^b	214.61 (11.49) ^b	174.93 (13.97) ^a	227.06 (13.46) ^c	7.79	0.05
Bare ground-MiPS (cm)*	127.99 (7.56) ^c	79.48 (7.95) ^a	127.06 (13.31) ^{bc}	100.33 (8.59) ^b	30.71	<0.0001

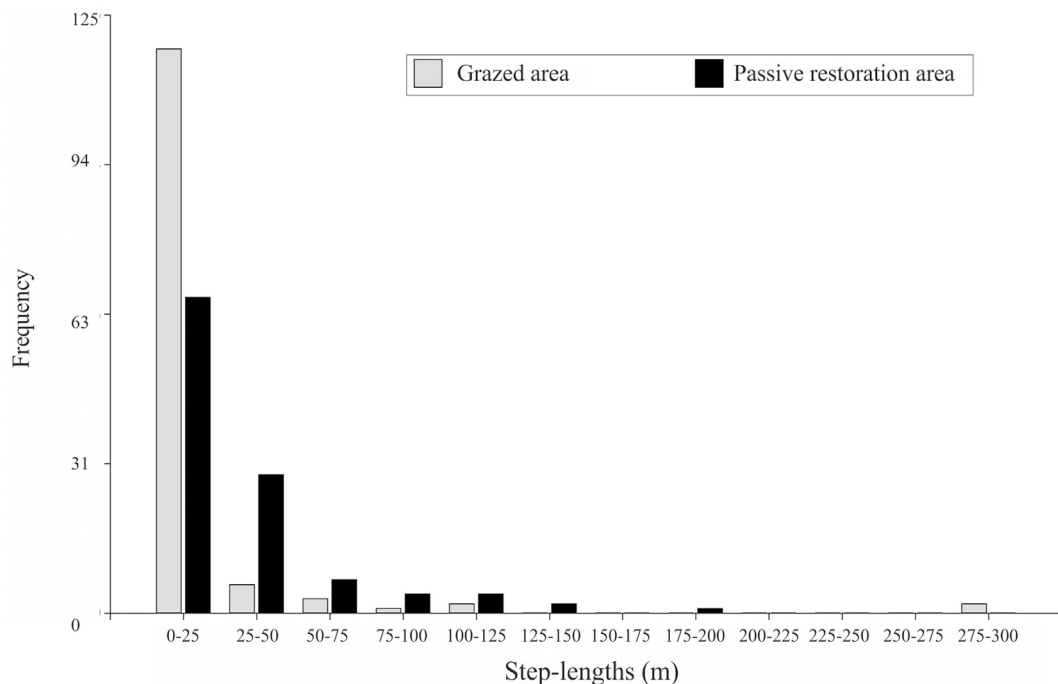


Fig. 1. Distribution of nighttime step-lengths (m), each assigned to a 2-hr sampling period, of *G. griseoflavus* in grazed and passive restoration areas in the Monte Desert, Argentina. Data were pooled among animals and seasons for this display.

3.4. Used area

The area used by *G. griseoflavus* was highly variable among animals in both management regimes, but especially in the grazed area (Fig. 3). The median value of area used was 53 m²/h (SE = 225.9 m²/h) in the grazed area, which was nearly 7 times smaller than that in the passive restoration (368 m²/h; SE = 75.4 m²/h; Fig. 3). This difference approached statistical significance ($p = 0.149$, $W = 8$), suggesting a strong but variable pattern of greater used area by animals in the passive restoration treatment. One animal (number 1, Table 1) had an extremely large value for used area (1636 m²/h), >4 times greater than the next closest value, and illustrated the highly variable area of use among individuals within and across treatment types. We reran the Mann-Whitney-Wilcoxon test omitting this animal to better understand differences in space use between management conditions in the absence of this extreme value; these results were statistically significant ($p = 0.0303$, $W = 3$), further reinforcing the overall pattern of greater area used in the passive restoration treatment.

4. Discussion

Different responses of small mammals to grazing have been reported in drylands (Tabeni and Ojeda, 2005; Kelt, 2011), demonstrating how changes in landscape structure and resource availability can affect population demographics (Gonnet, 1998; Tabeni and Ojeda, 2005). In this paper we showed for the first time how changes in the spatial arrangement and

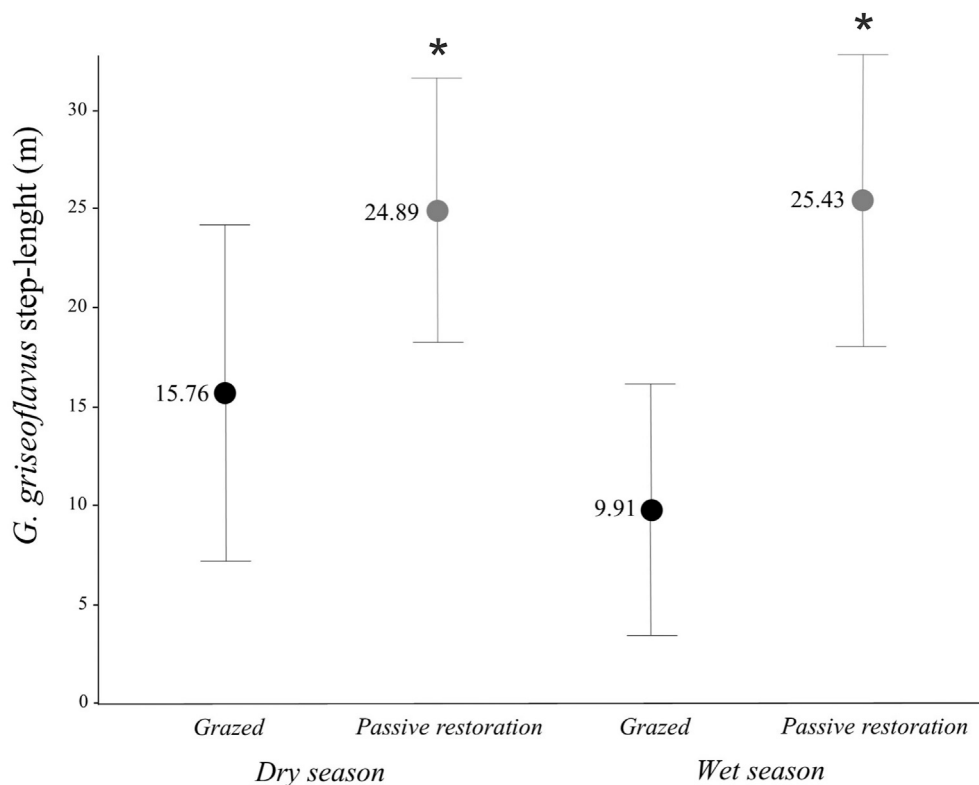


Fig. 2. Comparison of nighttime step-lengths (m), each assigned to a 2-hr sampling period, of *G. griseoflavus* between the passive restoration and grazed areas, for dry and wet seasons in the Monte Desert, Argentina. Values are means with Confidence Intervals. Significant results within a season are denoted by * ($p < 0.10$).

cover of vegetation affected movement of native small mammals in dry woodlands of South America. We focused on two contrasting land management conditions: dry woodlands under continuous grazing use and under long-term recovery from grazing cessation. Our results supported our prediction that step-lengths and used area by small mammals would be greater in landscapes whose spatial structure likely offers lower risk from predation during movement based on greater cover and smaller patches of bare ground, that is, the area under passive restoration from livestock grazing.

These results suggest that differences in resource availability between management conditions can influence the movement patterns and space use of the small mammal *G. griseoflavus* and may translate into greater access to the more abundant forage resources available in the restored area. This result agrees with previous studies reported in other mammals, in which animal movement is affected by land use (Stevens et al., 2004; Frair et al., 2005; Russell et al., 2007). As a habitat generalist species, previous evidence indicated that abundance of *G. griseoflavus* was not affected by grazing, showing their plasticity to inhabit disturbed woodlands (Tabeni et al., 2013). Authors have also noted their capacity for selecting vegetation patches under grazed conditions (Spirito et al., 2017). However, the availability of resources in the landscape does affect their movements and therefore the selection of resources among different management conditions.

We observed high variability in space use, as measured by step lengths and used area, in our study animals. It has been reported in the literature that small mammal movement can be characterized by short, regular movements and occasional long-distance movements (Robinson, 1987; Bentley, 2008). In Australian deserts, several studies suggest that long-distance (>1000 m) movements in rodents are very common (Dickman et al., 1995; Letnic, 2002). There is a complex set of factors that promote such large movements. Precipitation can be one of the most important triggers by producing an immediate increase in food by promoting access to buried seeds (Letnic et al., 2005; Dickman et al., 2011). In our work one animal (number 1, Table 1) traversed an extremely large area during the dry season. The reduction in available resources could partially explain these singular long-distance movements.

Landscapes can change in both space and time, with heterogeneous vegetation patches shifting during succession and over the growing season, presenting different structures for animals to move through and varying movement costs (Wells et al., 2006; Nathan et al., 2008; Marteinsdóttir et al., 2010; Searle et al., 2010). Our results suggest that environmental conditions in the restored area led to greater movements by *G. griseoflavus* year-round compared to the grazed area, presumably due to the effect of the long-term restoration of the vegetation, resulting in less bare ground and higher grass and forage cover, which promote a greater capacity of movement. We also expected that, given the typically more abundant vegetation cover in the wet season, step-lengths and used area would be greater during this season because the landscape

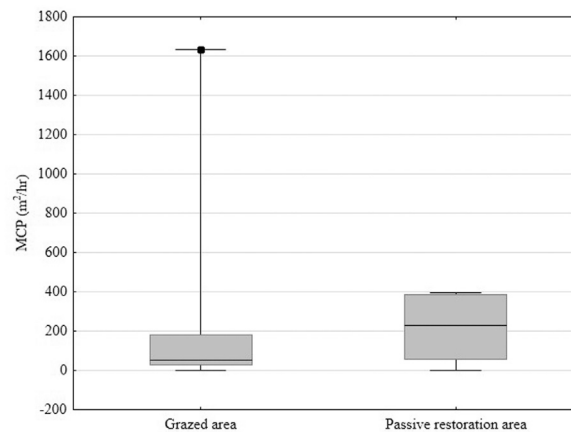


Fig. 3. Box-plot representation of used area sizes of *G. griseoflavus* calculated using a minimum convex polygon (MCP) under grazed and passive restoration conditions; total area (m²) across all days of tracking was divided by the hours of tracking for each individual. The horizontal line in the box represents the median, the box represents the 25th to 75th percentiles, the extensions represent the 10th and 90th percentiles, and solid circles represent the outliers.

offers greater structural connectivity that would facilitate movements to find forage resources. Although we did not formally test for seasonal differences due to small sample sizes, this prediction was not supported by our data. Small mammal step-lengths were somewhat shorter during the wet season in the grazed area, not longer, and step-length in the passive restoration was similar between seasons.

Differences and similarities in landscape structure also influenced animal movements. During the dry season, *G. griseoflavus* moved among forage patches of similar size in both management conditions, reflecting the similarities in forage patch sizes available in that season. However, they were unable to avoid the large inter-patches of bare ground in the grazed area. In deserts of Australia, the influence of structural connectivity in the movement of native species of rodents has been noted (Doerr et al., 2010). As a general pattern, most structurally connected sites are associated with increased movement of animals, matching the results of this study. Small mammals living in deserts are known to face challenges in moving through low-quality and risky landscape (Spencer et al., 2014). In addition to the vegetation type and patch characteristics of the habitat, the ability to move through and survive in these habitats involves other factors, not addressed here, such as perceptual and behavioral factors intrinsic to a given species that trigger decisions to move into habitat types to acquire resources as well as avoid predation and competition with conspecifics (Fahrig, 2007).

Our results from analysis of radio-telemetry data allowed us to describe space use of *G. griseoflavus* with greater precision than results from prior studies. Previous studies on the home range and movement of small mammals in the Monte Desert were carried out using fluorescent powder or live-trapping techniques (Corbalán and Ojeda, 2005; Corbalán and Debandi, 2009). Furthermore, our results provide fine-scale evidence on the fundamental role of vegetation during movement. Plant cover offers safe places for refuge and feeding sites for these prey populations in the Monte, data that were historically inferred only from trapping data (Ojeda et al., 2011). The passive restoration of plant communities leads to an increase in coverage, but at the same time to the recovery of the spatial arrangement of the vegetation. Thus, structural attributes of the landscape that we incorporated in our study, such as plant patch-size and inter-patches of bare ground, proved to be important ecological indicators for the dispersion of this species, not reported, until now.

Interpretations of our results, however, should be viewed with caution, given our small sample size of 13 animals that encompassed 2 management regimes, 2 seasons, and 2 sexes, low number of locations per animal, and limited number of days of telemetry data collection for each season. These factors combined led to high variability in movements observed in our study. These challenges are common with studies of small mammals that evaluate their movements, space use, and habitat use. Nonetheless each study contributes further to our limited knowledge on these topics, but at a slower pace than knowledge gain that is possible for most larger mammal species where more powerful data collection technologies have been developed and are commonly used. Our data limitations may contribute to a higher probability of Type II errors, and further studies are needed to improve precision of our estimates of movement distances, space use, and habitat use.

The findings of this study highlight the importance of considering animal movement in disturbed landscapes to ascertain effects of degradation on this key ecological process. Rodents decreased their movement in degraded sites, and only moved between sites providing high vegetation cover and large patches of forage species, which could indicate a reduction in the functional connectivity of the landscape with respect to *G. griseoflavus*. But connectivity is not a static process; rodents may change their movement patterns depending on vegetation cover that in turn is responding to seasonal changes in precipitation and temperature. Furthermore, the used area under passive restoration was characterized by greater connectivity both structurally and functionally. *G. griseoflavus* may perceive the restored area as a safer environment, venturing to explore the area more readily. This can promote important behaviors, such as scattering and capturing seeds and planting and germination of plants, among others (Yoshihara et al., 2009; Giannoni et al., 2013). Finally, identifying landscape structures that

facilitate small mammal movement may be an important tool to promote the restoration of degraded systems and the ecosystem services provided by these animals.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank B. Bender and all who helped with field sampling, as well the rangers at Ñacuñán Reserve for logistic support. Special thanks to B. Naylor and J. Hafer of the U.S. Forest Service, Pacific Northwest Research Station, for their invaluable help with GIS analyses. Many thanks to A. Ager and B. Johnson for discussion and comments on previous versions that greatly improved the clarity of this material. Thanks to R. Nielson and D. Johnson for help with data analysis, and to 2 anonymous reviewers whose comments greatly improved our manuscript. Thanks to L. Ebensperger and their 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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01348>.

References

- Albanese, S., Rodríguez, D., Ojeda, R.A., 2011. Differential use of vertical space by small mammals in the Monte Desert, Argentina. *J. Mammal.* 92, 1270–1277.
- Arnaez, J., Lasanta, T., Errea, M.P., Ortigosa, L., 2010. Land abandonment, landscape evolution, and soil erosion in a Spanish Mediterranean mountain region: the case of Camero Viejo. *Land Degrad. Dev.* 22, 537–550.
- Bastin, J.F., Berrahmouni, N., Grainger, A., Maniatis, D., Mollicone, D., et al., 2017. The extent of forest in dryland biomes. *Science* 356, 635–638.
- Bentley, J.M., 2008. Role of movement, interremnant dispersal and edge effects in determining sensitivity to habitat fragmentation in two forest-dependent rodents. *Austral Ecol.* 33, 184–196.
- Beyer, H.L., 2012. *Geospatial Modeling Environment*, version 0.7. 2.1. <http://www.spatialecology.com/gme>.
- Boshoven, J., Tognelli, M., 2001. El Desierto del Monte: La Reserva de Biosfera de Nacuñán. IADIZA-CONICET, MAB-UNESCO. In: Claver, S. y., Roig-JuñentS (Eds.), Córdoba: Editorial Trunfar.
- Campos, C., Ojeda, R., Monge, S., Dacar, M., 2001. Utilization of food resources by small and medium-sized mammals in the Monte Desert biome, Argentina. *Austral Ecol.* 26, 142–149.
- Corbalán, V.E., Ojeda, R.A., 2005. Áreas de acción en un ensamble de roedores del Desierto del Monte (Mendoza, Argentina). *Mastozool. Neotrop.* 12, 145–152.
- Corbalán, V.E., Debandi, G., 2009. Evaluating microhabitat selection by *Calomys musculinus* (Rodentia: Cricetidae) in western Argentina using luminous powders. *Mastozool. Neotrop.* 16, 205–210.
- Corbalán, V., Tabeni, S., Ojeda, R.A., 2006. Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina. *Mamm. Biol.* 71, 227–237.
- Dickman, C.R., Predavec, M., Downey, F.J., 1995. Long-range movements of small mammals in arid Australia: implications for land management. *J. Arid Environ.* 31, 441–452.
- Dickman, C.R., Greenville, A.C., Tamayo, B., Wardle, G.M., 2011. Spatial dynamics of small mammals in central Australian desert habitats: the role of drought refugia. *J. Mammal.* 92, 1193–1209.
- Doerr, V.A.J., Doerr, E.D., Davies, M.J., 2010. Does structural connectivity facilitate dispersal of native species in Australia's fragmented terrestrial landscapes. *CEE Rev.* 8, 70.
- Estrella, H., Boshoven, J., Tognelli, M., 2001. Características del clima regional y de la Reserva de Ñacuñán. *El desierto del Monte: La Reserva de Biosfera de Ñacuñán*, pp. 25–33. Mendoza, Argentina.
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015.
- Fernández, O.A., Busso, C.A., 1999. Arid and Semi-arid Rangelands: Two Thirds of Argentina. Agricultural Research Institute, Reykjavík, Iceland, pp. 41–60.
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L., Morales, J.M., 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc. Ecol.* 20, 273–287.
- Gehring, T.M., Swihart, R.K., 2004. Home range and movements of long-tailed weasels in a landscape fragmented by agriculture. *J. Mammal.* 85, 79–86.
- Gonnet, J.M., 1998. Impacto del pastoreo sobre poblaciones de aves y mamíferos herbívoros en la región de la Reserva de la Biosfera Ñacuñán. Mendoza, Argentina. PhD dissertation. Universidad Nacional de Córdoba, Argentina.
- Giannoni, S.M., Campos, V.E., Andino, N., Ramos-Castilla, M., Orofino, A., Borghi, C.E., Campos, C.M., 2013. Hoarding patterns of sigmodontine rodent species in the Central Monte Desert (Argentina). *Austral Ecol.* 38, 485–492.
- Guevara, J.C., Grünwaldt, E.G., Estevez, O.R., Bisigato, A.J., Blanco, L.J., Biurrun, F.N., Allegretti, L.L., 2009. Range and livestock production in the Monte Desert, Argentina. *J. Arid Environ.* 73, 228–237.
- Harrel, F.E., 2016. *Hmisc: Harrell Miscellaneous*, R Package, version 4.0-2.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., Wray, S., 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mamm Rev.* 20, 97–123.
- Hobbs, R.J., Cramer, V.A., 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annu. Rev. Environ. Resour.* 33, 39–61.
- Kelt, D.A., 2011. Comparative ecology of desert small mammals: a selective review of the past 30 years. *J. Mammal.* 92, 1158–1178.
- Kranstauber, B., Smolla, M., 2016. *Move: Visualizing and Analyzing Animal Track Data*, vol. 2. R package version, 0.
- Labraga, J.C., Villalba, R., 2009. Climate in the Monte Desert: past trends, present conditions, and future projections. *J. Arid Environ.* 73, 154–163.
- Letnic, M., 2002. Long distance movements and the use of fire mosaics by small mammals in the Simpson Desert, Australia. *Aust. Mammal.* 23, 125–134.
- Letnic, M., Tamayo, B., Dickman, C.R., 2005. The responses of mammals to La Niña (El Niño Southern Oscillation)-associated rainfall, predation, and wildfire in central Australia. *J. Mammal.* 86, 689–703.

- Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conserv. Biol.* 14, 941–950.
- Lockard, R.B., Owings, D.H., 1974. Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and Fresno (*D. nitratoides*) kangaroo rats. *Anim. Behav.* 22, 262–273.
- Lundberg, J., Moberg, F., 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6, 87–98.
- Marteinsdóttir, B., Svavarsdóttir, K., Thórhallsdóttir, T.E., 2010. Development of vegetation patterns in early primary succession. *J. Veg. Sci.* 21, 531–540.
- McCallum, K.P., Lowe, A.J., Breed, M.F., Paton, D.C., 2018. Spatially designed revegetation—why the spatial arrangement of plants should be as important to revegetation as they are to natural systems. *Restor. Ecol.* 26, 446–455.
- Miguel, M.F., Tabeni, S., Cona, M.I., Campos, C.M., 2018a. Secondary seed dispersal by mammals between protected and grazed semiarid woodland. *For. Ecol. Manag.* 422, 41–48.
- Miguel, M.F., Jordano, P., Tabeni, S., Campos, C.M., 2018b. Context-dependency and anthropogenic effects on individual plant–frugivore networks. *Oikos* 127, 1045–1059.
- Nams, V.O., 2005. Using animal movement paths to measure response to spatial scale. *Oecologia* 143, 179–188.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement. *Ojeda, R.A., Tabeni, S., 2009. The mammals of the Monte Desert revisited. J. Arid Environ.* 73, 173–181.
- Ojeda, R.A., Tabeni, S., Corbalán, V., 2011. Mammals of the Monte Desert: from regional to local assemblages. *J. Mammal.* 92, 1236–1244.
- Otis, D.L., White, G.C., 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *J. Wildl. Manag.* 63, 1039–1044.
- Redford, K.H., Eisenberg, J.F., 1992. Mammals of the Neotropics. In: *The Southern Cone: Chile, Argentina, Uruguay, Paraguay*, vol. 2. University Chicago Press, Chicago.
- Robinson, A.C., 1987. The ecology of the bush rat, *Rattus fuscipes* (Rodentia: Muridae). Sherbrooke forest, Victoria. *Aust. Mammal.* 11, 35–49.
- Roig, F.A., Roig-Juñent, S., Corbalán, V., 2009. Biogeography of the Monte Desert. *J. Arid Environ.* 73, 164–172.
- Rossi, B.E., 2004. Flora y vegetación de la Reserva de Biosfera de Nacuñán después de 25 años de clausura. Heterogeneidad espacial a distintas escalas. PhD dissertation. Universidad Nacional de Cuyo, Mendoza. Argentina.
- Ruecker, G., Schad, P., Alcubill, M.M., Ferrer, C., 1998. Natural regeneration of degraded soils and site changes on abandoned agricultural terraces in Mediterranean Spain. *Land Degrad. Dev.* 9, 179–188.
- Russell, R.E., Swihart, R.K., Craig, B.A., 2007. The effects of matrix structure on movement decisions of meadow voles (*Microtus pennsylvanicus*). *J. Mammal.* 88, 573–579.
- Searle, K.R., Hobbs, N.T., Jaronski, S.R., 2010. Asynchrony, fragmentation, and scale determine benefits of landscape heterogeneity to mobile herbivores. *Oecologia* 163, 815–824.
- Shanley, C.S., Pyare, S., Smith, W.P., 2013. Response of an ecological indicator to landscape composition and structure: implications for functional units of temperate rainforest ecosystems. *Ecol. Indic.* 24, 68–2016.
- Sikes, R.S., 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mammal.* 97, 663–688.
- Spencer, W.D., 2012. Home ranges and the value of spatial information. *J. Mammal.* 93, 929–947.
- Spencer, E.E., Crowther, M.S., Dickman, C.R., 2014. Risky business: do native rodents use habitat and odor cues to manage predation risk in Australian deserts? *PLoS One* 9, e90566. <https://doi.org/10.1371/journal.pone.0090566>.
- Spirito, F., Rowland, M., Nielson, R., Wisdom, M., Tabeni, S., 2017. Influence of grazing management on resource selection by a small mammal in a temperate desert of South America. *J. Mammal.* 98, 1768–1779.
- Spirito, F., Tabeni, S., 2016. Impacts of socio-political boundaries on small desert mammals of west-central Argentina. *J. Arid Environ.* 131, 6–14.
- Stevens, V.M., Polus, E., Wesselingh, R.A., Schtickzelle, N., Baguette, M., 2004. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). *Landscape Ecol.* 19, 829–842.
- Tabeni, S., Mastrantonio, L., Ojeda, R.A., 2007. Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte, Argentina. *Acta Oecol.* 31, 259–269.
- Tabeni, S., Ojeda, R.A., 2005. Ecology of the Monte Desert small mammals in disturbed and undisturbed habitats. *J. Arid Environ.* 63, 244–255.
- Tabeni, S., Spirito, F., Ojeda, R.A., 2013. Conservation of small and medium-sized mammals following native woodland regrowth: a case study in a long-term UNESCO Biosphere Reserve, Argentina. *J. Arid Environ.* 88, 250–253.
- Taraborelli, P., Corbalán, V., Giannoni, S., 2003. Locomotion and escape modes in rodents of the Monte Desert (Argentina). *Ethology* 109, 475–485.
- Tongway, D.J., Hindley, N., 2004. *Landscape Function Analysis Manual: Procedures for Monitoring and Assessing Landscapes with Special Reference to Minesites and Rangelands*. CSIRO Sustainable Ecosystems, Canberra.
- Turchin, P., 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Plants and Animals*.
- Udrizar Sauthier, D.E., Formoso, A.E., Teta, P., Pardiñas, U.F.J., 2011. Enlarging the knowledge on *Graomys griseoflavus* (Rodentia: Sigmodontinae) in Patagonia: distribution and environments. *Mammalia* 75, 185–193.
- Valone, T.J., Sauter, P., 2005. Effects of long-term cattle enclosure on vegetation and rodents at a desertified arid grassland site. *J. Arid Environ.* 61, 161–170.
- Villagra, P.E., Defossé, G.E., Del Valle, H.F., Tabeni, S., Rostagno, M., Cesca, E., Abraham, E., 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: implications for their management. *J. Arid Environ.* 73, 202–211.
- Webster, B., Brooks, R.J., 1981. Daily movements and short activity periods of free-ranging meadow voles *Microtus pennsylvanicus*. *Oikos* 37, 80–87.
- Wells, K., Pfeiffer, M., Lakim, M.B., Kalko, E.K.V., 2006. Movement trajectories and habitat partitioning of small mammals in logged and unlogged rainforests on Borneo. *J. Anim. Ecol.* 75, 1212–1223.
- Wickham, H., Francois, R., Henry, L., Müller, K., 2015. *Dplyr: a grammar of data Manipulation*. R Package Version 0.4.3.
- Wilson, A.D., Wikelski, M., Wilson, R.P., Cooke, S.J., 2015. Utility of biological sensor tags in animal conservation. *Conserv. Biol.* 29, 1065–1075.
- Yahnke, C.J., 2006. Habitat use and natural history of small mammals in the central Paraguayan chaco. *Mastozool. Neotrop.* 13, 103–116.
- Yoshihara, Y., Okuro, T., Undarmaa, J., Sasaki, T., Takeuchi, K., 2009. Are small rodents key promoters of ecosystem restoration in harsh environments? A case study of abandoned croplands on Mongolian grasslands. *J. Arid Environ.* 73, 364–368.
- Zar, J.H., 2019. *Biostatistical Analysis*. Pearson Education, Incorporated.
- Zollner, P.A., Lima, S.L., 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80, 51–60.