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Original Contribution

Mechanisms of Hantavirus Transmission in *Oligoryzomys longicaudatus*

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Abstract: The cricetid rodent *Oligoryzomys longicaudatus* is the species host of Andes virus (ANDV) which causes hantavirus pulmonary syndrome in southern Argentina and Chile. Population density, behavioral interactions, and spacing patterns are factors that affect viral transmission among wild rodents. We predict that the highest prevalence of hantavirus antibody positive would be found among wounded, reproductive males and that, at high population densities, wounded, reproductive males would be dispersers rather than resident individuals. The study was conducted seasonally from October (spring) 2011 to October (spring) 2013 in a shrubland habitat of Cholila, Argentina. During each trapping session, we classified captured *O. longicaudatus* as resident or disperser individuals, estimated population density, and recorded wounds as an indicator of aggression among individuals. We obtained blood samples from each individual for serological testing. We used generalized linear models to test the statistical significance of association between antibody prevalence, and sex, resident/dispersal status, wounds and trapping session. The highest proportion of seropositive *O. longicaudatus* individuals was among wounded reproductive males during periods of the greatest population density, and the characteristics of seroconverted individuals support that transmission is horizontal through male intrasexual competition. A positive association between dispersing individuals and hantavirus antibody was detected at high population density. Our study design allowed us to obtain data on a large number of individuals that are seroconverted, enabling a better understanding of the ecology and epidemiology of the ANDV host system.

Keywords: Hantavirus prevalence, Seroconversion, *Oligoryzomys longicaudatus*, Dispersion

Introduction

The aim of this study was to investigate whether there is a relationship between sexes, resident or transient status, presence of wounds, population density and ANDV anti-

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body prevalence in *O. longicaudatus*. On the American continent, the genus *Orthohantavirus* (Family Hantaviridae) is a group of rodent-borne viruses that cause the human disease, hantavirus pulmonary syndrome (HPS) (Levis et al. 1997; Mills et al. 2010; Maes et al. 2019). Infection by hantaviruses usually results in an asymptomatic chronic infection in their rodent hosts and is transmitted to humans through inhalation of aerosolized particles from virus contaminated rodent excreta (Glass 1997; Schmaljohn and Hjelle 1997). It has been suggested that changes in climatic conditions may cause the rapid spread of the virus from focal "safe havens" (Mills et al. 1999; Abbot et al. 1999; Glass et al. 2007). Besides, both field and laboratory studies suggest that nearly all hantavirus transmission is via horizontal routes (Young et al. 1998; Padula et al. 2004). According to Young et al. (1998), the virus would be transmitted among individuals in rodent populations through fighting and social grooming. Several researchers have found that the presence of hantavirus antibodies is more frequent in adult males and that it is correlated with the presence of scars or wounds (Glass et al. 1988; Hinson et al. 2004; Bagamian et al. 2012).

In the southern regions of Argentina and Chile, *Oligoryzomys longicaudatus* has been identified as the principal host of Andes virus (ANDV), which is the main cause of HPS in the region (Levis et al. 1998; Calderón et al. 1999; Cantoni et al. 2001; Polop et al. 2010; Andreo et al. 2011, 2014). In Argentina, this rodent species inhabits multiple habitat types such as pastures, shrublands, Andean Patagonian forest and peridomestic settings (Piudo et al. 2005, 2011; Polop et al. 2010, 2014a; Andreo et al. 2012). Although the mechanism of transmission for ANDV infection is not fully understood, both laboratory and field studies indicate that infection is chronic in the host who excretes the virus in its urine, feces and saliva (Padula et al. 2004; Lázaro et al. 2007). Several studies have documented a positive relationship between *O. longicaudatus* population abundance and the prevalence of ANDV (Pearson 2002; Murúa et al. 2003; Murúa and Briones 2005; Sage et al. 2007; Polop et al. 2010). In this virus-host system, Piudo et al. (2012) and Polop et al. (2018) found that population structure (age and sex), the reproductive status of the host, and the presence of wounds were fundamental predictors when modelling the probability that the virus enters and/or persists in a population. However, Padula et al. (2004) expressed that it is likely that other factors, such as grooming or aerosol transmission, are required for efficient virus transmission. Recently, in a study of space use, Juan et al. (2018) found that *O. longicaudatus* males and females use space differently: Males have mutually exclusive home ranges which are not only larger than females' but also extensively overlap with several female home ranges. Based on these space patterns, Juan et al. (2018) suggested that this species may follow a polygynous mating system, in which dispersion is strongly biased toward males due to the avoidance of intrasexual local competition for breeding opportunities (Emlen and Oring 1977; Agrell et al. 1996; Waterman 2007; Wolff 2007). Thus, male-biased reproductive dispersion in *O. longicaudatus* would be primarily related to its mating system, beyond that infection may increase dispersion, as suggested by Douglass et al. (2007) and Lonner et al. (2008) for *Peromyscus maniculatus*.

The proliferation of the virus in an environment can have two phases: the spread within the host population and the dispersal between populations. Dispersal may occur more quickly in some populations, possibly because of differences in the early stages of infection, the population composition or the dispersal behavior of individuals (Abbot et al. 1999; Mills et al. 1999; Glass et al. 2007; Polop et al. 2018). Increasing the understanding of wild population dynamics and host dispersal are crucial to better characterize disease dynamics and devise ways to protect human health.

Dispersal depends on the degree of habitat saturation and the food, refuge and vacant reproductive territories available (Bondrup-Nielsen 1985; Lambin et al. 2001). Thus, high population density can lead to increased dispersal of voles (Lidicker 1975; Wolff 1999) and mice (Wolff 2003; Austrich et al. 2014). Many researchers study animal dispersal through the identification and quantification of resident and transient individuals present in the study population (Douglass et al. 2003; Priotto et al. 2004; Steinmann et al. 2006a, b; Lonner et al. 2008; Austrich et al. 2014). *Transients* or *dispersers* are individuals that do not establish a home range and move a minimum unidirectional distance equal to the average home range diameter of the population, both within and between populations. *Residents* are individuals that settle in a patch area and keep their movements within their home range's area (Stickel 1968a, b).

Several authors propose that underlying causes of dispersal are linked to mating systems and intrasexual competition and have important ecological consequences that affect both population dynamics and disease transmission (Lidicker and Stenseth 1992; Stenseth and Lidicker 1992; Clobert et al. 2012). According to Farias et al. (2006)

and Schooley and Branch (2006), both behavioral interactions and patterns of space use are factors that affect viral transmission. Thus, under the hypothesis that ANDV transmission is horizontal through *O. longicaudatus* male intrasexual competition we expect that the highest proportion of antibody-positive individuals: (1) is more likely to be males, (2) is more likely to be reproductively active, (3) is more likely to have wounds. Also, we expect that individuals with these features would be more common at higher population densities. Regarding the maintenance of ANDV in relation to dispersal, we expect a greater number of transient or disperser individuals to be hantavirus antibody-positive than residents at high population densities.

Materials and Methods

Study Area

We conducted this study at Rivadavia Lake valley (42°31 S; 71°27 W), Cholila, Andean region, Chubut Province. This province has been associated with human cases of HPS attributed to ANDV infection (Levis et al. 1998; Enría and Pinheiro 2000; Padula et al. 2000). The study area is a steppe-rainforest transition zone (for a detailed description of the study area, see Juan et al. 2018). Rodent populations were sampled in a shrubland habitat, characterized by native species, such as calafate (*Berberis buxifolia*), romerillo (*Acanthostyles buniifolius*), espino negro (*Rhamnus lycioides*) and Laura (*Schinus patagonicus*), and exotic species, such as rosa mosqueta (*Rosa* spp.). In this habitat, *Rosa* spp. prevails and high population abundances of *O. longicaudatus* occurred (Polop et al. 2010, 2014b; Andreo et al. 2012).

Rodent Trapping and Processing

We performed rodent trapping sessions in spring, summer, autumn and winter from spring 2011 (October) to spring 2013 (October), except in winter 2012 (due to weather conditions), on two capture-marked-recapture (CMR) grids of 10 × 10 traps, with an interstation distance of 20 m. Each grid was 3.24 ha and they were 150 m away from each other. Two live traps (8 × 9 × 23 cm) similar to a Sherman trap (Alejandro Möller manufacturer, Argentina) were placed at each station and baited with rolled oats, bovine fat and vanilla essence. To obtain enough recaptures to estimate individual's home range, each trapping session included ten consecutive nights (Juan et al. 2018). Traps were checked each morning. To identify captured animals, individuals were foot tagged with numbered metal rings. Trapped animals were weighed, and body and tail length were recorded. Sex and reproductive status (for males, scrotal or abdominal testicles; for females, perforate or non-perforate vagina, nipples visible or not and evidence of pregnancy) were recorded.

In this study, individuals without evidence of reproductive activity and a body mass less than 14 g, or between 14 and 19.9 g were considered juveniles and subadults, respectively; those individuals with evidence of reproductive activity (males with scrotal testes, and females with perforate vagina, visible nipples and/or evidence of pregnancy) and with a body mass greater or equal than 20 g were considered adults.

Wounds were considered an indicator of aggression among individuals. Thus, in each trapping session and in all captured *O. longicaudatus*, the presence of any peeling on the body surface, bites in ears, at the base of the tail, and/or at snout and flanks was recorded. For serological testing, blood samples were obtained from the retro-orbital sinus from each individual (only once per session trapping) using capillary tubes. Rodent blood samples were collected in cryovials, which were then centrifuged in the field, and stored in liquid nitrogen until further testing at the Instituto Nacional de Enfermedades Virales Humanas "Dr. Julio Maiztegui" (INEVH).

In each trapping session captured *O. longicaudatus* were classified as residents or transients. Residents were those individuals who maintained a home range during a trapping session without exploratory displacements. Transients were those individuals who did not maintained a home range (animals caught less than 3 times in the same trapping session) or moved a minimum unidirectional distance equal to the average home range diameter of the population. Home range configuration of each animal was calculated following the boundary strip methods (Stickel 1954). Transient and resident status of individuals was determined for each trapping session (Priotto et al. 2004).

Oligoryzomys longicaudatus population density was expressed for each trapping session as the number of unique individuals captured per hectare. Handling of rodents followed standardized safety guidelines recommended by the Centers for Disease Control and Prevention (Mills et al. 1995). The animals were treated in a humane manner according to the current Argentinean Laws (National Law 14346).

Serology

Hantavirus IgG antibodies were detected by an ELISA test using whole Maciel virus antigen (Guzman et al. 2013). Briefly, 96-well polyvinyl microplates were coated with Maciel hantavirus Vero E6 cell lysate and control antigens overnight; then, serum samples and positive and negative controls were applied, followed by a mix of peroxidase-conjugated anti-*Rattus norvegicus* and anti-*P. maniculatus* IgG. Additionally, in 8 of the MACV IgG ELISA positive *O. longicaudatus* samples, the ANDV genome was characterized by using RT-PCR and sequencing the amplicons of 303 nucleotides from the viral M segment obtained by Levis et al. (1998). The substrate applied was 2.20-azino-di(3-etilbentiazolin sulfonate) (ABTS, Kierkegaard & Perry Laboratories, Inc., Gaithersburg, MD). Absorbance was measured at 405 and 450 nm. Serum dilutions were considered positive if the optical density was > 0.2 after subtraction of the corresponding negative-antigen optical density. Serum samples with titers ≥ 400 were considered positive; cross-reactive IgG antibodies to Maciel virus were considered as a marker of infection with ANDV in *O. longicaudatus*, the primary ANDV reservoir in Southern Argentina.

Data Analysis

Prevalence of hantavirus antibodies over the course of the entire study and also by each trapping session was calculated as the number of antibody-positive animals divided by the total number tested, and it was expressed as a percentage. We considered seroconversion to have occurred when an antibody-negative individual captured during one trapping session was antibody-positive at a following trapping session. To assess the relationship between seroprevalence and sex, resident/transient status, or trapping session, a χ^2 test was used (Zar 1996). We used generalized linear models (GLM) (binomial distribution) to determine which variables are most associated with the condition of being infected or not. First, we evaluated all possible additive models and a null model using the R package MuMIn (Barton 2018). The response variable was seroprevalence status (positive or negative) and the predictor variables were: sex (fixed factor with two levels; male or female), population density by trapping session (fixed factor with two levels; high or low density), wounds (fixed factor with two levels; presence or absence) and status (fixed factor with two levels; resident or transient). Akaike information criterion was used as a measure of a model fit (the smaller the AIC, the better the fit). Weights of each model were considered to select the best in the set of candidate models (Burnham and Anderson 2002). Statistical analyses were carried out using R version 3.0.3 library (nlme) (R Development Core Team 2009, www.r-project.org).

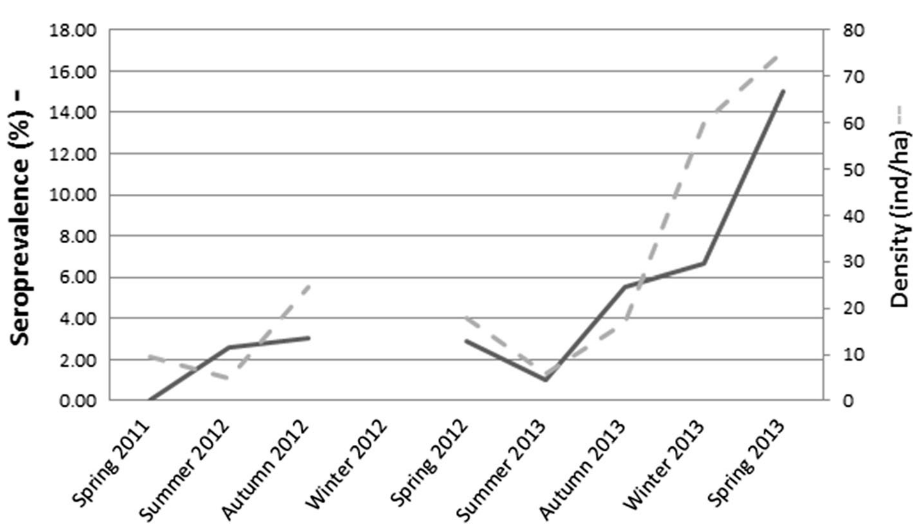

Fig. 1. Seroprevalence of IgG antibodies specific for Hantavirus (Andes), detected by ELISA tests for rodent assembly in a shrubland habitat (valley of the Rivadavia Lake, Chubut-Argentina Province), registered in each of the trapping sessions, from spring 2011 to spring 2013. The absence of values corresponding to winter 2012 is due to the fact that there was no sampling at that station. Line gray and discontinuous indicates seroprevalence; line black and continuous indicates population density values.

Table 1. Model Selection Based on AIC Comparison of Generalized Linear Models (GLM) Describing Seroprevalence of *Oligoryzomys longicaudatus*, in a Shrubland Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina).

Model	(Intercept)	Wounds	Resident	Sex	Trapping session	*df*	logLik	AICc	Delta	Weight
6	**− 4.168**	+		+		**3**	**− 259.17**	**524.4**	**0**	**0.424**
14	**− 4.107**	+		+	+	**4**	**− 258.57**	**525.2**	**0.81**	**0.283**
8	**− 4.204**	+	+	+		**4**	**− 259.04**	**526.1**	**1.76**	**0.175**
16	− 4.143	+	+	+	+	5	− 258.43	526.9	2.56	0.175
2	− 3.343	+				2	− 270.03	544.1	19.72	0
10	− 3.281	+			+	3	− 269.24	544.5	20.14	0
4	− 3.38	+	+			3	− 269.9	545.8	21.46	0
12	− 3.319	+	+		+	4	− 269.08	546.2	21.84	0
5	− 3.681			+		2	− 274.92	553.8	29.49	0
13	− 3.617			+	+	3	− 274.17	554.4	30	0
7	− 3.732		+	+		3	− 274.68	555.4	31.03	0
15	− 3.67		+	+	+	4	− 273.88	555.8	31.44	0
9	− 2.54				+	2	− 290.29	584.6	60.23	0
1	− 2.605					1	− 291.32	584.6	60.29	0
11	− 2.6		+		+	3	− 289.93	585.9	61.53	0
3	− 2.66		+			2	− 291.06	586.1	61.76	0

Models are ordered by ΔAIC. The best models are indicated in boldface type and + signs, variables which were included in models.

Table 2. Coefficients (β) for Best Linear Models for Seroprevalence of *Oligoryzomys longicaudatus*, in a Shrubland Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina).

Response variable	Factors	β (SE)	*t* value	*P* value
(a) Model 6 (Seroprevalence ∼ wounds + sex + 1, family = binomial)				
Seroprevalence	Intercept	**− 4.1681 (0.3098)**	**− 13.455**	**< 2e−16*****
	Wounds	**1.3568 (0.2496)**	**5.435**	**5.48e−08*****
	Sex	**1.3138 (0.3141)**	**4.183**	**2.88e−05*****
(b) Model 14 (Seroprevalence ∼ wounds + sex + trapping session + 1, family = binomial)				
Seroprevalence	Intercept	**− 4.1071 (0.3136)**	**− 13.098**	**< 2e−16*****
	Wounds	**1.3516 (0.2498)**	**5.41**	**6.29e−08*****
	Sex	**1.3044 (0.3143)**	**4.15**	**3.33e−05*****
	Trapping session	− 0.4112 (0.3913)	− 1.051	0.293
(c) Model 8 (Seroprevalence ∼ wounds + status + sex + 1, family = binomial)				
Seroprevalence	Intercept	**− 4.2043 (0.3189)**	**− 13.185**	**< 2e−16*****
	Wounds	**1.353 (0.2498)**	**5.417**	**6.07e−08*****
	Status	0.1304 (0.2591)	0.503	0.6150
	Sex	**1.3136 (0.3141)**	**4.181**	**2.90e−05*****

Standard errors (in parentheses) and the significance of the coefficients are also shown; $P < 0.05$ shown in boldface type. The effect of each term in the model is tested. *P* values tested the null hypothesis that $\beta = 0$. The terms with $P < 0.05$ have some discernable effect.

Results

During the study, 1411 different individuals were captured with a total effort of 26,517 trap nights. The assemblage was comprised of 8 small rodent species: *Oligoryzomys longicaudatus* (1072), *Abrothrix longipilis* (188), *A. olivaceus* (109), *Loxodontomys micropus* (20), *Reithrodon auritus* (11), *Chelemys macronyx* (7), *Irenomys tarsalis* (3) and

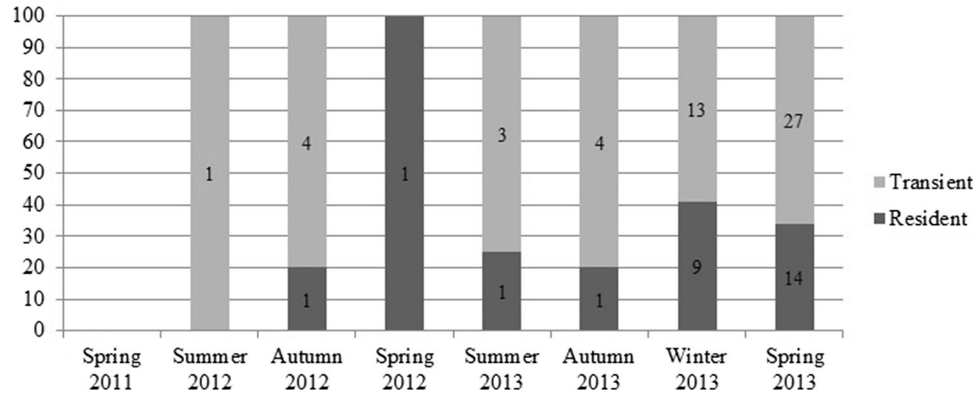

Fig. 2. Percentage of males of *Oligoryzomys longicaudatus* with presence of IgG antibodies specific for Hantavirus (Andes) discriminated by their condition of resident or transient, registered in each of the trapping sessions, between spring 2011 and spring 2013, in a shrubland habitat in the valley of Lake Rivadavia (Province of Chubut, Argentina). The numbers within the columns represent the totality of individuals of each condition.

Geoxus valdivianus (1). Eighty-eight percent of the total *O. longicaudatus* captured were adults. During the study period, population density fluctuated between 5.00 and 75.46 individuals/hectare (Fig. 1). For the first year (2012), the lowest density occurred during the summer (5.00 ind/ha) and the highest was detected in the autumn (24.69 ind/ha), while for the second year (2013) the lowest density was in summer (5.71 ind/ha), and the maximum density was in spring (75.46 ind/ha). High percentages of transient individuals of both sexes of *O. longicaudatus* were recorded, reaching values higher than 70%.

We analyzed 1327 blood samples from captured and recaptured rodents, and specific IgG antibodies to hantavirus were detected in 98 individuals of three species (96/1115 *O. longicaudatus*, 1/164 *Abrothrix olivaceus* and 1/48 *A. longipilis*). The total prevalence of hantavirus antibodies in *O. longicaudatus* for the study period was 8.61% (83 males and 13 females/1115 individuals), with minimum prevalence in spring 2011 and summer 2013, and maximum in spring 2013 (62/413 = 15.38%) (Fig. 1). In this study, we found that the highest seroprevalence values were obtained at highest population densities (autumn 2012; spring 2013) (Fig. 1).

Models were obtained to determine which variables had a stronger relationship with the condition of being infected are detailed in Table 1, and those that showed the lowest AICc values were selected to draw inferences. Wounds and sex were present in the 3 most parsimonious models. Trapping session (model 14) and resident/transient status (model 8) also influence serologic condition increasing the probability for *O. longicaudatus* to be seropositive (Table 1). The coefficients for the best models are shown in Table 2.

Prevalence of hantavirus antibodies was more frequent in adult males (86.7% infected males) ($\chi^2 = 49.6$, $df = 1$, $p < 0.001$). No association was found regarding resident or transient status ($\chi^2 = 0.42$, d.f = 1, $p = 0.52$). Nevertheless, during the study period, the percentage of seropositive transient males (66%) was greater than resident males (Fig. 2).

However, when trapping sessions were included in the analysis, there was a significant association between antibody prevalence and being male in winter 2013 ($\chi^2 = 10.62$, $df = 1$, $p = 0.0011$) and spring 2013 ($\chi^2 = 11.72$, $df = 1$, $p = 0.0006$). Although both the number of seropositive transient and resident males increased during these trapping sessions, the increase in transients was much greater (Fig. 2). Considering all *O. longicaudatus* individuals, our results showed that although both sexes exhibited wounds, the percentage of males with wounds was almost double compared to females (45.09 ± 21.60 and 25.87 ± 9.82%, respectively).

The highest percentages of seroconversions were among males captured in winter and spring of 2013 (85.7% seroconverted individuals) (Table 3), coinciding both with the highest population densities (59.88–75.5 ind/ha, respectively) and a greater percentage of males with wounds (> 40%). The average weight of seroconverted males captured in autumn and spring 2013 (37.68 ± 4.38 g) was greater than the mean weight value for *O. longicaudatus* adult males (33 ± 8 g).

Table 3. Seroconversions Recorded for *Oligoryzomys longicaudatus* by Sex and Age in a Shrublands Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina), from Spring 2011 to Spring 2013.

Sex	Foot-tag number	Summer 2013	Autumn 2013	Winter 2013	Spring 2013
Female	1945		Subadult (−)		**Adult** (+)
	1528			Adult (−)	**Adult** (+)
	1800			Adult (−)	**Adult** (+)
Male	1530			Adult (−)	**Adult** (+)
	1539			Adult (−)	**Adult** (+)
	1547			Adult (−)	**Adult** (+)
	1661			Adult (−)	**Adult** (+)
	1718			Adult (−)	**Adult** (+)
	1809	Juvenile (−)	**Adult** (+)		
	2000		Adult (−)	Adult (−)	**Adult** (+)
	1490			Adult (−)	**Adult** (+)
	1554			Adult (−)	**Adult** (+)
	1695			Adult (−)	**Adult** (+)
	1875	Adult (−)	**Adult** (+)		

Bold indicates seroconversions

Discussion

Our results showed that reproductively active males with wounds constitute the highest proportion of hantavirus antibody-positive *O. longicaudatus*, supporting our hypothesis that ANDV transmission is horizontal through male intrasexual competition. However, other indirect transmission routes were not tested in this study. The average prevalence for hantavirus antibody found in this study was 8.79% (range 0–15%), which is within the range reported by other authors for sigmodontine rodents from Argentina and other areas of America (3–15%) (Levis et al. 1997; Williams et al.1997; Cantoni et al. 2001; Padula et al. 2004; Enría and Levis 2004; Torres-Perez et al. 2004; Mills et al. 2007). Although other studies found an association between seasonal and annual seroprevalence values and population density in *O. longicaudatus* (Piudo et al. 2005; Polop et al. 2010), *O. flavescens* (Mills et al. 2007) and *Peromyscus maniculatus* (Kuenzi et al. 1999), in ours this association was only evident in 2013. In our study, a larger percentage of adult males were antibody-positive. This could be explained by male intrasexual competition of *O. longicaudatus* mating system (Juan et al. 2018), in which a minority of males monopolizes several fertile females leaving other males without access to them. Several authors have found that the presence of wounds is a good indicator of aggressive interactions in voles and mice (Blanchard and Blanchard 1977; Van Zegeren 1980; Dewsbury 1988; Wolff and Summerlin 1993; Steinmann et al. 2009; Steinmann and Priotto 2011). In *O. longicaudatus*, the high percentage of males with wounds could indicate agonistic interactions between active reproductively males. The association between the presence of wounds and infections has been observed in different species: SNV, in *P. maniculatus* (Mills et al. 1997), Seoul Virus, in *Rattus norvergicus* (Glass et al. 1988) and Oliveros Virus (an arenavirus), in *Akodon azarae* (Mills et al. 1994). Biggs et al. (2000) proposed that wounding would occur because at high population densities the probability of contact between individuals increases, increasing the chances of transmission of the virus to susceptible rodents. This is also consistent with a polygynous mating system in which intrasexual competition between males to gain access to receptive females increase with population density (Clutton-Brock 1989; Loughran 2007; Korpela et al. 2011; Bonatto et al. 2013, 2015). Other studies have suggested that the frequent association between wounds and seroprevalence could be the result of a post-infection phenomenon (Glass et al. 1988; Calisher et al. 1999; Douglas et al. 2001; Hinson et al. 2004; Kallio et al. 2006), that at high population density could increase transmission by viral contamination of the environment (spill-over), more than by intraspecific behavioral interactions. In our study, this last mechanism could be proposed for the other two positive species of *Abrothrix* recorded.

Our results indicate that *O. longicaudatus* adult males are more like to be dispersers and seropositive. We captured few (13) seropositive *O. longicaudatus* adult females as compared to adult males (83). Seropositive disperser males, together with the high rate of exogamy found for this species by Ortiz et al. (unpublished data), would favor an increase in the contact rate between males, and therefore, increase the probability of dispersion of the virus among populations. These authors found that males did not show significant genetic structuring in any of the years compared (the distribution of their genotypes was always random) and proposed that *O. longicaudatus* females have a philopatric behavior, while males represent the dispersing sex. This is consistent with *O. longicaudatus*' polygynous mating system, in which, faced with an increase in intrasexual competition, males that fail in the competitive interactions, would disperse from their original area in search of exclusive reproductive spaces to monopolize receptive females (Emlen and Oring 1977; Clutton-Brock 1989). Thus, because adult *O. longicaudatus* males have higher infection rates of ANDV compared with females, those males are more likely to transmit the virus as they disperse. On the other hand, seropositive resident males of *O. longicuadatus* would be responsible for maintaining the infection within the population. Calisher et al. (1999) found that long-lived, persistently infected *P. maniculatus* by SNV serve as reservoirs within populations, reintroducing the virus into susceptible animals every spring.

In our study, body mass of adult males *O. longicaudatus* that seroconverted were similar to those reported by Piudo et al. (2012) and Polop et al. (2018). Piudo et al. (2012) found that adult males with a body mass greater than 37 g had a probability greater than 50% of presenting IgG antibodies specific for ANDV, increasing this probability to 80% in individuals with a body mass greater than 44 g. The highest number of seroconversions was between August and October 2013 (late winter–spring), when there was a higher population density and a greater percentage of males with wounds. Douglass et al. (2007) found that the seroconversion rate for *P. maniculatus* began to increase in late winter through spring, but contrary to our results, they found that seroconversion rates remained constant through summer. This difference in seroconversion rate between *P. maniculatus* and *O. longicaudatus* could be the result of differing sampling frequencies between both studies, being monthly that carried out by Douglass et al. (2007) and seasonal ours. We acknowledge that a more intense sampling frequency would be optimal, but the distances between the area of study and our University, in addition to the logistics involved, prevented it. In relation to seroconversion and the presence of wounds, these authors did not find a strong association between them. Instead they suggested that wounds might be inflicted by infected rodents whose behaviors were influenced by the virus. In our study, the high percentage of seroconverted adult males with wounds at high population density periods could be related to an increase in intrasexual competition associated with their mating strategies.

Conclusion

Our study supports the hypothesis that ANDV transmission is horizontal through male intrasexual competition, similar to what has been found for other hantaviruses, although alternatives indirect transmission routes were not tested in this study. Our data also allow us to support the hypothesis that hantavirus antibody-positive transient individuals disperse the virus between populations; meanwhile, seropositive resident males of *O. longicuadatus* would be responsible for maintaining the infection within a population. Our study was able to follow many more individuals that seroconverted as compared with previous ANDV CMR studies and thus enabled a better understanding of the ecology and epidemiology of the ANDV host system.

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