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Where do Norway rats live? Movement patterns and habitat selection in livestock farms in Argentina

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Abstract

Context. The Norway rat (*Rattus norvegicus*) is recognised as one of the most harmful invasive mammal species in natural, urban and rural environments worldwide. Prevention and control of pest species in livestock farms is necessary to protect animal and human health, but control practices usually do not take into account the biology and ecology of the species to be controlled. The understanding of the biological requirements of Norway rats is necessary for the implementation of efficient management actions.

Aims. The aim of this research was to study movement patterns and habitat selection of Norway rats on livestock farms in central Argentina. We hypothesised that rats selected specific areas within the farms according to the farm's structure and to the availability of resources.

Methods. We conducted live-trapping of rats in a pig farm and a dairy farm, during each of four seasons over 1 year. Traps were active for three consecutive days at each trapping session. Movements and habitat selection were assessed by spool-and-line technique combined with environmental surveys and GIS tools.

Key results. We captured a total of 133 Norway rats and evaluated the movements of 47 individuals. The mean length travelled, registered for one night, was 84.28 ± 38.21 m. They did not travel great linear distances within the farms, but instead performed tortuous trajectories around specific sites. Norway rats selected sites containing food, water and refuges; and avoided travelling across areas with short vegetation. Sites containing food sources were most preferred.

Conclusions. Because food sources for rats were present *ad libitum* in farms, our findings strongly support the idea that management strategies of prevention and control of this species must include adequate rodent-proof food storage. Also, because rats are found close to livestock, improvement in preventing rats' access to animal sheds is necessary to prevent contamination of livestock feeders with pathogens carried by rats.

Implications. The present study provides novel information about the ecology of Norway rats on livestock farms. We encourage farmers to follow our recommendations in order to improve rodent-control strategies.

Additional keywords: habitat preference, locomotion, pest ecology, pest management, spatial ecology.

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Introduction

The overall objective of this study was to describe movements and habitat use of Norway rats in livestock farms in Buenos Aires province, Argentina. Animals evaluate and use certain physical and biological resources over others through a series of innate and learned behavioural decisions, by searching for those that ensure their reproduction and survival. These decisions define whether they are being selective (Block and Brennan 1993). Animal movement studies provide a detailed description of how individuals use and select the area – information that is essential to understand structure and dynamics of populations (Nathan *et al.* 2008). Small mammals present variations in movements and home-range (HR) areas. Mature males of many small mammal species are reported to occupy bigger areas (Ryser 1995; Hanski *et al.* 2013). Also, resource availability (McMillan and Kaufman 1995; Stapp 1997; Hanski *et al.* 2013), foraging habits, risk of predation (Barnett and Spencer 1951; Kelt and Van Vuren 2001) and social interactions influence small mammals movements and HR areas, while juveniles are displaced to lower quality areas in populations with social hierarchy (Keen 1982; Block and Brennan 1993).

The Norway rat (*Rattus norvegicus*) is one of the most abundant vertebrate pest species found in livestock farms (Lambert *et al.* 2008; Lovera *et al.* 2015). It causes economic losses (Drummond 2001) and represents a serious livestock and human health risk worldwide (Webster *et al.* 1995; Glass 1997; Kosoy *et al.* 2015). There are few scientific studies concerning the movements and HR of Norway rat populations in rural areas. In urban environments, available literature highlights a patchy distribution and a restriction to small areas with natural soils, food and water (Davis *et al*. 1948; Traweger and Slotta-Bachmayr 2005; Traweger *et al*. 2006). Although studies performed in urban areas describe factors that promote rat infestations, such as poor living standards and inadequate hygiene (Traweger *et al*. 2006; Feng and Himsworth 2014), scarce information in rural habitats, particularly in animal production systems, is available. Rural Norway rat populations remained near food sources and had smaller HR than those living along field margins of arable lands and natural habitats (Taylor and Quy 1978; Hardy and Taylor 1979; Moors 1985; Macdonald and Fenn 1995). Also, in livestock farms, shorter movements were reported close to animal buildings, and open areas were usually avoided (Gómez Villafañe *et al*. 2008; Lambert *et al*. 2008). Cowan *et al*. (2003) have described larger HR in places where resources were more widely dispersed. Moreover, Akande (2011) described in detail the movements of two Norway rats in a pig farm in Sweden, using a video camera, and showed a high activity inside pig sheds and along drainages.

Chemical and mechanical control methods are widely used to prevent rodent infestations. However, many problems associated with rodent populations still persist, especially if key factors like foraging decisions and social interactions are not taken into account (Singleton and Brown 1999). Ecological-based rodent management has been proposed as a more effective method to prevent or mitigate rodent infestation (Singleton *et al*. 2007). Knowledge about the factors that influence movements and habitat use of rodent pests can provide useful strategies for ecologically based management practices, such as the modification of some structural characteristics of the rural buildings where rodents were mostly found (Lambert *et al*. 2008).

In this work, we aimed first to analyse habitat distribution and movements according to sex, body size, habitat type and season, and second, we proposed to evaluate habitat selection by this species. We set the following hypotheses: (1) rodents do not move randomly within the farms but travel near places that provide resources, making non-linear trajectories; (2) rodents living near resource-rich areas make more tortuous trajectories than those living in marginal areas; (3) in relation to sex and body size, mature males to travel longer distances than females; (4) a greater abundance of old adults (>261 days) occur in resource-rich areas, and juveniles (<70 days) occupy marginal areas; (5) food and water sources, as well as refuges, are the main factors associated with habitat selection; and (6) factors that affect habitat selection change with time.

Materials and methods

Study area and farms description

This study was conducted in two livestock farms (a pig and a dairy farm) located in a rural area outside the city of Buenos Aires. The pig farm was located in San Andrés de Giles (34°26′S, 59°26′W) and the dairy farm in Marcos Paz (34°46′S, 58°50′W), Buenos Aires province, Argentina. The study area is in the Rolling Pampa, a subdivision of the Pampas region (Soriano *et al*. 1992). The slopes are moderate and the climate is temperate, with a mean annual temperature of 17.4°C (IGM 1998). Intensive poultry, bovine, and other livestock farming are common activities in this region. Pig and dairy farms typically consist of numerous dwellings such as animal sheds, food storage sheds, silos, warehouses and farmer's houses. Dwellings are surrounded by herbaceous spontaneous vegetated areas (for detailed description of these dwellings see Lovera *et al*. 2015). On farms studied, livestock food was present *ad libitum* mainly in feeders inside animal sheds and stored in large bags inside food storage sheds. Because these farms did not have automatic feeding systems, a large amount of food was routinely spilled on the floor by farmers, providing suitable conditions for rodent establishment. Animal sheds were frequently washed to ensure hygienic conditions and to prevent contamination and disease transmission. Drainage channels containing remnants of food together with faeces, hair and urine carried wastewater from sheds into a pond for wastewater treatment.

Trapping procedure and animal tracking

Live-trapping of Norway rats was conducted in both farms during 2012. Each farm was sampled for four consecutive seasons. A total of 40 cage traps (15 cm × 16 cm × 31 cm) at the dairy farm and 50 at the pig farm were set at each trapping session. Because the availability and distribution of resources in the farms influence the distribution of rats (Lovera *et al*. 2015), four different habitat types were defined *a priori* in each farm: (1) the 'high resource level' habitat type corresponded to the food storage sheds and/or silos; (2) the 'high to moderate resource level' habitat type corresponded to the pig sheds or milking enclosure and adjacent areas; (3) the 'moderate to low resource level' habitat type corresponded to the drainage channel or ditches; and (4) the 'low resource level' habitat type corresponded to areas and dwellings away (at least 100 m) from the main sources of food and water. Cage traps were placed in these habitat types, on both farms and during each seasonal trapping session. Traps were set every 10 m along 50–100 m trap lines and their position remained the same in all trapping sessions. In order to avoid the bias due to neophobia and to increase trap success, trapping was carried out following a pre-baiting period over three nights (Cowan 1977; Gurnell 1980). Then, baits (meat and carrot) were replaced and traps were activated for three consecutive nights. Early each morning, traps were checked for captures. Individuals were kept in a comfortable place with food and water until late afternoon. At that time, they were anesthetised by means of inhalation of isoflurane, ear-tagged, sexed and weighted, and their body–tail length was measured. Animals were equipped with a spool-and-line device (Miles *et al*. 1981; Boonstra and Craine 1986) and released at the same site of capture, with the free end of the thread tied off to a fixed point. When the number of animals captured exceeded our capacity for tracking (see below), some rats were released without the device. Nylon threads were dyed with different colours to identify the animal to which it belonged. Threads were followed and collected 1 day after the animals were released. Distances travelled were recorded using a measuring tape and the trajectories were mapped on Google Earth high-resolution aerial images of each farm, printed at 1 : 50 scale. In cases where a thread appeared going in and/or out of two close burrows – after ensuring it was the same thread by pulling both extremes of the burrow holes – a linear trajectory below ground between them was recorded. Trapping and handling conformed to guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and to the Argentine Law for Animal Care (National Law 14346; see http://www.sarem.org.ar, accessed dd mmm yyyy).

Habitat distribution and movement patterns

To analyse habitat distribution, trap success was used to measure the relative abundance in each habitat type (Mills *et al*. 1991). Trapping effort used for trap success estimation was adjusted according to the number of sprung traps without captures, as in Nelson and Clark (1973) and Cavia *et al*. (2012). This adjustment was necessary because domestic animals and farmers accidentally disabled the traps. Relative abundance of individuals of different age classes was compared among habitat types, taking into account possible seasonal effects (see below). The age of Norway rats was estimated based on head–body length using the equation proposed by Gómez Villafañe *et al*. (2013). We defined age classes as follows: juveniles, 0–70 days (the upper limit corresponds to the age of sexual maturity according to Coto (1997); young adults, 71–260 days; and old adults, >261 days. Generalised Linear Mixed Models (GLMM; Zuur *et al*. 2009) with binomial error structure were used to compare the relative abundance of rats of different age classes among seasons and habitat types. The effect of the farms was included as the random effect because each farm was sampled four consecutive times. This analysis was conducted using *nlme* package (Pinheiro *et al*. 2011) from R software (R Core Team 2013).

Recorded movements of Norway rats were imported into ArcView GIS 3.2 (ESRI 1999) as polyline shapefiles. Polylines consisted of straight line segments created between vertices (direction changes), and were used to represent the linear and curvilinear movements of rats (Fig. 1). We analysed the linearity of the movements among sexes, seasons and habitat types using a linearity index (LI; Shanahan *et al*. 2007). This index was defined as the total linear distance between the start and end points of the trajectory, divided by its total length ($LI = 1$ for linear trajectories and $LI < 1$ for tortuous trajectories). A Generalised Least Square (GLS; Crawley 2007) model was performed to compare LI among sexes, seasons and habitat types. Also, to determine whether rats moved through their HR randomly or made directional choices, we compared the LI of individual trajectories with the LI of random trajectories. We generated three random trajectories for each individual using the Alternate Animal Movement Routes *v*.2.1 (Jenness Enterprises, xxx), an extension to ArcView GIS 3.2 (ESRI 1999). With this tool, the original step-length and distance travelled were kept constant but the angles of direction change were randomised. This means that individuals were assumed to search with no previous information (Berg 1993) and were equally likely to move in each possible direction and uncorrelated in direction, meaning that the direction taken at a given time is independent of the direction at all preceding times. A GLS was performed to evaluate whether LI of individual trajectories differed from LI of random trajectories.

Daily activity areas were computed for each animal using the Minimum Convex Polygon method (MCP; Mohr 1947). For this, we used a tool in the Animal Movement Analysis extension (Hooge and Eichenlaub 2000) for ArcView 3.2 (ESRI 1999). Minimum Convex Polygons were compared among sexes, body sizes (body–tail length) and seasons using a GLS model (Crawley 2007). Minimum Convex Polygons and LI data were log-transformed to satisfy normality and homoscedasticity.

Environmental factors that could affect habitat selection were evaluated in two ways. First, along their trajectories, 24 environmental variables were recorded within a 4-m^2 area every 10 m (Table 1). Also, to estimate environmental availability, we randomly selected 4-m^2 areas, located within the limits of the farms, in which we measured the same variables. For each individual tracked, at least three random areas were chosen. Random areas close to each other were joined together in order to simulate a random trajectory. Mean values for each environmental variable were used to evaluate habitat selection. A stepwise forward multiple regression analysis using GLM with a binomial distribution was performed (McCullagh and Nelder 1999; Zuur *et al*. 2009). For this analysis and according to Manly *et al*. (1993), a binary response variable was tested (individual and random trajectories, given a value of 1 and 0, respectively); the 24 environmental variables were used as explanatory variables.

Second, the study area within each farm was classified in nine habitat elements (Table 2) and mapped onto Google Earth high-resolution images of the farms, printed at 1 : 500 scale (https://www.google.com.ar/intl/es/earth/, accessed dd mmm yyyy).

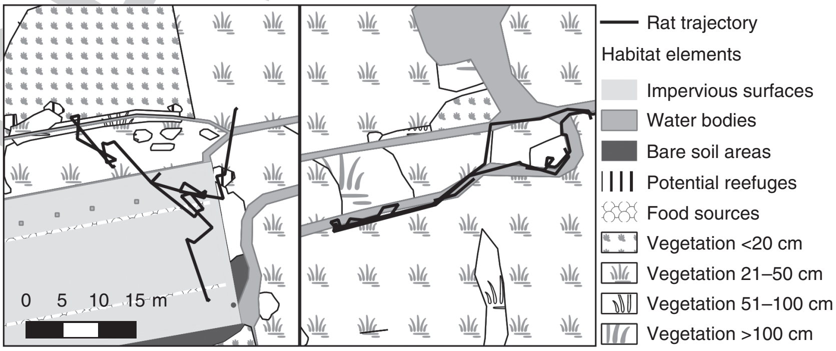

Fig. 1. Examples of two rat trajectories represented by black solid lines and the habitat elements represented by polygons within a farm. These examples corresponded to autumn 2012 in the pig farm, Buenos Aires province, Argentina.

Table 1. Description of the 24 environmental variables recorded within 4-m^2 area explaining habitat selection of Norway rats on both a dairy and a pig farm of Buenos Aires province, Argentina, in 2012

Variable	Description
Bare soils	Proportion of area covered by bare soils.
Water	Proportion of area covered by water.
	Presence or absence of water bodies.
Vegetation	
0–20 cm	Proportion of area covered by vegetation between 0 and 20 cm above ground.
21–50 cm^A	Proportion of area covered by vegetation between 21 and 50 cm above ground.
>50 cm^A	Proportion of area covered by vegetation over 50 cm above ground.
Vertical solid elements	Proportion of area covered by vertical solid elements (i.e. pile of bricks, trunks, etc.).
	Amount of vertical solid elements.
Horizontal solid elements	Proportion of area covered by horizontal solid elements.
	Amount of horizontal solid elements.
Vertical hollow elements	Proportion of area covered by vertical hollow elements (i.e. wood trunks, barrels, etc.).
	Amount of vertical hollow elements.
Horizontal hollow elements	Proportion of area covered by horizontal hollow elements (i.e. sheet, bags, etc.).
	Amount of horizontal hollow elements.
Impervious surfaces^A	Proportion of area covered by impervious surfaces.
Wall	Proportion of area covered by wall.
	Presence or absence of wall.
	Height of the wall (m).
Food^A	Proportion of area covered by food.
	Presence or absence of food sources.
Distance to refuge	Distance (m) to the closest potential refuge (i.e. burrows, plant cover, etc.).
Distance to food	Distance (m) to the closest food source.
Proximity to refuge^A	1/ distance (m) to the closest potential refuge.
Proximity to food	1/ distance (m) to the closest food source.

^{A}Variables that were excluded from the GLM models because they were correlated with $r > |0.6|$ to another variable that had higher explanatory value.

Table 2. Description of the nine habitat elements of the farms that were mapped onto Google Earth high-resolution images of the farms printed at 1 : 500 scale to explain habitat selection of Norway rats on both a dairy and a pig farm of Buenos Aires province, Argentina, in 2012

Habitat elements	Description
Water bodies	Surfaces covered with water bodies (i.e. streams, ponds, drainage channels).
Food sources	Surfaces covered with food sources (i.e. food in storage sheds, food spread on the floor, feeders).
Impervious surfaces	Impervious surfaces such as cemented floors.
Potential refuges	Non-vegetated surfaces covered with elements that provide refuges (i.e. branches, garbage, machinery sheds, machinery in disuse or sites where rats could protect themselves from other animals and people).
Bare soil areas	Surfaces covered with bare soil areas (i.e. ground soils).
Vegetation	
0–20 cm	Surfaces covered with herbaceous or shrub vegetated areas less than 20 cm above ground.
21–50 cm	Surfaces covered with herbaceous or shrub vegetated areas between 21 and 50 cm above ground.
51–100 cm	Surfaces covered with herbaceous or shrub vegetated areas between 51 and 100 cm above ground.
>100 cm	Surfaces covered with herbaceous or shrub vegetated areas over 100 cm above ground.

Thematic maps were created in each trapping session and digitised *a posteriori* using ArcView GIS 3.2 (ESRI 1999). The nine habitat elements were represented as polygons. To quantify the relative proportion of the habitat elements used and available, individual and random trajectories (already digitised) were overlaid on the thematic maps of the farms (Fig. 1). For this, we used the Alternate Animal Movement Routes v.2.1 extension for ArcView (Jenness Enterprises) that estimates the proportion of a trajectory that intersects with the different habitat elements. To analyse the selection of these elements, we used two statistical methods: the compositional analysis described by Aebischer *et al*. (1993), and a forward stepwise multiple regression analysis (see below). The proportions of the habitat elements along the individual's trajectories were compared with the random trajectories. The *adehabitat* package from R software (Calenge 2006; R Core Team 2013) was used to perform the compositional analysis. The regression analysis was performed using GLM with binomial distribution (Crawley 2007). In order to compare the proximity of individual and random trajectories with food and water sources, spatial distance maps using the Spatial Analyst tool for ArcView were generated. For each trajectory, mean distances were estimated and also included in the GLM as explanatory variables. This analysis was performed with R software (R Core Team 2013).

Results

A total of 133 Norway rats were captured (99 rats in the dairy farm with a total trapping effort of 432 cage live trap-nights, and 34 rats in the pig farm with a total trapping effort of 538 cage live trap-nights). The percentage of traps that were set off at each farm was similar (10% and 10.3% respectively). Individuals were captured in the four habitat types defined *a priori*. According to the observed movements, the animal sheds and the drainage channels were equally used by the rats (data not shown), so both habitat types were considered the same for the statistical analysis named ‘moderate resource level’ habitat type.

Abundance patterns of juveniles and young adults differed among habitat types (Likelihood Ratio Test, $LRT_2 = 61.33$, $P < 0.001$; $LRT_2 = 12.39$, $P = 0.002$, respectively). Juveniles were less abundant in the ‘high resource level’ habitat type than in the other two ($P < 0.001$; Fig. 2), whereas young adults were more represented in the ‘moderated resource level’ habitat type ($P < 0.001$; Fig. 2). Old adults showed no significant differences in their abundances among habitat types but differed among seasons ($LRT_2 = 12.26$, $P = 0.007$; Fig. 3). Old adults were more abundant during autumn (May and June) and spring (December) compared with summer (February and March) and winter (July and September) ($P = 0.006$; Fig. 3). Juveniles tended to be more abundant in summer ($P = 0.051$; Fig. 3) and the abundance of young adults did not differ throughout the year ($P > 0.050$; Fig. 3).

We applied the spool-and-line device to 79 of the 133 Norway rats captured. The individuals entered and exited to animal sheds throughout available entrances at ground level, including open doors, burrows, holes in the walls and sewers. Only one individual made vertical use of space, by climbing a tree to reach the roof of a pig shed. Trajectories of 47 rats (26 male and 21 female) were longer than 30 m. Two rats were recaptured two consecutive nights on the margins of the drainage channel. Each rat used the same area each night, overlapping 90% of their first and second night MCP. Daily activity areas (estimated by MCP) were similar among all seasons and for both sexes (mean MCP: 118 m^2, range MCP: 13 m^2–462 m^2, $P > 0.050$ in both cases). Individuals with greater head–body length showed larger MCPs ($r_{\mathrm{Pearson}} > 0.6$, $P < 0.050$). The mean length travelled registered for one night was 84.28 ± 38.21 m. In the pig farm, three individuals presented considerably larger daily activity areas (MCPs: 984 m^2, 794 m^2, 712 m^2). These individuals visited different habitat types over one night and their trajectories were almost linear; this behaviour differed from the rest of the individuals, who instead performed tortuous paths around only one habitat type (see below). Therefore, the movements of the three individuals were considered exploratory behaviours and were therefore not included in the statistical analysis related to MCPs (already informed) and tortuosity. More tortuous paths were observed during winter ($F_3 = 2.91$, $P = 0.040$), but we did not find differences between sexes ($P > 0.050$) or habitat types ($P > 0.050$). Also, we found that the trajectories were more tortuous than expected if they were moving randomly (mean LI value ± s.e. for individual and random trajectories: 0.150 ± 0.020 and 0.230 ± 0.005 respectively; $F_3 = 19.99$; $P < 0.050$).

Forward multiple regression analysis for the variables recorded within 4-m^2 areas along rat trajectories showed that Norway rats moved close to elements that provide potential

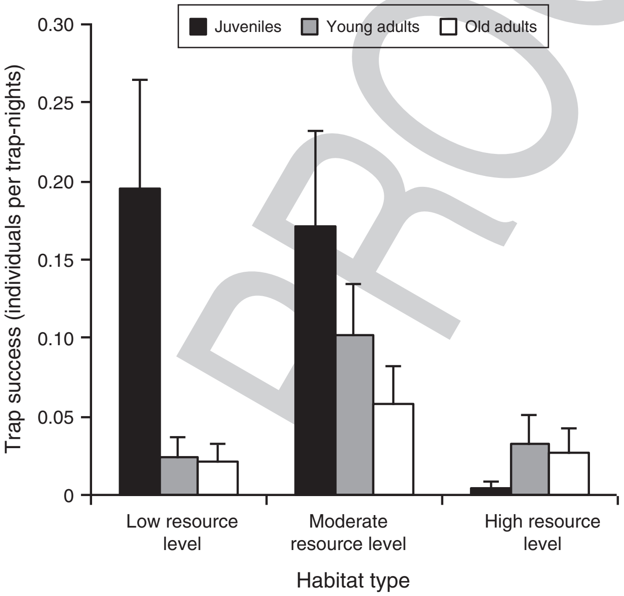

Fig. 2. Habitat type variations in trap success (mean ± standard error) of Norway rats of different age classes on both a dairy and a pig farm in Buenos Aires province, Argentina, in 2012.

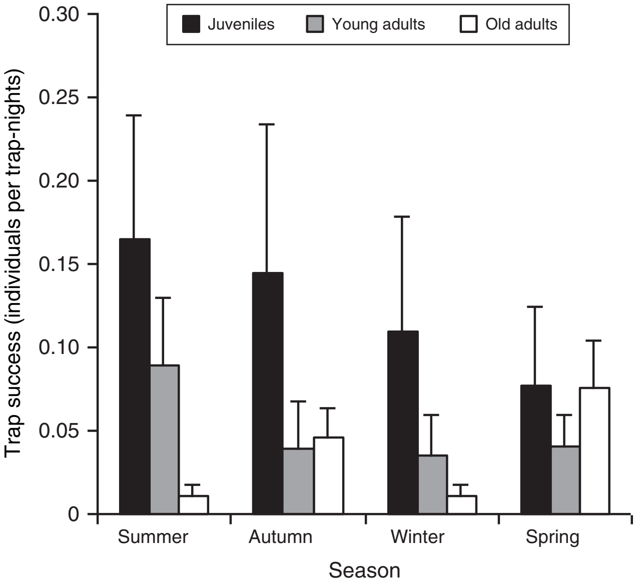

Fig. 3. Seasonal variations in trap success (mean ± standard error) of Norway rats of different age classes on both a dairy and a pig farm of Buenos Aires province, Argentina, in 2012.

refuge and food sources (Table 3). They also moved along building walls while simultaneously avoiding areas with low vegetation height (Table 3). Compositional analysis showed that rats travelled more over food sources, water bodies and impervious surfaces than over vegetated areas and sites with potential refuges, being less used to the vegetated areas and potential refuge patches (Table 4). Similarly, multiple regression analysis showed that habitat elements were not equally used. This analysis also indicated that rats moved over food sources, water bodies and impervious surfaces, as well as through potential refuges (Table 5).

Discussion

In this study we demonstrated that Norway rats selected specific areas within the farms according to the farm's structure and the availability of food, water and refuge. It has been proposed that in resource-rich areas, Norway rats tend to exhibit high site fidelity and smaller HR (Taylor and Quy 1978; Hardy and Taylor 1979; Klemann and Pelz 2006; Gardner-Santana *et al.* 2009). In accordance with this, we found that Norway rats living in one habitat did not travel to another habitat, instead concentrating their movements to some specific sites making tortuous trajectories. Although we expected less tortuous movements in the 'low resource level' habitat as reported in previous studies (Gómez Villafañe *et al.* 2008), we did not find differences among habitats. Also, tortuous trajectories observed indicate that animals did not move throughout the entire area (within the farms), possibly to decrease the risk of predation. The tracking threads showed a high association with the presence of walls because Norway rats use their sense of touch, as well as smell, to locate, recognise and memorise pathways and safety

Table 3. Results of the multiple regression analysis by GLM for habitat selection of Norway rats on both a dairy and a pig farm of Buenos Aires province, Argentina, in 2012

Only significant variables are reported ($P < 0.050$). df, degrees of freedom

	Coefficients	*z*	*P*	Residual deviance	df	Change in deviance	df	*P*
Null				154.693	111			
Distance to potential refuge (m)	–1.808	–2.332	0.020	96.446	110	58.247	1	<0.001
Proximity to food (m)	10.600	1.952	0.051	64.503	109	31.943	1	<0.001
Wall	182.138	2.276	0.023	47.795	108	16.707	1	<0.001
Vegetation 0–20 cm	–15.803	2.428	0.015	31.915	107	15.880	1	<0.001
Distance to potential refuge (m) × Proximity to food (m)	–3.437	1.914	0.056	24.778	106	7.137	1	<0.001

Table 4. Results of the compositional analysis based on comparing proportional habitat elements used and available within individual and random trajectories, respectively, by Norway rats on both a dairy and a pig farm in Buenos Aires province, Argentina, in 2012

Habitat elements are ranked in order of relative preference (8, highest; 0, lowest). The signs of *t*-values are indicated with positive or negative signs. The sign '+' signifies a higher usage of the element that appears in the row rather than the element of the column, both being equally available. A triple sign signifies non-random habitat use at $P < 0.050$. Table format is adapted from Aebischer *et al.* (1993)

	Habitat element									
Habitat element	Food sources	Water bodies	Impervious surfaces	Bare soil areas	Vegetation 21–50 cm	Vegetation 51–100 cm	Potential refuges	Vegetation <20 cm	Vegetation >100 cm	Rank order
Food sources		+	+	+++	+++	+++	+++	+++	+++	8
Water bodies	–		+	+	+++	+++	+++	+++	+++	7
Impervious surfaces	–	–		+	+++	+++	+++	+++	+++	6
Bare soil areas	—	–	–		+	+++	+++	+++	+++	5
Vegetation 21–50 cm	—	—	—	–		+	+	+	+	4
Vegetation 51–100 cm	—	—	—	—	–		+	+	+	3
Potential refuges	—	—	—	—	–	–		+	+	2
Vegetation <20 cm	—	—	—	—	–	–	–		+	1
Vegetation >100 cm	—	—	—	—	–	–	–	–		0

Table 5. Results of the Multiple Regression Analysis by GLM for habitat selection of Norway rats on a dairy and a pig farm of Buenos Aires province, Argentina, in 2012

Only significant variables are reported ($P < 0.050$). df, degrees of freedom

	Coefficients	*z*	*P*	Residual deviance	df	Change in deviance	df	*P*
Null				235.650	210			
Vegetation <20 cm	–4.320	–2.711	0.006	209.850	209	25.790	1	<0.001
Food sources	17.623	3.427	<0.001	197.680	208	12.171	1	<0.001
Water bodies	6.338	4.618	<0.001	184.700	207	12.981	1	<0.001
Impervious surfaces	14.534	3.944	<0.001	171.470	206	13.235	1	<0.001
Potential refuges	6.205	3.553	<0.001	157.030	205	14.434	1	<0.001

places (Timm 1994). Additionally, rats used burrows, holes in the walls and sewers to enter and exit the animal sheds, all at ground level (D. P. Montes de Oca, R. Lovera, R. Cavia, unpubl. data). We found that many individuals shared the same runways for moving as well as the same tunnels. These behaviours are typically found in social animals that share their nests (Timm 1994; Macdonald *et al*. 1999). Our results agree with those observed in poultry farms where movements were restricted to farm boundaries, and short displacements near sheds were observed (Gómez Villafañe *et al*. 2008). Since poultry farms have lower abundances (Gómez Villafañe and Busch 2007), future studies should evaluate if factors associated with habitat selection reported in this work also determine habitat selection in poultry farms, or other systems with lower densities.

Besides the few individuals that made exploratory movements, we found the activity areas of rats living in one habitat type did not overlap with the activity areas of rats living in another habitat type. Moreover, we found that the sizes of the activity areas were similar across all seasons and habitat types. Estimated sizes of activity areas were similar to those described for Norway rats in urban environments where they travelled short distances and the main activity area had a 25–150-m radius (Macdonald *et al*. 1999), but were smaller than those in natural environments where the distances that rats travelled to reach food were longer (Moors 1985). The fact that we found larger individuals in greater activity areas suggests that adults need greater areas to satisfy their basic requirements, such as making their territory, and also that larger body size provides greater locomotion capacity.

Norway rats of all age classes were captured during all seasons. However, seasonal differences in abundance of the different age classes suggest differences in reproductive investment along the year. These results agree with previous studies that showed that reproductive investment may change along with the seasons in livestock farms in temperate and cold climates, even though a constant supply of food in these systems was present throughout the year (Vadell *et al*. 2010; Vadell *et al*. 2014). Juveniles and young adults differed in their spatial distribution among habitat types. The behaviour of dominant rats influences the behaviour of other rats in the colony (Barnett and Spencer 1951; Calhoun 1963); dominant rats often occupy the best habitats, while the subordinates are relegated to marginal habitats and tend to feed when dominant rats are not present (Marsh 1994; Clapperton 2006). Accordingly, we observed that juveniles mainly occupied marginal areas, primarily with lower levels of resources. Future studies could focus on the behaviour of juveniles in marginal areas of farms, because wild animals such as opossums approach the periphery of the farms, but are less frequent in farm buildings where people and domestic animals are present (Lovera *et al*. 2015).

Food sources were the most preferred patches, including unbagged food in storage sheds, and food spread on the floor and over animal feeders. This indicates that rats could be significant disease sources for livestock because they frequently visit livestock feeders and are commonly infected by pathogens in the Pampas region (R. Lovera, M. S. Fernández, J. Jacob, N. Lucero, G. Morici, B. Brihuega, M. I. Farace, J. Caracostantogolo, R. Cavia, unpubl. data). We also found that rats avoided moving through areas with short vegetation, where the risk of being detected by domestic and wild predators is higher. On the farms in our study, cats and dogs were commonly present. Among wild predators, two opossums (*Lutreolina crassicaudata* (Desmarest, 1804) and *Didelphis albiventris* (Lund, 1840)) were common in pig and dairy farms (Lovera *et al*. 2015), and have been described as potential predators of *Rattus* spp. (Abas 2015). Massa *et al*. (2014) and Leveau *et al*. (2006) studied the diet of the barn owl (*Tyto alba* (Scopoli, 1769)) in the Pampas region, and found that it preyed on *Rattus* spp. as well. These results support the hypothesis that small mammals avoid patches with high predation risk (Brown 1988; Abrahams and Dill 1989; Lima 2002). We observed that the total area of the farms' short vegetation was greater in winter compared with warmer seasons (data not shown). Thus, fewer places were available for rats to move in winter and this probably resulted in the most tortuous trajectories. Nevertheless, we found that rats moved over cemented floors and bare soils. This can be explained if we consider that food was more abundant inside buildings with cemented floors and bare soil was common at the edges of water bodies, enabling the rats to create their burrows (Lore and Schultz 1989). Norway rats probably used these two substrates to reach food and water resources intensively, assuming the risk of being detected by predators.

The spool-and-line technique provided accurate information about the sites visited during one night, in contrast to other techniques that are commonly used to explain fine-scale habitat usage by evaluating only the information of the capture and recapture sites and/or radio-tracked sites. These other techniques, when used with most radio-tracking equipment, cannot record continuous movements and probably overestimate real habitat usage and miss a great quantity of data (Berry *et al*. 1987). However, spool-and-line technique, unlike radio-tracking, does not provide a time component in its analysis, although it is possible to compare distances travelled over different areas within the home-range and provide an estimate of the time spent in each one (Anderson *et al*. 1988). Nevertheless, paths travelled by rats showed evidence of regular usage because they appeared well worn, and animals tracked over two nights showed similar movement patterns on each occasion. Tracking the same animal a greater number of times would provide information regarding time spent in each area. Additionally, understanding the underlying processes affecting the core activities of the organisms tracked requires the ability to classify trajectory segments in terms of some basic functional units (Nathan *et al*. 2008).

Rodenticides are widely used by livestock farmers to manage rodents. There is a consensus that the amount of rodenticide used must be reduced (Singleton *et al*. 1999). The consequences of the misuse of rodenticides may result in genetic resistance, behavioural avoidance, non-target poison and environmental risks (Dowding *et al*. 1999; Noble *et al*. 2001; Cowan *et al*. 2003; Jackson and Van Aarde 2003; Guidobono *et al*. 2010). Reduced reliance on their usage should be accompanied by an understanding of the ecological processes involved. Lambert *et al*. (2008) have modified characteristics of some farms and concluded that targeted habitat management has the potential to reduce the size of rat populations. Our results suggest several management actions for this purpose. We propose that on farms, food should be bagged or stored in containers where rodents have no access, and that feeders should ideally be emptied and cleaned after feeding animals. Also, in animal and food storage sheds, doors should be sealed and the holes in the walls covered to prevent access by rodents (Gómez Villafañe *et al*. 2003). It is important to avoid accumulating discarded materials and rubbish that provide refuge. Recognition of burrows is important – usually there are paths leading to them. Also, as previously described, information related to the rats' preferred areas can be used to select the optimal places to set traps and bait stations. In this study, we found that rats avoided areas with low vegetation coverage, suggesting the importance of maintaining short vegetation around buildings (by frequent mowing) and resources free from vegetation in order to reduce the number of suitable sites for this species (Gómez Villafañe *et al*. 2001; Cowan *et al*. 2003; Jacob 2008; Lambert *et al*. 2008). According to the daily activity areas observed in this study, vegetation should be kept short around animal buildings up to a distance of 12 to 24 m, which takes into account the diameters of the mean to the maximum activity area registered, respectively. All these recommendations may contribute to reduce rat abundance, and consequently to diminish disease transmission and other rodent damages on farms. Since these actions entail an increase in labour investment and economic costs, cost–benefit studies are needed to evaluate its adoption. Finally, since juveniles were mostly found in marginal areas, there is probably an effect of density in their habitat distribution. If chemical rodent control is applied only in resource-rich areas, such as food and animal sheds, it should take into account the probable recolonisation from those environments.

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