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Differences in population parameters of *Rattus norvegicus* in urban and rural habitats of central Argentina

Abstract: Life history characteristics are influenced by both biotic and abiotic factors of the environment. The aim of this study was to compare the life history strategies of *Rattus norvegicus* populations in urban and rural habitats in central-east Argentina. Live trapping of rodents was conducted over 1 year in a shanty town and for 2 years on poultry farms. Abundance did not differ between habitats. Age structure was similar in both habitats but varied among seasons. Rats on poultry farms had better body condition, produced larger litters and had a higher reproductive potential than rats from the shanty town. These differences may be due to differences in habitat favourability or in selection pressures between the two habitats. Our results show that rats may adopt different life history strategies according to habitat conditions.

Keywords: life history; rats; reproduction; rural; urban.

Introduction

The knowledge of a species' life history is of key importance in predicting population responses to management (Williams et al. 2002), and it is useful for understanding how populations respond to changes in the environment (Dobson and Oli 2007). Life history traits include body size at birth, growth pattern, age and body size at maturity, number and sex ratio of offspring, reproductive investment, age-specific mortality schedules and length of life (Stearns 1992, Williams et al. 2002). These life history characteristics are influenced by both biotic and abiotic factors of the environment (Williams et al. 2002). For example, in mammals, food availability, ambient temperature and humidity, among other factors, interact to determine an individual's rate of growth and indirectly determine its reproductive development (Bronson 1989).

Rattus norvegicus Berkenhout, 1769 is a cosmopolitan rat that occupies habitats ranging from areas with commensal to natural conditions (Stroud 1982, Aplin et al. 2003). Population parameters such as litter size, sexual maturation and growth rate differ among populations inhabiting different habitats within the same region (Davis 1949, Glass et al. 1988, 1989). Davis (1949) showed that the striking differences in size between individuals living in residential areas and on a horse-breeding farm were largely phenotypic, and Davis (1951) detected that rats living in residential areas grew larger, attained reproductive maturity at a smaller size and had more embryos per female than rats living on farms. Glass et al. (1988) observed that individuals in parkland populations grow more slowly, were smaller, attained reproductive maturity at an older age and lived at lower densities than rats in

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residential areas. Both authors suggested that these differences may be the consequence of plastic phenotypic responses to differences between habitats in food quality and availability, and concluded that the city is a more favourable habitat for rodents than horse-breeding farms or parklands (Davis 1951, Glass et al. 1988).

In Argentina, *Rattus norvegicus* is considered a pest species both in rural and urban habitats (Jackson 1988, Gómez Villafañe et al. 2005, Fernández et al. 2007, Gómez Villafañe and Busch 2007). In rural areas, it is associated with animal-breeding farms (dairy, poultry and pig farms), where rats consume commercial animal food and organic refuse, and find refuge in barns and sheds (Gómez Villafañe and Busch 2007). These rural buildings represent favourable habitats inside a matrix of cultivated fields and pastures where rats are rarely found (Gómez Villafañe and Busch 2007).

On the poultry farms of Exaltación de la Cruz, in the province of Buenos Aires, rats are found inside and outside breeding sheds, which are surrounded by short grass, while a perimeter of tall grass or hedgerow is usually kept uncut along the wire fences that separate the farms from the surrounding crop or pasture fields (Gómez Villafañe et al. 2001, Gómez Villafañe and Busch 2007). Farm managers usually live with their family on the farm, while other extra workers come to work from the nearby village. Sheds are treated periodically with an anticoagulant rodenticide for rodent control, although they may remain untreated for several months (Gómez Villafañe et al. 2001).

In urban areas, rats are found in households, warehouses, stores, rubbish dumps, vacant areas and parklands, among other habitats (Castillo et al. 2003, Sequeira et al. 2003, Cavia et al. 2009, Vadell et al. 2010). In the city of Buenos Aires, *Rattus norvegicus* is the dominant rodent species in shanty towns and parklands (Cavia et al. 2009). Shanty towns in Buenos Aires are densely inhabited and precarious urban settlements with poor housing conditions, a lack or deficiency of basic public services, and the presence of spontaneous plant cover (Fernández et al. 2007, Cavia et al. 2009, Vadell et al. 2010). Poor housing conditions in residential areas are known to provide an accessible refuge for rodents (Lambropoulos et al. 1999, Pocock et al. 2004) where garbage represents their major food resource (Schein and Orgain 1953). In contrast to areas with a high abundance of buildings, shanty towns present unpaved streets and backyards, and therefore provide suitable conditions for the construction of ground burrows (Fernández et al. 2007). According to the habitat characteristics and the life history theory, we expect life history strategies of *R. norvegicus* to be different on farm and in shanty-town habitats.

The aim of this study was to compare the life history traits of *Rattus norvegicus* in a rural and an urban habitat in central-east Argentina by comparing population abundance, age structure, reproduction, individual body condition and growth rate.

Materials and methods

Study area

This study was conducted in 229 dwellings (houses or shops) in a shanty town in the city of Buenos Aires (34°37′ S, 58°24′ W) and on 48 poultry farms located in the rural area of Exaltación de la Cruz (34°28′ S, 59°12′ W), Buenos Aires, Argentina (Figure 1). The rural area is located 100 km to the north of the urban area. Both areas are located in the Rolling Pampa, a subdivision of the Pampas region, which has a temperate climate with four well-defined seasons (Soriano et al. 1992). The mean annual temperature in the study area is 17.4°C, and its mean annual precipitation is 1014 mm (Instituto Geográfico Militar 1998).

The shanty town is located in a north-eastern neighbourhood of the city of Buenos Aires, close to a railway and to harbour warehouses and surrounded by vegetated areas (Fernández et al. 2007). It comprises an area of about 190,000 m^2 and is inhabited by 12,242 people [Instituto Nacional de Estadística y Censos (INDEC) 2001]. Its

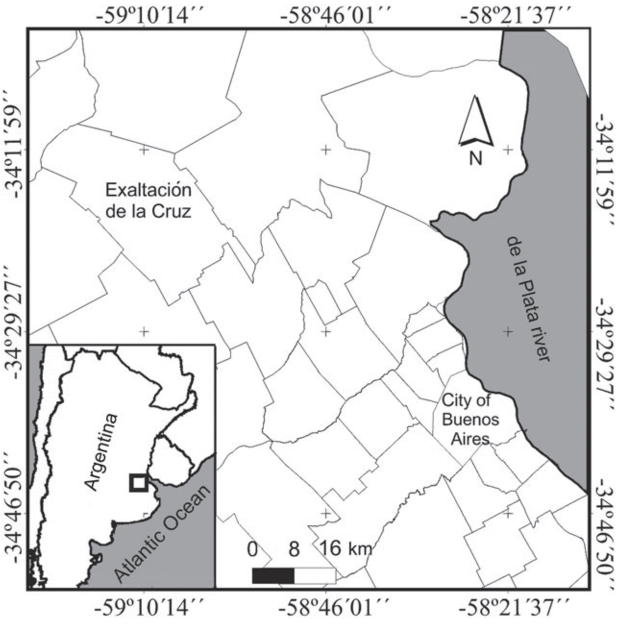

Figure 1 Location of the rural (Exaltación de la Cruz) and urban (City of Buenos Aires) sampling sites for *Rattus norvegicus* in Argentina.

dwellings are small, generally unfinished, and many of them have yards where garbage and unused objects are kept. The streets are unpaved and rainwater is frequently accumulated in puddles (INDEC 2001, Fernández et al. 2007, Vadell et al. 2010).

Poultry farms are located in a rural area that is intensely cultivated with maize, soybean, sunflower and sorghum. Other activities in the area include extensive cattle breeding and intensive pig farming. On poultry farms, chickens receive food and water *ad libitum* and are maintained at a comfortable temperature throughout the year (for more information about the management of the farms and sheds description, see Gómez Villafañe et al. 2001).

Although samplings were conducted in different years in the two habitats, we considered that there was not an effect of time in the life history parameters of *Rattus norvegicus* because weather conditions were similar both during the year preceding the start of each study (mean monthly temperature: 16.4°C and annual precipitation: 891 mm for poultry farms; 16.6°C and 1015 mm for the shanty town) and during the studied periods (mean monthly temperature: 17.1°C and annual precipitation: 1100 mm for poultry farms; 16.5°C and 1131 mm for the shanty town).

Rodent surveys

Live trapping of rodents was conducted with cage traps (15×16×31 cm) every 2 months from September 2006 to August 2007 in the shanty town, with a total trapping effort of 1723 trap-nights, and every 3 months from September 1999 to July 2001 on the poultry farms, with a total trapping effort of 4282 trap-nights. Cage traps were baited with meat and carrot, set for 3 and 4 consecutive nights (on farms and in the shanty town, respectively), and checked for captures every morning. In the shanty town, the total area was divided into four homogenous sectors in order to facilitate the trapping. Traps were placed in a group of 10 dwellings in each sector. These groups of dwellings were sampled only once to avoid the effect of rodent removal. In the rural area, six farms were studied per season each year. Traps were set at 20-m intervals surrounding the poultry sheds. Three sheds were sampled on each farm. When a farm had more than three sheds, the sheds to be sampled were randomly chosen.

Captured rats were anaesthetised with an intramuscular dose of ketamine hydrochloride (40 mg/kg) and acepromazine (2.5 mg/kg), and sacrificed by cervical dislocation. Animals were handled according to the 14,346 Argentinean National Law of Animal Care. The species, sex, weight, age, and body and tail lengths were recorded for each animal caught. Reproductively active females (pregnant, with evidence of lactation or with open vaginas) and reproductively active males (with scrotal testes) were distinguished from those which were reproductively inactive (females with closed vaginas and males with abdominal testes). Additionally, we registered the numbers of embryos present in the uteri of pregnant females. We collected the eye lens of each individual following Lord (1959), and the age (in days) was estimated according to their weight using the equation proposed by Hardy et al. (1983).

We defined age classes as follows: class 1, between 0 and 70 days (juveniles, the upper limit corresponds to the age of sexual maturation according to Coto 1997); class 2, between 71 and 260 days (young adults); and class 3, older than 261 days (old adults).

To estimate an index of physical condition (IPC), we first performed a linear regression between the logarithm ($\log_{10}$) of the body mass (dependent variable) and the head-body length (independent variable) of all individuals independently of the habitat. We used the logarithmic transformation of the head-body length in order to linearise the relation between the variables. Then, we calculated the IPC for each animal as the ratio between the observed and predicted values (Krebs and Singleton 1993). Values of this index >1 were considered evidence of good physical condition.

Trap success was estimated as follows: number of rodents captured×100/(number of traps×number of nights). To make the trap success of the farms and the shanty town comparable, we computed the trap success in the shanty town only with the captures of the first 3 nights.

Data analysis

Rattus norvegicus abundance was compared between the shanty town and the farms and among seasons (summer: December 21 to March 21; autumn: March 21 to June 21; winter: June 21 to September 21; and spring: September 21 to December 21) by means of a two-factor analysis of deviance using generalised linear models (Crawley 1993, McCullagh and Nelder 1999). According to the sampling design, both factors were considered fixed effects (habitat and season). We assumed a binomial distribution of errors and applied the logistic function as a link for the response variable (Crawley 1993).

Age composition was compared between habitats by means of an analysis of variance (Zar 1996). To analyse the difference between habitats in age structure a Cochran-Mantel-Haenszel (C-M-H) test was conducted, considering the seasons (summer, autumn, winter and spring) as strata (Quinn and Keough 2002). We also analysed the variation in age structure according to seasons (summer, autumn, winter and spring) by means of a C-M-H test, considering habitats (farms and the shanty town) as strata (Quinn and Keough 2002).

Head-body length and body mass were compared between the shanty town and the poultry farms by means of an ANCOVA test using the logarithm of the age as a co-variable (Quinn and Keough 2002). Logarithm was applied to age in order to linearise the relation between age and head-body length and body mass. IPC was compared between habitats by means of a one-way analysis of variance (Zar 1996).

To compare the reproductive activity (proportion of active or inactive individuals) between habitats (farms or shanty town), a C-M-H test was conducted, defining the seasons (summer, autumn, winter and spring) as strata (Quinn and Keough 2002). The proportion of reproductively active females with respect to the total of individuals in both habitats, and with respect to the total females in warm (spring and summer) and cold (autumn and winter) seasons were compared by means of a χ^2-test (Zar 1996). An annual potential rate of increase (PRI) based on offspring production was calculated for each habitat (based on Chernousova 2002) as follows: PRI=(number of sexually active females captured×mean number of embryos per female)/number of total of captured individuals. Adjustment to the 1:1 sex ratio was tested by means of a χ^2-test for each habitat (Zar 1996). All these analyses were done using InfoStat software (InfoStat group, FCA, Córdoba, Argentina) (Di Rienzo et al. 2012).

Results

A total of 51 individuals of *Rattus norvegicus* were captured in the shanty town, while 152 individuals were captured on the farms. The abundance did not differ significantly between habitats ($TS_{farms}=3.47$; $TS_{shanty\ town}=3.04$; deviance change=0.121; df=1; p=0.73; Table 1) nor among seasons (deviance change=5.12; df=3; p=0.16; Figure 2). There was no significant interaction between habitat and season (deviance change=3.196; df=3; p=0.36).

	Poultry farms	Shanty town	Difference
Abundance (TS)	3.47	3.04	NS
Mean age (days±SE)	130±7.4	131±12.3	NS
Age structure (1:2:3)	3.4:8.3:1	2.8:6.4:1	NS
Mean head-body length (cm±SE)	207±3.4	207±5.3	NS
Mean body mass (g±SE)	269.9±11.1	215.3±15.0	S
IPC	1.01±0.01	0.96±0.01	S
Sex ratio (male:female)	1.3:1	1:1.4	NS
Proportion of reproductively active individuals	0.86	0.95	NS
Active females/total no. of individuals	0.48	0.33	S
Mean number of embryos/female (±SE)	11.6±0.8	7.5±1.32	S
PRI	5.5	2.5	–

Table 1 Summary of the results for the comparison of life history traits between rat (*Rattus norvegicus*) populations on poultry farms and a shanty town in central Argentina.
NS, non-significant differences; S, significant differences; SE, standard error.

The mean age of rats did not differ significantly between habitats ($F_{1,176}=0.01$; p=0.90; Table 1) and was 130 days on poultry farms (standard deviation, SD: 83 days; maximum age: 452 days; Table 1) and 131 days in the shanty town (SD: 88 days; maximum age: 356 days; Table 1). Age structure was independent of the habitat (C-M-H; $\chi^2=0.31$; df=2; p=0.857), but varied among seasons (C-M-H; $\chi^2=13.9$; df=6; p=0.03). Juveniles and older adults were more represented in spring, while young adults were equally represented in summer, autumn and winter.

Head-body length was equal in both habitats (adjusted mean for farms: 207 cm, SD: 38.43 cm; adj. mean for shanty town=207 cm, SD=37.87 cm; $F_{1,177}=0.01$; p=0.93; Table 1) and increased with age according to the following equations:

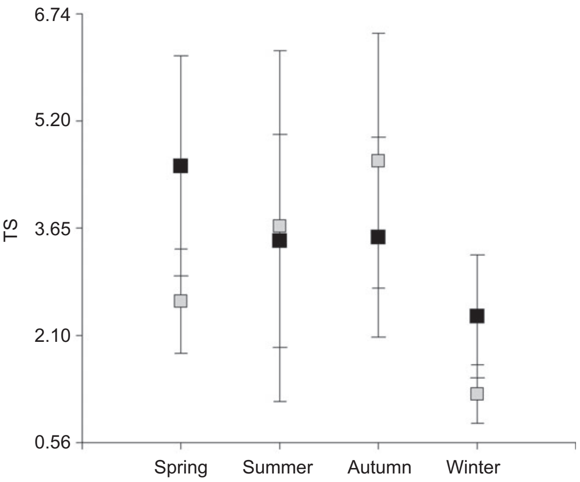

Figure 2 Seasonal variations in the trap success (mean±SD) in the shanty town (grey squares) and poultry farms (black squares).

$$\text{Head-body length}_{\text{farms}} = 16.5\ \text{cm} + 94.45 \times \log \text{age (in days)} \quad (R^2 = 0.55)$$

$$\text{Head-body length}_{\text{shanty town}} = 3.3\ \text{cm} + 100.95 \times \log \text{age (in days)} \quad (R^2 = 0.77)$$

Body mass was significantly higher ($F_{1,\ 177} = 18.38$; $p < 0.0001$) on poultry farms (adj. mean=269.9 g; SD=126.44 g; Table 1) than in the shanty town (adj. mean=215.3 g; SD=107.30 g; Table 1). Body mass increased with age according to the following equations in rural and urban habitats:

$$\text{Body mass}_{\text{farms}} = -393.4\ \text{g} + 328.23 \times \log \text{age (in days)} \quad (R^2 = 0.61)$$

$$\text{Body mass}_{\text{shanty town}} = -336\ \text{g} + 272.74 \times \log \text{age (in days)} \quad (R^2 = 0.70)$$

There was a significant positive relation between body mass and the logarithm of head-body length ($R^2 = 0.75$; n=161; $p < 0.0001$). The IPC was significantly higher for individuals of the poultry farms than the shanty town ($F_{1,\ 159} = 29.92$; $p < 0.0001$). In the first habitat, 64% of the individuals showed an index >1, while in the second only 19% of individuals exceeded this value.

The age of reproductive active males and females did not differ significantly between habitats, although reproductive active females tended to be younger on the poultry farms (males: mean $\text{age}_{\text{farms}} = 143$ days; SD=81.8; mean $\text{age}_{\text{shanty town}} = 142.92$ days; SD=81.8; $F_{1,55} = 0.93$; p=0.33; and females: mean $\text{age}_{\text{farms}} = 150$ days; SD=80.5; mean $\text{age}_{\text{shanty town}} = 189$ days; SD=106.6; $F_{1,\ 77} = 2.42$; p=0.12. The youngest reproductively active males and females were found on the farms (28 days for females and 31 days for males, while in the shanty town the youngest active individuals were 55 days old for females and 45 days old for males).

We detected pregnant females throughout the year in both habitats, and the proportion of reproductively active individuals (without discriminating into male or female) did not differ between habitats in any season (0.86 on farms; 0.95 in shanty town; C-M-H; $\chi^2 = 3.24$; df=1; p=0.072; Table 1). However, the proportion of active females with respect to the total females was greater in the warm season with respect to the cold season in both habitats ($\chi^2_{\text{farms}} = 2.02$, p=0.15; $\chi^2_{\text{shanty town}} = 3.71$, p=0.05).

The proportion of active females with respect to the total number of animals captured was significantly higher on poultry farms than in the shanty town (0.48 vs. 0.33, $\chi^2 = 4.45$, p=0.035; Table 1), and the number of embryos per female was higher on farms (mean: 11.6 embryos; SD=3.0; n=14) than in the shanty town (mean: 7.5 embryos; SD=2.7; n=4; H=4.29; p=0.038; Table 1). Therefore, the potential rate of increase was more than double on the farms (PRI=5.5; Table 1) than in the shanty town (PRI=2.5; Table 1). The sex ratio did not differ from the expected 1:1 in any habitat (shanty town: $\chi^2 = 1.58$, gl=1, p=0.21; farms: $\chi^2 = 2.33$, gl=1, p=0.13; Table 1).

Discussion

Rats on poultry farms had a higher body mass, a better physical condition and produced larger litters (based on the numbers of embryos) than rats from the shanty town. Larger litters and a higher proportion of active females in farm populations resulted in a higher potential rate of increase than in the shanty town; however, this higher reproductive potential was not translated to a higher abundance. As abundance is mainly the balance between natality and mortality, it is probable that the higher reproductive potential of rats on farms may be a compensation for a higher mortality, as rodent control is more intense in the breeding sheds than in the shanty town (personal observations).

The differences in reproductive parameters between habitats may be related to differences in resource availability, as rats on poultry farms showed higher body mass and a better physical condition, which in turns allow a higher reproductive investment (Bronson 1985, Ricklefs and Wikelski 2002). In many species, reproduction is not triggered by age but depends on the physical condition, allowing a plastic response in habitats with fluctuating resources (Stearns 1972, Bronson 1985, Metcalfe and Monaghan 2001). However, high mortality rates on farms can be a selective pressure for an increase in reproductive investment at each reproductive event, as was evidenced by the high number of embryos per female in comparison to shanty-town females. Large reproductive investment in each reproductive event may be at the expense of adult longevity (Stearns 1992), and may be favoured when food resources are abundant and the probability of survival is low, as may be the case on poultry farms. Although the age of the oldest individual was higher for the poultry farms, there were few individuals that attained this age (three individuals); thus, we cannot discard the possibility of this being due to a higher chance of capturing old individuals on the farms because of its higher sample size.

As was found in similar habitats with low seasonal variations and mild climatic conditions (Davis 1951, Bishop and Hartley 1976, Glass et al. 1989, Villa et al. 1997), in this study we found that rats reproduced throughout the year both on farms and in the shanty town. The variations found in age structure in both habitats are therefore not due to a break in their reproductive cycle but could be explained by changes in the intensity of reproduction throughout the year, as suggested by the differences in the proportion of active females between warm and cold seasons. In addition, changes in climatic conditions throughout the year could be affecting rodent survival and consequently generating differences in age structure.

In conclusion, we found that the studied rat populations in the shanty town and on poultry farms exhibited different life history traits probably related to variations in resource availability and in the intensity of pest control between habitats. Although we compared populations in different years, we consider that environmental conditions did not vary among the years of study in such a way to account for the observed results.

Our results may be relevant to management because the idea that a reproductive response may compensate the mortality due to control with rodenticides highlights the need for a more integrated control programme that addresses the need for reducing the access of rats to food, and that evaluates the use of alternative methods for reducing abundance, such as chemical inhibitors of reproduction (Dell'Omo and Palmery 2002, Hinds et al. 2003, Jacob et al. 2008). However, we consider that the management of this pest species must be done according to the characteristics of the habitats and populations involved, meaning that there are no universal recipes for control that can be applied without the knowledge of the particular system where they are applied.

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