

Original Contribution

Long-Term Study of a Hantavirus Reservoir Population in an Urban Protected Area, Argentina

Emiliano Muschetto,¹ Gerardo Rubén Cueto,¹ Regino Cavia,¹ Paula Julieta Padula,² and Olga Virginia Suárez¹

¹Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Instituto de Ecología, Genética y Evolución de Buenos Aires, (IEGEB) UBA-CONICET, Universidad de Buenos Aires, Intendente Güiraldes 2160 (Ciudad Universitaria), PB II, 4to piso, Ciudad Autónoma de Buenos Aires, Argentina

²CONICET, Instituto Nacional de Enfermedades Infecciosas ANLIS “Dr. Carlos G. Malbrán”, Buenos Aires, Argentina

Abstract: Green spaces in urban areas can play a key role in protecting wildlife. However, the presence of wildlife in urban areas can lead to human health risks. Although the presence of the rodent species *Oligoryzomys flavescens* (hantavirus reservoir) has been recorded in cities of Argentina, its population dynamics in this type of habitat is still unknown. Here, we evaluated: (1) long-term spatial and temporal patterns of *O. flavescens* abundance and how these patterns were influenced by weather factors and (2) the seroprevalence of hantavirus and the identity of the viral lineage circulating in the population that inhabits the Costanera Sur Ecological Reserve, a protected area in the city of Buenos Aires. Genetic results confirmed that the pathogenic ANDES Central Lechiguanas virus is present in *O. flavescens* populations inhabiting this urban reserve. Abundance of *O. flavescens* showed interannual and seasonal fluctuations, with maximum values in winter and spring and minimum ones in summer and autumn. Summers with the highest abundances of *O. flavescens* were preceded by warmer winters, while winters with lower abundances were preceded by warmer summers. On the other hand, accumulated precipitations in the previous 6 months positively affected winter abundance. These results could help the authorities in charge of the green spaces of Buenos Aires to identify priority areas and times of the year for the implementation of preventive measures that minimize the contact of rodents with visitors. Such measures could be intensified when winters are warmer than normal, and summers are cooler and wetter than normal.

Keywords: Rodents, Seroprevalence, Population dynamics, Urban ecosystem, Meteorological variables, Control measures, GAM models

INTRODUCTION

Parks and other types of green spaces immersed in the urban matrix are providers of ecosystem services of crucial

importance for the promotion and conservation of biodiversity (Bolund and Hunhammar 1999; Shanahan et al. 2015). They are important suppliers of wildlife habitat in the urban landscape (Zhou and Chu 2012) and can play a key role in wildlife protection (Nielsen et al. 2014). In addition, they contribute to people’s well-being by encouraging recreation, reflection and social interaction

Correspondence to: Emiliano Muschetto, e-mail: emuschetto@hotmail.com

(Shanahan et al. 2015). However, despite these widely recognized benefits, the health risks associated with the presence of wildlife in urban areas have been explored in only a limited number of studies (Riley et al. 1998; Matuschka et al. 1996; Mahan and O'Connell 2005; Dizney et al. 2010; Chernousova 2013).

Rodents are intermediate hosts of numerous species of parasites and reservoirs of virus and bacteria that may spillover to humans and their domestic animals (Begon 2003; Meerburg et al. 2009). In urban ecosystems, most ecological and parasitological studies have focused on synanthropic rodent species (Cueto et al. 2008; Hancke et al. 2011; Himsworth et al. 2013; Froeschke and Matthee 2014; Cavia et al. 2015), although wild species are often present (Cavia et al. 2009; Chernousova 2013) and responsible for various emerging infectious diseases.

In Argentina, in the central-eastern part of the country, *O. flavescens* is the main reservoir of ANDES Central Lechiguanas virus (AND Cent Lec) (Suárez et al. 2003), the causal agent of hantavirus pulmonary syndrome, a severe disease often fatal in humans (Martínez et al. 2010). In addition to the AND Cent Lec, two more lineages have been found in this area, the ANDES Central Buenos Aires near the river regions and the ANDES Central Plata which was characterized from cases from both sides of the Río de la Plata River (Argentina and Uruguay). Nucleotide and amino acid identities among AND lineages ranged from 76.5 to 86.6% and 91.9 to 96.9%, respectively (Padula et al. 2000a). Studies on populations of *O. flavescens* have been conducted in natural environments (Gómez Villafaña et al. 2012; Vadell and Gómez Villafaña 2016; Maroli et al. 2018) and agricultural ecosystems (Mills et al. 1991; Busch and Kravetz 1992; Suárez and Bonaventura 2001; Bonaventura et al. 2003). Although the occurrence of this species was reported in cities of Argentina (Gómez et al. 2008; Cavia et al. 2009), there is a lack of data on their population dynamics in urban habitats, as well as the influence of environmental factors on their abundance is unknown. Ecological studies that contribute to the understanding of the factors and mechanisms responsible for population fluctuations can help to predict how the population may respond to changes in the environment and aid in developing policies and practices that may allow reducing the likelihood of associated zoonotic diseases.

In the city of Buenos Aires, *O. flavescens* have been recorded in large green spaces (surface areas over 25 ha) located in the basin of the Río de la Plata and Riachuelo

river, the two rivers that surround the city (Cavia et al. 2009). Among these green spaces, the presence of this species is particularly important in the Costanera Sur Ecological Reserve, a protected area that, because of its location in the urban matrix and its large area (350 ha), receives between 10,000 and 30,000 visitors every weekend, who carry out various activities including, recreation, sports (mainly walking and cycling), relaxation, biological research, photographic safaris, etc. The general objective of this work was to study the population dynamics of this species in order to obtain information that may help in the design of measures aimed to reduce the health risk to the reserve visitors. To this end, we evaluated (1) the spatial and temporal variation in abundance of *O. flavescens* over 10 years; (2) the effect of weather factors on abundance; and (3) the seroprevalence of hantavirus and the identity of the viral lineage circulating in the population.

MATERIALS AND METHODS

Study Area

Fieldwork was conducted at the Costanera Sur Ecological Reserve (34°36'S, 58°27'W), Buenos Aires, Argentina. This reserve is a coastal protected area, next to the Río de la Plata River, located a few blocks away from the heart of the city and government buildings, and built by gaining land to the river using demolition debris and river silts (Marcomini and López 2004). The reserve encompasses 350 ha, with a mean annual temperature of 17.6°C, and mean annual precipitation of 1062 mm. The reserve contains a complex mosaic of habitats including tall grasslands, humid prairies and shallow floodplain lakes mixed with small woods of *Tessaria integrifolia* and *Salix humboldtiana*, and coastal bushy patches dominated by *Ricinus communis*, *Baccharis salicifolia* and *Erythrina crista-galli*. The community of small rodents (species < 500 g) in this area is dominated by the sigmodontines *O. flavescens*, *Deltamys kempi* and *Scapteromys aquaticus*, the caviid *Cavia aperea* and the non-native murines *Mus musculus* and *Rattus norvegicus* (Teta et al. 2007). The study was conducted in three different habitats: 1) tall grasslands (*Cortaderia selloana*); 2) forest of *T. integrifolia*, *Ligustrum lucidum* and *Ligustrum sinense*; and 3) coastal bushy areas (locally known as “matorrales ribereños”), dominated by the exotic *R. communis* and the native species *B. salicifolia* and *E. crista-galli*.

Rodent Survey

Rodent trapping surveys were carried out in two phases (Table 1). In the first phase, eight capture sessions were conducted seasonally during two consecutive periods: the first one included trappings in April (middle autumn), June (early winter), October 2004 (middle spring) and February 2005 (late summer), while the second included trappings in May (late autumn), August (late winter), November (late spring) 2005 and February 2006 (late summer), in the three habitats mentioned above. In this phase, we used two or three transects, spaced at 150 m, of 20 Sherman live traps in each habitat during each trapping survey, with a capture effort of 540 trap-nights and 360 trap-nights in each trapping survey for the first and second period, respectively. We decided to remove at random one transect per habitat due to logistic and safety reasons. Transects were randomly assigned once at the beginning of the first capture session in April 2004 and then repeated until the last sampling in February 2006. Traps were active during three consecutive nights.

In the second phase, 25 capture sessions were conducted in edge habitats (coastal bushy areas, roadsides and edges of ponds) throughout spring 2008 to winter 2014. In this phase, the number of transects ranged from one to six transects per sampling ($N = 99$, Table 1). Transects were randomized in each capture session, although some were repeated between samplings due to the limitation of available space to arrange them. The length of transects and the distance between them varied in some samplings, but

the minimum distance between transects was always 150 m. The trapping effort varied between 135 and 480 traps-nights according to each sampling, and traps were active during four consecutive nights. In both phases, traps were baited with peanut butter and cow fat and the distance between neighboring traps was 10 m.

Captured animals were marked with a numbered ear tag for individual identification and then released at the point of capture. Animals were treated in accordance with the guidelines of the Sociedad Argentina para el Estudio de los Mamíferos (Giannoni et al. 2003).

We used trap success (TS) as an index of *O. flavescens* abundance. Trap success was calculated for each season using the formula $TS = [\text{number of captures}/(\text{number of traps} \times \text{number of nights}) - \frac{1}{2} a] \times 100$, where a is the number of shut traps without captures (Seber 1973).

Weather data including monthly precipitation (mm), days per month with precipitation, and minimum and maximum temperatures ($^{\circ}\text{C}$), were retrieved from the Buenos Aires bureau of Statistics and Censuses (<https://www.estadisticaciudad.gob.ar/eyc/?cat=128>).

Hantavirus Detection

Captured rodents were anesthetized before taking blood samples from the retroorbital capillary plexus. Animals recaptured a second, third or fourth time during a 4-day trapping event were not bled again. Blood samples were immediately carried to the National Microbiology Institute Dr. Carlos Malbrán to be screened for Andes (AND) virus-specific immunoglobulin G (IgG) antibodies using enzyme-linked immunosorbent assays (ELISA), as previously described by Padula et al. (2000b). Meanwhile in the field, our team waited for approximately 2 h the results of this test, and then all antibody-positive animals were sacrificed and lung samples were preserved at -30°C to be transported to the laboratory where they were stored at -80°C until tested. Seronegative individuals were released at the point of capture. Total RNA was extracted from lung tissues of seropositive rodents. Reverse transcription (RT) procedure and hemi-nested polymerase chain reaction (PCR) were performed to amplify a partial fragment from hantavirus genome (Nichol et al. 1993). The S segment (N protein 396 nts) and the M segment (Gn protein 368 nts) were amplified and sequenced for comparisons with AND Cent viral RNA from previous human cases and rodents captured in the study area (up to 100 km away). Multiple nucleotide and amino sequence alignments were done

Table 1. Number of Seasonal Trapping Surveys of *O. flavescens* Conducted from Autumn 2004 Until Summer 2006 (Phase 1) and from Spring 2008 Until Winter 2014 (phase 2) in Costanera Sur Ecological Reserve, city of Buenos Aires, Argentina. The Total Number of Transects per Season is Reported in Parentheses.

Year	Summer	Autumn	Winter	Spring
2004	–	1 (3)	1 (3)	1 (3)
2005	1 (3)	1 (2)	1 (2)	1 (2)
2006	1 (2)	–	–	–
2008	–	–	–	3 (5)
2009	1 (3)	1 (4)	1 (5)	1 (3)
2010	1 (2)	1 (3)	1 (3)	1 (3)
2011	1 (3)	1 (5)	1 (5)	1 (5)
2012	1 (3)	1 (5)	1 (5)	1 (4)
2013	1 (4)	1 (4)	1 (4)	1 (6)
2014	1 (6)	1 (5)	1 (4)	–

using MEGA 5 software package (<http://www.megasoftware.net>).

Seroprevalence is reported as the proportion of individuals with hantavirus antibodies (seropositives) over the total number of blood samples analyzed.

Statistical Analysis

To analyze what factors influenced abundance of *O. flavescens* for the first phase, we fitted a generalized linear mixed-effect model (GLMM) with Poisson error distribution using the *lme4* package (Bates 2010) for R software (R Development Core Team 2013). The response variable was the number of different individuals of *O. flavescens* in each trap line. Habitat type (coastal bushy areas, grassland and forest), season (spring, summer, autumn and winter), period (2004–2005 and 2005–2006), weather variables and their interactions were included as explanatory variables in the GLMM. Monthly rainfall and mean, minimum and maximum temperatures during the month before each trapping survey were considered. These variables were also used with time lags of 3 and 6 months. Also, the accumulated precipitations in the last 3 and 6 months prior to each sampling were analyzed. Since abundance was recorded on the same transects every season, a random factor (transect) was included. The DGC multiple comparison test (Di Rienzo et al. 2002) was used to analyze differences between factor levels when necessary.

Intra- and interannual changes in the estimated abundance of *O. flavescens* (trend and seasonality) in edge habitats over the entire study period were evaluated through generalized additive mixed models (GAMM) with a Poisson distribution, using data from for the first and the second phases (autumn 2004 to winter 2014). We used GAMM models because they accommodate smooth, non-linear changes over time in population size (Fewster et al. 2000). Since the number of animals that were caught depended on trap-effort and it was not constant in each trap line, we used the logarithm of this value as Poisson offset according to Zuur et al. (2009). Two GAMM models were tested. A base model tested *O. flavescens* abundance versus a smoothed function of time: monthly variation with 12 levels (intra-annual) and year variation (interannual), whereas the second one included seasons, weather variables and their interactions as explanatory variables. The highest order interactions and factors were removed sequentially until we reached the model with the lowest AIC. A random factor (transect) was included with temporally auto-cor-

related errors with a separate fit for each transect. GAMMs were conducted using the *mgcv* package (Wood 2011) for R (R Development Core Team 2013).

RESULTS

A total of 233 individuals of *O. flavescens* were captured with a trapping effort of 12,754 trap-nights. Hantavirus antibodies were detected in 6% (14/233) of the captured *O. flavescens* individuals. All seropositive individuals were captured during the reproductive season (spring–summer, Table 2, Fig. 1a, b). The viral genome could be detected and amplified, in one of 14 seropositive individuals. A comparison of the 396 nt generated from the N–S segment showed high nucleotide identity (97.28–100%) with AND Cent Lec virus obtained from human cases occurred in the study area with an amino acid identity of (100%). The nucleotide and amino acid similarity with rodent AND Cent Lec virus was 95.39 and 99.18%, respectively [Lechiguanas (LEC) virus strain, Af028022]. Also, a comparison of the 368 nt generated from the Gn–M segment showed high nucleotide identity (97.2–99.24%), with an amino acid identity of 100%. The nucleotide and amino acid similarity of this segment with rodent AND Cent Lec virus was 98.73 and 100%, respectively.

Table 2. Capture Data and Characteristics of 14 *O. flavescens* Individuals Serologically Positive for ANDES Central Lechiguanas Virus in Costanera Sur Ecological Reserve, city of Buenos Aires, Argentina.

Year	Season	Sex	Reproductive status	Body mass (g)
2004	Spring	Male	Scrotal testes	30
2004	Spring	Male	Scrotal testes	35
2005	Spring	Male	Scrotal testes	24
2005	Spring	Female	Opened vagina	22
2005	Spring	Male	Scrotal testes	20
2006	Summer	Male	Scrotal testes	27
2008	Spring	Male	Scrotal testes	15
2008	Spring	Male	Scrotal testes	15
2008	Spring	Male	Scrotal testes	23
2008	Spring	Male	Scrotal testes	20
2008	Spring	Male	Scrotal testes	15
2008	Spring	Male	Scrotal testes	16
2013	Spring	Male	Scrotal testes	17
2013	Spring	Male	Scrotal testes	34

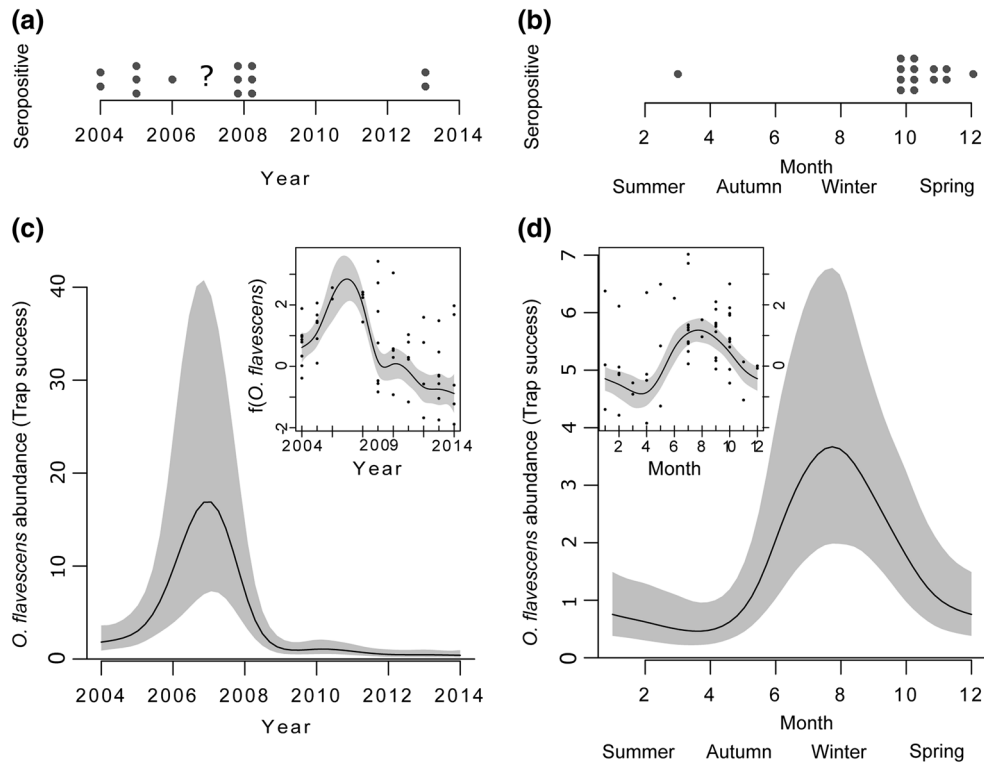


Figure 1. Seropositive individuals (represented as dots) by years (a) or months (b) and inter- (c) and intra-annual (d) trends in *O. flavescens* abundance [inset: as a function of the logarithm of *O. flavescens* abundance, $f(O. flavescens)$] from autumn 2004 to spring 2014 (phase 1 and phase 2) in Costanera Sur Ecological Reserve, city of Buenos Aires, Argentina. Smooth functions (solid lines) for a typical month (May) or year (2011) with 95% credible region (gray area) estimated for (c) interannual and (d) intra-annual trends. The question mark shows the lack of data during 2007.

Population Dynamics of *Oligoryzomys flavescens*

In the first phase of the study (2004–2006), *O. flavescens* showed the highest abundances in winter and spring (Mean \pm SE = 1.63 ± 0.41 and 2.21 ± 0.62 , respectively) and the lowest ones in summer and autumn (0.51 ± 0.13 and 0.60 ± 0.21 , respectively, likelihood ratio test (LRT) = 31.22, $df = 3$, $P < 0.001$). Seasonal pattern was similar for the three habitats and in both study periods ($P > 0.05$). The coastal bushy areas showed the highest abundance of *O. flavescens* (2.33 ± 0.35), followed by the tall grassland (0.95 ± 0.21) and the forest (0.43 ± 0.13 , (LRT) = 14.02, $df = 2$, $P < 0.001$). Abundance differences between habitats were maintained in both study periods ($P > 0.05$). *Oligoryzomys flavescens* abundance was influenced by the difference, compared to normal values, of accumulated rains in the 3 months prior to the sampling period (LRT) = 14.46, $df = 1$, $P < 0.001$). This variable was positively associated with *O. flavescens* abundance and explained both the increase in abundance recorded in winter 2005 (when the rainfall during the previous autumn

was 183 mm higher than normal) and the subsequent decrease the following spring due to a drought period recorded during the previous winter (189 mm lower than normal, Fig. 2).

Regarding the intra- and interannual variations in *O. flavescens* abundance in edge habitats throughout the entire study period (phase 1 and 2), we observed an interannual fluctuation ($F = 20.93$, estimated degrees of freedom [edf] = 6.87, $P < 0.01$) with maximum values between 2006 and 2008 and minimum values between 2012 and 2014 (Fig. 1c). In turn, intra-annual abundance cycles were observed ($F = 6.33$, edf = 3.92, $P < 0.01$), with maximum values between June and September (winter in the Southern Hemisphere) and minimum between March and May (late summer and mid-autumn) (Fig. 1d). These intra- and interannual variations represented 47% (adjusted R^2) of *O. flavescens* abundance fluctuations.

When weather variables were included, the highest abundances of *O. flavescens* in summers occurred when they were preceded by warmer winters (higher values of minimum temperature than normal, $F = 9.22$, edf = 1,

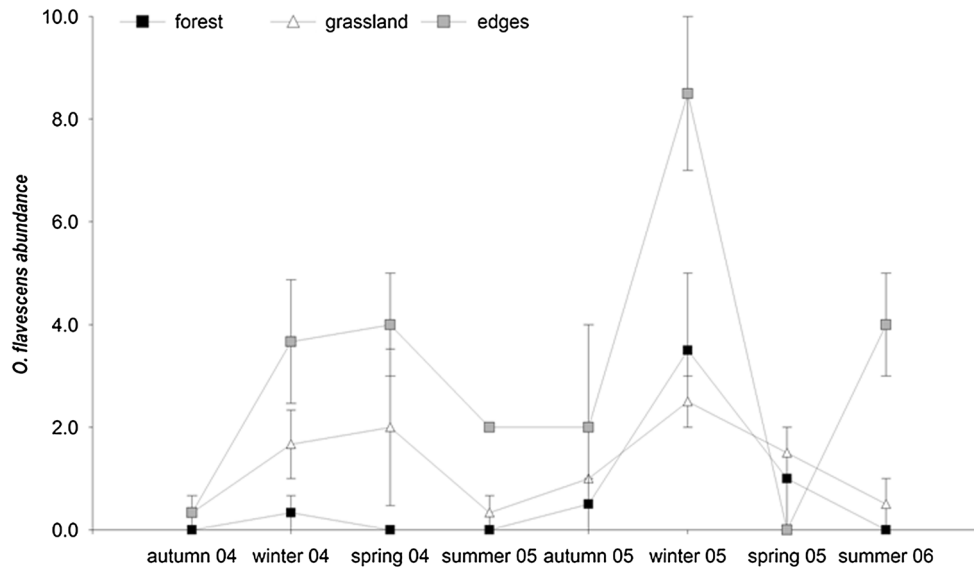


Figure 2. Abundance of *O. flavescens* (trap success \pm SE) from autumn 2004 to summer 2006 (first phase) according to habitat type in Costanera Sur Ecological Reserve, city of Buenos Aires, Argentina.

$P < 0.01$, Fig. 3). In addition, abundances recorded in winters were lower than normal when they were preceded by warmer summers ($F = 6.10$, $edf = 1$, $P = 0.01$, Fig. 3). *Oligoryzomys flavescens* abundances were greater during winters that presented the highest accumulated rainfall in the previous 6 months ($F = 13.27$, $edf = 1$, $P < 0.01$, Fig. 3), and lower in springs that were preceded by wet periods (with higher accumulated rainfall in the previous 6 months, $F = 10.79$, $edf = 1$, $P < 0.01$, Fig. 3). In addition, there was a decrease in the abundance of *O. flavescens* over the 10 years studied ($F = 76.28$, $edf = 1$, $P < 0.01$, Fig. 3) that could not be explained by the climatic variables analyzed. All these factors affected *O. flavescens* abundance in a linear way (the better smooth function for all explanatory variables was the linear one). By incorporating the seasons and weather variables into the model, we were able to explain 60% (adjusted R^2) of the fluctuations in *O. flavescens* abundance.

DISCUSSION

Abundance of *O. flavescens* in an urban reserve in the city of Buenos Aires showed interannual and seasonal fluctuations with maximum values in winter and spring and minimum values in summer and autumn. In addition to seasonal differences, these fluctuations were associated with variations in weather conditions that partially explained interannual variations. Moreover, there was a decrease in

the abundance of this rodent throughout the study period that could not be explained through the weather variables analyzed. *Oligoryzomys flavescens* was more abundant in the edge habitat corresponding to the riparian thicket within the reserve. On the other hand, genetic results confirmed that the pathogenic AND Cent Lec virus is present in *O. flavescens* populations inhabiting this urban reserve. The high virus similarity with those obtained from human cases registered in localities as far as 100 km away from the study area suggests the existence of connectivity between the populations of *O. flavescens* from this urban reserve and the surrounding ones. This could be explained by the passive transport of individuals through the rivers (see below).

We found seasonal abundance variations in *O. flavescens*, pattern which is commonly observed in small rodents (Singleton et al. 2001; Stenseth et al. 2003; Andreo et al. 2009; Vadell et al. 2014). In our study, maximum abundance was recorded during winter and spring, whereas this species in a near protected area (Maroli et al. 2018) as well as other species of sigmodontine rodents typical of agricultural ecosystems in central Argentina (i.e., *Akodon azarae* and *Calomys laucha*) reach their highest abundances before the beginning of frosts during late autumn and winter (Crespo 1966; Zuleta et al. 1988; Mills et al. 1991; Busch and Kravetz 1992; Andreo et al. 2009). This lag could be due to the location of the study area in a coastal environment in close proximity to the city of Buenos Aires, which would temper climatic conditions and generate a microclimate where frosts are rare. As a consequence, the

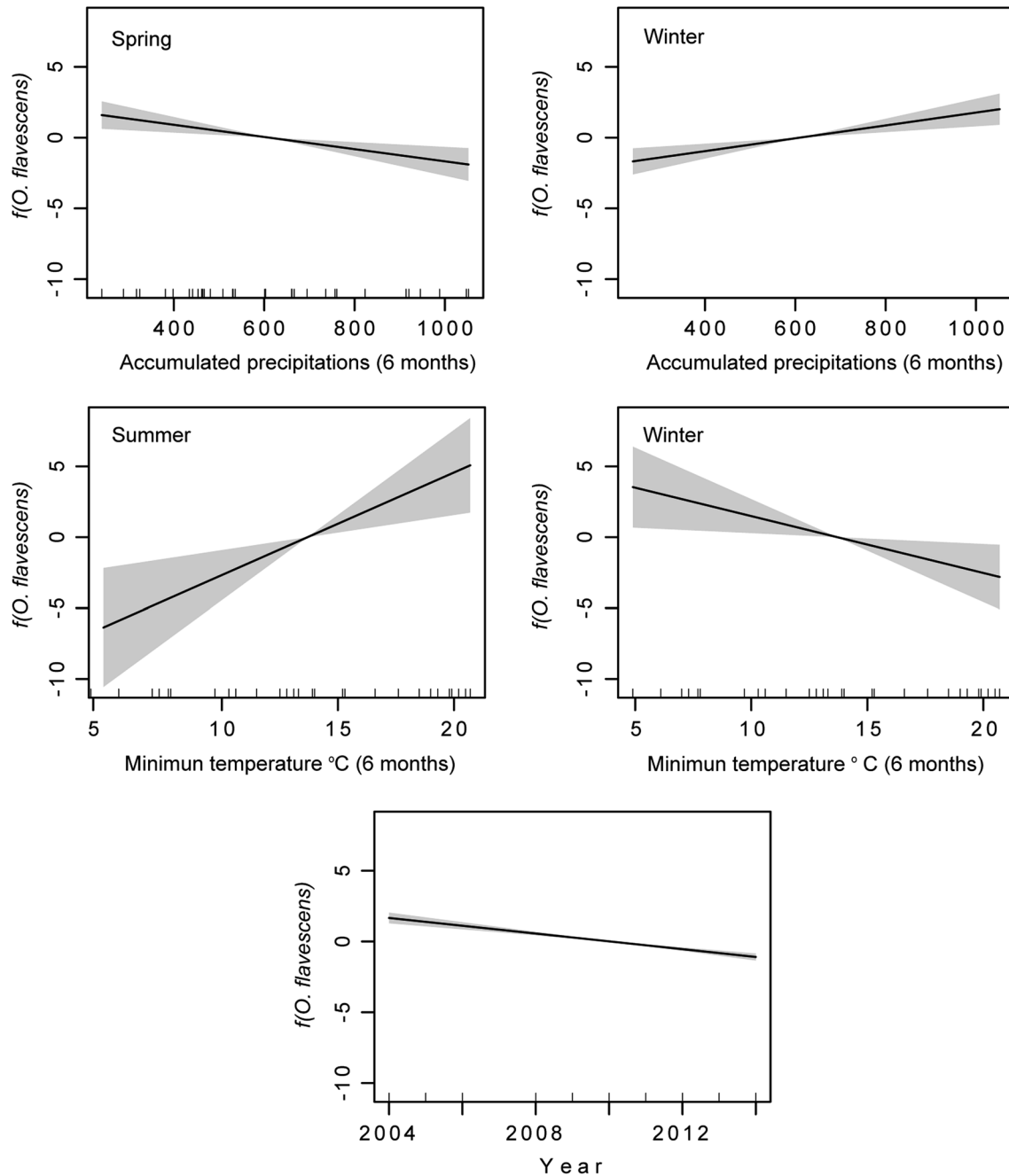


Figure 3. Seasonal abundance of *O. flavescens* [expressed as a function of the logarithm of *O. flavescens* abundance, $f(O. flavescens)$] from autumn 2004 to spring 2014 (phase 1 and phase 2) according to weather variables in Costanera Sur Ecological Reserve, city of Buenos Aires, Argentina. Only the significant relationships are reported. The figure shows the adjusted values proposed by the model for a typical transect with 95% credible region (gray area).

main cause of mortality would not be due to winter frosts, and the decline in population abundance would be due to death of overwintering individuals during late spring and summer. This would generate a maximum abundance peak during winter and spring, when individuals born in two

successive reproductive seasons are still present simultaneously.

The interannual variation in the abundance of *O. flavescens* was partially explained by the minimum temperature and the precipitations recorded with a delay period of

two seasons. The minimum temperature recorded during winter and summer would be affecting the abundance of *O. flavescens* in the summer and the following winter, respectively. Thus, when more benevolent winters or summers occur (higher minimum temperature or lower minimum temperature, respectively), the abundance of *O. flavescens* in the next summer or winter would be higher. This would indicate that for this species in these urban ecosystems there are two critical seasons. In general, for small rodents in temperate climates, it has been described that the winter season represents the critical time for their survival, with increased mortality associated with winter frosts (Crespo 1966; Garsd and Howard 1981, 1982; Mills et al. 1991; Calisher et al. 2005). The low efficiency in thermoregulation as a consequence of the small body size of sigmodontine rodents would make them vulnerable to low temperatures in the cold seasons (Crespo 1966; Andreo et al. 2009) but also to high temperatures in the warm seasons. Regarding the decreasing trend in the abundance that could not be explained by the weather variables, it is possible that it was related to cycles of abundance that exceed the study period and/or to local factors and management decisions that occur within the reserve and/or inbreeding depression due to isolation. Accidental fires and intentional floods on the flooded plains and lakes occurred during the study period, which would have an amplified effect on inbreeding depression of these rodents as a consequence of some degree of isolation in which they would be in this urban reserve.

The precipitations recorded in the previous months would also have an important role in the observed fluctuations. The effect of rainfall in previous seasons has been widely studied in many species of rodents, both at a seasonal (Ernest et al. 2000; Stenseth et al. 2003; Calisher et al. 2005; Madsen et al. 2006) and at an interannual scale (Meserve et al. 2003; Stenseth et al. 2003; Holmgren et al. 2006). In a rural area of central Argentina, Andreo et al. (2009) described a delay period of one or two seasons in the response of population densities of *A. azarae* to precipitation. The delay may be due to the relationship between vegetation cover and precipitation either during the same season or during the previous season (Ernest et al. 2000), which increases the plant biomass and consequently increases food availability and shelter for rodents. In addition, the greater abundance observed during the winters preceded by rainier summers can be the consequence of the influence of the flooding pulses occurred upstream in the delta of the Río de la Plata River. It is likely that during these periods, which usually occur during

the summer, immigration of individuals that may travel on floating plants (passive transport) may increase (Chiappero et al. 1997).

Our results suggest that individuals of *O. flavescens* would make a differential use of the studied habitats. These rodents showed greater preference for habitats that presented a tree-shrub stratum, such as the riparian thicket, and, to a lesser extent, for grasslands, than for those with low vegetation cover, such as the forest understory. Similar results have been observed by other authors in another natural protected area (Maroli et al. 2015; Vadell et al. 2016). This preference would be based on the fact that their long tail and hind legs are possible adaptations to scansorial habits and would favor their life in habitats where the tree-shrub stratum predominates (Massoia and Fornes 1965; Udrizar Sauthier et al. 2010; Maroli et al. 2015). In general, in natural reserves, the habitats that receive a greater number of visitors are those that are close to water courses (rivers, streams, etc.) because areas for recreation, rest and in some cases camping are usually available. Therefore, the preference of *O. flavescens* for these habitats in the Costanera Sur Ecological Reserve could increase the risk of hantavirus pulmonary syndrome transmission as a consequence of the greater probability of rodent-person contact allowed by such habitats.

The fact that almost all seropositive individuals were males is in agreement with previous studies in sigmodontine rodents that suggest a horizontal virus transmission mechanism where adult males are more likely to become infected (Glass et al. 1998; Douglass et al. 2007; Vadell et al. 2011). This is probably because aggressive contacts among males increase the probability of transmission (Padula et al. 2004). In addition, as was also observed by Mills et al. (2007), seropositive *O. flavescens* individuals occurred during the reproductive season (spring–summer), when aggressive interactions are supposed to increase. By last, the fact that 7 of 14 seropositive individuals were clustered during the period of high abundance registered between 2006 and 2008 could be suggesting a positive relation between abundance and number of infected individuals, and therefore an increased risk for transmission to humans (Maroli et al. 2018). The opposite relationship was found for this species in Argentina (Mills et al. 2007) and other sigmodontine rodents in North America (Abbott et al. 1999; Douglass et al. 2001). However, it is necessary to point out that sample sizes of antibody-positive *O. flavescens* in this study were small, and additional studies will be required to confirm these observed trends.

In general, natural reserves, particularly those within an urban matrix, have the main objective of promoting both human well-being and community awareness of the importance of regional biodiversity conservation. In this context, the dilemma arises as to whether or not management strategies should be applied to control native species that inhabit natural reserves, because the species may represent a risk to the health of visitors and local workers. However, beyond the decisions, information on the ecology of native species is indispensable for their management (Singleton et al. 1999). This requires long-term studies that can provide information that contributes to the knowledge of the ecology of these species and are useful for decision makers in the government.

In addition to contributing to partially filling the gap of existing knowledge regarding the ecology of *O. flavescens*, these results will also contribute to the understanding of what causes population fluctuations in large green spaces present in the urban landscape of the city of Buenos Aires. These results can be used to determine when to take preventive measures. For example, preventive measures may be maximized when warmer than normal winters and cooler and wetter than normal summers occur. These measures could include the closure of certain areas to the public, the generation of a buffer zone between recreational areas and the surrounding vegetation to prevent rodents from approaching people, or removal of individuals that are positive for hantavirus. Some of these management measures have been proposed by Vadell et al. (2016) for the control of *Oligoryzomys nigripes* in another natural reserve in Argentina. We consider that the implementation of strategic prevention measures would at present minimize the likelihood of rodent-person contact and thus the transmission of diseases to visitors of this urban reserve. These measures would not affect the conservation of this species or others related through the food web (raptors, opossums, etc.).

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REFERENCES

- Abbott KD, Ksiazek TG, Mills JN (1999) Long-term hantavirus persistence in rodent populations in central Arizona. *Emerging Infectious Diseases* 5:102–112
- Andreo V, Provencal C, Scavuzzo M, Lamfri M, Polop J (2009) Environmental factors and population fluctuations of *Akodon azarae* (Muridae: Sigmodontinae) in central Argentina. *Austral Ecology* 34:132–142
- Bates DM (2010) *lme4: Mixed-effects modeling with R*. <http://lme4.r-forge.r-project.org/book>. Last Accessed August 2016.
- Begon M (2003) Disease: health effects on humans, population effects on rodents. In: *Rats, mice and people: rodent biology and management*, Grant R, Singleton LA, Hinds C, Krebs J, Spratt DM (editors), Canberra: Australian Center for International Agricultural Research, Monograph No. 96, pp 13–19.
- Bolund P, Hunhammar S (1999) Ecosystem services in urban areas. *Ecological Economics* 29:293–301
- Bonaventura SM, Pancotto V, Madanes N, Vicari R (2003) Microhabitat use and density of sigmodontine rodents in *Spartina densiflora* freshwater marshes, Argentina. *Mammalia* 67:367–378
- Busch M, Kravetz FO (1992) Competitive interactions among rodents (*Akodon azarae*, *Calomys laucha*, *C. musculus* and *O. flavescens*) in a two-habitat system. I. Spatial and numerical relationships. *Mammalia* 56:45–56
- Calisher CH, Mills JN, Sweeney WP, et al. (2005) Population dynamics of a diverse rodent assemblage in mixed grass-shrub habitat, Southeastern Colorado, 1995–2000. *Journal of Wildlife Diseases* 41:12–28
- Cavia R, Cueto GR, Suárez OV (2009) Changes in rodent communities according to the landscape structure in an urban ecosystem. *Landscape and Urban Planning* 90:11–19
- Cavia R, Muschetto E, Cueto GR, Suárez OV (2015) Commensal rodents in the city of Buenos Aires: A temporal, spatial, and environmental analysis at the whole city level. *EcoHealth* 12:468–479
- Chernousova N (2013) Role of wildlife small rodents of the city parks and park-forests in helminth epizootology by the example of *Apodemus Uralensis* Pallas, 1811. *Beiträge zur Jagd-und Wildforschung* 38:341–347
- Chiappero MB, Caldero GE, Gardenal CN (1997) *Oligoryzomys flavescens* (Rodentia, Muridae): Gene flow among populations from central-eastern Argentina. *Genetica* 101:105–113
- Crespo JA (1966) Ecología de una comunidad de roedores silvestres en el Partido de Rojas, Provincia de Buenos Aires. *Revista del Museo Argentino de Ciencias Naturales* 1:73–134
- Cueto GR, Cavia R, Bellomo C, Padula PJ, Suárez OV (2008) Prevalence of hantavirus infection in wild *Rattus norvegicus* and *R. rattus* populations of Buenos Aires City, Argentina. *Tropical Medicine and International Health* 13:46–51
- Di Rienzo JA, Guzmán AW, Casanoves F (2002) A multiple comparisons method based on the distribution of the root node distance of a binary tree. *Journal of Agricultural, Biological, and Environmental Statistics* 7:129–142
- Dizney L, Philip DJ, Ruedas LA (2010) Natural history of Sin Nombre virus infection in deer mice in urban parks in Oregon. *Journal of Wildlife Diseases* 46:433–441
- Douglass RJ, Calisher CH, Wagoner KD, Mills JN (2007) Sin Nombre virus infection of deer mice in Montana: characteristics

- of newly infected mice, incidence, and temporal pattern of infection. *Journal of Wildlife Diseases* 43:12–22
- Douglass RJ, Wilson T, Semmens WJ, Zanto SN, Bond CW, Van Horn RC, Mills JN (2001) Longitudinal studies of Sin Nombre virus in deer mouse-dominated ecosystems of Montana. *The American Journal of Tropical Medicine and Hygiene* 65:33–41
- Ernest SKM, Brown JH, Parmenter RR (2000) Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88:470–482
- Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD (2000) Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81:1970–1984
- Froeschke G, Matthee S (2014) Landscape characteristics influence helminth infestations in a peri-domestic rodent-implications for possible zoonotic disease. *Parasite Vector* 7:393
- Garsd A, Howard WE (1981) A 19-year study of microtine population fluctuations using time-series analysis. *Ecology* 62:930–937
- Garsd A, Howard WE (1982) Microtine population fluctuations: an ecosystem approach based on time-series analysis. *Journal of Animal Ecology* 51:225–234
- Giannoni SM, Mera Sierra R, Brengio S, Jiménez Baigorria L (2003) Guía para el uso de animales en investigaciones de campo y en cautiverio, Comisión de Ética de la Sociedad Argentina para el Estudio de los Mamíferos. <http://www.sarem.org.ar/legislacion/>. Last Accessed March 2015.
- Glass GE, Livingstone W, Mills JN, Hlady WG, Fine JB, Biggler W, Coke T, Frazier D, Atherley S, Rollin PE, Ksiazek TG, Peters CJ, Childs JE (1998) Black Creek Canal virus infection in *Sigmodon hispidus* in southern Florida. *The American Journal of Tropical Medicine and Hygiene* 59:699–703.
- Gómez MD, Provenzal MC, Polop JJ (2008) Effects of interest-specific competition on *Mus musculus* in an urban area. *Journal of Pest Science* 81:235–240
- Gómez Villafañe IE, Expósito Y, San Martín Á, Picca P, Busch M (2012) Rodent diversity and habitat use in a protected area of Buenos Aires province, Argentina. *Revista Mexicana de Biodiversidad* 83:762–771
- Hancke D, Navone G, Suárez O (2011) Endoparasite community of *Rattus norvegicus* captured in a shantytown of Buenos Aires City, Argentina. *Helminthologia* 48:167–173
- Holmgren M, Stapp P, Dickman CR, et al. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment* 4:87–95
- Himsworth CG, Parsons KL, Jardine C, Patrick DM (2013) Rats, cities, people, and pathogens: a systematic review and narrative synthesis of literature regarding the ecology of rat-associated zoonoses in urban centers. *Vector-Borne and Zoonotic Diseases* 13:349–359
- Madsen T, Ujvari B, Shine R, Olsson M (2006) Rain, rats and pythons: Climate-driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* 31:30–37
- Mahan CG, O'Connell TJ (2005) Small mammal use of suburban and urban parks in central Pennsylvania. *Northeastern Naturalist* 12:307–314
- Marcomini SC, López RA (2004) Generación de nuevos ecosistemas litorales por albardones de relleno en la costa de la ciudad de Buenos Aires. *Revista de la Asociación Geológica Argentina* 59:261–272
- Maroli M, Vadell MV, Iglesias A, Padula PJ, Gómez Villafañe IE (2015) Daily movements and microhabitat selection of hantavirus reservoirs and other sigmodontinae rodent species that inhabit a protected natural area of Argentina. *Ecohealth* 12(3):421–431
- Maroli M, Vadell MV, Padula PJ, Gómez Villafañe IE (2018) Rodent abundance and hantavirus infection in protect area, east-central Argentina. *Emerging infectious diseases* 24:131–134
- Martínez VP, Bellomo CM, Cacace ML, Suárez P, Bogni L, Padula PJ (2010) Hantavirus pulmonary syndrome in Argentina, 1995–2008. *Emerging infectious diseases* 16:1853–1859
- Massoia E, Fornes A (1965) *Nuevos datos sistemáticos, biológicos y etoecológicos de Oryzomys (Oligoryzomys) delticola* Thomas (Rodentia-Cricetidae), Delta del Paraná: Investigaciones Agrícolas, pp 4
- Matuschka FR, Endepols S, Richter D, Ohlenbusch A, Eiffert H, Spielman A (1996) Risk of urban lyme disease enhanced by the presence of rats. *Journal of Infectious Diseases* 174:1108–1111
- Meerburg BG, Singleton GR, Kijlstra A (2009) Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology* 35:221–270
- Meserve PL, Kelt DA, Milstead WB, Gutiérrez JR (2003) Thirteen years of shifting top-down and bottom-up control. *BioScience* 53:633–646
- Mills JN, Ellis BA, Mckee KT, Maiztegui JI, Childs JE (1991) Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. *Journal of Mammalogy* 72:470–479
- Mills JN, Schmidt K, Ellis BA, Calderón G, Enría DA, Ksiazek TG (2007) A longitudinal study of hantavirus infection in three sympatric reservoir species in agroecosystems on the Argentine pampa. *Vector-Borne and Zoonotic Diseases* 7:229–240
- Nichol ST, Spiropoulou CF, Morzunov S, Rollin PE, Ksiazek GT, Feldmann H, Sanchez A, Childs J, Zaki S, Peters CJ (1993) Genetic identification of a hantavirus associated with an outbreak of acute respiratory illness. *Science* 262:914–917
- Nielsen AB, van den Bosch M, Maruthaveeran S, van den Bosch CK (2014) Species richness in urban parks and its drivers: A review of empirical evidence. *Urban Ecosystems* 17:305–327
- Padula PJ, Colavecchia SB, Martínez VP, Della Valle MG, Edelstein A, Miguel SDL, Russi J, Riquelme JM, Colucci N, Almirón M, Rabinovich RD (2000) Genetic diversity, distribution, and serological features of hantavirus infection in five countries in South America. *Journal of Clinical Microbiology* 38:3029–3035
- Padula PJ, Figueroa R, Navarrete M, Pizarro E, Cadiz R, Bellomo C, Jofre C, Zaror L, Rodriguez E, Murúa R (2004) Transmission study of andes hantavirus infection in wild Sigmodontinae rodents. *Journal of Virology* 78:11972–11979
- Padula PJ, Rossi CM, Della Valle MO, Martinez PV, Colavecchia SB, Edelstein A, Miguel SDL, Rabinovich RD, Segura EL (2000) Development and evaluation of a solid-phase enzyme immunoassay based on Andes hantavirus recombinant nucleoprotein. *Journal of medical microbiology* 49:149–155
- R Development Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>. Last Accessed June 2016.
- Riley SPD, Hadidian J, Manski DA (1998) Population density, survival, and rabies in raccoons in an urban national park. *Canadian Journal of Zoology* 76:1153–1164
- Seber GAF (1973) *The estimation of animal abundance and related parameters*, London: Charles Griffin & Company Limited

- Shanahan DF, Lin BB, Gaston KJ, Bush R, Fuller RA (2015) What is the role of trees and remnant vegetation in attracting people to urban parks? *Landscape Ecology* 30:153–165
- Singleton GR, Leirs H, Hinds LA, Zhang Z (1999) Ecologically-based management of rodent pests—Re-evaluating our approach to an old problem. In: *Ecologically-based management of rodent pests*, Singleton GR, Hinds LA, Leirs H, Zhang Z (editors), Camberra: Australian Centre for International Agricultural Research, pp 17–29
- Singleton G, Krebs CJ, Davis S, Chambers L, Brown P (2001) Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society of London B: Biological Sciences* 268:1741–1748
- Senseth NC, Leirs H, Skonhofs A, et al. (2003) Mice and rats: the dynamics and bioeconomics of agricultural rodents pests. *Frontiers in Ecology and the Environment* 1:367–375
- Suárez OV, Bonaventura SM (2001) Habitat use and diet in sympatric species of rodents of the low Paraná delta, Argentina. *Mammalia* 65:167–176
- Suárez OV, Cueto GR, Cavia R, Gómez Villafaña IE, Bilenca DN, Edelstein A, Martínez P, Miguel S, Bellomo C, Padula PJ, Busch M (2003) Prevalence of infection with hantavirus in rodent populations of central Argentina. *Memórias do Instituto Oswaldo Cruz* 98:727–732
- Teta P, Cueto G, Suárez O (2007) New data on morphology and natural history of *Deltamys kempi* Thomas, 1919 (Cricetidae, Sigmodontinae) from central-eastern Argentina. *Zootaxa* 1665:43–51
- Udrizar Sauthier WO, Abba AM, Udrizar Sauthier DE (2010) Nidos de *Oligoryzomys* sp. y *Holochilus brasiliensis* (Rodentia, Cricetidae) en el este de la provincia de Entre Ríos. *Argentina. Mastozoología Neotropical* 17:207–211
- Vadell M, Bellomo C, San Martín A, Padula PJ, Gómez Villafaña IE (2011) Hantavirus ecology in rodent populations in three protected areas of Argentina. *Tropical Medicine & International Health* 16:1342–1352
- Vadell MV, Erize FG, Gómez Villafaña IE (2016) Evaluation of habitat requirements of small rodents and effectiveness of an ecologically-based management in a hantavirus-endemic natural protected area in Argentina. *Integrative Zoology* 12:77–94
- Vadell MV, Gómez Villafaña IE (2016) Environmental variables associated with hantavirus reservoirs and other small rodent species in two national parks in the Paraná delta, Argentina: implications for disease prevention. *EcoHealth* 13:248–260
- Vadell MV, Gómez Villafaña IE, Cavia R (2014) Are life-history strategies of Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*) dependent on environmental characteristics? *Wildlife Research* 41:172–184
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73:3–36
- Zhou D, Chu LM (2012) How would size, age, human disturbance, and vegetation structure affect bird communities of urban parks in different seasons? *Journal of Ornithology* 153:1101–1112
- Zuleta GA, Kravetz FO, Busch M, Percich RE (1988) Dinámica poblacional del ratón del pastizal pampeano (*Akodon azarae*) en ecosistemas agrarios de Argentina. *Revista Chilena de Historia Natural* 61:231–244
- Zuur AF (2009) *Mixed Effects Models and Extensions in Ecology with R*, New York: Springer