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The influence of sugarcane pre-harvest fire on hantavirus prevalence in Neotropical small mammals

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Abstract

The use of pre-harvest fire in sugarcane fields surprisingly results in an increase in the abundance of Neotropical Sigmodontinae rodents, which might carry hantavirus. By contrast, fire suspension induces a decline in rodents in the first 5 years. The present study aimed to evaluate the effect of sugarcane harvest regimes on hantavirus prevalence in wild rodents. Field collections were carried out on a sugarcane production area in Northeast São Paulo, which is responsible for 30% of the ethanol production in Brazil. A few years after pre-harvest fire suspension, a high prevalence of hantavirus was found in small rodents at lower population density, but apparently higher population growth rate. Differences in life cycle between the rodents and their predators may explain such density patterns, as small rodents can breed twice or even three times each year, whereas their predators usually breed only once a year. Similarly, the temporal dynamics of the predator–prey relationship suggests that hantavirus prevalence is related to small rodent's population growth and not density. Only *Akodon montensis*, *Calomys tener*, and *Necromys lasiurus* contained immunoglobulin G antibodies

against the recombinant nucleoprotein of *Araraquara orthohantavirus*, a genotype of *Andes orthohantavirus*, with no interspecific variation in seroprevalence among these species. However, males presented higher prevalence rate than females, possibly due to a male-biased dispersal pattern and a higher frequency of antagonistic interactions. Governance measures to mitigate the role of small wild rodents on the emergence of hantavirus in agricultural landscapes dominated by sugarcane plantations should include the use of wildlife-friendly management techniques (e.g., to mitigate the mortality of the predators of small rodents), human capacity building concerning wildlife-related conflicts, and multifunctionality of agricultural landscapes. Future studies should prioritize the possible relationship between microhabitat structure and hantavirus prevalence in small rodents in agricultural landscapes dominated by sugarcane fields.

INTRODUCTION

Land use change and agricultural expansion have been impacting wildlife in many ways including direct habitat loss (Kehoe et al., 2017), environmental contamination (Matthiessen et al., 2018), antibiotics resistance by microorganisms (Semedo-Lemsaddek et al., 2018), and the spread of emerging infectious diseases (Verdade & Ferraz, 2013). However, despite these impacts, agricultural landscapes are fundamental for the conservation of a relevant part of biodiversity as conservation units like national parks and biological reserves are unable to provide integral conservation for the native biota (Verdade et al., 2016). In such context, agricultural landscapes should be managed multifunctionally keeping their primary mission of biological production, and also a secondary mission of accomplishing biological conservation (Martinelli et al., 2010; Verdade, Penteado, et al., 2014).

Small rodents are usually the basis of the food web in agricultural landscapes of Southeast Brazil (Verdade et al., 2011). Anthropogenic land-use change favors opportunistic and/or generalist species of rodents that are known to be natural hosts of hantavirus (Dearing & Dizney, 2010; Figueiredo et al., 2003; Gheler-Costa et al., 2013; Martin et al., 2012; Riquelme et al., 2015; Ruedas et al., 2004; Yahnke et al., 2001).

In such circumstance, by hypothesis, the agricultural management of sugarcane plantations might affect their use of space. In fact, the use of fire pre-harvest in sugarcane fields even increases the local abundance of wild rodents (Gheler-Costa et al., 2013).

Small rodents can host pathogens relevant to human health such as *Leptospira* (Vieira et al., 2019), Ricketsia

(Lopes et al., 2018), and hantavirus (Camp et al., 2021). This highlights their importance to One Health concept in which the human–animal–ecosystem interface may determine the evolution and emergence of pathogens (Destoumieux-Garzón et al., 2018).

Orthohantaviruses cause a decline in fitness within natural rodent hosts (Kallio et al., 2007; Luis et al., 2012). However, transmission to humans can lead to renal and cardiopulmonary compromise (Clement et al., 2014). Orthohantaviruses are spread by aerosolized rodent excreta. The main transmission route to humans occurs by inhaling viral particles, or by direct contact with blood or saliva of infected animals (Jonsson et al., 2010).

Hantavirus epidemiology is affected by the ecological characteristics of the hosts, such as body size, age distribution, and abundance. Such variables may affect hantaviral prevalence by horizontal transmission between hosts (Anderson & May, 1991; Gieseke, 1994). For instance, large male deer mice tend to be more infected than small ones due to their larger territories and more frequent agonistic interactions related to territorial defense (Hjelle & Yates, 2001). In addition, hantavirus prevalence has been reported to be density-dependent (Olsson et al., 2002; Riquelme et al., 2015).

The emergence of hantavirus in Brazil in the last two decades is likely due to agricultural intensification and urbanization (De Sousa et al., 2008; Figueiredo et al., 2008; Oliveira, Guterres, et al., 2014). Agricultural landscapes dominated by sugarcane fields in Southeast Brazil contain potential rodent reservoirs of hantavirus such as *Necromy lasiurus*, *Oligoryzomys nigripes*, *Calomy tener*, and *Akodon montensis* (Figueiredo et al., 2008, 2009; Gheler-Costa et al., 2012, 2013; Martin et al., 2012). As a matter of fact, a

combination of pre-harvest fire and manual harvest of sugarcane plantations can apparently result in an increase in human hantavirus infection (Figueiredo et al., 2009).

Sugarcane fields are harvested for ethanol/sugar industry from April through November in the state of São Paulo, which corresponds to 54% of the ethanol and 61% of the sugar produced in Brazil (Ramos & Nachiluk, 2016). Traditional sugarcane plantation management included pre-harvest fire, in order to facilitate manual harvest. Attempts to change harvest from manual to mechanic—to ban the use of pre-harvest fire—have been made in the state of São Paulo in the last decade to minimize the environmental pollution and human respiratory problems of local populations (Gheler-Costa et al., 2013). However, an agreement between the ethanol industry and the local government has never been fully achieved, resulting only in the partial suspension of pre-harvest fire.

The present study aimed to evaluate the effect of sugarcane pre-harvest fire on orthohantaviral prevalence among wild rodents. We tested the following hypotheses: (1) hantavirus prevalence in small rodents varies according to the sugarcane harvest regime; (2) hantavirus prevalence in small rodents varies according to species, sex, and age class (juveniles or adults); and (3) the suspension of pre-harvest fire may result in a decrease of the current prevalence rate of hantavirus in rodents due to a possible asynchrony in life cycle between predators and prey (Boone et al., 1998; Singleton, 2000; Sutherland & Dickman, 1999) (Figure 1).

STUDY AREA

This study was carried out at Usina Santa Elisa Vale (21°04′34″ S, 48°00′22″ W), located at Sertãozinho municipality in the northeast region of the state of São Paulo, in southeastern Brazil, which is responsible for 60% of the ethanol production (Scheer & Rocha, 2006), with a human population of approximately 1.2 million people. The study area extent is 1090 ha, with 844 ha of sugarcane plantations, 125 ha of native forest restoration areas, 85 ha of native forest remnants, and 36 ha of artificial water reservoir (Figure 2). The local climate is considered as tropical savanna (Aw according to Koeppen), with a minimum average temperature of 16°C and maximum of 25°C, and an average annual rainfall of 1500 mm (CEPAGRI, 2018).

METHODOLOGY

Sampling methodology

Four distinct types of sugarcane harvest regimes were considered: (1) manual harvest with the use of pre-harvest fire (PHF); (2) mechanical harvest without the use of fire in the last 3 years (Y3); (3) mechanical harvest without the use of fire in the last 5 years (Y5); and (4) mechanical harvest without the use of fire in the last 10 years (Y10). For each of these management schemes, four stands were selected, totaling 16 sampling plots. These areas were at
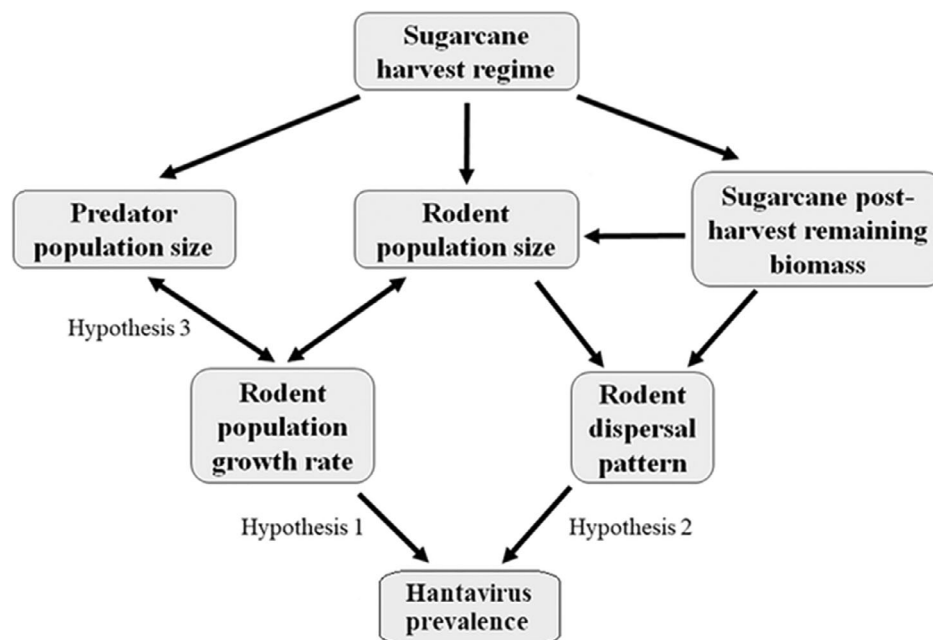
FIGURE 1 Relationship between harvest regime and hantavirus prevalence in wild rodents. Relationship between fire management in sugarcane fields in southeastern Brazil and rodents, predators, and hantavirus prevalence. For hypotheses description, see text. Arrow directions refer to causal effect.
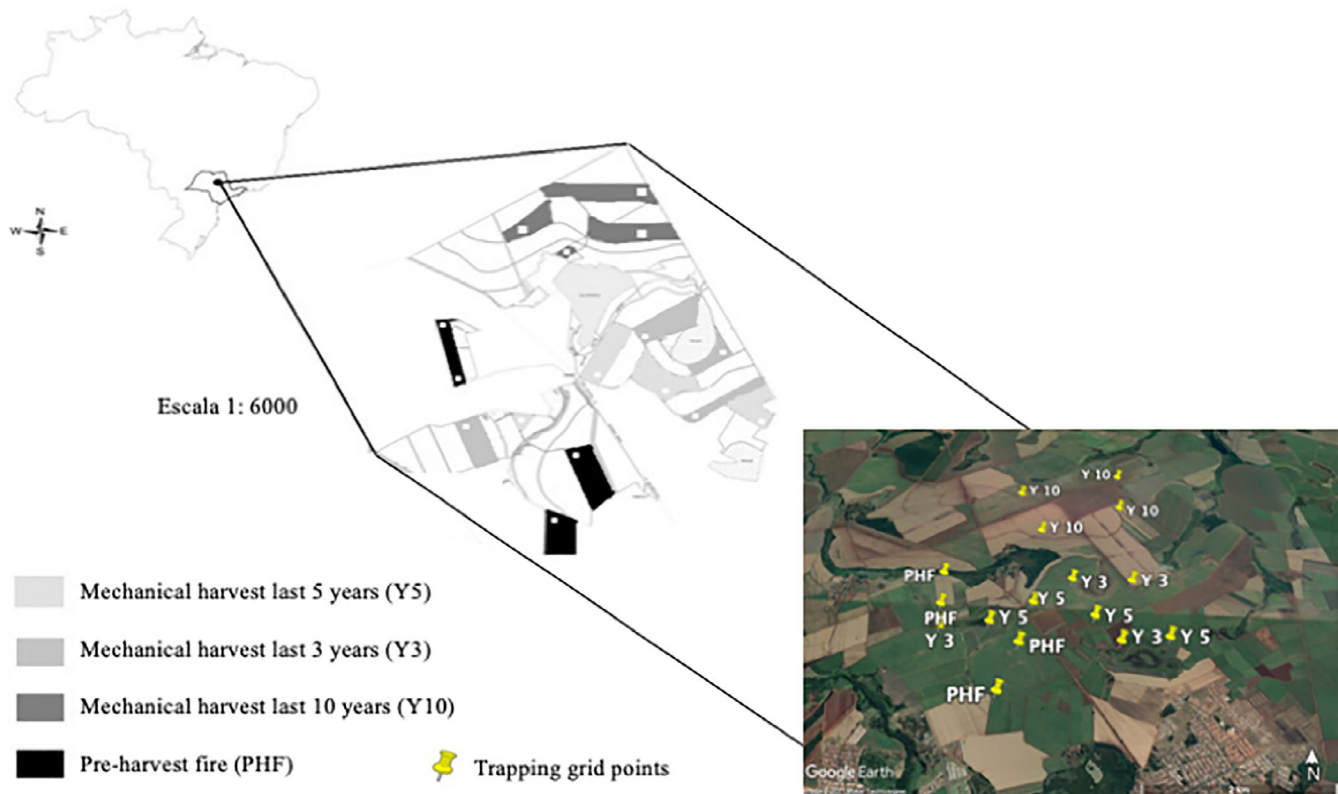
FIGURE 2 Study area and trapping grids in sugarcane stands.

least 500 m apart and were located further 500 m from native forest remnants in order to provide independent sampling (see Martin et al., 2012, p. 186). Within each of the 16 sampling plots, a 4 × 4 trapping grid was set, with Sherman live traps (8 × 9 × 23 cm) separated 20 m from each other (Figure 1). The trapping grids were located more than 100 m from the border of the stands. Each trap was baited with a mixture of oatmeal, vanilla essence, and Brazilian peanut flour candy. Seven bimonthly trapping campaigns were carried out between February 2009 and February 2010 (February, March, April, June, August, October, December from 2009 and February 2010), with traps remaining active for three consecutive nights and checked every morning (Gheler-Costa et al., 2012; Martin et al., 2012). The owners allowed captures only 10 days after fire. After 10 years of data collection, the same sugarcane stands remain operative in the study area.

The specimens were anesthetized with Halothane and blood was collected from the retro-orbital sinus, using capillary tubes. Blood samples were collected into separate, labeled cryovials using clean, sterilized instruments for each animal and placed immediately into liquid nitrogen (Mills et al., 1999). The following data were recorded from each specimen: species, sex (by direct observation of the gonads), and age class (juvenile or adult, according to the specimens' body mass and pelage color). The identification to species level was based on morphometric characteristics (Ramos & Nachiluk, 2016) and complemented by molecular data (e.g., fragment of *cyt-b* gene) (Salazar-Bravo et al., 2013). Each animal was marked using subcutaneous transponders (Digital Angel, dimension: 11.5 × 2 mm) to prevent multiple sampling of the same individual (Ramos & Nachiluk, 2016). After processing, each specimen was released at the trap site. All animals were handled and sampled according to previous recommendations (Mills et al., 1995) under protocols approved by the Chico Mendes Institute of Biodiversity Conservation and Ethics Committee for Animal Research of the School of Medicine of Ribeirão Preto, University of São Paulo (refs. 0115/2007, 115/2008, and 19364/2009).

Analytical methodology

The family Hantaviridae comprises seven genera according to its evolutionary history and distinct host reservoirs: Actinovirus (fish), Aganathovirus (jawless fish), Loanvirus (bat), Mobatvirus (bat or mole), Orthohantavirus (rodent), Thottimvirus (shrew), and Reptillovirus (reptile) (Adams et al., 2017; Bennett et al., 2014; Sabino-Santos et al., 2015, 2018). The genus Orthohantavirus is the only one so far reported to infect humans (Laenen et al., 2019;

Sabino-Santos et al., 2019). In South America, hantaviruses are zoonoses associated with wild rodents of the family Cricetidae, subfamily Sigmodontinae; however, recently, natural infections of bats have been reported, with no evidence of transmission to humans (Sabino-Santos et al., 2018, 2019).

To date, in Brazil, there are two species of hantavirus associated with human disease: *Andes orthohantavirus* (ANDV) and *Laguna-Negra orthohantavirus* (LNV) (Sabino-Santos et al., 2019). Within ANDV there are three genotypes: *Araraquara orthohantavirus* (ARQV), *Castelo dos Sonhos orthohantavirus* (CASV), and *Juquitiba orthohantavirus* (JUQV). On the other hand, within LNV there are two genotypes: *Anajatuba orthohantavirus* (ANJV) and *Rio Mamore orthohantavirus* (RIOMV) (Colombo et al., 2019; Delfraro et al., 2017; Firth et al., 2012; Oliveira, Guterres, et al., 2014). The ARQV genotype is the most virulent hantavirus in the Brazilian Cerrado and possibly in the world, with lethality of approximately 50% (Figueiredo et al., 2009; Oliveira, Gentile, et al., 2014; Raboni et al., 2009; Travassos da Rosa et al., 2012).

All samples were screened for the presence of specific immunoglobulin G (IgG) antibodies for hantavirus by an indirect enzyme-linked immunosorbent assay (ELISA), using as antigen a recombinant nucleoprotein (rN) of ARQV produced at the Center for Virology Research, School of Medicine of the University of São Paulo, at Ribeirão Preto. This assay was performed as previously described in the literature (Homes et al., 2000). As secondary antibodies for rodents, we used a mix of anti-*Rattus rattus* for subfamily Murinae and anti-*Peromyscus leucopus* for subfamily Sigmodontinae (KPL, Gaithersburg, MD, USA), and for marsupials, family Didelphidae, we used an anti-opossum (Alpha Diagnostics Intl. Inc., San Antonio, TX, USA). This ELISA assay was supported by 97.2% sensitivity, 100% specificity, 100% positive predictive value, and 98.1% negative predictive value when compared with an indirect IgG-ELISA using rN antigen of ANDV, which is the most used serological test for hantavirus in South America (Figueiredo et al., 2009; Gheler-Costa et al., 2013). For detection of hantavirus infection in rodent serology followed by immunoblotting and reverse transcription–polymerase chain reaction, detection of viral RNA may be used, and followed by sequencing and virus isolation, if required. However, in the present study, we only used serological test for hantavirus.

The prevalence of animals with antibodies against hantavirus, according to each species, was calculated by dividing the number of positives by the total number of analyzed animals of each species. However, the nature of the data is binary, that is, 0 when the collected specimen was not infected by hantavirus and 1 when it was. Hence, we evaluated the effect of harvest regime (PHF, Y3, Y5, and Y10),

species, sex, and age class on hantavirus prevalence in Neotropical small mammals living in sugarcane plots, as suggested previously (Abbott et al., 1999; Olsson et al., 2002), fitting binomial generalized linear models with a logit kink function, including these effects in the linear predictor. Since hantavirus prevalence was very sparse when splitting the data by age, sex, and harvest regime, the two-way interactions between age and harvest regime, as well as sex and harvest regime, were not estimable. Therefore, our maximal linear predictor included the additive effects of harvest regime, species, sex, and age. The significance of the effects was assessed using an analysis of deviance (McCullagh & Nelder, 1989). Multiple comparisons were performed by obtaining the 95% confidence intervals for the linear predictor. When all observations within a level of an explanatory variable were zero, this level was omitted from the analysis since it did not contribute to variability.

The possible influence of predator–prey relationship on the small mammals' demography along the years after pre-harvest fire suspension on sugarcane fields was checked using a modified Lotka–Volterra predator–prey model, given by:

$$\begin{cases} \dfrac{dR}{dt} = \alpha R - \beta RP - \theta_R RK(t) \\ \dfrac{dP}{dt} = -\gamma P + \delta RP - \theta_P PK(t) \end{cases},$$

where R and P represent prey and predator populations, respectively, t is the time (in years), α is the prey growth rate, β is the mortality rate for the prey due to encounter with the predator, γ is the predator natural mortality rate, δ is the predator growth rate due to prey consumption, and θ_R and θ_P are parameters associated with the mortality rates of prey and predator, respectively, due to pre-harvest fire.

The original Lotka–Volterra model was adapted in this study to introduce sudden perturbations in dynamics representing prey and predator mortality caused by the pre-harvesting fire. Such perturbations had the duration of few days ($d = 10$) and were described by a sum of Gaussian kernel functions, $K(t)$, written as follows:

$$K(t) = \sum_{i=1}^{b} \exp\left\{\frac{-1}{2}\left(\frac{t - \mu_i}{\sigma}\right)^2\right\},$$

where b is the number of times pre-harvest fire was performed and μ_i is when (in years) the ith fire took place. The duration of each fire event was set as 4σ (in years), then $\sigma = d/(4 \times 365)$. The kernel function represents fire intensity, assuming the value 0 when no fire is

taking place and a maximum value of 1 during an intense fire process.

For the simulation procedure, parameters were set as $\alpha = 3$, $\beta = 0.4$, $\gamma = 2$, $\delta = 0.1$, $\theta_R = 50$, $\theta_P = 20$, and $d = 10$. The initial conditions were $R = 20$ and $P = 5$. We simulated the population dynamics for 10 years under four different scenarios related to a previous study (Figueiredo et al., 2003): (1) no fire over the last 10 years ($K(t) = 0$, for all $t > 0$); (2) no fire over the last 5 years and annual pre-harvest fire before that ($\mu_i = i, b = 5$); (3) no fire over the last 3 years and annual pre-harvest fire before that ($\mu_i = i, b = 7$); and (4) annual fire over the last 10 years ($\mu_i = i, b = 10$). Simulations were performed in software R (R Core Team, 2018) using the package simecol (Petzoldt & Rinke, 2007) and phase-plan studies were carried out with the package phaseR (Grayling & Burger, 2018). All R codes used to analyze the data and produce the simulations of the modified Lotka–Volterra model are available in Data S1.

RESULTS

A total of 396 individuals were captured over 5376 trap nights, with a capture success of approximately 7.4%. The number of captures varied from 48 in Y5 to 153 in PHF (see Table 1). There was a significant effect of harvest regime on hantavirus prevalence (deviance = 28.32, df = 2, $p < 0.0001$), with higher prevalence found in Y5 (25%, 12 out of 48), than on the other treatments (PHF: 1.31%, 2 of 153; Y3: 4.17%, 3 of 72, and Y10: 0 of 123) (Table 1, Figure 2). These results corroborate Hypothesis 1.

Only *A. montensis*, *Calomys tener*, and *Necromys lasiurus* (all Sigmodontinae rodents) contained IgG antibodies to the rN of ARQV, respectively, with 3.03% (1 of 33), 3.68% (6 of 163), and 6.37% (10 of 157), totaling 17 individuals, with no relevant interspecific variation in seroprevalence (deviance = 0.99, df = 2, $p = 0.6110$) (Table 1, Figure 4). There was also no significant effect of age class (deviance = 1.30, df = 1, $p = 0.2536$), with 8% (12 of 150) for adults and 4.76% (5 of 105) for juveniles (Figure 2). However, males presented a significantly higher seroprevalence than females (deviance = 4.83, df = 1, $p = 0.0280$), with 10.43% (12 of 115) for males and 3.57% (5 of 140) for females (Figure 3). These results partially corroborate Hypothesis 2.

Based on the simulation results, the populations eventually drop near to the origin of the phase plane in response to the fire effects and, consequently, the trajectories followed by the populations become wider after these fire events (Figures 4 and 5). The population sizes of prey and predator can rapidly decrease due to fire effects. A consequence of these events is an intense growth rate of the prey population in the absence of predators in the area, given the rodents reproduce much faster than their predators (Eisenberg & Redford, 1999). Past a certain time without fire, the predator is able to respond to prey growth and population sizes fluctuate again, as predicted by the classical Lotka–Volterra equations (Figure 4). However, the fluctuations observed before and after pre-harvest fire are not necessarily similar. Simulation results indicate that the prey population size often reaches higher values than those observed before the burning events and, consequently, the fluctuations become more intense.

Such patterns may be explained by the fact that, in the Lotka–Volterra model, lower values of population sizes for prey and predators are associated with wider trajectories in the phase space (Figure 4). Therefore, after

TABLE 1 Prevalence of hantavirus immunoglobulin G antibodies in small mammals against the recombinant nucleoprotein protein of *Araraquara orthohantavirus* according to the sugarcane harvest regime in Southeast Brazil.

| | Harvest regimes | | | | | | | | | | Body mass (g) | |
| | PHF | | Y3 | | Y5 | | Y10 | | Total | | | |
Species	Nt	Ni	Nt	Ni	Nt	Ni	Nt	Ni	Nt	Ni	Females	Males
Am	17	0	6	1	7	0	3	0	33	1	19.1 ± 3.3	17.3 ± 2.8
Ct	61	2	31	2	23	2	48	0	163	6	13.3 ± 4.0	15.4 ± 3.7
Mm	5	0	0	0	0	0	7	0	12	0	14.0 ± 4.1	16.0 ± 2.3
Nl	70	0	29	0	13	10	45	0	157	10	38.0 ± 15.4	35.1 ± 16.4
On	0	0	6	0	5	0	18	0	29	0	14.3 ± 2.3	17.4 ± 2.7
Total	153	2	72	3	48	12	123	0	396	17		

Note: Nt, total no. collected specimens; Ni, no. infected specimens. Harvest regimes: PHF, pre-harvest fire; Y3, harvest without fire in the last 3 years; Y5, harvest without fire in the last 5 years; Y10, harvest without fire in the last 10 years. Species: Am, *Akodon montensis*; Ct, *Calomys tener*; Mm, *Mus musculus*; Nl, *Necromys lasiurus*; On, *Oligoryzomys nigripes*.
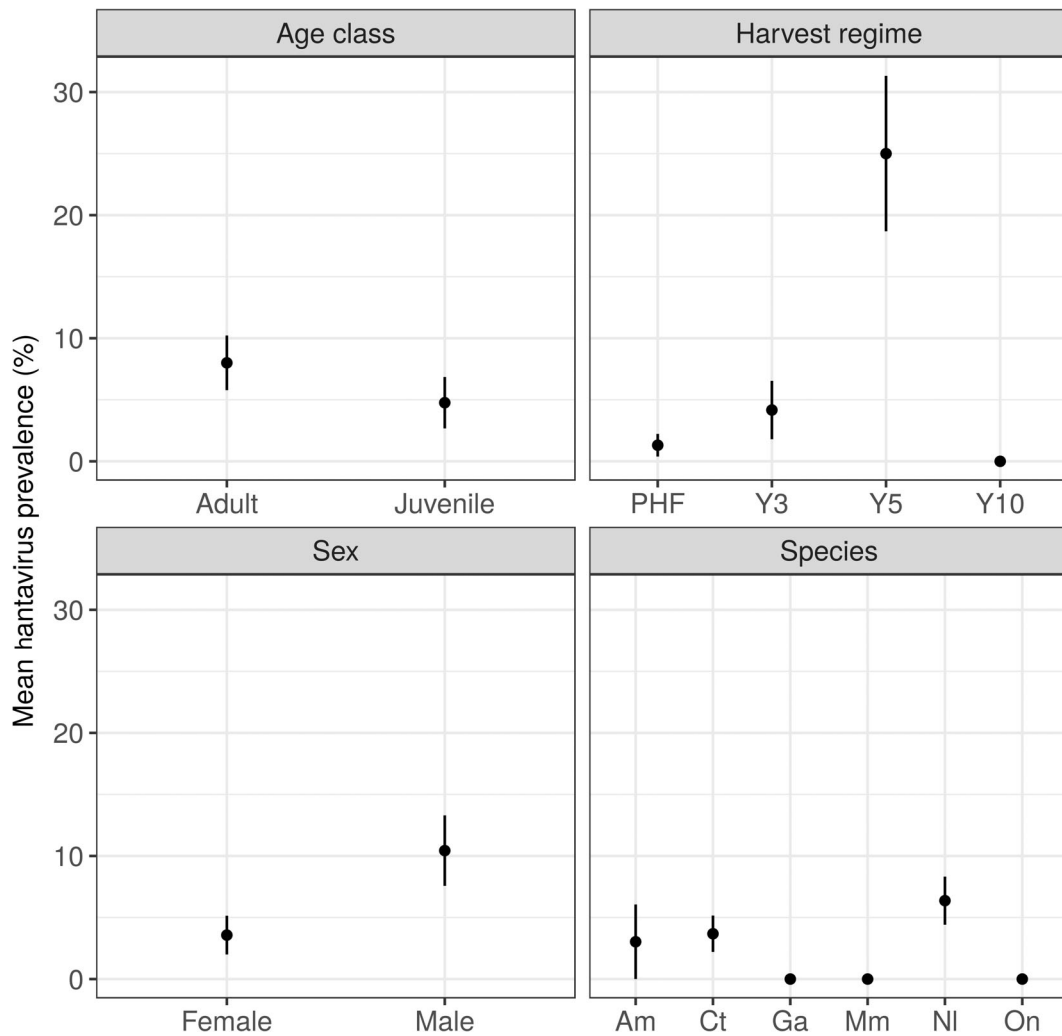
FIGURE 3 Predicted mean prevalence of hantavirus immunoglobulin G (IgG) antibodies in small mammals and associated 95% CIs obtained from the binomial generalized linear model fit. Mean prevalence of hantavirus IgG antibodies in small mammals against the recombinant nucleoprotein (rN) protein of *Araraquara orthohantavirus* according to the sugarcane harvest regime in southeastern Brazil. Harvest regimes: PHF, pre-harvest fire; Y3, harvest without fire in the last 3 years; Y5, harvest without fire in the last 5 years; Y10, harvest without fire in the last 10 years. Species: Am, *Akodon montensis*; Ct, *Calomys tener*; Ga, *Gracilinanus agilis*; Mm, *Mus musculus*; Nl, *Necromys lasiurus*; On, *Oligoryzomys nigripes*.

the fire events, the model predicts that rodent populations will rapidly increase.

DISCUSSION

Previous studies have shown that the harvest regime of sugarcane determines the abundance of rodents in sugarcane fields (De Sousa et al., 2008; Gheler-Costa et al., 2012; Prist et al., 2016; Verdade et al., 2012). The present results show that the sugarcane harvest regime can also determine the seroprevalence of hantavirus in small rodents of sugarcane fields. In the present study, the highest prevalence level was found at the lowest rodent abundance (Y5), contrary to what has

been described for bank-voles (*Myodes glareolus*) in Sweden (Olsson et al., 2002) and for the Central Arizona's brush mouse (*Peromyscus boylii*) (Kuenzi et al., 2007). In both cases, higher densities of rodents were associated with higher prevalence of hantavirus. Our data highlight that besides individuals inhabiting Y5 plots, Y3 small rodents also presented a relatively low population density. However, our simulation models suggest that their growth rate is likely lower than at Y5, suggesting that prevalence might be directly related to small rodent population growth and not density.

Hantavirus seroprevalence has been detected in only a few species of Sigmodontinae rodents: *A. montensis*, *C. tener*, and *N. lasiurus*. Rodents in the family Cricetidae, like *A. montensis*, *C. tener*, and *N. lasiurus*, are the most
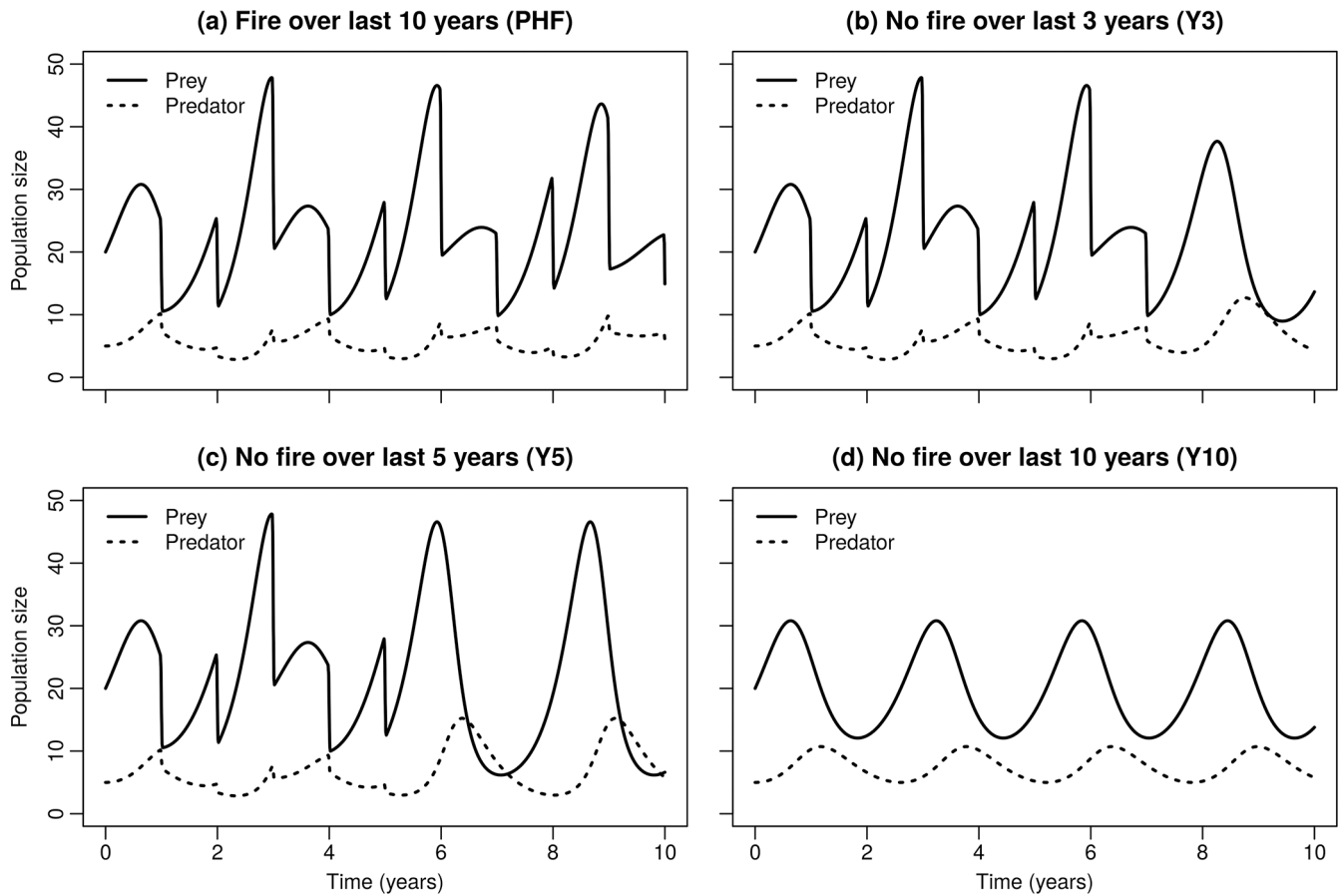
FIGURE 4 Simulated population dynamics from the modified Lotka–Volterra model when (a) there were yearly fire events over the last 10 years; (b) there were no fire events over the last 3 years; (c) there were no fire events over the last 5 years; and, (d) there were no fire events over the last 10 years.
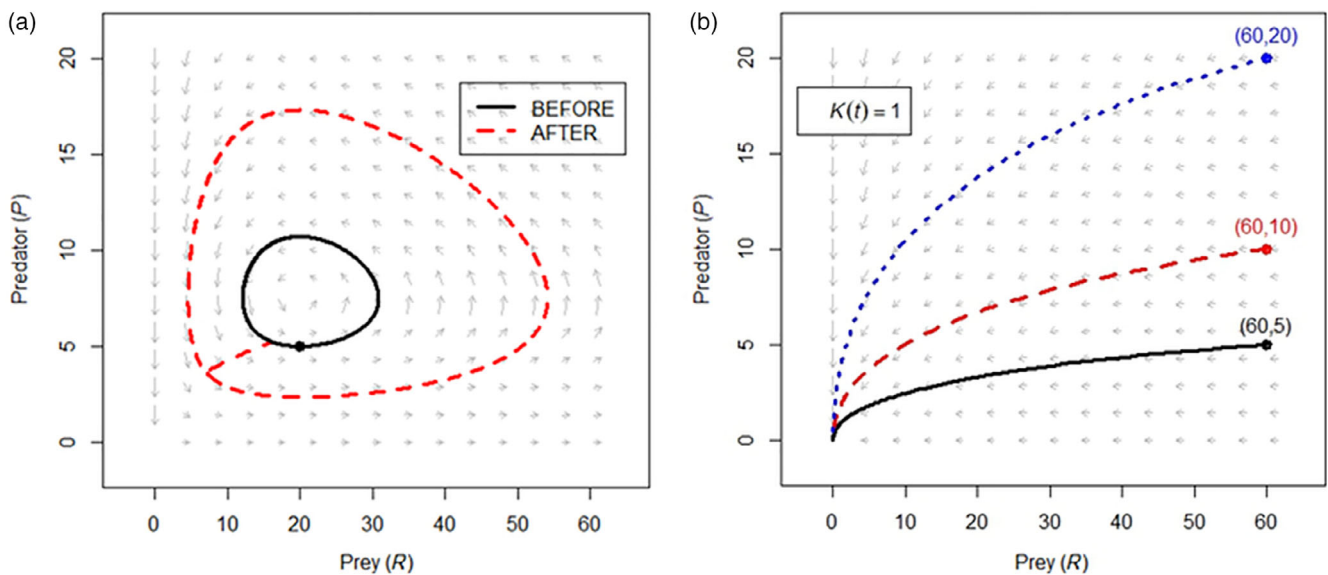
FIGURE 5 Prey–predator dynamics: (a) Phase plane and trajectory of population sizes of prey (R) and predator (P) through time, after and before a pre-harvest fire, and the direction field of the classical Lotka–Volterra differential equations (i.e., $K[t] = 0$). (b) Direction field and trajectories for three population size combinations for predators and prey during an intense fire process (i.e., $K[t] = 1$).

abundant species in sugarcane fields in southeastern Brazil (Gheler-Costa et al., 2012, 2013) and are the primary hosts of hantavirus pulmonary syndrome in Brazil (Figueiredo et al., 2003; Jonsson et al., 2010; Mills et al., 1999). They are generalist species that tend to adapt to environmental changes. Although among them no significant interspecific variation was found in hantavirus prevalence, intraspecific (i.e., sexual) difference occurs. By hypothesis, a male-biased dispersal pattern results in male-biased hantavirus prevalence in these species. Such a pattern would tend to involve males, likely because of their longer dispersal (young) and larger home range and higher frequency of agonistic interaction (adults) than females (Maroli et al., 2020). However, no significant variation in age class was detected in this study, possibly due to the relatively small number of infected individuals. In a larger scale, the area covered by sugarcane plantations is causally related to a higher prevalence (Prist et al., 2016). In addition, by hypothesis, spatial disposition of plantation lines might affect the dispersal of small rodents in agricultural landscapes (Prevedello & Vieira, 2010). Future studies should prioritize the possible relationship between microhabitat structure and hantavirus prevalence in small mammals as their movement between the matrix and surrounding areas of native vegetation must affect virus spread.

Rodents are the basis of the food web in agricultural landscapes of southeastern Brazil (Verdade et al., 2011). Therefore, the population dynamics of rodents tends to affect the population dynamics of their predators. The generalist small mammals that can carry hantavirus tend to be more abundant in the matrix than in the native vegetation around it (Ramos & Nachiluk, 2016).

The use of pre-harvest fire in sugarcane fields surprisingly results in an increase in rodent abundance. By contrast, fire suspension results in a decline of their abundance in the first 5 years and then a certain recovery after 10 years (Figueiredo et al., 2003). This decline in abundance is associated with an increase in the prevalence rate of hantavirus, which rejects our third hypothesis (Figure 1), although these results support the dilution effect since species diversity and predators tend to decrease in disturbed ecosystems favoring opportunistic/generalist species, and therefore, pathogen prevalence is higher (Khalil et al., 2016). Differences in life cycle between rodents and their predators may explain such patterns (and the relationship between prevalence and small rodent's population growth) as small rodents can breed twice or even three times each year, whereas their predators usually breed only once a year (Eisenberg & Redford, 1999). The present predator–prey models corroborate such a hypothesis (Figures 3 and 4). Future studies should focus on the long-term (>10 years)

effect of fire suspension on small rodents and their predators, as well as their hantavirus prevalence.

The present results are relevant not only for public health but also for agriculture and wildlife management. Hantavirus infection is a mandatory reportable disease in many countries as it can have a high virulence and lethality, which may result in the loss of human life and an increase in the cost of public health service (Olsson et al., 2003). All cases of hantavirus, confirmed by laboratory analysis (positive antibodies) reported by hospitals in the 645 municipalities in the state of São Paulo, are considered. Official data from the Ministry of Health for confirmed cases of hantavirus in the state of São Paulo are from 2017, and most municipalities had 0 or 1 case in this year (98.3% and 1.7%, respectively) (DATASUS, 2020). In 2017, 11 confirmed cases were recorded in the state of São Paulo, with one in the city of Ribeirão Preto, which is about 34 km from the study area. The most recent confirmed cases for the municipality of Sertãozinho, according to official data, are from 2014, 2015, and 2016, with three, one, and one confirmed cases, respectively (DATASUS, 2020). Considering the expansion of the area covered by sugarcane plantations, a long-term monitoring program of hantavirus prevalence in small rodents should be part of the environmental certification initiatives associated with the Brazilian biofuel program (Verdade et al., 2015; Verdade, Lyra-Jorge, & Piña, 2014). Such a monitoring program should also include agricultural management techniques and their role in containing disease spread, and not only the area covered by sugarcane plantations.

Despite the impacts caused by sugarcane expansion and intensification on biodiversity, agricultural landscapes are still crucial for biodiversity conservation (Verdade, Penteado, et al., 2014). As plantations can be considered a habitat for a relevant part of the wildlife found in agricultural landscapes, they should be managed as such (Verdade et al., 2020). This would only be possible in multifunctional agricultural landscapes (Martinelli et al., 2010; Verdade, Lyra-Jorge, & Piña, 2014). Furthermore, monitoring programs targeting wildlife in these productive landscapes are also crucial for the One Health approach to increase human livelihood (Lebov et al., 2017), and thus fulfill Goal 3 of the UN Development Sustainable Goals, which is good health and well-being (https://sustainabledevelopment.un.org/). However, the inevitable conflict between wildlife and humans would require human capacity building and solid institutions in support of the decision-making process associated with governance (Verdade, 2004).

The following measures should be prioritized at the governance level in order to minimize the role of small wild mammals as hosts of hantavirus in agricultural landscapes dominated by sugarcane plantations: (1) establishment of a

long-term monitoring program of hantavirus prevalence in small mammals as part of the environmental certification initiatives associated with the Brazilian biofuel program; (2) use of wildlife-friendly techniques in sugarcane plantations to mitigate the mortality of small rodent predators; and (3) improvement of human capacity building in wildlife management in agricultural landscapes in Brazil.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.