

Rodent Community Structure and Andes Virus Infection in Sylvan and Peridomestic Habitats in Northwestern Patagonia, Argentina

Luciana Piudo,¹ Martin J. Monteverde,¹ R. Susan Walker,² and Richard J. Douglass³

Abstract

Modifications of natural habitat in peridomestic rural areas could affect original rodent community composition, diversity, and evenness. In zoonoses such as hantavirus pulmonary syndrome, the presence of a diverse community can dilute the impact of the principal reservoir, reducing risk to humans. The goal of this study was to examine rodent community composition, abundance of Andes virus (ANDV) host (*Oligoryzomys longicaudatus*), ANDV prevalence, and temporal variability associated with rural peridomestic settings in Patagonia, Argentina. We trapped rodents in peridomestic settings and nearby sylvan areas for 2 years. The numerically dominant species differed between peridomestic and sylvan settings. *O. longicaudatus* was the most abundant species in peridomestic settings (>50% of individuals). Diversity and evenness in peridomestic settings fluctuated temporally, with an abrupt decline in evenness coinciding with peaks in ANDV prevalence. The probability of finding an ANDV-positive mouse in peridomestic settings was 2.44 times greater than in sylvan habitats. Changes in rodent communities in peridomestic settings may increase the probability for human exposure to ANDV because those settings promote the presence of *O. longicaudatus* with high ANDV antibody prevalence. High *O. longicaudatus* relative abundance in an unstable community associated with peridomestic settings may favor intraspecific contact, leading to a higher probability of virus transmission.

Key Words: Diversity—Habitat modification—Hantavirus—*Oligoryzomys longicaudatus*—Temporal fluctuations.

Introduction

HABITAT MODIFICATION BY HUMANS constitutes a major impact on ecosystems, and the effect of habitat modification on wildlife is a prominent conservation issue (Saunders et al. 1991). However, the impact of anthropogenic habitat changes on zoonoses is not well understood. In the present study, we examined the effect of peridomestic habitat modifications on the ecology of the Andes virus (ANDV), a hantavirus that causes hantavirus pulmonary syndrome (HPS) in humans.

ANDV and other hantaviruses are directly transmitted to humans by rodent reservoirs (Mills et al. 1997). The structure of a rodent community may affect disease transmission within the community and to humans. Rodent communities can be affected by human habitat modifications that reduce abundance of host populations, lower species diversity of rodent

communities, or alter host dispersal patterns, possibly impacting emerging diseases (Ostfeld and Keesing 2000a, 2000b, Daszak et al. 2001, Schmidt and Ostfeld 2001). A diverse vertebrate assemblage may “dilute” the impact of the reservoir, thus reducing disease risk to humans. In directly transmitted zoonoses (e.g., HPS) where horizontal transmission is associated with intraspecific contact (Mills and Childs 1998), high rodent diversity may reduce intraspecific contact (Ostfeld and Keesing 2000b), reducing transmission within the host population.

HPS is primarily contracted by humans in rural peridomestic settings (Armstrong et al. 1995, Pini et al. 2003, Torres-Perez et al. 2004). The disease can cause severe respiratory disease, with a 44% fatality rate in Argentine Patagonia. In Neuquén Province, 41 cases of HPS have been identified since 1997 (Dr. Ignacio Canevari, Neuquén Public Health Service, pers. comm.). The sigmodontine rodent *Oligoryzomys*

¹Departamento Fauna Terrestre, Centro de Ecología Aplicada del Neuquén (CEAN), Junín de los Andes, Neuquén, Argentina.

²Patagonian and Andean Steppe Program, Wildlife Conservation Society, Junín de los Andes, Neuquén, Argentina.

³Department of Biology, Montana Tech of the University of Montana, Butte, Montana.

longicaudatus is the reservoir for the ANDV in Neuquén (Lopez et al. 1996, Levis et al. 1998, Murua 1998). Three other species have been found to have antibodies against ANDV (antibody positive) in Argentina: *Abrothrix longipilis*, *Abrothrix olivaceus*, *Loxodontomys micropus* (Cantoni et al. 2001, Piudo et al. 2005). There are no reports of these species transmitting ANDV to humans. The primary host occurs in a broad range of habitats including forests (Pearson 1982), the ecotone between forests and shrublands (Guthmann et al. 1997), and steppe (Corley et al. 1995, Monjeau et al. 1997, Piudo et al. 2005). In Neuquén, *O. longicaudatus* is found in peridomestic settings in all ecoregions except for the high Andean steppe (Piudo et al. 2005). *O. longicaudatus* is highly mobile (Kelt et al. 1994, Murua et al. 1996), with home ranges that are, in many cases, twice the size of those of sympatric species such as *A. olivaceus* (González et al. 2000).

Rural peridomestic settings have several effects on rodent habitat. Compared with adjacent sylvan areas, temperature and humidity are moderate and less seasonally variable in buildings (houses, woodsheds, and barns) found in these settings. In addition, rodent food supply is less seasonal, readily available, and often continuously abundant in peridomestic settings compared with sylvan areas. Rodent control (snap-traps and toxic baits) is frequently attempted in and around buildings, but is only effective when structures are rodent proofed, preventing the entrance of new rodents (Glass et al. 1997). Otherwise, rodents that are removed from these structures are quickly replaced by individuals dispersing from nearby sylvan areas (Calisher et al. 1999, Douglass et al. 2003). Differences in environmental conditions and food availability, as well as rodent control in peridomestic settings, may alter the rodent community associated with the original sylvan environment.

We examined rodent community composition, abundance, and temporal variability associated with rural peridomestic settings in northwestern Patagonia, Argentina. We hypothesize that the peridomestic habitat favors *O. longicaudatus*, as human modification of natural habitats and removal of rodents from peridomestic rural settings increase the abundance of species with high dispersal ability, such as *O. longicaudatus*. At the same time, abundance of less-mobile species and species more sensitive to disturbance decreases, thus altering diversity and evenness of the rodent community. These alterations in the rodent community may increase the transmission of ANDV among host rodents by increasing intra-specific contact. Therefore, we further hypothesize that peridomestic settings favor the presence of rodents infected with ANDV.

Most studies of multispecies effects on the ecology of hantaviruses focus on the effects of spatial variability on diversity/transmission (Ruedas et al. 2004, Mills 2005, Suzan et al. 2009). However, temporal variation in ecological processes can also influence ecological/transmission patterns (Mengue and Olson 1990). In the present study, we examined both spatial and temporal patterns of variability within the rodent community and ANDV transmission.

Materials and Methods

Study sites

We established three study sites in Neuquén Province, Argentina. Each study site contained both a sylvan and ad-

jacent peridomestic setting. Paraje El Contra (CONTRA: south shore of Huechulafquen Lake, 39° 46' 47.1" S, 71° 22' 8.8" W, 938 m.a.s.l.) is in the subantarctic forest and is comprised of radial (*Lomatia hirsuta*), cypress (*Austrocedrus chilensis*), and an understory of dry bamboo (*Chusquea culeou*) and michay (*Berberis darwini*). Paraje San Cabao (SC: 39° 54' 20.7" S, 71° 07' 51.2" W, 814 m.a.s.l.) is in the patagonian steppe and is comprised of a homogeneous matrix of neneos (*Mulinum spinosum*), sweet bunchgrass (*Festuca* sp. and *Stipa* sp.), and groundsel (*Senecio* sp.). Villa La Angostura (VLA: 40° 44' 47.7" S, 71° 35' 20.1" W, 961 m.a.s.l.) is in the subantarctic forest, dominated by coihue (*Notophagus dombeyi*) and with an understory of green bamboo (*C. culeou*), wild rose (*Rosa rubiginosa*), ñire (*Nothofagus antarctica*), radial (*L. hirsuta*), and *Berberis* sp.

At each study site, peridomestic settings were located ~300 m from the sylvan settings. All peridomestic settings included storage buildings, vegetable gardens, henhouses, and covered corrals. Structures were constructed of wooden planks, or brick and concrete, and were not rodent proofed. Most buildings were used by people on a daily basis, although some storage buildings were entered only irregularly.

Trapping

We trapped simultaneously in peridomestic and nearby sylvan settings at each site. Trapping was carried out for three consecutive nights, every month, between February 2003 and December 2004, with the exception of July 2004 at CONTRA, when trapping was not possible because of deep snow. In each sylvan setting, we placed one 10×10 grid consisting of 100 Sherman live traps at 10-m intervals. Traps were baited with rolled oats, bovine fat, and vanilla extract, with cotton bedding added during cold seasons. At the peridomestic settings, traps were set inside buildings and around perimeters of buildings. The number of traps placed depended on the size of buildings and perimeter areas, but was sufficient to assure that there were always traps available (CONTRA = 34, SC = 32, and VLA = 25). The number of traps at each site remained constant throughout the study. Traps from all buildings for each site were treated as a group for the analysis.

Captured rodents were identified to species and permanently marked with uniquely numbered ear tags (National Band and Tag Co., Newport, KY). Blood samples for antibody testing were obtained from the retroorbital sinus of each rodent, using a heparinized capillary tube. Individuals were bled only once during a monthly trapping session. Blood samples were placed in cryovials and frozen until they were tested for antibodies against ANDV in rodent blood serum samples using an enzyme-linked immunosorbent assay (ELISA) (Feldmann et al. 1993) as described by Padula et al. (2000).

Captured rodents were weighed and classified as adult, subadult, or juvenile according to body mass and breeding condition (males: testes scrotal or abdominal; females: non-perforate, perforate vagina, pregnant, and/or lactating) (Meserve and Le Boulengé 1987, Guthmann et al. 1997). Individuals captured in sylvan settings were released at the site of capture. Rodents captured in peridomestic settings were subjected to the same handling procedures, but were then sacrificed by cervical dislocation. Handling of rodents followed the guidelines described by Mills et al. (1995).

In our absence, the human inhabitants at each study site continuously removed rodents from peridomestic settings by snap trapping. Despite these removal efforts, the continuous presence of rodents was evident.

Data analysis

We compared total capture frequencies of the most abundant species in peridomestic versus sylvan settings at each site using chi-square analysis (Zar 1996). We did not include less-common species in this analysis, to avoid violating chi-square test assumptions concerning minimum expected numbers. *O. longicaudatus*, *A. olivaceus*, and *A. longipilis* were the species compared between settings at CONTRA and VLA, and *O. longicaudatus*, *Eligmodontia morgani*, *Akodon iniscatus*, and *Reithrodon auritus* at SC.

We estimated species diversity (*H*) using the conversion of Shannon-Wiener entropy index to true diversity [$H = \exp(-\sum p_i \ln p_i)$] (Jost 2006), where p_i is the proportion of the total sample belonging to the *i*th species. We quantified evenness (*J*) as [$H/\ln(\text{Richness})$] and defined richness as the number of species. We compared average diversity in sylvan and peridomestic settings using a *t*-test (Zar 1996). We compared temporal fluctuation in species diversity and evenness between peridomestic and sylvan settings with a sign test for two related samples (Daniel 1978). Coefficients of variation (CV) for diversity and evenness indices (Zar 1996) were estimated for peridomestic and sylvan settings of all sites combined over all sampling periods. We expressed abundance as the number of individuals of each species captured per trapping period. Time series cross-correlation analysis was used to determine relationships among ANDV prevalence as well as number of antibody-positive individuals and species diversity as well as evenness at different times. Only the sites where antibody-positive *O. longicaudatus* were present at >3 months were used for the analysis. We estimated odds ratios for antibody status with a binomial logistic model (Infostat 2009).

Results

Rodent communities

Between January 2003 and December 2004, we captured 343 individuals of 14 species in 6375 trap-nights (TN) (5.4 ind./100 TN) in peridomestic settings. During the same time period, we captured 1020 individuals of 13 species in sylvan habitats in 20,700 TN (4.9 ind./100 TN).

Although some species were present at all study sites, many occurred at only one or two of our sites. The three species reported to have antibodies against ANDV in this region, *O. longicaudatus*, *A. olivaceus*, and *A. longipilis*, were the only species captured in peridomestic settings at all three study sites. These three species accounted for over 87% of all individuals captured (Fig. 1). *O. longicaudatus* was the most abundant species in peridomestic settings, comprising 50% of the total individuals, whereas in sylvan settings they accounted for <22% of rodents captured.

Rodent communities varied among and within the three sites. We found significant differences in the numerically dominant species between peridomestic and sylvan settings for all sites combined ($\chi^2 = 187.77$, $p < 0.001$) and for each of the three sites separately (CONTRA: $\chi^2 = 62.7$, $p < 0.001$; SC:

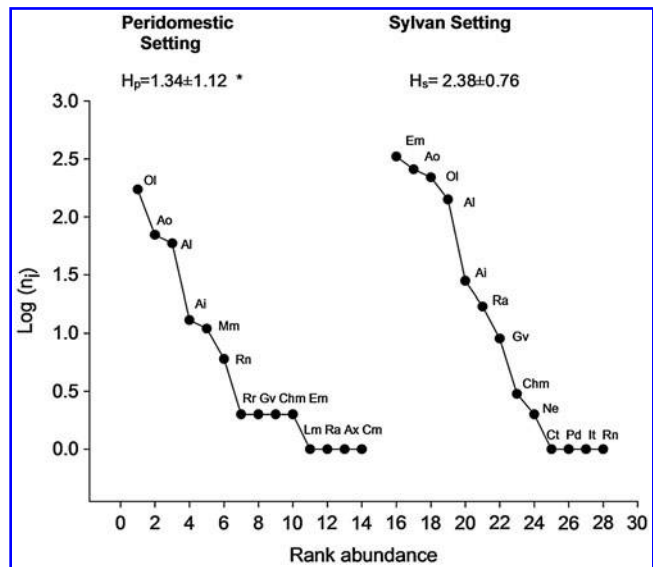


FIG. 1. Species ranked from most to least abundant (highest to lowest log of the abundance of each species [n_i]) for rodents captured in sylvan and peridomestic settings in northwestern Patagonia, Argentina, from 2003 through 2004. Em, *Eligmodontia morgani*; Ao, *Abrothrix olivaceus*; Ol, *Oligorizomys longicaudatus*; Al, *Abrothrix longipilis*; Ai, *Akodon iniscatus*; Ra, *Reithrodon auritus*; Gv, *Geoxus valdivianus*; Chm, *Chelemys macronix*; Ne, unidentified species; Ct, *Ctenomys* sp; Pd, *Phyllotis darwini*; It, *Irenomys tarsalis*; Rn, *Rattus norvegicus*; Mm, *Mus musculus*; Rr, *Rattus rattus*; Lm, *Loxodontomys micropus*; Ax, *Abrothrix xanthorhinus*; Cm, *Calomys musculinus*. *Statistically different peridomestic (H_p) and sylvan diversity (H_s); $p < 0.001$.

$\chi^2 = 239.4$, $p < 0.001$; VLA: $\chi^2 = 10.6$, $p = 0.014$). Diversity (Fig. 2a) and evenness (Fig. 2b) fluctuated over time in all peridomestic settings combined ($CV_{(H)} = 0.83$; $CV_{(J)} = 0.69$), but remained more stable in sylvan settings ($CV_{(H)} = 0.31$; $CV_{(J)} = 0.37$). Species diversity over time was greater in sylvan than in peridomestic settings ($Z = 3.75$, $p < 0.001$) (Fig. 2a). Average monthly diversity for the entire study was also significantly lower in peridomestic settings ($t_{(42)} = 5.21$, $p < 0.001$) (Fig. 1). Evenness in peridomestic settings was not consistently different from that in sylvan settings over time ($Z = 0.21$, $p = 0.831$) (Fig. 2b).

Temporal variation in *O. longicaudatus* abundance and ANDV antibodies

At CONTRA, *O. longicaudatus* was present in most sampling periods in both peridomestic and sylvan settings (Fig. 3a, b). Peaks in total community abundance (all species combined) occurred in winter 2003 (from June to August/September) and in April 2004 in both settings. These peaks in abundance coincided with peaks in abundance of *O. longicaudatus* and two pulses in antibody prevalence (July to October 2003 and April to May 2004) in the peridomestic setting (Fig. 3a). *O. longicaudatus* was the most abundant species captured at the CONTRA peridomestic settings (50%–81% total captures), whereas in sylvan settings it was never the most abundant species (<45% of total captures) (Fig. 3a, b). In the sylvan setting, ANDV antibodies within rodent populations appeared intermittently and prevalence was more

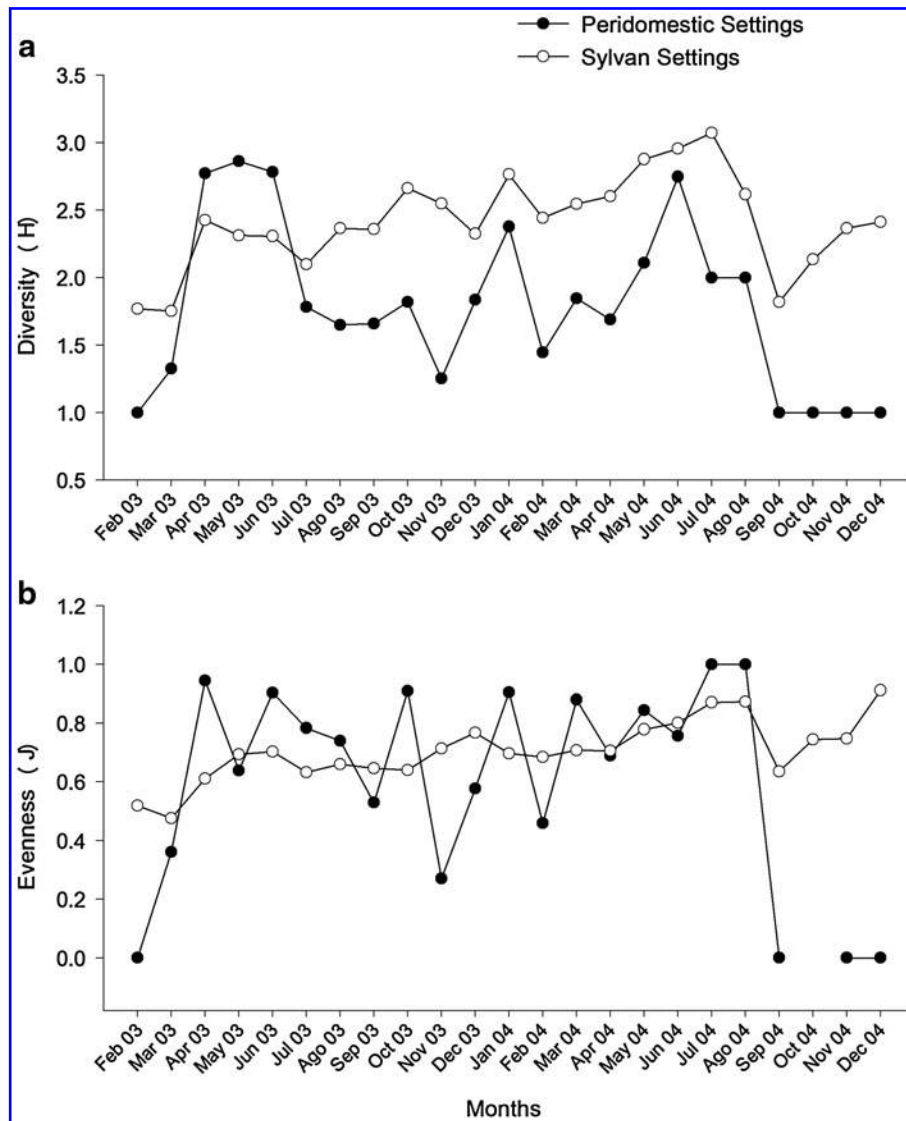


FIG. 2. Temporal fluctuation in average rodent diversity (H) (a) and average rodent evenness (J) (b) in sylvan and peridomestic settings. Data were averaged for the three sites located in Neuquén, northwestern Patagonia, Argentina, during 2003 and 2004.

evenly distributed among the ANDV antibody-positive species, *O. longicaudatus*, *A. longipilis*, and *A. olivaceus*, than in peridomestic setting (Table 1). Except for one, *A. olivaceus*, all rodents positive for ANDV antibodies in peridomestic setting were *O. longicaudatus* (Table 1).

Although species composition at VLA was similar to CONTRA, overall abundance at VLA was less than half of that at CONTRA (Fig. 3a–d). In the sylvan setting, total community abundance reached its maximum value in May 2003 and remained relatively constant until April 2004, when it decreased until August 2004 (Fig. 3c, d). *O. longicaudatus* was present during all seasons in the peridomestic setting, except winter 2004 (June to August), and it was the most abundant species during 5 months (>60% of total captures) (Fig. 3c). An *A. longipilis* that was trapped during March 2003 (Table 1) was the only antibody-positive mouse captured in the VLA peridomestic setting. In the sylvan setting, *O. longicaudatus* was always present and was the most abundant species (>50% of total captures) during winter 2003 (July and

August 2003) and September and October 2004 (Fig. 3d). In the sylvan setting, ANDV antibody-positive rodents, mostly *O. longicaudatus*, were present during May 2003 and from September to December 2004 (Table 1).

Although *O. longicaudatus* was not captured in the sylvan setting at SC, it was present in the peridomestic setting in 12 of 23 months sampled, whereas other species such as *Mus musculus* and *A. olivaceus* were only captured during 8 months of the study (Fig. 3e, f). Moreover, *O. longicaudatus* was the most abundant species in this setting (>50% of the captures) during 6 months (Fig. 3e). An antibody-positive *O. longicaudatus* was present in the peridomestic setting at SC during June 2003 (Table 1).

Sylvan versus peridomestic prevalence of ANDV antibodies

We tested 1584 blood samples for ANDV antibodies from all individuals (with the exception of murid species) captured

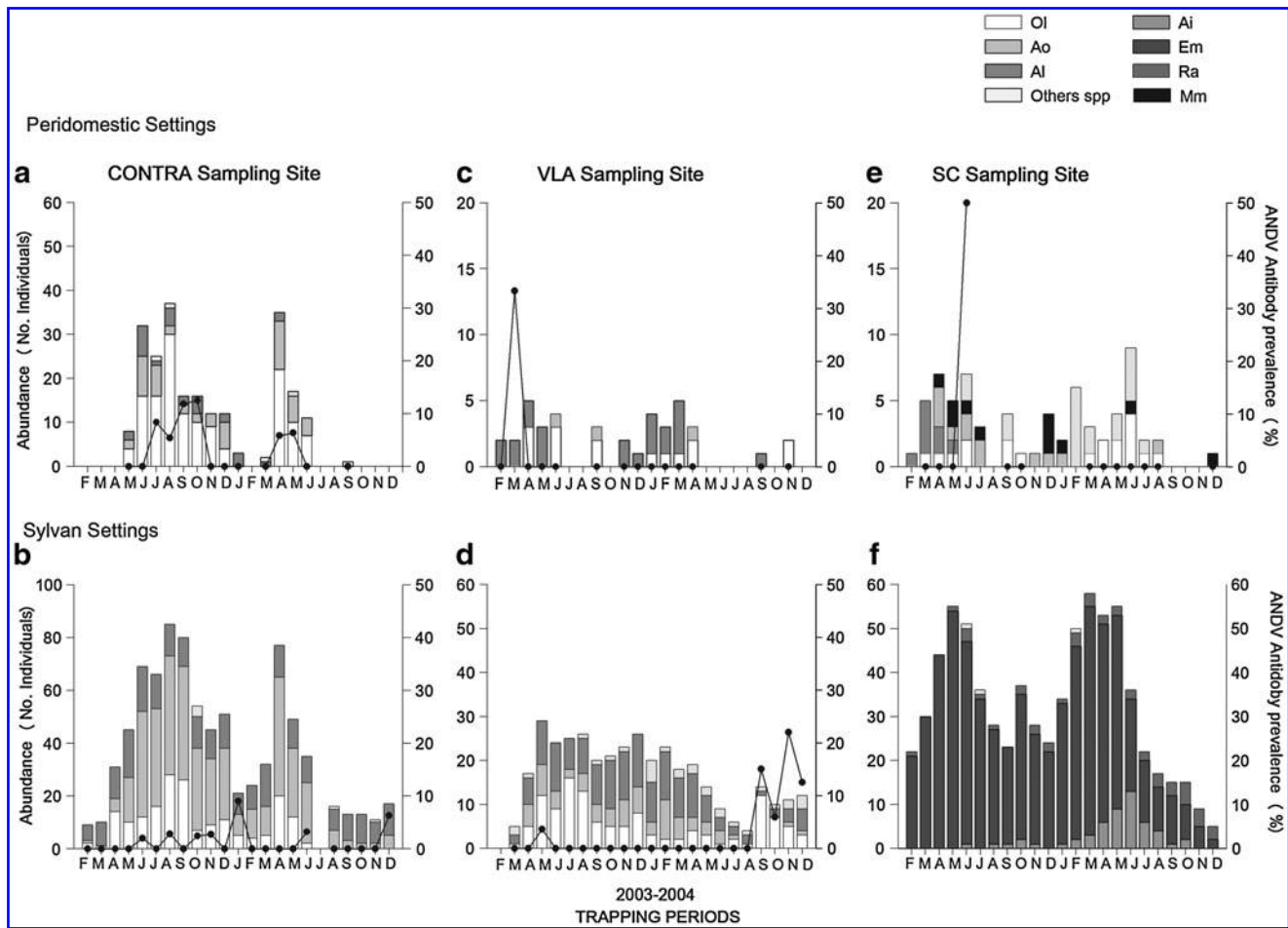


FIG. 3. Monthly variation in rodent abundance (bars) and total Andes virus antibody prevalence % (line) from February 2003 to December 2004, expressed as number of captures in peridomestic and sylvan settings of (a, b) Pje el Contra (CONTRA), (c, d) Villa la Angostura (VLA), and (e, f) Pje San Cabao (SC), northwestern Patagonia, Argentina.

in sylvan and peridomestic settings. Of those, 22 of 405 *O. longicaudatus* (5.4%), 4 of 206 *A. longipilis* (1.9%), and 4 of 478 *A. olivaceus* (0.8%) had detectable ANDV antibody prevalence. None of the positive *O. longicaudatus* were recaptured during subsequent trapping periods. All antibody-positive individuals were adult, and in the case of *O. longicaudatus*, all were male, whereas all antibody-positive *A. olivaceus* were female. Antibody-positive *A. longipilis* were both male and female (three males and one female).

Total rodents captured (all species combined) in peridomestic settings had twice the probability of being antibody positive than rodents captured in sylvan areas (Wald stat = 17.12; $p < 0.001$; OR = 2.16; OR_{min} = 1.5; OR_{max} = 3.12). Overall *O. longicaudatus* antibody status was not associated with either sylvan or peridomestic settings (Wald stat = 1.71; $p = 0.189$). However, at CONTRA, the only site with a sufficient number of *O. longicaudatus* in both settings for statistical comparisons, the probability of finding an ANDV antibody-positive rodent in the peridomestic setting was 2.44 times higher than on the sylvan grid for all species (Wald stat = 14.40; $p < 0.001$; OR_{min} = 1.54; OR_{max} = 3.88), and 2.07 times higher for *O. longicaudatus* (Wald stat = 4.76; $p < 0.001$; OR_{min} = 1.07; OR_{max} = 4).

Temporal fluctuation in community indices and ANDV antibody-positive *O. longicaudatus*

Because rodent populations fluctuated markedly, especially in peridomestic settings (Fig. 2a, b), we did the cross-correlation analysis of temporal relationships between ANDV infection and diversity or evenness. The presence of ANDV antibodies in *O. longicaudatus* seemed to be more related to extreme fluctuations in diversity than to low values of the diversity index *per se*. Coincidentally, most of the peaks in *O. longicaudatus* seroprevalence coincided with abrupt decreases in evenness (Fig. 4a, b). However, we did not find a significant correlation between species diversity or evenness and *O. longicaudatus* ANDV antibody prevalence at any time (Table 2). However, the number of antibody-positive *O. longicaudatus* was negatively associated with diversity during the same month (time zero) and one and two previous months ($H_t = 0$, $r = -0.35$, $T = -2.49$, $p = 0.015$; $H_t = -1$, $r = -0.40$, $T = -2.83$, $p = 0.006$; $H_t = -2$, $r = -0.33$, $T = -2.28$, $p = 0.026$). The number of *O. longicaudatus* was also negatively correlated with evenness at time zero and the previous month ($H_t = 0$, $r = -0.41$, $T = -2.96$, $p = 0.004$; $H_t = -1$, $r = -0.36$, $T = -2.50$, $p = 0.015$) (Table 2).

TABLE 1. MONTHLY ANDES VIRUS ANTIBODY PREVALENCE OF INFECTION, EXPRESSED AS PERCENTAGES

Months	CONTRA						SC						VLA						
	Peridomestic			Sylvan			Peridomestic			Sylvan			Peridomestic			Sylvan			
	Ol	Ao	Total	Ol	Al	Ao	Total	Ol	Total	Ao	Total	Ol	Al	Ao	Total	Ol	Ao	Total	
2003																			
February	—	—	—	0	0	0	0	—	0	0	0	—	—	—	0	ND	ND	0	ND
March	—	—	—	0	0	—	0	0	0	0	0	0	—	—	0	0	—	0	0
April	—	—	—	0	0	0	0	0	0	0	0	0	—	—	0	0	0	0	0
May	0	0	0	0	0	0	0	0	0	0	0	0	—	—	0	0	0	0	3.6 (1)
June	0	0	0	20.0 (1)	0	0	2.0 (1)	50.0 (1)	16.7 (1)	0	0	0	—	—	0	0	0	0	0
July	11.7 (2)	0	8.3 (2)	0	0	0	0	—	0	0	0	—	—	—	—	—	—	—	0
August	6.9 (2)	0	5.4 (2)	4.0 (1)	0	2.0 (1)	2.8 (2)	—	0	0	0	—	—	—	—	—	—	—	0
September	16.6 (2)	0	11.8 (2)	0	0	0	0	0	0	0	0	0	—	—	—	—	—	—	0
October	10.0 (1)	16.6 (1)	12.5 (2)	0	11.0 (1)	0	2.4 (1)	0	0	0	0	—	—	—	—	—	—	—	0
November	0	0	0	0	0	5.0 (1)	2.7 (1)	—	—	—	—	—	—	—	—	—	—	—	0
December	0	0	0	0	0	0	0	—	0	0	0	—	—	—	—	—	—	—	0
2004																			
January	—	—	0	50.0 (1)	0	0	9.0 (1)	—	0	0	0	—	—	—	0	0	0	0	0
February	—	—	—	0	0	0	0	—	0	0	0	—	—	—	0	0	0	0	0
March	—	—	—	0	0	0	0	—	0	0	0	—	—	—	0	0	0	0	0
April	9.5 (2)	0	5.8 (2)	0	0	0	0	0	0	0	0	0	—	—	—	—	—	—	0
May	14.3 (1)	0	6.3 (1)	0	0	0	0	0	0	0	0	—	—	—	—	—	—	—	0
June	0	0	0	0	17.0 (1)	0	3.2 (1)	0	0	0	0	—	—	—	—	—	—	—	0
July	ND	ND	ND	ND	ND	ND	ND	0	0	0	0	—	—	—	—	—	—	—	0
August	—	—	—	—	0	0	0	0	0	0	0	—	—	—	—	—	—	—	0
September	—	—	—	—	0	0	0	—	—	—	—	—	—	—	0	0	0	0	15.0 (3)
October	—	—	—	—	0	0	0	—	—	—	—	—	—	—	0	0	0	0	5.9 (1)
November	—	—	—	—	0	0	0	—	—	—	—	—	—	—	0	0	0	0	22.0 (2)
December	—	—	—	—	8.0 (1)	0	6.3 (1)	0	0	0	0	—	—	—	—	—	—	—	0
Seroprev (%)	7.6	1.9	5.0	2.0	1.6	0.5	1.1	7.7	2.0	0	0	0	4.5	1.6	2.6	7.9	1.6	3.1	3.1
Positives	10	1	11	3	3	2	8	1	1	1	1	1	1	1	1	8	1	1	9
Analyzed	131	52	219	150	184	362	684	13	51	300	10	22	38	64	292	101	64	292	292

Values in parentheses are the numbers of infected *Oligoryzomys longicaudatus* (Ol), *Abrothrix olivaceus* (Ao), and *Abrothrix longipilis* (Al) and total combined species, for three sites (Pje el Contra [CONTRA], Pje San Cabao [SC], and Villa La Angostura [VLA]) and in both sylvan and peridomestic by month for 2003 and 2004 in northwestern Patagonia, Argentina. ND, no data because no traps were set in that month; —, no captures were registered in that month.

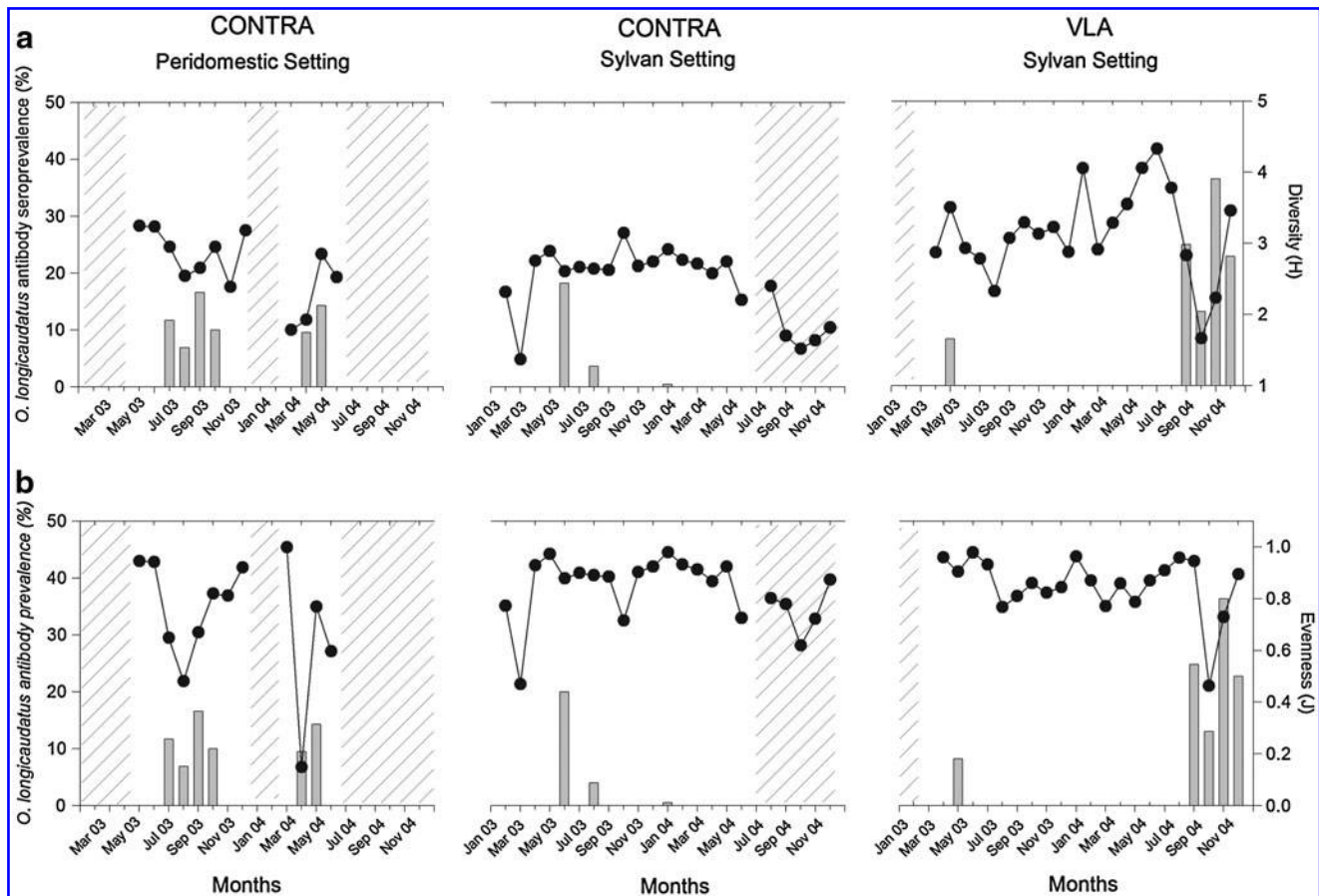


FIG. 4. Temporal fluctuation in *O. longicaudatus* Andes virus antibody prevalence and (a) diversity (H') or (b) evenness in CONTRA peridomestic and sylvan setting and VLA sylvan setting, northwestern Patagonia Argentina. Hatching denotes months in which there were no *Oligoryzomys longicaudatus* captures. Continuous lines indicate diversity (a) or evenness (b) and bars indicate antibody prevalence.

TABLE 2. CROSS-CORRELATION ANALYSIS BETWEEN DIVERSITY (H) OR EVENNESS (J) AND *Oligoryzomys longicaudatus* ANDES VIRUS ANTIBODY PREVALENCE (%) OR NUMBER OF INFECTED *Oligoryzomys longicaudatus* AT DIFFERENT LAG TIMES

	Lag	Coefficient	T	p
<i>H</i> vs. <i>O. longicaudatus</i> seroprevalence (%)	-3	-0.15	-0.96	0.342
	-2	-0.14	-0.97	0.337
	-1	-0.16	-1.10	0.276
	0	-0.15	-1.06	0.294
<i>J</i> vs. <i>O. longicaudatus</i> seroprevalence (%)	-3	-0.06	-0.40	0.691
	-2	0.03	0.21	0.831
	-1	-0.09	-0.60	0.549
	0	-0.09	-0.61	0.542
<i>H</i> vs. no. of infected <i>O. longicaudatus</i>	-3	-0.22	-1.43	0.157
	-2	-0.33	-2.28	0.026
	-1	-0.40	-2.83	0.006
	0	-0.35	-2.49	0.015
<i>J</i> vs. no. of infected <i>O. longicaudatus</i>	-3	-0.05	-0.34	0.731
	-2	-0.17	-1.13	0.261
	-1	-0.36	-2.50	0.015
	0	-0.41	-2.96	0.004

Statistically significant values are emphasized in bold type.

Discussion

The modification of previously continuous natural habitats into peridomestic rural settings, as well as the systematic removal of rodents from these settings, appears to favor the presence of *O. longicaudatus*. *O. longicaudatus* was more abundant in peridomestic settings, and other species, presumably more sensitive to disturbance, were less abundant, as indicated by the low species diversity of these settings. Rodent communities in peridomestic settings were highly unstable with temporal fluctuations in abundance, species diversity, and evenness. The low diversity and high abundance of *O. longicaudatus* in peridomestic settings may favor intraspecific transmission of virus, resulting in the high seroprevalence found in these settings. The rodent community in peridomestic settings was twice as likely to contain antibody-positive individuals than the rodent community in sylvan areas.

Total rodent abundance in peridomestic sites was likely regulated by abundance in nearby sylvan areas. The peridomestic rodent populations seem to act as sinks, with sylvan areas acting as sources. As with deer mice (*Peromyscus maniculatus*) in Montana (Douglass et al. 2003), continuous removal of rodents from buildings generated a constant turnover in peridomestic rodent populations, which may produce important changes in community composition. However, the ability of *O. longicaudatus* to disperse into and survive in altered habitats is demonstrated by the fact that it was present in the peridomestic setting and not the sylvan setting at SC. When the population of one species increases in abundance, it may reduce the relative abundance of populations of other species, without necessarily changing total community abundance, resulting in lower evenness and diversity (Brady and Slade 2001). Temporal fluctuations in abundance of *O. longicaudatus*, the most abundant species in the peridomestic settings, probably caused the observed evenness and diversity fluctuations in these settings.

Species evenness and diversity seem to be important parameters affecting host–pathogen dynamics. Communities with low evenness and high abundance of the primary host may present favorable conditions for intraspecific contact, leading to increased probability of virus transmission. In this study, we found that the number of *O. longicaudatus* with ANDV antibodies was negatively correlated with diversity and evenness during the same month, as well as with previous months. Other studies (Mills 2005, Clay et al. 2009, Suzan et al. 2009) have reported similar relationships between species diversity and prevalence of infection with hantavirus. We did not, however, find statistical support for the relationship between ANDV antibody prevalence and community parameters. Of the three ANDV antibody-positive species, *O. longicaudatus* was the most abundant. However, *O. longicaudatus* abundance and antibody prevalence varied greatly both temporally and spatially. Despite relatively small sample sizes, the hypothesis that habitat modifications of rural peridomestic settings favor the presence of *O. longicaudatus* was supported in that the abundance of this species was higher in peridomestic versus sylvan settings for both within and between species comparisons. This is especially evident at the SC site where *O. longicaudatus* was captured only in the peridomestic setting. A similar situation was found in Panama (Suzan et al. 2008), where changes in natural environments

due to deforestation were associated with increases in the abundance of the principal reservoirs of Choclo and Calabazo hantavirus.

Regarding spatial variability, each site varied according to the level and timing of risk of exposure for humans. Because of a high abundance of *O. longicaudatus* and high total antibody prevalence, the risk of HPS exposure for humans was high in the peridomestic setting at the CONTRA site, especially during the coldest months of the year. However, at VLA, people maybe at higher risk of exposure to ANDV during spring months (September to December) in sylvan areas because the relative abundance and ANDV antibody prevalence of *O. longicaudatus* were higher during those months. Overall, the prevalence of ANDV antibodies tended to be high in sylvan sites during warm months of the year (spring and summer). This high spring/summer prevalence is of particular relevance to human risk of infection because both CONTRA and VLA are areas frequented by summer campers.

High relative abundance and high ANDV antibody presence in populations of *O. longicaudatus* living in peridomestic settings may increase the probability of human exposure to ANDV. *O. longicaudatus* is a habitat generalist highly capable of adapting to peridomestic habitats. Its propensity for high relative abundance in unstable communities favors intraspecific contact, resulting in higher probabilities of virus transmission. The high ANDV antibody prevalences in populations of *O. longicaudatus* in peridomestic settings in northern Patagonia, Argentina, may increase the probability of human exposure to ANDV. Similar high prevalence of Sin Nombre Virus in peridomestic settings in North American populations of *P. maniculatus* and the associated risk to human health were described by Kuenzi et al. (2001).

Acknowledgments

The authors thank the Neira and Briceño families (Pje El Contra) and Meli-Hue (VLA) for hospitality and logistical support during the entire study. The authors greatly appreciate the permission to work on their properties and at the Centro Integral San Ignacio, San Pedro Ranch, and lote Pascotto. Lorena Laffitte provided useful advice on statistical analysis. Pablo Carmanchahi and Martin Funes helped at the beginning of the study. The authors thank J. Mills and A. Kuenzi for reviewing an earlier version of this manuscript. Antibody analysis was performed by Paula Padula and staff of the Dpto de Hantavirus, INEI-ANLIS “Dr. Carlos G. Malbran,” Buenos Aires, Argentina. This research was funded by the Centro de Ecología Aplicada del Neuquén, Montana Tech University, the National Institutes of Health (grant No. P20RR16455-05 from the INBRE–BRIN program), and the U.S. Centers for Disease Control and Prevention (Atlanta, GA) through cooperative agreement No. US3/CCU813599 and VIGIA (No. 282).

Disclosure Statement

No competing financial interests exist.

References

Armstrong, LR, Zaki, SR, Goldoft, MH, Todd, RL, et al. Hantavirus pulmonary syndrome associated with entering or

- cleaning rarely used rodent-infected structures. *J Infect Dis* 1995; 172:1166.
- Brady, MJ, Slade, NA. Diversity of grassland rodent community at varying temporal scale: the role of ecologically dominant species. *J Mamm* 2001; 82:974–983.
- Calisher, CH, Sweeney, WP, Root, JJ, Beaty, BJ. Navigational instinct: a reason not to live traps deer mice in residences. *Emerg Infect Dis* 1999; 5:175–176.
- Cantoni, G, Padula, P, Calderon, G, Mills, JN, et al. Seasonal variation in prevalence of antibody to hantaviruses in rodents from southern Argentina. *Trop Med Int Health* 2001; 6:811–816.
- Clay, CA, Lehmer, EM, St. Jeor, S, Dearing, MD. Sin Nombre virus and rodent species diversity: a test of dilution and amplification hypotheses. *PLoS ONE* 2009; 4:e6467.
- Corley, JC, Fernandez, GJ, Capurro, AF, Novaro, AJ, et al. Selection of cricetine prey by the culpeo fox in Patagonia: a differential prey vulnerability hypothesis. *Mammalia* 1995; 59:315–325.
- Daniel, Wayne W. *Applied Nonparametric Statistics*. Boston: Houghton Mifflin, 1978.
- Daszak, P, Cunningham, AA, Hyatt, AD. Anthropogenic environmental change and the emergence of infectious diseases in wildlife. *Acta Trop* 2001; 78:103–116.
- Douglass, RJ, Kuenzi, AJ, Williams, CY, Douglass, SJ, et al. Removing deer mice from buildings and the risk for human exposure to Sin Nombre virus. *Emerg Infect Dis* 2003; 9:390–392.
- Feldmann, H, Sánchez, A, Morzunov, S, Spiropoulou, CF, Rollin, PE, Ksiazek, TG, Peters, CJ, Nichol, ST. Utilization of autopsy RNA for the synthesis of the nucleocapsid antigen of a newly recognized virus associated with hantavirus pulmonary syndrome. *Virus Res* 1993; 30:351–367.
- Glass, GE, Johnson, JS, Hodenbach, GA, Disalvo, C, et al. Experimental evaluation of rodent exclusion methods to reduce hantavirus transmission to humans in rural housing. *Am J Trop Med Hyg* 1997; 56:359–364.
- González, LA, Murua, R, Jofre, C. Habitat utilization of two species in relation to population outbreaks in southern temperate forests of Chile. *Rev Chil Hist Nat* 2000; 73:489–495.
- Guthmann, N, Lozada, M, Monjeau, JA, Heinemann, KM. Population dynamics of five sigmodontine rodents of northwestern Patagonia. *Acta Theriol* 1997; 42:143–152.
- InfoStat. *InfoStat Versión 2009*. Grupo InfoStat, FCA. Argentina: Universidad Nacional de Córdoba, 2009.
- Jost, L. Entropy and diversity. *Oikos* 2006; 113:363–375.
- Kelt, DA, Meserve, L, Lang, BK. Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. *J Mammal* 1994; 75:890–904.
- Kuenzi, AJ, Douglass, RJ, White, D, Bond, CW, et al. Antibody to Sin Nombre virus in rodents associated with peridomestic habitats in west central Montana. *Am J Trop Med Hyg* 2001; 64:137–146.
- Levis, S, Morzunov, SP, Rowe, JE, Enria, D, et al. Genetic diversity and epidemiology of hantaviruses in Argentina. *J Infect Dis* 1998; 177:529–538.
- Lopez, N, Padula, P, Rossi, C, et al. Genetic identification of a new hantavirus causing severe pulmonary syndrome in Argentina. *Virology* 1996; 220:223–226.
- Mengue, BA, Olson, AM. Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* 1990; 5:52–57.
- Meserve, PL, Le Boulengé, E. Population dynamics and ecology of small mammals in the northern Chilean semiarid region. *Fieldiana: Zoology, New Series*, 39:413–431. In: Paterson, BD, Timm, RM, eds. *Studies in Neotropical Mammalogy: Essays in Honor of Philip Hershkovitz*.
- Mills, JN. Regulation of rodent-borne virus in the natural host: implications for human disease. *Arch Virol* 2005; suppl 19:45–57.
- Mills, JN, Childs, JE. Ecologic studies of rodents reservoirs: their relevance for human health. *Emerg Infect Dis* 1998; 4:529–538.
- Mills, JN, Childs, JE, Ksiazek, TG, Peters, CJ. Guidelines for working with rodents potentially infected with hantavirus. *J Mammal* 1995; 76:716–722.
- Mills, JN, Ksiazek, TG, Ellis, BA, Rollin, PE, et al. Pattern of association with host and habitat: antibody reactive with Sin Nombre virus in small mammals in the major biotic communities of the southern United States. *Am J Trop Med Hyg* 1997; 56:273–284.
- Monjeau, JA, Sikes, RS, Birney, EC, Guthmann, N, et al. Small mammal community composition within the mayor landscape divisions of Patagonia, southern Argentina. *Mastozool Neotropical* 1997; 4:113–127.
- Murua, R. Ecología de los reservorios silvestres de hantavirus en Chile. *Rev Chil Inf* 1998; 15:79–83.
- Murua, R, Gonzalez, LA, Gonzalez, M, Jofre, C. Efectos del florecimiento del arbusto Chusquea quila bambucea) sobre la demografía de poblaciones de roedores de los bosques templados fríos del sur chileno. *Bol Soc Biol Concepción* 1996; 67:37–42.
- Ostfeld, RS, Keesing, F. Biodiversity and disease risk: the case of Lyme disease. *Conserv Biol* 2000a; 14:722–728.
- Ostfeld, RS, Keesing, F. The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Can J Zool* 2000b; 78:2061–2078.
- Padula, PJ, Rosi, CM, Della Valle, MO, Martinez, PV, et al. Development and evolution of a solid-phase enzyme immunoassay based on Andes hantavirus recombinant nucleoprotein. *J Med Microbiol* 2000; 49:149–155.
- Pearson, OP, Pearson, AK. Ecology and biogeography of the southern rainforest of Argentina. In: Mares, MA., Genoways, HH, eds. *Mammalian Biology in South America*. Special Publications Series. Sp. Publ. Pymatuning Lab Ecol. University of Pittsburgh 1982; 6:129–142.
- Pini, N, Levis, S, Calderon, G, Ramirez, J, et al. Hantavirus infection in humans and rodents, Northwestern Argentina. *Emerg Infect Dis* 2003; 9:1070–1076.
- Piudo, L, Monteverde, MJ, Gonzalez Capria, S, Padula, P, et al. Distribution and abundance of sigmodontine rodents in relation to hantavirus in Neuquén, Argentina. *J Vector Ecol* 2005; 30:119–125.
- Ruedas, LA, Salazar-Bravo, J, Tinnin, DS, Armien, B, et al. Community ecology of small mammal population in Panama following an outbreak of hantavirus pulmonary syndrome. *J Vector Ecol* 2004; 29:177–191.
- Saunders, DA, Hobbs, RJ, Margules, CR. Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 1991; 5:19–35.
- Schmidt, KA, Ostfeld, RS. Biodiversity and dilution effect. *Ecology* 2001; 82:609–619.
- Suzan, G, Armien, A, Mills, JN, Marce, E, et al. Epidemiological considerations of rodent community composition in fragmented landscapes in Panama. *J Mammal* 2008; 89:684–690.

- Suzan, G, Marcé, E, Giermakowski, JT, Mills, JN, et al. Experimental evidence for reduced rodent diversity causing increased hantavirus prevalence. *PLoS ONE* 2009; 4:e5461.
- Torres-Perez, F, Navarrete-Droguett, R, Aldunate, R, Yates, TL, et al. Peridomestic small mammals associated with confirmed cases of human hantavirus disease in southcentral Chile. *Am J Trop Med Hyg* 2004; 70:305–309.
- Zar, JH. *Biostatistical Analysis*. Third ed. Eaglewood Cliffs, NJ: Prentice-Hall, Inc., 1996.

Address correspondence to:
Luciana Piudo
Departamento de Fauna Terrestre
Centro de Ecología Aplicada del Neuquén (CEAN)
ruta 61 km 3
San Cabao
Junín de los Andes 8371
Neuquén
Argentina
E-mail: lupiudo@gmail.com