Are life-history strategies of Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*) dependent on environmental characteristics?

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Abstract

Context. Life-history theory attempts to explain the way in which an organism is adapted to its environment as well as explaining the differences in life-history strategies among and within species.

Aims. The aim of this paper was to compare life-history traits of the Norway rat and the house mouse living in different habitats and geographic regions so as to find patterns related to environmental characteristics on the basis of published ecological studies conducted before 2011.

Methods. The environments where rodent populations lived were characterised according to climate type, occurrence of freezing temperatures and frost, degree of anthropisation and trapping location. Four demographic characteristics were analysed. A canonical correspondence analysis was performed to explain the effects of environmental variables on the demographic characteristics of rodents. Information was gathered from 35 articles published between 1945 and 2010.

Key results. Most populations of both species showed differences in abundance throughout the year, but no defined pattern was common among populations. The pregnancy rate of Norway rat was highest during spring and autumn in urban environments, during spring and winter in rural environments and during summer in sylvan habitats. House mouse populations were most frequently reported to experience high pregnancy rates during summer. Contrary to urban and rural populations, in sylvan environments the occurrence of a reproductive break was the most commonly reported pattern for both species. Litter size of Norway rat depended on the degree of anthropisation and the occurrence of freezing temperatures and frost. Litter size was greater in rural environments and in areas without freezing temperatures and frost. House mouse did not show differences in litter size resulting from any of the environmental characteristics analysed.

Conclusions. Both species are able to modify their reproductive strategies according to environmental characteristics, especially according to the degree of anthropisation of the environment. In sylvan areas, where animals are more exposed to seasonal changes in weather conditions, changes in reproductive investment are more evident.

Implications. Regarding the implications for rodent control, the best time to apply control measures could be winter in sylvan and urban environments. In rural environments, the best time for conducting control efforts is less clear, although cold seasons seem also to be the best.

Additional keywords: abundance, demography, life-history traits, reproduction.

Introduction

Organisms have evolved many different ways of combining reproduction and survival to affect fitness (Stearns 1992) and, in turn, reproductive investment and survival respond to intrinsic and extrinsic factors such as population density, food supply and temperature (Bronson 1979; Stearns 1992). Similarly, litter size in small rodents is influenced by nutritional factors such as food quality and quantity and population densities, additionally to age and parity of females (Bomford 1987; Bronson and Perrigo 1987).

Life-history theory attempts to explain the way in which an organism is adapted to its environment and it studies the various investments in growth, reproduction and survivorship that define the life-history strategy of an organism (Dobson and Oli 2007). Life-history theory aims to explain differences in life-history strategies among species and groups of species, but also

among populations within species. In an interspecific approach, life-history strategies are constrained by the evolutionary history of the organisms involved (Read and Harvey 1989; Stearns 1992). However, such constraints should be relatively unimportant in intraspecific studies because of the greater degree of shared history among conspecific populations. Different life-history patterns within a species are therefore likely to reflect the ways in which populations respond to changes in the environment (Dobson and Murie 1987; Dobson and Oli 2007).

Body size itself might be the causal influence on life-history traits (Stearns 1983; Dobson and Oli 2007). Gaillard *et al.* (1989) and Dobson and Oli (2007) suggested that measurement was the principal characteristic associated with life-history traits such as age maturity, reproductive lifespan, fecundity and juvenile and adult survival rates. Food availability and weather conditions interact to determine an individual's rate of growth and thus, indirectly, these factors determine its rate of reproductive development (Bronson 1989). For example, many mammals live in environments that change seasonally where they reproduce during only part of the year, responding strictly to dietary and climatic conditions (Bronson 1989).

The Norway rat (*Rattus norvegicus*) and the house mouse (*Mus musculus*) are two originally Asiatic rodent species that have become adapted to close association with humans, and have hence become distributed worldwide (Bronson 1979; Berry 1981; Lund 1994; Aplin *et al.* 2003*b*). The Norway rat and the house mouse are considered to be important pest species because they pose a risk to human health, cause economic losses from food and crop consumption and contamination, damage to buildings and equipment, and they also affect negatively the native fauna of the places invaded by them (Atkinson 1985; Lund 1994; Robinet *et al.* 1998; Thorsen *et al.* 2000; Aplin *et al.* 2003*b*; Singleton *et al.* 2003; Stenseth *et al.* 2003).

They are found on all continents except Antarctica and can exploit urban, rural and sylvan environments in a wide variety of regions and climates (Bronson 1979; Berry 1981; Coto 1997; Macdonald *et al.* 1999). The success of Norway rats and house mice has been largely attributed to their commensal behaviour and to their adaptability (Rowe 1973; Lund 1994; Coto 1997; Macdonald *et al.* 1999). In urban environments, they are found inside houses, stores and industries where they thrive on human food and garbage (Laurie 1946; Schein and Orgain 1953; Glass *et al.* 1989; Vadell *et al.* 2010), and in parklands and vacant lots (Glass *et al.* 1989; Gómez Villafañe *et al.* 2008; Cavia *et al.* 2009; Vadell *et al.* 2010). In rural environments, they often exploit animal breeding farms where they find available food and refuge in barns, granaries and sheds (Rowe *et al.* 1983; Lund 1994; Chou *et al.* 1998; Gómez Villafañe and Busch 2007) but they are also found exploiting crop fields (Meehan 1984; Macdonald *et al.* 1999; Singleton *et al.* 2005; McGuire *et al.* 2006; León *et al.* 2013). Norway rats and house mice can also inhabit a wide variety of sylvan habitats, ranging from deserts and swamps to sub-Antarctic islands (Bronson 1979; Pye and Bonner 1980; Berry 1981; Matthewson *et al.* 1994). In sylvan habitats, Norway rats are known to consume a wide variety of food items, including terrestrial vegetation, invertebrates, eggs, birds and other small vertebrates (Bettesworth and Anderson 1972; Lund 1994; Major *et al.* 2007), whereas house mice feed mostly on terrestrial invertebrates and seeds (Badan 1986; Copson 1986; Le Roux *et al.* 2002).

Norway rat and house mouse populations have been widely studied throughout the second half of the 20th century, and information about demographic parameters of mice and rats inhabiting different environments is well known. Davis (1953) made a revision about different characteristics of the Norway rat; however, the analysis of each demographic characteristic was presented separately. Also, climate data were not included in his revision, even though he understood its importance, but these data were not as available as they are currently. Apart from his studies, few attempts have been made to try to identify patterns of life-history strategies common to specific environmental characteristics. A comparative analysis of life-history traits of closely related species may provide an important insight into the particular methods of adaptation of the species. It is particularly interesting to compare species that live in the same habitat and show different life-history strategies.

Norway rats and house mice showed the typical life-history strategies of most small mammal species (Stearns 1983). They are short-lived animals with short gestation periods, many small altricial young, high energetic investment during lactation, and early sexual maturation. Because of their small body sizes they have limitations in storing energy, having very short-term 'physiological memory' and therefore, reproduction depends on current income (Stearns 1989). For these reasons, they have limitations in assigning energy between actual reproduction and survival for future reproduction (Stearns 1989).

We hypothesised that these species have different life-history strategies according to their requirements, to their physical and physiologic characteristics, and to their capacity of adaptation to the environment. Therefore, according to this hypothesis, we predict that Norway rats and house mice living in the same habitat will show different life-history traits such as litter size, occurrence or not of a reproductive break, season of high prevalence of pregnancy or the season of high abundance. We also hypothesised that each individual species changes its life-history strategy according to the characteristics of the environment, presenting the highest reproductive investment in areas with better conditions and higher availability of resources. Therefore, we predict that Norway rats and house mice living in urban and rural areas, inside human dwellings, in temperate climates and in areas without freeze and frost will show no changes in abundance and pregnancy prevalence throughout the year, no reproductive break and highest litter size. Last, we hypothesise that the Norway rat has a higher capacity to modify its life-history strategy than the house mouse because of its larger body size. Therefore, we predict that Norway rats will change more demographic parameters than does house mice according to changes in the environment.

Thus, the objectives of our study are to analyse and compare life-history traits of Norway rats and house mice living in different habitats and geographic regions, so as to describe variations in life-history strategies related to environmental characteristics. There is a growing demand, particularly in developing countries, for rodent-control strategies that either have less reliance on chemical rodenticides or can better target their use (Singleton *et al.* 1999); therefore, this information will contribute to management decisions on these rodent pests.

Methods

Literature survey

All published studies on population ecology of the Norway rat and the house mouse that met our predetermined requirements (see below) were reviewed. For this purpose, the Google Scholar web search engine (accessed January 2011) was used with the following set of keywords: *Rattus norvegicus* or *Mus musculus*, ecology, reproduction and abundance. From the articles that met our search criteria, we further searched the references and selected those that met our criteria for inclusion (see below).

Criteria for inclusion

Ecological studies of Norway rat or house mouse populations based on trapping campaigns of at least 11 months duration were chosen. Shorter trapping periods were not included because we wanted to compare demographic parameters during four seasons. Most of the included studies used live traps but some used kill traps. Among the papers of acceptable duration, papers that contained information about abundance (trap success or number of individuals/ha) and at least one reproductive parameter (proportion of reproductive individuals or pregnancy prevalence or an estimator of litter size) during every season were selected.

Environmental and population characterisation

The environments where rodent trapping took place were classified as urban, rural or sylvan, according to their degree of anthropisation. Urban environments were defined as those inside a city or town, rural as those typically related to agricultural or livestock activities, and sylvan as those with very low (or without) human activity (e.g. national parks).

Populations were classified as living indoor or outdoor, according to whether the majority of the traps were placed inside or outside human dwellings. However, if traps were placed around dwellings, the location was classified as inside because we assumed rodents captured near or around dwellings were using the building.

The probability of occurrence of freezing temperatures (mean daily temperatures below 0°C) and/or frost (absolute daily temperatures below 0°C) in the studied locality was used to characterise weather conditions (WorldClimate 1996).

The studied areas were classified according to Köppen–Geiger's world climate map updated and published by Kottek *et al.* (2006). This classification has five main classes, including equatorial climates, arid climates, warm temperate climates, snow climates and polar climates. Each of these main classes have subclasses according to precipitation, except for the snow climates, which are subdivided according to the monthly mean temperature of the warmest month (see Kottek *et al.* 2006, for a full description).

Four demographic characteristics of the studied populations were recorded, including the season/s of high abundance, the season/s of high prevalence of pregnancy, the occurrence of a reproductive break and the mean number of embryos. Because not all the included studies contained statistical results and authors did not use the same parameters, specific criteria were selected to make results comparable. Season/s of high abundance were those with values at least twice as high as

those in other seasons. This criterion resulted in the inclusion of some works having more than one season with high abundance because several seasons had similar values. Season/s of high prevalence of pregnancy were those with values at least 25% higher than for other seasons. Some works having more than one season with high maximum values of pregnancy rates were included. The occurrence of a reproductive break was considered whenever there was an absence of reproductive females in at least one of the trapping sessions. Females were considered reproductive if they presented an open vagina, corpora lutea in their ovaries, embryos in their uterus or signs of lactation. In multi-year studies, we classified the population as having a reproductive break if the break occurred at least once along the study. The mean number of embryos determined for the total number of pregnant females captured in each study was used as the indicator of litter size.

Data analysis

Data were analysed graphically and with a canonical correspondence analysis (CCA; Legendre and Legendre 2012). The CCA was intended to explain demographic characteristics (season/s of high abundance, season/s of high prevalence of pregnancy, occurrence of a reproductive break and mean number of embryos) affected by environmental variables (degree of anthropisation, trapping location, occurrence of freezing temperatures and frost, and climate type). For the CCA, categorical environmental variables, such as degree of anthropisation and trapping location were divided into subvariables through the creation of dummy variables. The mean numbers of embryos were standardised by range (assigning 0 to the minimum number of embryos and 1 to the maximum number). Effects of each environmental parameter on rodent population characteristics was evaluated with the use of backward selection and a Monte Carlo resampling procedure with 999 permutations (Borcard *et al.* 2011). These analyses were conducted using *vegan* package (Oksanen *et al.* 2013) for R 3.0.1 (R-Core-Team 2013).

The mean number of embryos was compared among degrees of anthropisation, trapping locations, climate types and occurrence of freezing and frost for the two species by means of multi-factor ANOVA, or one-factor ANOVA when the sample size was insufficient for a multi-factor analysis (Zar 1996).

Results

A total of 35 articles published between 1945 and 2010 met the selection criteria. Information from 16 Norway rat and 27 house mouse populations were extracted from 13 publications from seven countries and 22 publications from nine countries, respectively. Seven Norway rat populations were from urban environments, six were from rural environments and three from sylvan environments (Table 1). House mouse populations included seven from urban environments, eight from rural environments and 12 from sylvan environments (Table 2).

The canonical correspondence analysis was statistically significant for both species (Norway rat: $P = 0.002$; house mouse: $P = 0.001$). The backward selection of the environmental characteristics for Norway rats retained the urban ($P = 0.02$), rural ($P = 0.01$) and sylvan ($P = 0.01$)

Table 1.   Ecological studies of Norway rat populations in different environments around the world

Reference	Type of environment	Habitat	Climate
Vadell *et al.* 2010	Urban	Shanty town (Buenos Aires, Argentina)	Warm temperate, fully humid, hot summer
Vadell *et al.* 2010	Urban	Parkland (Buenos Aires, Argentina)	Warm temperate, fully humid, hot summer
Villa *et al.* 1997	Urban	Poultry farm (Mexico D.F., Mexico)	Warm temperate, dry winter, warm summer
Glass *et al.* 1989	Urban	Residential area (Maryland, USA)	Warm temperate, fully humid, hot summer
Glass *et al.* 1989	Urban	Parkland (Maryland, USA)	Warm temperate, fully humid, hot summer
Farhang-Azad and Southwick 1979	Urban	Zoo (Maryland, USA)	Warm temperate, fully humid, hot summer
Davis 1951	Urban	Residential area (Maryland, USA)	Warm temperate, fully humid, hot summer
Gómez Villafañe and Busch 2007	Rural	Poultry farms (Buenos Aires, Argentina)	Warm temperate, fully humid, hot summer
McGuire *et al.* 2006	Rural	Barn (Illinois, USA)	Snow climate, fully humid, hot summer
Bishop and Hartley 1976	Rural	Farm buildings (Powys, Wales)	Warm temperate, fully humid, warm summer
Davis 1951	Rural	Farm (Maryland, USA)	Warm temperate, fully humid, hot summer
Leslie *et al.* 1952	Rural	Corn-ricks (Oxford, England)	Warm temperate, fully humid, warm summer
Venables and Leslie 1942	Rural	Corn-ricks (Oxford, England)	Warm temperate, fully humid, warm summer
Innes *et al.* 2001	Sylvan	Forest (North Island, New Zealand)	Warm temperate, fully humid, warm summer
Moors 1985	Sylvan	Noises and Motukawao islands, (Hauraki Gulf, New Zealand)	Warm temperate, fully humid, warm summer
Pye and Bonner 1980	Sylvan	South Georgia Island (South Atlantic Georgia)	Tundra

Table 2.   Ecological studies of house mice populations in different environments around the world

Reference	Type of environment	Habitat	Climate
Vadell *et al.* 2010	Urban	Shanty town (Buenos Aires, Argentina)	Warm temperate, fully humid, hot summer
Vadell *et al.* 2010	Urban	Parkland (Buenos Aires, Argentina)	Warm temperate, fully humid, hot summer
Gómez *et al.* 2008	Urban	Vacant lots (Córdoba, Argentina)	Warm temperate, fully humid, hot summer
Wu *et al.* 2006	Urban	Rice granaries (Ilan, Taiwan)	Warm temperate, fully humid, hot summer
Laurie 1946	Urban	Warehouses, restaurants, shops and houses (Oxford, England)	Warm temperate, fully humid, warm summer
Laurie 1946	Urban	Cold stores (Oxford, England)	Warm temperate, fully humid, warm summer
Laurie 1946	Urban	Buffer depots (Oxford, England)	Warm temperate, fully humid, warm summer
León *et al.* 2013	Rural	Poultry farm (Buenos Aires, Argentina)	Warm temperate, fully humid, hot summer
Pocock *et al.* 2004	Rural	Farm (Yorkshire, England)	Warm temperate, fully humid, warm summer
Singleton *et al.* 2001	Rural	Fields (Victoria, Australia)	Warm temperate, fully humid, warm summer
Boonstra and Redhead 1994	Rural	Irrigated rice growing area (Jerilderie, Australia)	Cold steepe, desert
Mills *et al.* 1991, 1992	Rural	Crop fields (Buenos Aires and Santa Fé, Argentina)	Warm temperate, fully humid, hot summer
Rowe *et al.* 1983	Rural	Mixed arable and dairy farm buildings (Sussex and Surrey, United Kindom)	Warm temperate, fully humid, warm summer
Stickel 1979	Rural	Cropfields (Maryland, USA)	Warm temperate, fully humid, hot summer
Laurie 1946	Rural	Corn ricks (United Kindom)	Warm temperate, fully humid, warm summer
King *et al.* 1996	Sylvan	Forest (North Island, New Zealand)	Warm temperate, fully humid, warm summer
Miller and Miller 1995	Sylvan	Forest (Rangitoto Island, New Zealand)	Warm temperate, fully humid, warm summer
Matthewson *et al.* 1994	Sylvan	Beach, vegetated black lava area and dry swamp (Marion Island, South Africa)	Tundra
Triggs 1991	Sylvan	Grassland with exposed rock (Isle of May, Scotland)	Warm temperate, fully humid, warm summer
Murphy 1992	Sylvan	Forest (South Island, New Zealand)	Warm temperate, fully humid, warm summer
Efford *et al.* 1988	Sylvan	Beach and forest (Mana Island, New Zealand)	Warm temperate, fully humid, warm summer
King 1983	Sylvan	Forest (South Island, New Zealand)	Warm temperate, fully humid, warm summer
Newsome 1969	Sylvan	Reed bed (Adelaide, Australia)	Warm temperate, fully humid, warm summer
Berry 1968	Sylvan	Cliffs and coastland (Skokholm Island, Wales)	Warm temperate, fully humid, warm summer
Lidicker 1966	Sylvan	Brush-grassland (San Francisco Bay, USA)	Warm temperate, dry and warm summer
Pearson 1963	Sylvan	Grassland (California, USA)	Warm temperate, dry and warm summer
Pearson 1963	Sylvan	Grassland (California, USA)	Warm temperate, dry and warm summer

condition of the environment to explain the population characteristics in the CCA. The constrained proportion of variance of the population characteristics was 31.65%, retaining the first two axes (CCA axis 1: $F = 3.87$, $P = 0.006$, total variance explained $= 20.37\%$; CCA axis 2: $F = 2.14$, $P = 0.040$, total variance explained $= 11.28\%$). Axis 1 was

related to the occurrence of a reproductive break and high pregnancy prevalence in summer associated with the sylvan environment, and the high pregnancy prevalence during spring, autumn and winter in urban and rural habitats (Fig. 1). Additionally, an absence of a reproductive break was associated with anthropogenically modified environments. Axis 2 was related to the high pregnancy prevalence in winter associated with rural habitats, and the high pregnancy prevalence in autumn associated with urban habitats (Fig. 1). The variability in the seasons with high abundance and large litter size was not explained with the variables included in the model.

The backward selection on the CCA of the environmental characteristics for house mice retained the sylvan condition of the environment ($P = 0.01$) and the occurrence of freezing ($P = 0.03$) to explain population characteristics. The constrained proportion of variance of the population characteristics was 18%, retaining the first two axes (CCA axis 1: $F = 3.73$, $P = 0.001$, total variance explained $= 12.65\%$; CCA axis 2: $F = 1.76$, $P = 0.072$, total variance explained $= 5.99\%$). Axis 1 was associated with a reproductive break associated with sylvan environments, and to the absence of a reproductive break in studies conducted in non-sylvan environments (Fig. 2). Axis 2 was related to high abundance in winter in areas with freezing temperatures, and to high abundance during summer and high pregnancy prevalence during autumn in areas without freezing temperatures (Fig. 2). Litter size was not explained with the variables included in the model.

Season of high abundance

Almost all Norway rat and house mouse populations showed differences in abundance throughout the year (92% of Norway rat and 96% of house mouse populations; Figs 3, 4). The only two populations that showed no difference in abundance throughout the year according to our criteria were one urban,
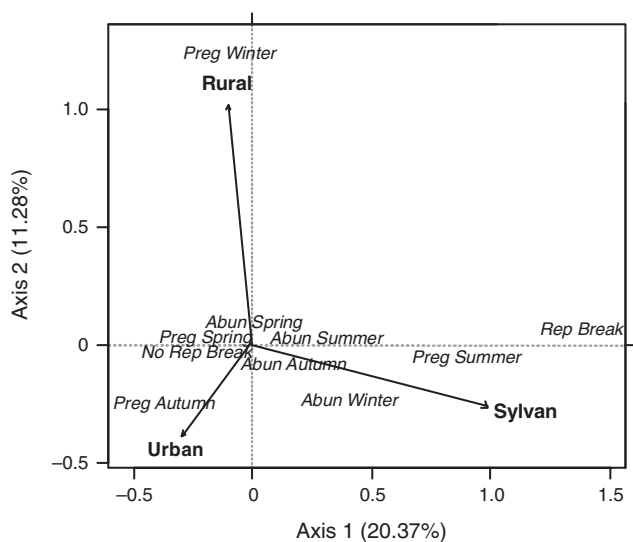
outdoor Norway rat population in a warm temperate fully humid climate with hot summer, in which freezing temperatures and frost occurred, and one rural, indoor house mouse population in a warm temperate fully humid climate with warm summer, in which freezing temperatures and frost occurred during winter.

High abundance of Norway rats was least common in winter. The other seasons contained equally frequent high abundance and did not show associations with any environmental characteristic (Figs 1, 3). High abundance of house mice occurred almost equally in every season. However, the occurrence of high abundance in winter was associated with the occurrence of freezing temperatures, and the occurrence of high abundance in summer was associated with the absence of freezing temperatures (Fig. 4c). The CCA analysis also showed that the occurrence of high abundance in winter, as the occurrence of freezing temperatures, is associated negatively with Axis 2, whereas the occurrence of high abundance in summer is associated positively with this axis, and consequently, with the absence of freezing temperatures (Fig. 2).

Pregnancy prevalence

Most Norway rat populations showed high pregnancy rates in spring (Fig. 5). Pregnancy rates of Norway rats were also high in autumn in urban environments and in winter in rural environments, whereas in sylvan habitats high pregnancy rates occurred mainly during summer (Fig. 5a). This pattern was also seen in the CCA analysis where high pregnancy rates in summer and sylvan environments were positively associated with Axis 1; high pregnancy rates in winter and rural environments were positively associated with Axis 2; high pregnancy rates in autumn and urban environments were negatively associated with Axis 2.

House mouse populations with high pregnancy prevalences in summer were the most frequently reported (Fig. 6). Populations
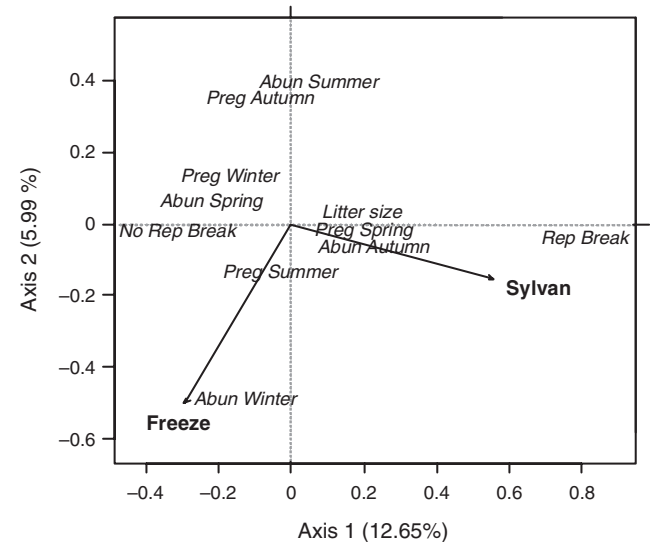

Fig. 1. Canonical correspondence analysis biplot for demographic population characteristics of the Norway rat explained by environmental variables. Abun, season with high abundance; Preg, season with high pregnancy prevalence; Rep, reproduction.

Fig. 2. Canonical correspondence analysis biplot for demographic population characteristics of the house mouse explained by environmental variables. Abun, season with high abundance; Preg, season with high pregnancy prevalence; Rep, reproduction.
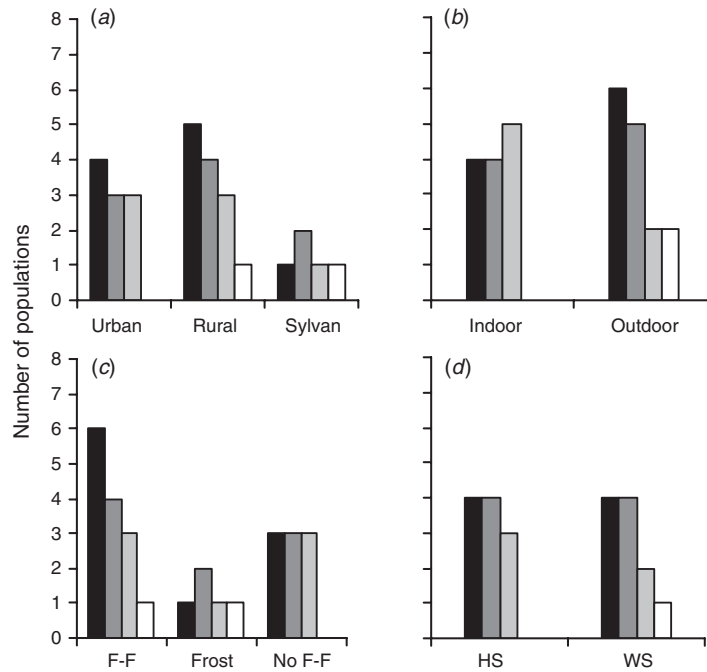
Fig. 3. Seasons of high abundance of Norway rats according to (*a*) degree of anthropisation, (*b*) trapping location, (*c*) occurrence of freezing and frost and (*d*) climate type in the studied locality. Bar colours stand for spring (black), summer (dark grey), autumn (light grey) and winter (white). F-F, freezing and frost; HS, warm temperate climate fully humid with hot summer; WS, warm temperate climate fully humid with warm summer.
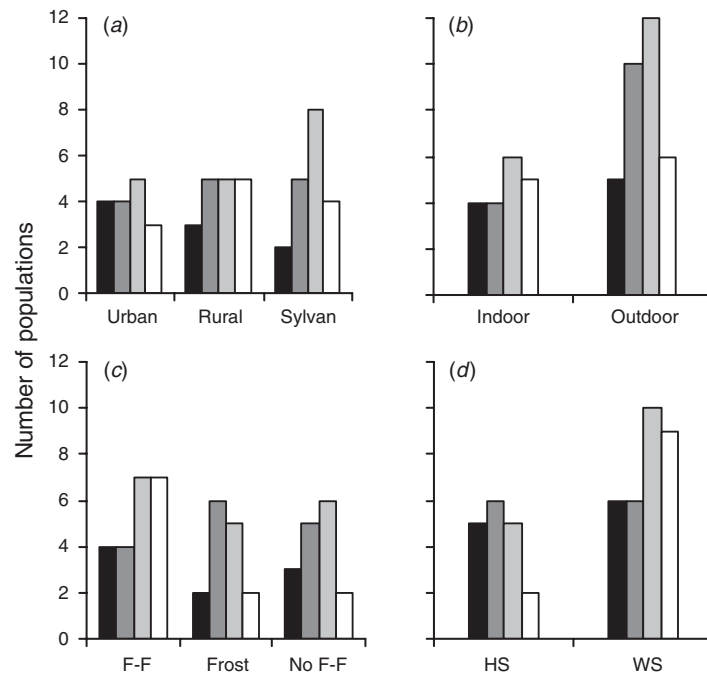

Fig. 4. Seasons of high abundance of house mice according to (*a*) degree of anthropisation, (*b*) trapping location, (*c*) occurrence of freezing and frost and (*d*) climate type in the studied locality. Bar colours stand for spring (black), summer (dark grey), autumn (light grey) and winter (white). F-F, freezing and frost; HS, warm temperate climate fully humid with hot summer; WS, warm temperate climate fully humid with warm summer.
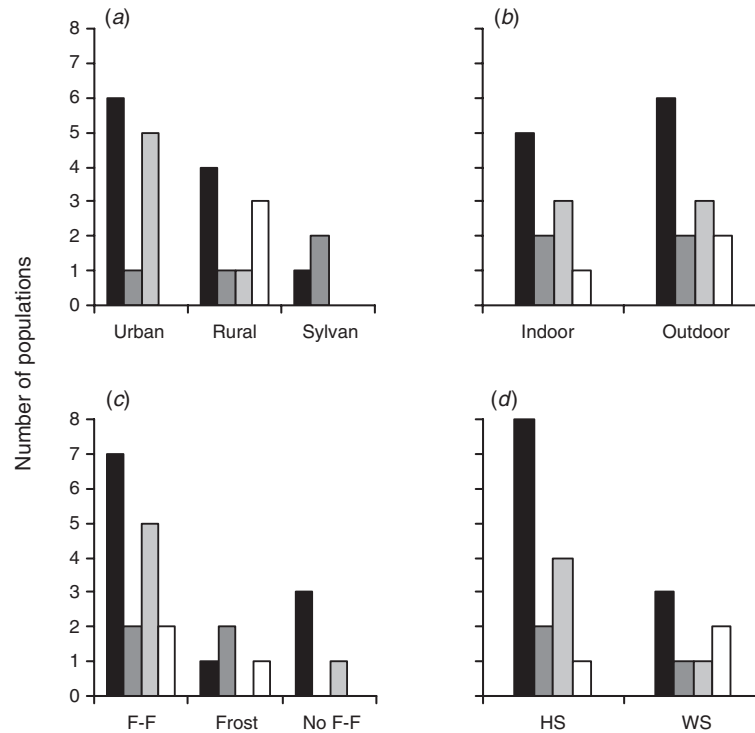
Fig. 5. Seasons of high prevalence of pregnancy of Norway rats according to (*a*) degree of anthropisation, (*b*) trapping location, (*c*) occurrence of freezing and frost in the studied locality and (*d*) climate type in the studied locality. Bar colours stand for spring (black), summer (dark grey), autumn (light grey) and winter (white). F-F, freezing and frost; HS, warm temperate climate fully humid with hot summer; WS, warm temperate climate fully humid with warm summer.

with high values in autumn and winter were least frequently reported in both urban and sylvan environments but not in rural environments (Fig. 6*a*). The pregnancy prevalence was twice as high during summer as during spring in places were freezing temperatures and frost occurred (Fig. 6*c*). According to the CCA, populations had high prevalence of pregnancy during autumn in areas without freezing temperatures (Fig. 2).

The prevalence of pregnancy did not show a different pattern for indoor and outdoor populations or according to the climate type for either species (Figs 5*b*, *d*, 6*b*, *d*).

Reproductive break

In all, 19% of all Norway rat populations studied and 41% of the house mouse populations studied showed an interruption in their breeding cycle. For both species, no urban and few rural populations showed breaks in the breeding cycle (Figs 7*a*, 8*a*). In sylvan environments, the occurrence of a reproductive break was more common (Figs 7*a*, 8*a*). This pattern was also observed in the CCA analysis for both species (Figs 1, 2). The occurrence of a reproductive break was positively associated with Axis 1 in the sylvan environment for the Norway rat (Fig. 1) and house mouse (Fig. 2).

Both indoor and outdoor populations of Norway rats showed a high frequency of continuous breeding (Fig. 7*b*), whereas the pattern for house mouse populations differed according to the

trapping location, with a high percentage of reproductive breaks occurring in outdoors populations (Fig. 8*b*). A break in the breeding cycle did not occur in Norway rat populations that inhabited localities without freezing temperatures and frost (Fig. 7*c*). Additionally, in warm temperate fully humid climates (both with hot or warm summers), where the greatest numbers of studies were concentrated, rodent populations tended to breed continuously (Figs 7*d*, 8*d*).

Litter size

The mean number of embryos per pregnant female of Norway rats was significantly higher in rural (mean = 9.64; s.d. = 1.69) than in sylvan (mean = 6.90; s.d. = 0.92; $F_{2,11}$ = 3.93, P = 0.05) environments. The mean number of embryos per pregnant female in urban areas did not differ from that in the other areas (mean = 9.14; s.d. = 1.22).

House mice did not show significant differences in the mean number of embryos among urban (mean = 5.92; s.d. = 0.75), rural (mean = 6.18; s.d. = 0.82) and sylvan (mean = 6.22; s.d. = 1.18; $F_{2,12}$ = 0.15, P = 0.86) environments. The mean number of embryos of both species did not differ between indoor (Norway rat: mean = 9.08; s.d. = 1.68; house mouse: mean = 5.60; s.d. = 0.46) and outdoor (Norway rat: mean = 8.68; s.d. = 1.79; house mouse: mean = 6.37; s.d. = 0.98) populations (Norway rat: $F_{1,12}$ = 0.29, P = 0.60; house mouse: $F_{1,13}$ = 2.71, P = 0.12).
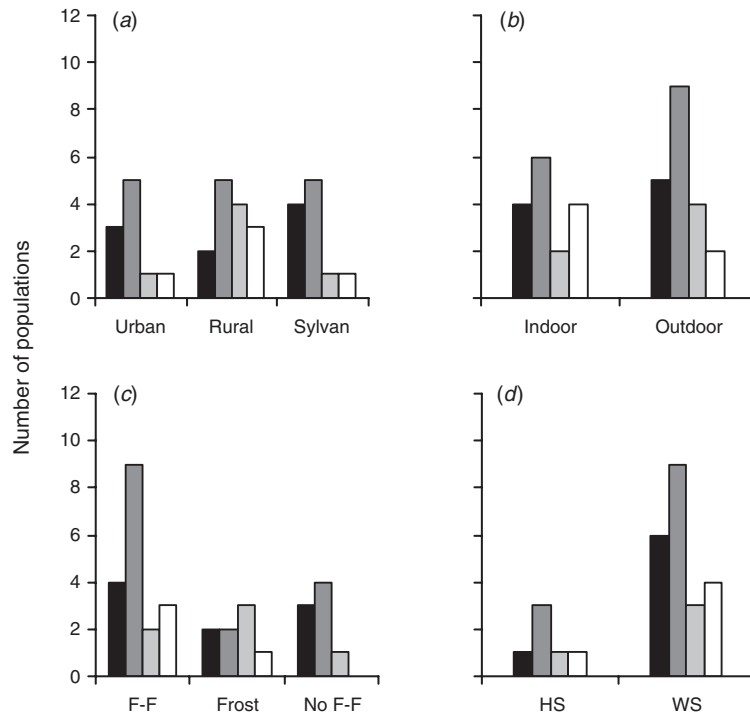
Fig. 6. Seasons of high prevalence of pregnancy of house mice according to (*a*) degree of anthropisation, (*b*) trapping location, (*c*) occurrence of freezing and frost in the studied locality and (*d*) climate type in the studied locality. Bar colours stand for spring (black), summer (dark grey), autumn (light grey) and winter (white). F-F, freezing and frost; HS, warm temperate climate fully humid with hot summer; WS, warm temperate climate fully humid with warm summer.

The mean number of embryos for Norway rats was significantly higher in regions without freezing temperatures and frost (mean = 7.80; s.d. = 1.73) than in regions where freezing temperatures and frost occur (mean = 9.48; s.d. = 0.95; $F_{1,10} = 6.68$, $P = 0.03$). Norway rat populations inhabiting regions where only frost occurs were excluded from the analysis because of the low sample size. The mean number of embryos of house mice did not differ among localities with freezing temperatures (mean = 6.64; s.d. = 0.84), freezing temperatures and frost (mean = 5.91; s.d. = 0.77) or without freezing temperatures and frost (mean = 5.93; s.d. = 1.10; $F_{2,12} = 0.89$, $P = 0.43$).

Discussion

Despite the fact that Norway rats and house mice have to exploit the energy recently obtained and they are limited to derive this energy among different traits, our results suggested that they have the capacity to modify their reproductive strategies according to the environment. A variety of responses in life-history traits were found in this research. The main feature that seems to determine the occurrence of different traits was the degree of anthropisation. The anthropisation of the environment changes the habitat for commensal rodents in two main aspects. First, it provides a more constant habitat through time compared with sylvan habitats. Second, some human activities provide food and refuge in quality and quantity that result in an improved habitat that can sustain a higher abundance of commensal rodents, in comparison to sylvan environments (Davis 1953). Therefore, we expected urban and rural populations of both species to have little or no changes in abundance and pregnancy prevalence throughout the year; however, these population parameters were not as stable as expected for the relatively more constant habitats.

Norway rats seemed more capable of changing their demographic characteristics in response to different environmental conditions than were house mice (Fig. 9), as was expected, probably because of their larger body size (Stearns 1983). The climate type, trapping location and the occurrence of freezing and frost were less critical in determining a particular life-history trait than was the anthropisation of the environment. However, it is worth noting that most ecological studies available for these species were conducted in warm temperate climates. Because of the disproportionate number of studies conducted in warm temperate climates, a comparison among all climate types was not possible.

Life-history traits directly influence reproduction and survival. Organisms have evolved many different ways of combining reproduction and survival to affect fitness (Stearns 1992). As Norway rats and house mice are potentially able to reproduce in nature in all seasons, the occurrence of a reproductive break in a given population must be the result of unfavourable conditions in a certain season (Calhoun 1963).
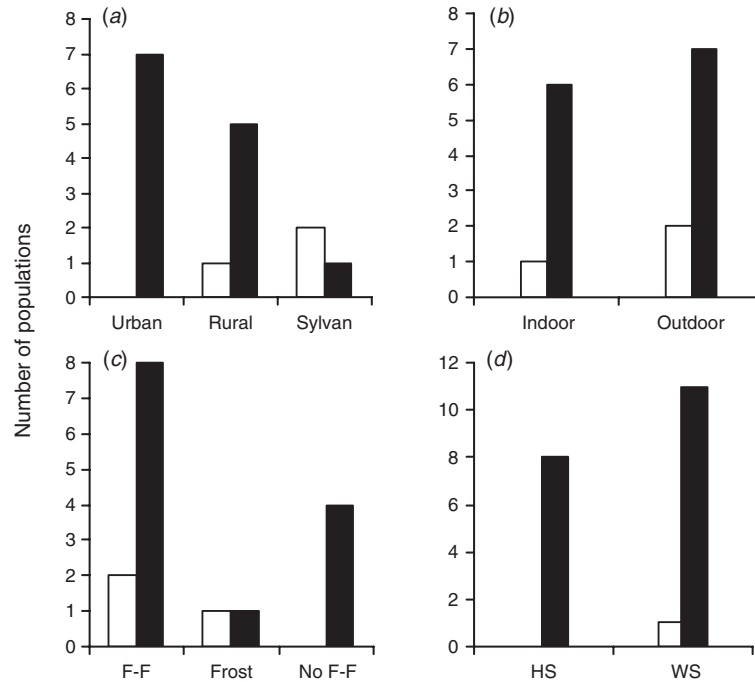
Fig. 7. Occurrence of reproductive break in Norway rats populations according to (*a*) degree of anthropisation, (*b*) trapping location, (*c*) occurrence of freezing and frost and (*d*) climate type. Bar colours stand for occurrence of reproductive break (white) and no reproductive break (black). F–F, freezing and frost; HS, warm temperate climate fully humid with hot summer; WS, warm temperate climate fully humid with warm summer.

Fig. 8. Occurrence of reproductive break in house mice populations according to (*a*) degree of anthropisation, (*b*) trapping location, (*c*) occurrence of freezing and frost and (*d*) climate type. Bar colours stand for occurrence of break in the breeding cycle (white) and continuous breeding (black). F–F, freezing and frost; HS, warm temperate climate fully humid with hot summer; WS, warm temperate climate fully humid with warm summer.
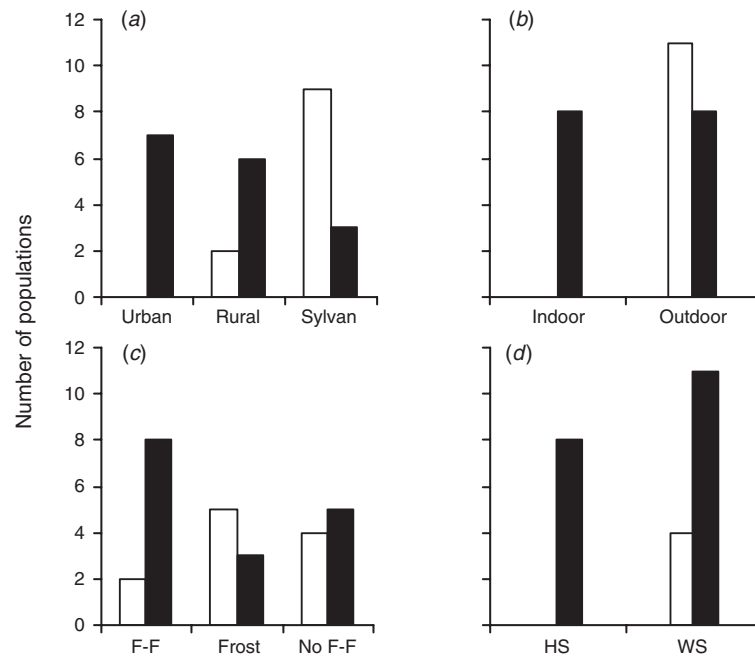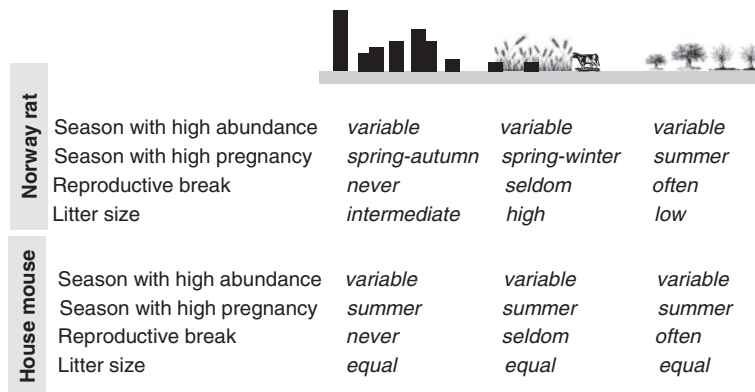
Norway rat			
Season with high abundance	*variable*	*variable*	*variable*
Season with high pregnancy	*spring-autumn*	*spring-winter*	*summer*
Reproductive break	*never*	*seldom*	*often*
Litter size	*intermediate*	*high*	*low*
House mouse			
Season with high abundance	*variable*	*variable*	*variable*
Season with high pregnancy	*summer*	*summer*	*summer*
Reproductive break	*never*	*seldom*	*often*
Litter size	*equal*	*equal*	*equal*

Fig. 9. Summary of life traits in urban, rural and sylvan environments (left to right) of the Norway rat and the house mouse.

Assuming this, the absence of a reproductive break in urban areas supports the idea that urban settings present the most favourable conditions for these species. Rural areas, with only a few cases of reproductive breaks, are second-most favourable, whereas sylvan environments represent the least favourable conditions. However, it should be noted that for Norway rats this last statement is based on only three populations living in sylvan environments. In addition, to be conclusive about the favourability of these environments, comparable abundances data are needed, because continuous reproduction throughout the year does not necessarily mean high abundance. The number of individuals actually alive in a given time will depend not only on the number of births but also on mortality and migration. Reproduction, mortality and migration, the three main factors that model a population, are influenced by the structural, climatic and nutritional characteristics of the habitat, as well as by predation and competition (Davis 1953). Therefore, urban areas would have the highest abundance of rodents only if mortality rates are similar to those in rural and sylvan settings, which is unlikely. A comparison of the absolute abundances was not possible in the present study because of the different methodologies employed in the diverse studies. In Buenos Aires, Argentina, Vadell *et al.* (2010) detected a higher abundance of these two species in a neighbourhood of the city, a highly anthropisated environment, than in parks in the same city. On the contrary, Gómez Villafañe *et al.* (2013) did not find differences in the abundances of Norway rats between urban and rural environments in the same region of Argentina. Also, although the comparison of patterns of mortality has been proposed as critical to understanding different life-history strategies among habitats (Stearns 1992), mortality data are very difficult to obtain and were unavailable in most reviewed papers.

Bronson (1979) proposed that commensal populations of house mice inhabiting man-made structures, where food is plentiful and stable and where the structure is complex, could endure at high densities for many months and even years. Although commensal environments seem to be more stable than sylvan ones for these rodent populations, the degree in which human activities compensate natural seasonal changes can vary greatly. The season with high abundance was variable for both Norway rats and house mice and a clear pattern was not detected with the environmental characteristics in this study. An exception was found for house mice where the season with high abundance was different according to the occurrence of freezing in the area. High abundances in summer observed in locations without freezing could be explained by the absence of an increased mortality during the cold months, resulting in the continuation of the increase phase of population growth to the summer months. A continuation of the increase phase is consistent with the high pregnancy prevalence observed in autumn in areas without freezing and in summer in areas with freezing and frost.

The variability detected in the season with high abundance could not be fully explained by the environmental characteristics examined in this study. As previously mentioned, the variability could be due to the fact that changes in abundance are a result of a complex interaction among reproduction, mortality, immigration and emigration (Davis 1953; Krebs 1978). The lack of information of the last three characteristics, but principally mortality, makes it difficult to develop a clear pattern of population dynamics. It is worth noting that almost every population included in the present study demonstrated changes in the abundance among seasons, indicating that even in the most anthropised environments these rodents responded to seasonal changes in their conditions and resources. These changes could be related to natural seasonal changes in temperature and photoperiod, or changes in anthropogenic factors such as poison application or food refuse availability, resulting in differences in mortality and/or reproduction (Krebs and Myers 1974; Aplin *et al.* 2003*a*).

Similarly, reproductive investment responds to population density, food supply and temperature (Stearns 1992). Several factors have been proposed to explain seasonal changes in reproduction. These include (1) seasonal variation in total caloric intake, (2) seasonal change in the availability of specific nutrients, (3) predictable changes in daylength; and (4) seasonal variation in the ambient temperature (Bronson 1979). Our results suggest that the prevalence of pregnancy in house mice and Norway rats show a seasonal pattern. Norway rat populations living in urban and rural environments had high pregnancy extending into autumn and winter, whereas in sylvan

areas, pregnancies were concentrated in summer. The differences observed in seasonality of pregnancy among urban, rural and sylvan environments seem to rule out the predictable changes in daylength as an important factor affecting reproduction in this species. The extreme situation of the reduction in the prevalence of pregnancy is the reproductive break. Because sylvan areas experience more thermal amplitude and adverse climate conditions, reproductive breaks occurred in most rat and mouse populations that inhabited sylvan areas. In rural areas, only a few populations showed a break in reproduction, and in urban areas, where environmental conditions are more constant and milder, no populations had reproductive breaks. It is important to note that, although reproductive breaks are uncommon in urban environments, these species do not have a constant reproductive investment throughout the year.

Similarly, litter size in small rodents is influenced by nutritional factors such as food quality and quantity and population densities, in addition to age and parity of females (Bomford 1987; Bronson and Perrigo 1987). Because age structure, parity, available food and population density are all characteristics that would generally differ among sylvan, rural and urban populations, the difference in litter size among environments detected only in Norway rats could be explained by any of these factors. The difference in litter size supports the previously mentioned idea that Norway rats are more capable of changing reproductive strategies in response to environmental conditions than house mice (Fig. 9).

Knowledge of life-history characteristics of a species is of key importance in predicting population responses to management, and thus should play an important role in management decisions (Williams *et al*. 2002). Under this approach, the best time to apply control measures would be when population abundance is low (Stenseth *et al*. 2001) and reproduction is absent or minimal, resulting in a slow recovery of the population. Hence, in sylvan and urban environments with warm temperate fully humid climates, control should be attempted during winter because low abundances and the absence or minimal reproduction in this season would make control measures more effective. In rural environments, the reproductive peaks found in spring for Norway rats and the absence of a seasonal pattern for house mice makes it difficult to find the best time for control. However, cold seasons seem to be the best time for control because reproductive breaks reported for these species took place in late autumn and winter months (Pearson 1963; Singleton *et al*. 2001; McGuire *et al*. 2006). Control measures of these species generally include trapping and poisoning, but they generally ignore demographic processes or ecological compensation mechanisms (Singleton *et al*. 1999). Our findings would therefore help in designing ecologically based pest management programs for Norway rats and house mice.

Acknowledgements

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