

University of São Paulo
"Luiz de Queiroz" College of Agriculture
Center for Nuclear Energy in Agriculture

Population dynamics of capybaras in human-modified landscapes and its
relationship with Brazilian spotted fever

Beatriz Lopes

Dissertation presented to obtain the degree of Master in
Science. Area: Applied Ecology

Piracicaba
2021

Beatriz Lopes
Bachelor of Science in Biology

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Advisor:
Profa. Dra. **KATIA MARIA PASCHOALETTO MICCHI DE BARROS FERRAZ**

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Dados Internacionais de Catalogação na Publicação
DIVISÃO DE BIBLIOTECA – DIBD/ESALQ/USP

Lopes, Beatriz

Population dynamics of capybaras in human-modified landscapes and its relationship with Brazilian spotted fever / Beatriz Lopes. - - Piracicaba, 2021.

64 p.

Dissertação (Mestrado) - - USP / Escola Superior de Agricultura “Luiz de Queiroz”.
Centro de Energia Nuclear na Agricultura.

1. *Hydrochoerus hydrochaeris* 2. Ecologia populacional 3. Flutuação populacional 4. Zoonoses 5. Influências antrópicas 6. Monitoramento populacional I. Título

DEDICATÓRIA

Aos meus pais, Benedito e Kátia. A minha irmã Bianca e Tia Cristina. A minha avó (in memoriam).

AGRADECIMENTOS

Agradeço primeiramente a Deus, por ter me agraciado com vida e saúde em tempos tão turbulentos. À minha família, por ser a minha força e o meu desabafo. Ao meu namorado, por ser meu melhor amigo e companheiro.

Obrigada a minha orientadora Katia Ferraz por todas as portas que me ajudou a abrir e por muitas vezes ter me acolhido. Ao meu co-orientador Marcelo Bahia Labruna, por todos os ensinamentos, e pelo entusiasmo com a minha evolução. Ao meu parceiro Ronaldo Morato pela sempre pronta ajuda e valiosa contribuição. Ao Alexandre Reis Percequillo, como membro do meu comitê de orientação, mas também como professor admirável que é. Ao Cristian Marcelo Villegas por me ajudar com a mão na massa, por todo aprendizado, paciência e evolução nas análises.

Obrigada aos membros da equipe “Capivaras, carrapatos e Febre Maculosa” que possibilitaram essa colheita, e muitas outras. Especialmente, aos amigos: Vanessa do Nascimento Ramos, Francisco Costa, Hermes Luz, Lidiani Correa, Hector Benatti, Thiago Dias, Lucas “Cansera”, Jardel, Ana Maria Nievas, Barbara Weck, Carolina Serpa....

Aos grandes amigos pessoais por momentos de lazer e descontração que me ajudavam a aliviar as partes difíceis. Em especial: Kayla Bernardo, Mariana Gil, Beatriz Menegali, Tatiane Mariote, Malu Baldo, Leticia Munhoes. E também aos grandes amigos do LEMaC, por me fazerem sentir pertencente a esse grupo de pessoas incríveis: Alex Bovo, Vinicius Roberto, Henrique Concone, Maristela Camolesi, Yuri Ribeiro, Leticia Munhoes (novamente), Fernanda Abra, Marcelo Magioli, Daiane Carreira, Roberta Paolino, Mariana Landis, Juliano Bogoni, Maria Augusta e Silvio Marchini.

Agradeço a CAPES e a FAPESP pelo financiamento desta pesquisa. A Prof^a. Vânia Galindo Massabni, por ter me dado uma oportunidade de trabalhar ao seu lado, na área da educação. A Prof^a. Silvia Molina e ao grupo de terapia Junguiana, por terem me oferecido todo o suporte emocional para superar esta etapa.

“Conheça todas as teorias, domine todas as técnicas, mas ao tocar uma alma humana, seja apenas outra alma humana”.

Carl Jung

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RESUMO

Dinâmica populacional de capivaras em paisagens modificadas pelo homem e sua relação com a Febre Maculosa Brasileira

A capivara (*Hydrochoerus hydrochaeris*) é o hospedeiro principal do carrapato-estrela (*Amblyomma sculptum*), que por sua vez é vetor da bactéria *Rickettsia rickettsii*, agente etiológico da Febre Maculosa Brasileira (FMB), uma doença altamente letal em humanos. Além de ser hospedeira do carrapato, a capivara também atua como amplificadora da bactéria através da contínua introdução de animais susceptíveis na população (i.e. filhotes). Estudos anteriores têm sugerido uma relação causal entre a ecologia populacional de capivaras e a emergência da FMB, já que foram encontradas maiores abundâncias de carrapatos em áreas endêmicas, e a importância dos filhotes como amplificadores da bactéria. Assim, objetivamos analisar a variação do número de indivíduos em populações de capivaras em paisagens modificadas pelo homem (HMLs) em áreas endêmicas ($n = 3$) e não-endêmicas ($n = 4$) da FMB, no estado de São Paulo. Nós realizamos contagens diretas dos indivíduos por 4 anos (de janeiro/2015 a dezembro/2018) para descrever a flutuação populacional e estimar os índices de abundância e densidade entre as áreas endêmicas e não-endêmicas para FMB. Não encontramos um padrão único de flutuação populacional, ao contrário, cada grupo monitorado mostrou um comportamento de variação de indivíduos específico. O único padrão observado foi o de incremento de filhotes, o qual diferiu entre áreas endêmicas e não-endêmicas. O período de incremento de filhotes na população ocorreu mais cedo nas áreas endêmicas, em julho/agosto, enquanto que nas áreas não endêmicas ocorreu após o mês de setembro. Os índices de abundância e densidade diferiram significativamente entre as áreas ($valor-P < 0.001$), sendo maiores em áreas endêmicas (24 ± 14 individuals and 85 ± 62 individuals/km²) do que não-endêmicas (12 ± 8 individuals and 33 ± 21 individuals/km²). Os resultados aqui apresentados são os primeiros sobre flutuação populacional de capivaras em HMLs, e também os primeiros a comparar índices de abundância e densidade entre áreas endêmicas e não endêmicas para a FMB. Nossos resultados são relevantes para compreender as relações ecológicas entre capivaras, carrapatos, ambiente e a emergência da FMB no estado de São Paulo. Reforçam ainda a necessidade de investigar melhor como as alterações antrópicas da paisagem determinam mudanças comportamentais e populacionais, as quais podem desencadear a incidência e o espalhamento da doença. Tais informações são essenciais para o estabelecimento de estratégias e programas de prevenção e controle da FMB.

Palavras-chave: *Hydrochoerus hydrochaeris*, Ecologia populacional, Flutuação populacional, Zoonoses, Influências antrópicas, Monitoramento populacional

ABSTRACT

Population dynamics of capybaras in human-modified landscapes and its relationship with Brazilian spotted fever

Capybara (*Hydrochoerus hydrochaeris*) is the main host of *Amblyomma sculptum* tick, which is the vector of *Rickettsia rickettsii* bacterium, etiological agent of Brazilian Spotted Fever (BSF), a very lethal disease for humans. Besides being tick hosts, capybaras also amplifies *R. rickettsii* in the environment through continuous introduction of susceptible animal in population (i.e. young). Previous studies have suggested a causal relationship between capybara population ecology and BSF emergence, since it was found greatest abundances of ticks in BSF-endemic areas than non-endemic and the known role of capybara young as bacterium amplifiers. We aimed to analyze variation in the number of individuals in capybara populations in human-modified landscapes (HMLs), in BSF-endemic ($n = 3$) and non-endemic areas ($n = 4$), in São Paulo state, Brazil. We made direct counts of capybaras (from January/2015 to December/2018) to describe population fluctuation and estimate abundance and ecological density indexes. We do not found a typical pattern of fluctuation among surveyed capybara groups. On the contrary, each monitored group showed a particular variation of individuals. The only pattern observed was in the increment of young, which differed in BSF-endemic compared to non-endemic areas. Increment of young occurred earlier in BSF-endemic areas, in July/August, while in BSF-non-endemic areas it occurred after September. We found significantly greater abundance (24 ± 14 individuals vs. 12 ± 8 individuals) and ecological density indexes (85 ± 62 individuals/km² vs. 33 ± 21 individuals/km²) in BSF-endemic than non-endemic areas (P -value < 0.001). This are the first study about population fluctuation of capybaras in HMLs and the first to compare abundance and ecological density indexes between BSF-endemic and non-endemic areas. These information are relevant to better understanding ecological relations between capybaras, ticks, environment and BSF emergence in São Paulo State. Our results reinforce the importance of investigating how HMLs alter capybaras behavior and population, which may influence disease occurrence and spread. Such information are essential to develop strategies and programs of BSF prevention and control.

Keywords: *Hydrochoerus hydrochaeris*, Population ecology, Population fluctuation, Zoonosis, Anthropogenic influence, Population monitoring

1. INTRODUCTION

More than ever, with the advent of COVID-19 pandemic (HAIDER et al., 2020) and its apparently relationship with bats (LU et al., 2020) and pangolins (LAM et al., 2020), zoonotic diseases have gained visibility around the world. Wildlife can be vehicle of diseases in different ways, such as by direct skin contact with infected animals (e.g. Tularemia), by bite (e.g. Rabies), by aerosols in dust (e.g. Hantavirus) and through vectors, as insects (e.g. Yellow fever, Leishmaniasis) and ticks (e.g. Lyme; KRUSE; KIRKEMO; HANDELAND, 2004). The origin of the majority of zoonosis is influenced by anthropogenic actions (WHITE; RAZGOUR, 2020), which includes expansion of human population, deforestation, reforestation, pollution and, climate changes (JONES et al., 2008). For example, Lyme, a tick-borne disease, has emerged because of increased white-tailed deer populations favored by reforestation of abandoned farms in the northeastern United States (BARBOUR; FISH, 1993; KILPATRICK et al., 2017), which, in addition, highlights the role of synanthropic species in terms of public health (MCFARLANE; SLEIGH; MCMICHAEL, 2012).

In Brazil, the capybara (*Hydrochoerus hydrochaeris*) plays an important role for public health (LABRUNA et al., 2013). It is the main host of *Amblyomma sculptum* ticks and acts as an amplifier of *Rickettsia rickettsii* infection, the etiologic agent of Brazilian Spotted Fever (BSF; SZABÓ; PINTER; LABRUNA, 2013). BSF is a very lethal disease, with an average of 54.4 % of infected people dying in the past 14 years in São Paulo state (official data from the State Health Secretary of São Paulo state, until October 2021). Especially in São Paulo state, the emergence of this disease is strictly associated with anthropogenic modifications, mainly triggered by sugarcane crops development (POLO; LABRUNA; FERREIRA, 2015). In human-modified landscapes (HMLs; MELO et al., 2013) capybaras found proper conditions for population increase: high spatial-temporal availability of vital resources (e.g. food and water) and low predation risk (FERRAZ et al., 2007, 2003; VERDADE et al., 2012).

However, not every HML in the state of São Paulo is endemic for BSF despite the presence of capybaras and *A. sculptum*, reinforcing the need of investigating which are the specific epidemiological conditions for determining *R. rickettsii* prevalence. A recent study has demonstrated higher burdens of *A. sculptum* in BSF endemic than non-endemic areas and suggested that it could be related to different population densities of capybaras between them

(LUZ et al., 2019). In addition, the number of young capybaras has a crucial role for BSF transmission (LABRUNA, 2013) and Polo et al. (2017) suggested an association between increased birth rates and the spread of BSF. All these evidences suggest a causal relationship between capybaras population ecology and the emergence of BSF.

Considering this, we monitored seven groups of capybaras living in HMLs across the São Paulo state, in southeastern Brazil, aiming to better understand their population dynamics. We performed direct counts to describe population fluctuations, focusing on identifying patterns, variations and peaks in group size and births, because we assume that these variations in population fluctuation could be important aspects of capybara population dynamics related to the BSF. We estimated abundance indexes and ecological densities per age classes for each capybara group and compared our results across BSF-endemic and non-endemic areas. Based on the results on higher tick burdens among BSF-endemic areas founded by Luz et al., (2019), which surveyed the same study areas, and as hypothesized by them, we expect to find greater capybara abundance indexes and densities of capybaras among BSF-endemic areas. This study provides important insights about the relations between capybaras, ticks and BSF-emergence and reinforce the need of better understanding the population dynamics of capybaras in HMLs.

2. LITERATURE REVIEW

2.1 Capybara: biology, ecology and behavior

Capybara is described as an exceptional and extraordinary mammal (MOREIRA et al., 2013a). Capybara means grass eater in Tupi indigenous language (MOREIRA et al., 2013b) and this is the common name for *Hydrochoerus hydrochaeris* (Linnaeus, 1766). This species is taxonomically classified within Rodentia order and Hydrochoeridae family. Capybara is the largest rodent in the world and they can only be found in South America, from Panama until Argentina, except in Chile (EMMONS, 1990).

Capybara has an robust and enlongated body shape of approximately 1.2 m in length and 0.6 m in height (MONES; OJASTI, 1986), body mass presents biogeographical variation being 50 kg in average (FERRAZ; BONACH; VERDADE, 2005; HERRERA, 1992; MONES; OJASTI, 1986; OJASTI, 1973). The head is large and enlongated (OJASTI, 1973) and there is a nasal scent gland, called morillo, which is more salient in adult males, although it is also seen in both sexes (MOREIRA et al., 2013b). The limbs are short and the toes are connected by a membrane used for water propulsion (MONES; OJASTI, 1986). Body is covered by thick brown/reddish hair (MONES; OJASTI, 1986).

Natural habitats for this species are characterized by seasonally flooded lowland open areas (MONES; OJASTI, 1986), for example, the Brazilian Pantanal (OJASTI, 1968) and Venezuelan Llanos (HERRERA, 1992). Capybara habitats are compound of three essential components: open areas used for foraging, a patch of forest used as shelter during rest and, proximity of water used for thermoregulation and reproduction (ALHO; RONDON, 1987; ALHO; CAMPOS; GONÇALVES, 1987; MACDONALD, 1981; OJASTI, 1968).

Capybara shows high food plasticity, feeding on grasses, bushes and aquatic plants in natural environments (ARTEAGA; JORGENSON, 2007; FORERO-MONTAÑA; BETANCUR; CAVELIER, 2003; OJASTI, 1973). This specie may adapt foraging strategies according to seasonal variation in habitat, being more selective during wet season, feeding on higher energetic and protein food than during dry season (BARRETO; HERRERA, 1998). In HMLs capybara adapts its diet to include agricultural crops, such as sugar cane and maize (ARTEAGA; JORGENSON, 2007; BOVO et al., 2016; FELIX et al., 2014; FERRAZ et al., 2003; MAGIOLI

et al., 2019; ROCHA et al., 2017). This anthropogenic food habit favored its proliferation and synanthropy in HMLs of Brazil.

As a gregarious and social species, capybara form groups with a dominance hierarchy that organizes the interactions between group members (HERRERA et al., 2011; HERRERA; MACDONALD, 1987, 1993; OJASTI, 1973). In small groups, typical of natural habitats, capybaras show a linear hierarchy dominance among males, while interactions among male-female and female-female are rare (HERRERA, 2013; HERRERA et al., 2011; HERRERA; MACDONALD, 1993). In larger groups, as the example of semi-confined conditions, capybara groups may show a non-linear and more flexible hierarchy dominance among males and females (FERRAZ et al., 2013). Dominant males tend to have a more prominent supra nasal gland and priority of access to receptive females, being responsible for more than 80% of copulations, characterizing a polygynous mating system (HERRERA; MACDONALD, 1993).

Capybaras are territorial, members from other groups are rejected by aggressive behavior which make each group as a closed and stable social unit in natural habitats, composed of males and females (HERRERA, 2013; HERRERA et al., 2011; HERRERA; MACDONALD, 1987). Territory is marked through a supra-nasal and anal glands secretions (MACDONALD; HERRERA, 2013). Some individuals may disperse and form new groups. Salas (1999) observed only male dispersal while Herrera (1992) observed dispersal in groups of subadults of both sexes including subordinate males. Herrera (2011) stated that dispersal is male-biased at high population densities. Recorded distances of dispersion varied from 3 to 5.6 km (HERRERA, 1992; HERRERA et al., 2011).

Capybara group size varies according to ecological characteristics of the particular habitat (HERRERA et al., 2011). While in natural habitats, such as the Brazilian Pantanal and the Venezuelan Llanos, groups are formed by 10 individuals in average; in HMLs, capybaras may form groups of more than 50 animals. In Brazilian Pantanal, mean group size varied from 3.6 to 5.8 individuals according to Schaller and Crawshaw (1981). Also in the Pantanal, Alho, Campos and Gonçalves (1987) reported an average of 5.68 ± 0.20 individuals per capybara group and 14 ± 0.6 individuals/km². In Venezuelan Llanos it was found a mean group size of 10.9 individuals and ecological densities of 25 individuals/km² (MACDONALD, 1981). Cordero and Ojasti (1981) found higher densities, 206 individuals/km² in forested habitats and 184 individuals/km² in savannas of Llanos. In HMLs, Verdade and Ferraz (2006) estimated an

abundance index of 50.55 ± 1.81 individuals and an ecological density of 124 ± 4 individuals/km², in Piracicaba, São Paulo. In this same city, it was found the highest record of capybara ecological density in HMLs (324 individuals/km²; BOVO et al., 2016). Vargas et al., (2007) found groups composed by a mean of 21 ± 5.6 individuals and a density of 58 ± 5 individuals/km² in Pirassununga, São Paulo. In Araras, São Paulo, Rocha et al., (2017) counted a maximum of 56 individuals in one capybara group. This variation in group size between natural and human-modified habitats is probably due to high availability of food resources from agricultural fields and low predation risk in HMLs (VERDADE; FERRAZ, 2006).

Population dynamics of capybara groups in natural habitats is dependent of seasonal variation of limiting resource, such as water and food (MOREIRA et al., 2013c). Alho and Rondon (1987) evaluated annual variation in density of capybaras in Brazilian Pantanal. They found highest ecological densities of capybaras during rainy season, when available dry space is reduced due to flooding. During wet season in flooded savannas capybara groups usually subdivides into smaller groups (ALHO; CAMPOS; GONÇALVES, 1987). In natural seasonal flooded habitats, wet season is the period of lower availability of grazing, therefore population tends to decrease (MOREIRA et al., 2013c). While, in other habitats, such as HMLs of Pirassununga the peak in population occurred in wet season, when possibly there is more availability of food in that type of habitat (VARGAS et al., 2007).

Similarly, the period of increase in birth in capybara population is related to high availability of food resource in association with low risk of mortality (MOREIRA et al., 2013c). Although capybaras are fertile all year around and capybara young are seen throughout the year (ALHO; RONDON, 1987; ALHO; CAMPOS; GONÇALVES, 1987; HERRERA, 1998; OJASTI, 1973), peaks in birth occurred at the end of rainy season in Venezuelan Llanos (MOREIRA et al., 2013c) and Brazilian Pantanal (ALHO; CAMPOS; GONÇALVES, 1987; SCHALLER; CRAWSHAW, 1981). This timing in birth peaks in seasonal flooded savannas habitats is also related to reduction in young risk of mortality due to floods (AZCARATE; ALVAREZ; BRAZA, 1980). In HMLs of São Paulo state, where there is not flood season, peaks in birth were detected at the beginning of rainy season (VARGAS et al., 2007; VERDADE; FERRAZ, 2006).

The first pregnancy of capybaras happens when females reach 30-40 kg, approximately with 1.5-2 years of age (OJASTI, 1973). In each litter, capybara may have birth to a mean of 4

young (HERRERA; MACDONALD, 1987; MIGLINO et al., 2013), but this number may vary from 1 to 7 individuals (OJASTI, 1973). In average, capybaras are pregnant 1.2 times per year (MOREIRA et al., 2013c).

Literature involving capybara biology and ecology in natural habitats started to be written from 1970. Nowadays capybara is a very well studied mammal in South America (MOREIRA et al., 2013a). However, the development of studies about capybara living in HMLs is later started in 2000 and many information, especially related to social organization and spatial ecology still lacks.

Especially the state of São Paulo undergone extensively land conversion from natural areas to agroecosystems (DEAN, 2000; DURIGAN; RATTER, 2006). The plantation of resources favorable for capybaras and reduction of top predators contributed to the proliferation of species close to urban areas (VERDADE; FERRAZ, 2006). Since then, some studies have emerged discussing the consequences and adaptations of capybaras living in close proximity to human population. Capybara is a species significantly affected by human activities, as the aforementioned alterations in diet (ARTEAGA; JORGENSON, 2007; BOVO et al., 2016; FELIX et al., 2014; FERRAZ et al., 2003; MAGIOLI et al., 2019; ROCHA et al., 2017) and group size (BOVO et al., 2016; ROCHA et al., 2017; VERDADE; FERRAZ, 2006).

Using GPS tracking technology Dias et al., (2020) analyzed and compared habitat selection among natural landscapes in Brazilian Pantanal and HMLs of São Paulo State. Results showed a positive selection for forests in HMLs especially during daytime to avoid human activities. Results in natural landscapes showed the opposite, capybaras selected open areas, avoiding forested areas during both day and nighttime.

Another studied carried out at the same locations also using GPS technology aimed to compare capybara home ranges and activity across natural landscapes and HMLs. Home ranges found in HMLs (35.85 ± 24.95 ha) were 2.43 times smaller than home ranges in natural landscapes (87.21 ± 60.1 ha; Lopes et al., 2021). Despite the infeasibility of comparing the results, Herrera and Macdonald (1989) estimated home ranges of 16.1 ha in Venezuelan Llanos, Schaller and Crawshaw (1981) estimated home ranges varying from 12 to 200 ha in Brazilian Pantanal and in the Paraguayan Chaco, Krauer (2009) found capybara home ranges of 183 ± 54 ha.

Analyses of activity pattern and displacement also have shown the influence of human activity in capybara behavior. In HMLS capybaras tend to be nocturnal (BARRETO; QUINTANA, 2013; LOPES et al., 2021; SERRA-MEDEIROS et al., 2021), again to avoid contact with humans. Capybara also presented lower displacement in HMLs than in natural landscapes, because of both the space restriction caused by human construction and less required movement due to high availability of agricultural food resources close to water bodies (LOPES et al., 2021). On the contrary, in natural landscapes capybaras tend to be diurnal (ALHO; RONDON, 1987; HERRERA; MACDONALD, 1989; KRAUER, 2009; MACDONALD, 1981).

Feeding from agriculture crops made capybaras gain weight due to fat deposit (BENATTI et al., 2021). According to Benatti et al., (2021) capybaras are heavier in HMLs (mean of 61.2 kg, range from 35 to 105.6 kg) than in natural landscapes (mean of 54.8 kg, range from 35.7 to 80.4 kg). It is discussed the possibility of heavier animals in HMLs may reproduce in larger scale and, consequently, form larger groups.

However, not only humans impact capybara ecology and behavior, but also capybara are involved in human-wildlife conflicts. Capybara is one of the most road killed animal, especially in the state of São Paulo, causing severe car accidents and fatally causing people direct mortality (HUIJSER; DELBORGO ABRA; DUFFIELD, 2013). Besides human health injury, capybaras can also be related to financial losses in two different ways. At first, capybara-vehicle crash generate costs for society on car fixing and victims compensation by road administrators (ABRA et al., 2019). Secondly, the species is considered an agricultural plague, causing financial losses for agricultural industry and small producers (FERRAZ et al., 2003). Lastly, capybaras are the main host of *A. sculptum* tick, which is the vector of *R. rickettsii* bacterium, the etiological agent of BSF in humans, a very lethal disease (LABRUNA, 2013).

2.1. Brazilian spotted fever

BSF is a zoonosis caused by the bacterium *R. rickettsii*, which is the most deadly rickettsiosis in the world. This bacterium is mainly transmitted to humans through *A. sculptum* tick bites, popularly known as “*carrapato estrela*” in Brazil (LABRUNA, 2013), but also may be transmitted by *A. aureolatum* ticks (PINTER; LABRUNA, 2006). BSF is reported as Rock mountain spotted fever in other locations in American continent, such as the United States, Mexico, Costa Rica, Panama, Colombia, Argentina and Canada, where this disease also occurs,

however associated with other tick species (CHAPMAN et al., 2006; CHEN; SEXTON, 2008; DANTAS-TORRES, 2007; LABRUNA, 2013).

Adult stages of *A. sculptum* preferentially parasitize equine species (CASTAGNOLLI et al., 2003). The immature stages (i.e. larvae and nymphs) are less selective about feeding preferences and may parasitize a broad range of domestic and wild mammals, such as opossums, small rodents, dogs and birds (LOPES et al., 1998; ROJAS; MARINI; COUTINHO, 1999; SERPA et al., 2021). Despite the variability of hosts, when taking BSF epidemiology into account, the main host to concern is the capybara (LABRUNA, 2013).

Although *R. rickettsii* may be inherited across tick generations, this bacterium is partially pathogenic for *A. sculptum* causing high mortality rates in infected ticks. Therefore, it requires an amplifier host to keep *R. rickettsii* active among ticks (BURGDORFER, 1988). The major role of amplifier host of *R. rickettsii* is played by capybaras, which are able to maintain the bacterium in their bloodstream after the first contact with an infected tick – a process called rickettssemia - for 10 days, when they infect about 25% of ticks parasitizing them (SOUZA et al., 2009).

Labruna (2009, p. 158) described some requirements to be followed by an efficient amplifier:

- “1. It has to be abundant in the *R. rickettsii*-endemic area.
2. It has to be a major host for the tick vector.
3. It has to be susceptible to the *R. rickettsii* infection.
4. Once infected by *R. rickettsii*, the host has to develop a rickettsemia of sufficient length and degree to infect ticks that feed on this host.
5. It has to be a prolific species, in order to have a continuous introduction of nonimmune animals in the host population”

Such requirements is perfectly filled by capybaras (LABRUNA, 2013). The requirement number five highlights the importance of continuous introduction of susceptible capybaras to *R. rickettsii* infection, which are represented especially by young individuals introduction (LABRUNA, 2009, 2013). Indeed, mathematical models have shown the positive correlation between increased birth rates of capybaras and population size of infected ticks (POLO et al., 2017).

Confirmed cases of BSF increase during the second half of the year, from June to November (KATZ et al., 2009; SOUZA; PINTER; DONALISIO, 2015). This seasonality coincides with the presence of immature stages of *A. sculptum* in the environment (BARBIERI et al., 2019), which, as mentioned before, are less selective to choose host and eventually parasitize humans (LABRUNA, 2013). Also, there is a higher transovarial transmission of *R. rickettsii* when *R. rickettsii*-acquisition feeding occurs during the nymphal stage (GERARDI et al., 2019; SOARES et al., 2012). Once a person get an infected tick attached to the skin, it takes 4-6h to have the bacterium inoculated in blood (LABRUNA, 2013). The symptoms of illness are non-specific and include high fever, headache, malaise, chills and myalgia, which can result in misdiagnosis (CHEN; SEXTON, 2008).

The occurrence of spotted fever is directly related to the size of vector (LABRUNA, 2013) and host populations (ARNEBERG, 2001). Luz et al., (2019) has demonstrated this association by founding higher abundance of *A. sculptum* ticks in BSF-endemic areas than non-endemic areas. The combination of high densities of capybaras and *A. sculptum* ticks is directly associated with *R. rickettsii* circulation (NUNES et al., 2019).

The Brazilian southeast is the most numerous region in BSF cases (DEL FIOLE et al., 2010). There are 1092 diagnosis of BSF reported only in the São Paulo state (data from 2007 to October/2021), of which approximately 54.4% were fatal (official data from the State Health Secretary of São Paulo state 2021). São Paulo state underwent intensive land cover change from natural to agricultural crops in the last century, especially for sugar cane cultivation (DEAN, 2000; DURIGAN; RATTER, 2006). This high energetic food for capybara favored its proliferation in this state (VERDADE; FERRAZ, 2006), which have contributed to the increase of BSF cases in the last decades in association with sugar cane crops increment (POLO; LABRUNA; FERREIRA, 2015).

3. OBJECTIVE

The general objective of this study is to analyze variation in the number of individuals in capybara populations in HMLs of the São Paulo State, Brazil and to compare the results between BSF-endemic and non-endemic areas.

The specific objectives are:

- 1) Analyze the population fluctuation of capybara groups
- 2) Analyze the increment of young in the capybara groups
- 3) Estimate abundance and ecological density indexes of capybara groups

4. MATERIALS AND METHODS

4.1. Study areas

We selected five HMLs in the state of São Paulo, Brazil (Figure 1, Table 1). Study areas were identified as HMLs as being compound by isolated and disconnected forest remnants, surrounded by agricultural fields, pasture and/or urban areas, where native biodiversity is low (MELO et al., 2013). This state is the most urbanized, populated and economically developed in Brazil (IBGE, 2017). At the same time that São Paulo is the main industrial hub in the country, it is also the main producer of ethanol by sugar cane with more than 25% of its territory being used for this crop cultivation (SOUZA et al., 2020).

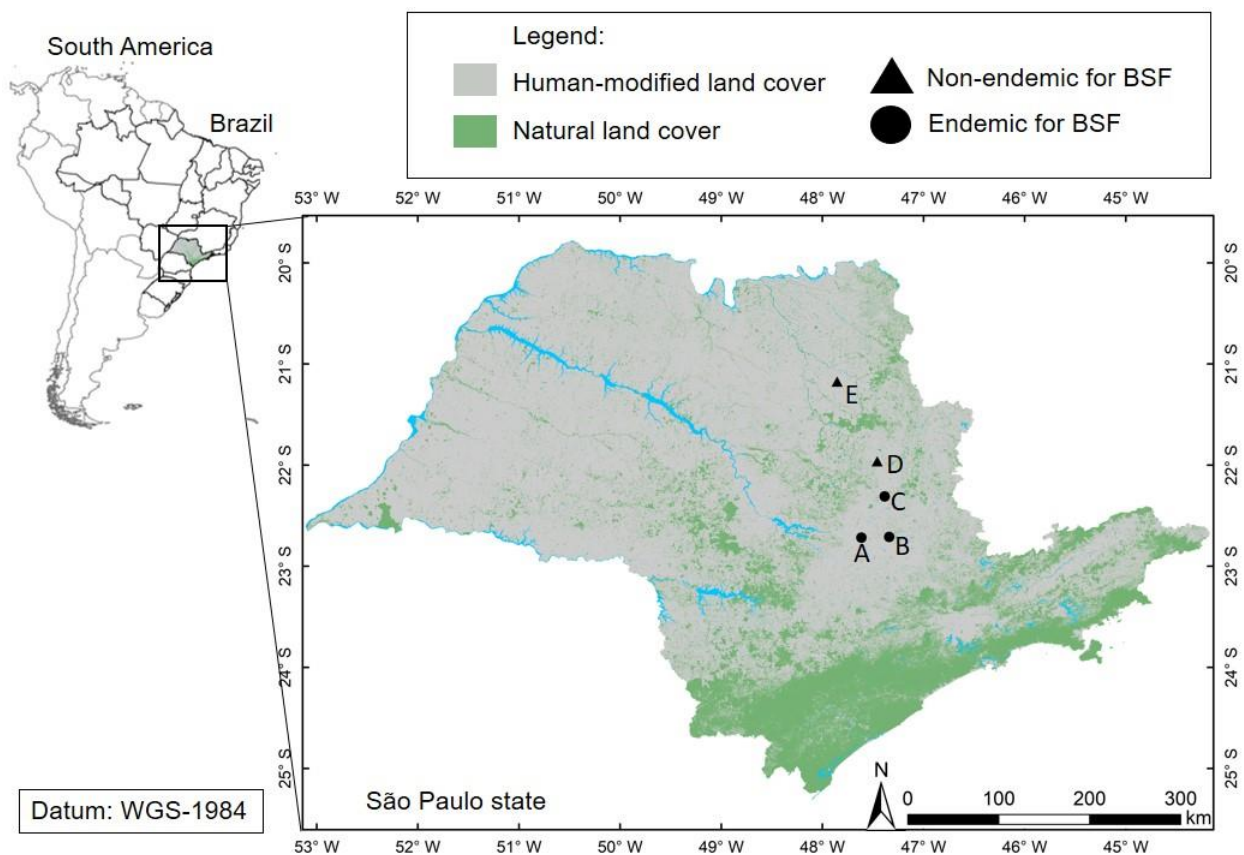


Figure 1. Study areas for monitoring capybara (*Hydrochoerus hydrochaeris*) populations in human-modified landscapes in São Paulo state, Brazil, Brazilian Spotted Fever (BSF)-endemic and non-endemic. Study areas are identified as A) Piracicaba, B) Americana, C) Araras, D) Pirassununga and E) Ribeirão Preto. We show natural and human-modified land covers according to MapBiomas Collections (SOUZA et al., 2020).

The increment of sugar cane plantations in the last century has been related to the emergence of BSF in the state of São Paulo, where it was registered 1092 diagnosis from 2007 to 2021 with an average lethality of 54.4% (official data from the State Health Secretary of São Paulo State 2021). Our study areas encompass three endemic and two non-endemic municipalities for BSF. The cities of Piracicaba, Americana, and Araras are considered BSF-endemic, with recently occurrence of BSF transmission to humans (official data from the State Health Secretary of São Paulo State 2021) and high proportion of seropositive capybaras for *R. rickettsii* bacteria (LUZ et al., 2019). While study areas in Pirassununga and Ribeirão Preto have no human case report or *R. rickettsii* circulation between ticks and capybaras (HORTA et al., 2007; LUZ et al., 2019; OGRZEWALSKA et al., 2012; SANGIONI et al., 2005; SOUZA et al., 2008).

Table 1. Description of study areas in São Paulo state in Brazil including location, Brazilian Spotted Fever status of endemism, capybara group name, capybara group home range, types of land cover/use in home ranges and surroundings, land cover composition of home ranges, type and size of water bodies used by capybara group (where measured). Adapted from Lopes et al., (2021).

	Study Area						
	Piracicaba	Americana	Araras	Pirassununga			Ribeirão Preto
Localization (longitude, latitude)	Universidade de São Paulo, campus “Luiz de Queiroz” (-47.612613, -22.718953)	Carioba Distrito Industrial (-47.338966, -22.710518)	Universidade Federal de São Carlos, campus Araras (-47.383967, -22.309933)	Universidade de São Paulo, campus “Fernando Costa”			Universidade de São Paulo, campus Ribeirão Preto (-47.852565, -21.173109)
				Subarea 1 - (-47.473345, -21.955670)	Subarea 2 – (-47.449615, -21.956841)	Subarea 3 - (-47.460785, -21.963396)	
BSF-status (E – endemic and NE – non-endemic)	E	E	E	NE	NE	NE	NE
Capybara group name	Aeroporto	Carioba	UFSCar	Captação	Risca Faca	CEPTOX	USPRP
Capybara group home range (mean in km ²)*	0.56	0.22	0.23	0.42	0.64	0.53	0.18
Types of Land use/cover in home ranges and surroundings	Agricultural crops (sugar cane and maize), pasture, artificial water reservoirs, silviculture plantation, urban areas, road, fence, natural vegetation, riparian forest, Piracicaba River, Piracicamirim Riverside	Industries, artificial water reservoirs used by a sewage treatment station, railroad, riparian forest, Piracicaba River, Quilombo Riverside	Agricultural crops (sugar cane), pasture, silviculture plantation, artificial water reservoirs, road, fence, natural vegetation	Agricultural crops (sugar cane, maize), artificial water reservoir, road, fence, natural vegetation	Agricultural crops (maize), artificial water reservoir road, fence, natural vegetation	Agricultural crops (maize), artificial water reservoir, road, fence, natural vegetation	Road, fence, urban area, riparian forest, streams
Land cover composition of home ranges	37,33% of forest, 41.49% of grasses/shrubs,	54.59% of forest, 13.01% of grasses/shrubs,	55.14% of forest, 25.19% of grasses/shrubs,	57.93% of forest, 28.50% of grasses/shrubs,	38.32 of forest, 31.81% of grasses/shrubs,	Not available	88.34% of forest, 8.87% of grasses/shrubs,

(mean in %) **	1.79% roads/settlements, 11.48% bare soil, 7.91% of water	6.17% roads/settlements, 1.64% bare soil, 24.59% of water	4.44% roads/settlements, 1.44% bare soil, 7.79% of water	4.93% roads/settlements, 0.41% bare soil, 8.23% of water	21.45% roads/settlements, 1.16% bare soil, 7.25% of water		1.78% roads/settlements, 1.01% bare soil, 0% of water
Water body type and size (approx. area in km ²)	Artificial water reservoir (3.35 ha)	Piracicaba River (2.63 ha) and artificial water reservoirs (0.15 ha)	Artificial water reservoir (1.56 ha)	Artificial water reservoir (2.23 ha)	Two Artificial Water reservoirs (10.9 ha)	Artificial water reservoir (4.17 ha)	Two small streams (few meters, not measured, undetectable via satellite images)

*Home range values are used in data analysis. These values are calculated averages per capybara group available in LOPES et al., (2021), except by capybara group CEPTOX, in Pirassununga, which is a mean of home range values of other two groups in the same municipality (Captação and Risca faca groups).

**Land cover composition (mean in %) were calculated in ArcGis software according to DIAS et al., 2020 land cover classification.

4.2. Capybara groups monitoring

We monitored population dynamics of seven groups of capybaras, three in endemic and four in non-endemic areas for BSF. Population monitoring were made through direct counts, a widely used method to monitor capybara populations (FERRAZ; MANLY; VERDADE, 2010; VARGAS et al., 2007; VERDADE; FERRAZ, 2006). This method consists in counting visible animals in a pre-selected area (VERDADE; MOREIRA; FERRAZ, 2013).

We counted animals during the last 3 hours of sunlight, between 4 p.m and 7 p.m. At this period of the day, capybaras were aggregated into a single group and could be observed resting in open areas or near water bodies, before increasing their foraging activity (LOPES et al., 2021). For each study area we defined a stationary point for sampling, choosing strategic locations and periods for best sighting and counting of individuals. Once the group was located, we performed point counts until the observer was confident that all visible animals were counted, which took 20-40 minutes, in general.

Distances of observation varied from 10 to 150 meters, for distances greater than 15 meters, observers used a binocular. We classified observed capybaras per age class based on body size as adults and juveniles (> 10 kg) or young (< 10 kg; OJASTI, 1973; VERDADE; FERRAZ, 2006). There was one observer responsible for counting animals in each study area. Before starting data collection, all observers were trained during one week to conduct capybara monitoring. At the end of training period, we assumed everyone was able to detect the same number of animals and classify them per age class, avoiding bias.

In Ribeirão Preto study area (USPRP group), fences were built by the campus administration to prevent capybaras from accessing areas where people circulate (NIEVAS, 2019), restricting animal movement inside a forest patch and preventing direct observations. Therefore, capybaras from this group were attracted to a corral baited twice a week with 10 kg of sugarcane. A camera-trap (Bushnell HD ®) was installed inside the corral and another at its entrance, programmed to record videos full time and collecting data ad libitum. Capybaras were counted when there was the largest number of animals in the same scene, which happened between 5 and 8 p.m.. As for direct counts, capybaras were classified per age class based on body size. A recent study have not found significant differences between camera trap monitoring and direct counts for capybara surveys (CORREA, 2021), so we assumed that this alternative method did not interfere with our results.

We planned to monitor capybara groups during 48 months (from January/2015 to December/2018) with an interval of 14 days between consecutive counts. However, due to inherent logistical problems (e.g. team losses, difficulties of transportation and study area accesses) of each study area and adverse weather conditions, some counts were missed and the monitoring was interrupted earlier in some study sites, which resulted in different sampling efforts among study areas.

We accomplished four-year population monitoring, as initially planned, for the groups Aeroporto, in Piracicaba, Carioba, in Americana, UFSCar, in Araras and USPRP, in Ribeirão Preto. All the groups in Pirassununga (i.e. Captação, Risca Faca and CEPTOX) had population monitoring interrupted in November/2016 or December/2016. We dealt with this sampling differences in statistical analysis by selecting comparable database.

4.3. DATA ANALYSES

To perform all data analyses we selected only the count when it was detected the largest number of individuals for each month. We assumed we did not over count animals; instead, we could underestimate individuals during count caused by errors in detection. Therefore, selecting maximum values better represented the state of populations than calculating means.

Then, we described the observed pattern of population fluctuation per capybara group, focusing on the variations in the number of individuals counted, and identifying peaks of increased number of individuals counted, especially in births (i.e. number of young) in all areas. Our description aimed to find patterns, differences, particularities and similarities between capybaras groups. We analyzed population fluctuation using all available data of each capybara group.

To describe and compare annual population fluctuation between BSF-endemic and non-endemic situations, we calculated the mean of the maximum numbers of individuals counted per month, independently of the year. For this analysis, we considered only the years that all capybara groups were simultaneously sampled (i.e. 2015 and 2016). Our description of annual fluctuations followed the same criteria described above.

From counts, we estimated abundance and ecological density indexes per age class for each capybara group. Such indexes are not an actual representation of population size or density, but it is assumed that there is a strong correlation between them, allowing comparisons across study areas and years, for example (POLLOCK et al., 2002; SINCLAIR;

FRYXELL; CAUGHLEY, 2006). This assumption is made based on the concept that by using the same amount of sampling effort the researcher will detect the same proportion of population (WITMER, 2005).

To access group abundance indexes, we calculated monthly maximums of counted capybaras without considering counts equal to zero, as they do not represent true variation in the number of individuals. According to GPS collar group monitoring (DIAS et al., 2021; LOPES et al., 2021), when the count was equal to zero the group was using another portion of its home range, other than the focus area. This situation was common when there were human disturbances just before counts (e.g. lumbering, machines working) or presence of cattle, but the individuals could be detected again in the counts. Ecological densities were calculated per month by dividing monthly abundances per group home range (Table 1; Lopes et al., 2021). We considered home ranges estimated for these same groups by Lopes et al., (2021). Since we did not have home range data for the group CEPTOX in Pirassununga, we used the mean home range size of the other two groups of that municipality. To estimate and compare abundance and density indexes among our study sites we considered only the years that were simultaneously sampled (i.e. 2015 and 2016).

We examined non-normality of our database using Shapiro-Wilk tests and inspecting Q-Q plots. We compared monthly averages of abundance and ecological density indexes per age between BSF-status by Kruskal-wallis non-parametric test, using a level of significance of 5%. Analysis were performed using R programming environment version 4.1.0 (R CORE TEAM, 2014).

5. RESULTS

5.1. Data collection

The number of counts per capybara group varied from 38 counts in the group CEPTOX to 94 counts in the group Carioba (Table 2). The mean interval between consecutive counts in database used for fluctuation analyses varied from 14.69 ± 3.7 days to 17.57 ± 13.67 days. While the mean interval between consecutive counts in the database used for abundance and density indexes estimation varied from 14.6 ± 2.84 days to 17.61 ± 9.26 days. In both databases, the interval ranged from the minimum of 7 to the maximum of 95 days. More details about the number of counts per group, month and year are available in Appendix.

Table 2. Monitoring period and number of counts per capybara group. Groups are identified by study area and BSF-status (E – endemic; NE – non-endemic).

BSF-status	Study area	Capybara group name	Monitoring period (month/year)	Number of counts	Interval of days between consecutive counts used for:					
					Fluctuation analysis			Abundance and density indexes estimation		
					Mean \pm SD	Minimum	Maximum	Mean \pm SD	Minimum	Maximum
E	Piracicaba	Aeroporto	02/15 to 12/18	88	16 \pm 7.9	7	63	14.6 \pm 2.84	10	26
E	Americana	Carioba	01/15 to 12/18	94	14.69 \pm 3.7	11	43	15.39 \pm 5.2	11	43
E	Araras	UFSCar	02/15 to 12/18	89	15.82 \pm 5.29	7	33	16.7 \pm 5.22	7	30
NE	Pirassununga	1-Captação	01/15 to 11/16	40	17.57 \pm 13.67	8	95	17.57 \pm 13.67	8	95
NE	Pirassununga	2-Risca Faca	01/15 to 12/16	43	16.31 \pm 7.3	8	50	16.31 \pm 7.3	8	50
NE	Pirassununga	3-CEPTOX	01/15 to 11/16	38	17.51 \pm 10.73	8	61	17.51 \pm 10.73	8	61
NE	Ribeirão Preto	USPRP*	01/15 to 12/18	86	16.75 \pm 7.95	7	65	17.61 \pm 9.26	8	65

*We do not have information of date from March/2018 to December/2018; calculations were made using available data.

5.2. Capybara population fluctuation

In the group Aeroporto, located in Piracicaba, we found similarities in population fluctuation across the four-year population monitoring (Figure 2). We observed a tendency of populational decrease, from a maximum of 59 individuals in October/2015 to a maximum of 25 individuals in October/2018. In 2015 and 2016, population reached its maximum in October and minimum in May and April. In 2017 and 2018, we counted very few animals in May and July, and again in October/2018 we noted a peak of the population. In 2015, we observed a larger number of young than in the other three years. In this same year, we noted an increase in the number of young two times, first in March/April and again in July/August, reaching a maximum of 31 young individuals. In the following years, we observed a decrease in the number of young, close to zero, not overpassing 7 young individuals (in July/2018).

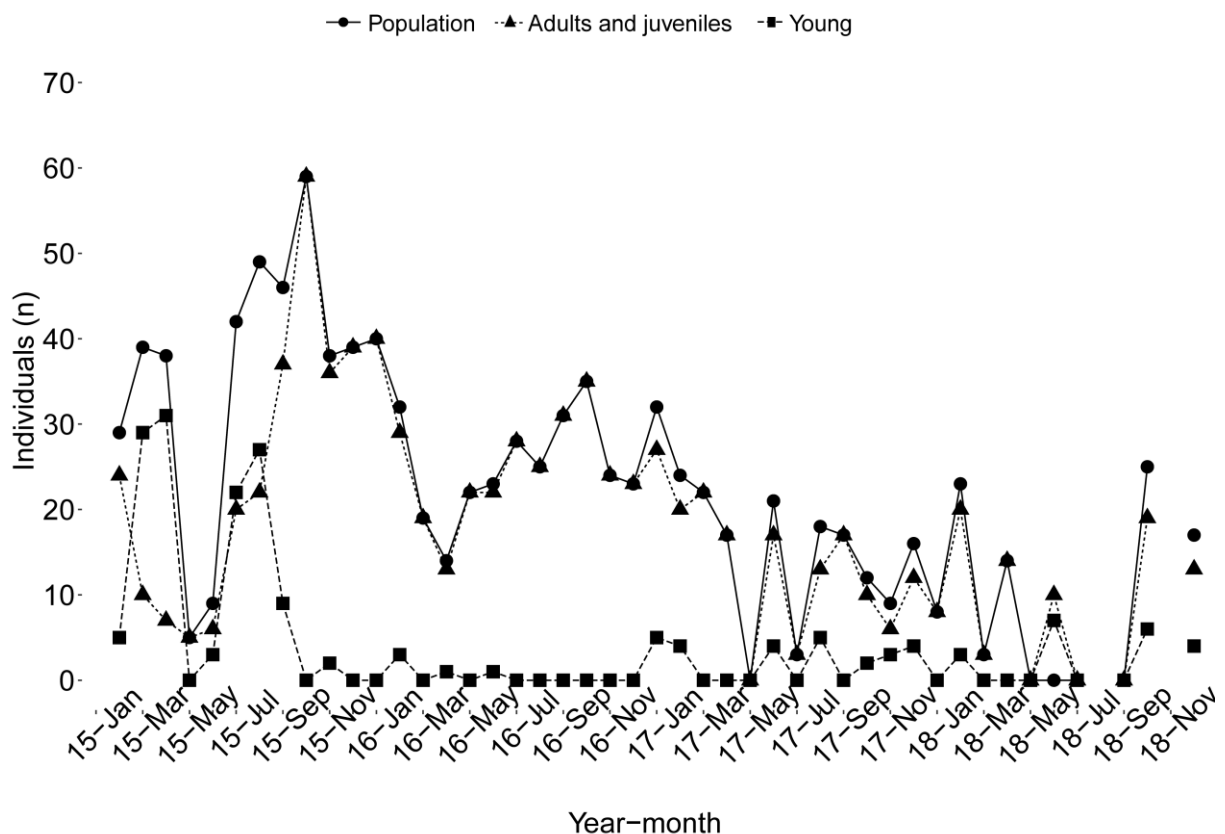


Figure 2. Population fluctuation of capybaras monitored in Piracicaba – Group Aeroporto, from February/2015 to December/2018.

The capybara group Carioba, in Americana, also showed a tendency of decreasing in group size along the monitoring period, from a maximum of 49 in January/2015 to a

maximum of 25 individuals in February/2018 (Figure 3). Besides this general tendency, there were variations in group size in specific periods. At the beginning of the population monitoring, we observed the maximums of young individuals, in January/2015 and April/2015. In 2015, we observed a continuous decrease in the number of individuals counted from April until July. In August/2015 there was an increment of young individuals and population increased again. In next year, we observed a similar pattern, population decreased from December/2015 until June/2016, and the increment of young occurred earlier, in July. In 2017, we counted few animals from January until April. We noted an increase in birth in August. In 2018, the peak of birth happened in February and from June onwards we counted few animals, with a maximum of 11 individuals, in December/2018.

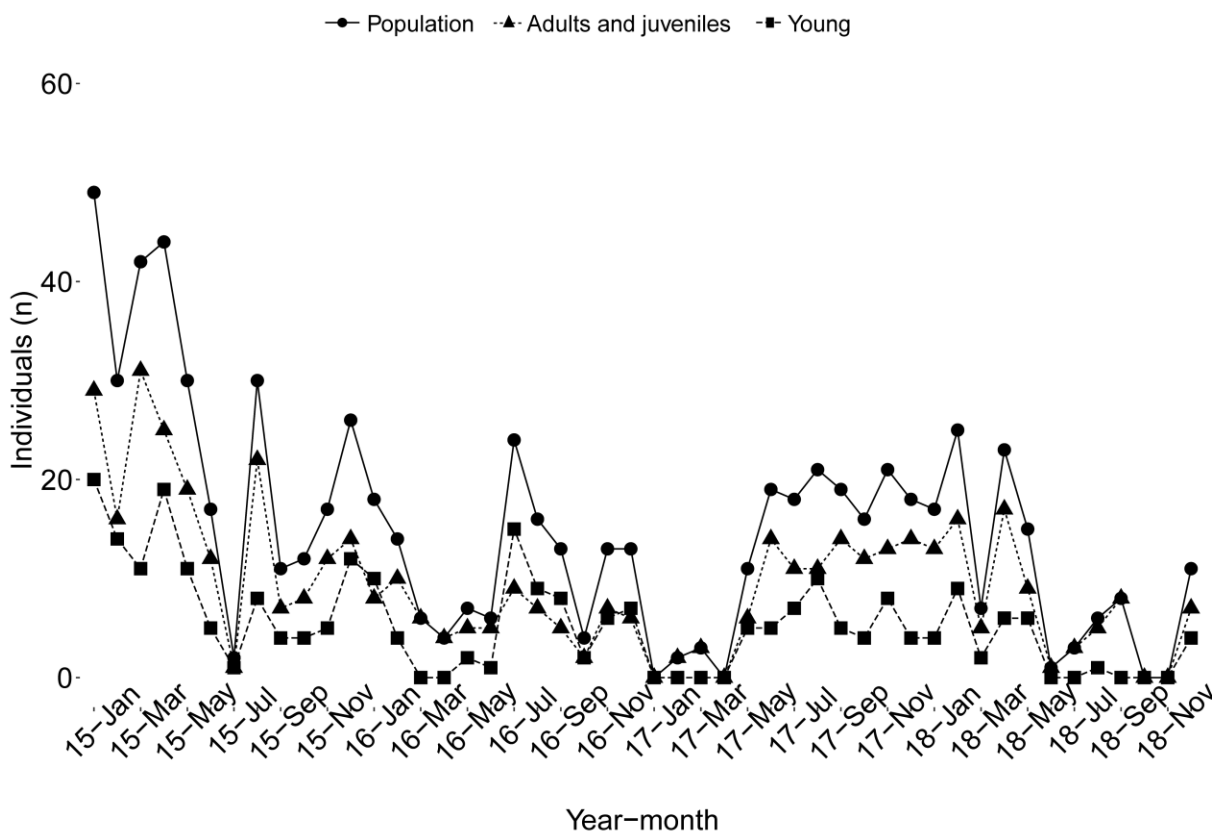


Figure 3. Population fluctuation of capybaras monitored in Americana – Group Carioba, from January/2015 to December/2016.

In the capybara group UFSCar, in Araras, we observed a stability in the number of individuals counted, especially in 2017 and 2018 (Figure 4). During the first year of monitoring, in 2015, we noted a larger variation in the number of individuals counted, when it was observed sharp decreases in population in June and August. In July/2015, there was a

peak in the number of individuals as well as in February and November/December. From October/2015 until April/2016 we counted a consistent number of young individuals (ranged from 12 to 21 individuals). From May/2016 until October/2016 the number of young individuals decreased (ranged from 0 to 10 individuals). From November/2017 until December/2018, the number of young increased again (range from 10 to 22 individuals), with a maximum of individuals observed in March and June. In general, young individuals were observed through the whole year.

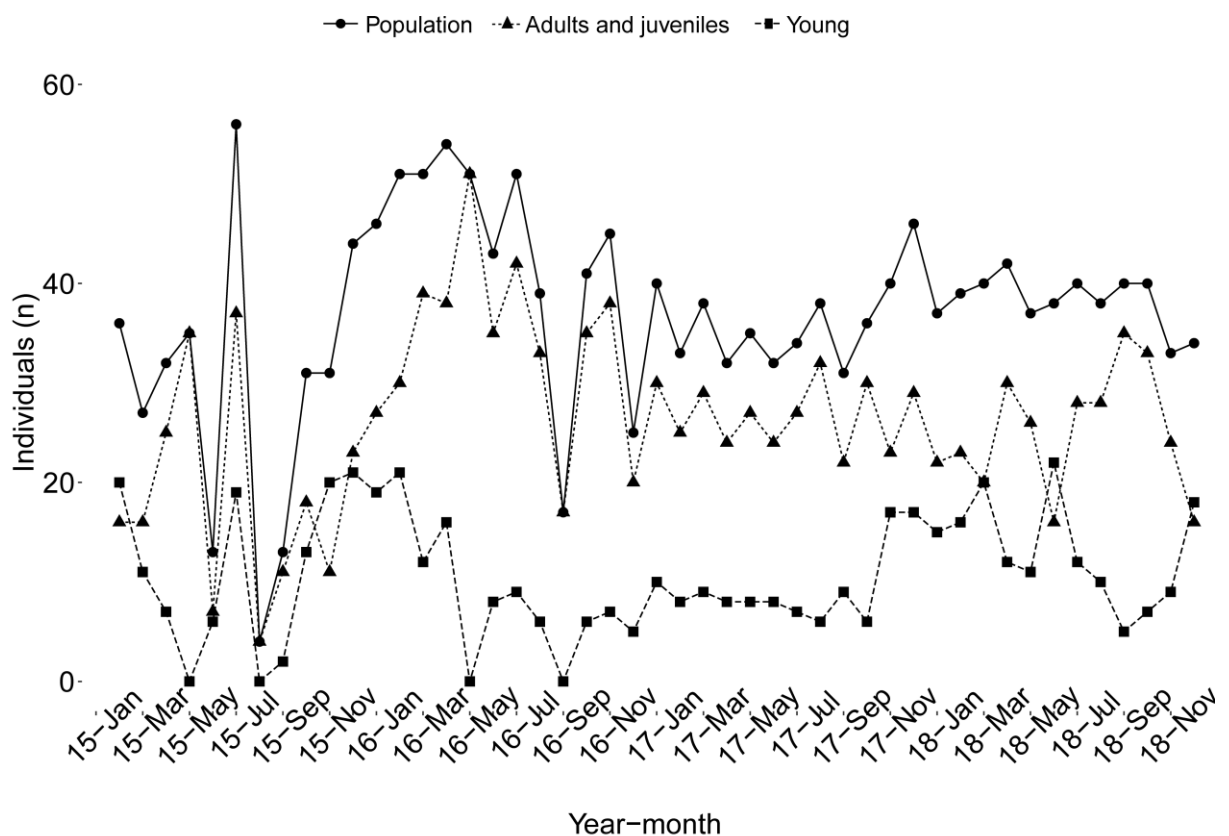


Figure 4. Population fluctuation of capybaras monitored in Araras – Group UFSCar, from February/2015 to December/2018.

In the group Captação, in Pirassununga, population reached its maximum ($n = 27$ individuals) in September/2015 (Figure 5). At this same time, we recorded the greatest number of young individuals ($n = 12$). From December/2015, population started to decrease constantly, until July 2016. The smallest numbers of individuals, which varied from zero to seven, were recorded in February and April/2015, May of both years, June and July/2016. We

do not have records for July, August and December/2016. However, in October/2016 population increased to 12 individuals, compared to the last record made in June/2016.

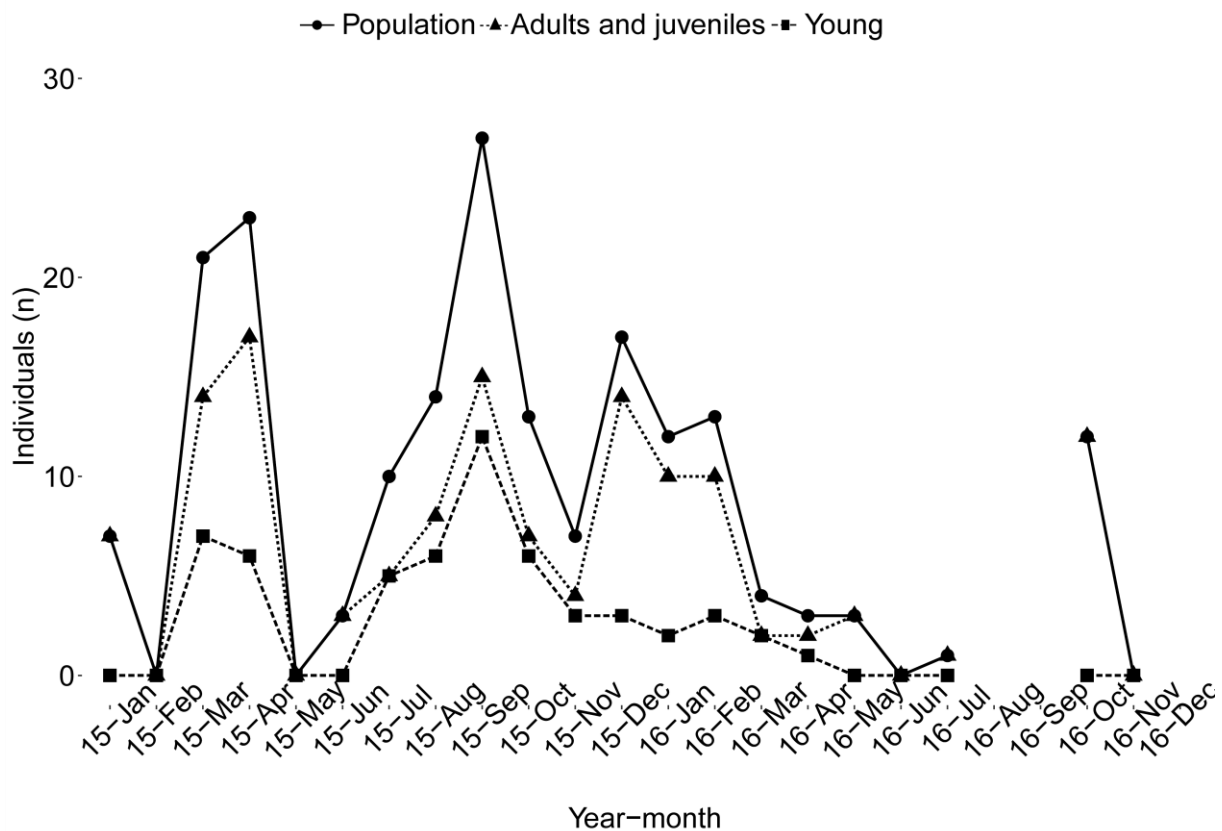


Figure 5. Population fluctuation of capybaras monitored in Pirassununga – Group Captação, from January/2015 to December/2016.

In the group Risca Faca, in Pirassununga, we found large variation in the number of individuals counted from January/2015 until December/2015 (Figure 6). During this period, the number of individuals varied from 1 to 50 individuals. The peak in the number of individuals occurred in December/2015 ($n = 50$ individuals). The maximum number of young was observed in March/2016 ($n = 24$ individuals). There was also an increase of young in March/2015 ($n = 21$ individuals) and December/2015 ($n = 18$ individuals). From January/2016 until December/2016 the maximum number of individuals counted was 28. We did not count this group in November/2016.

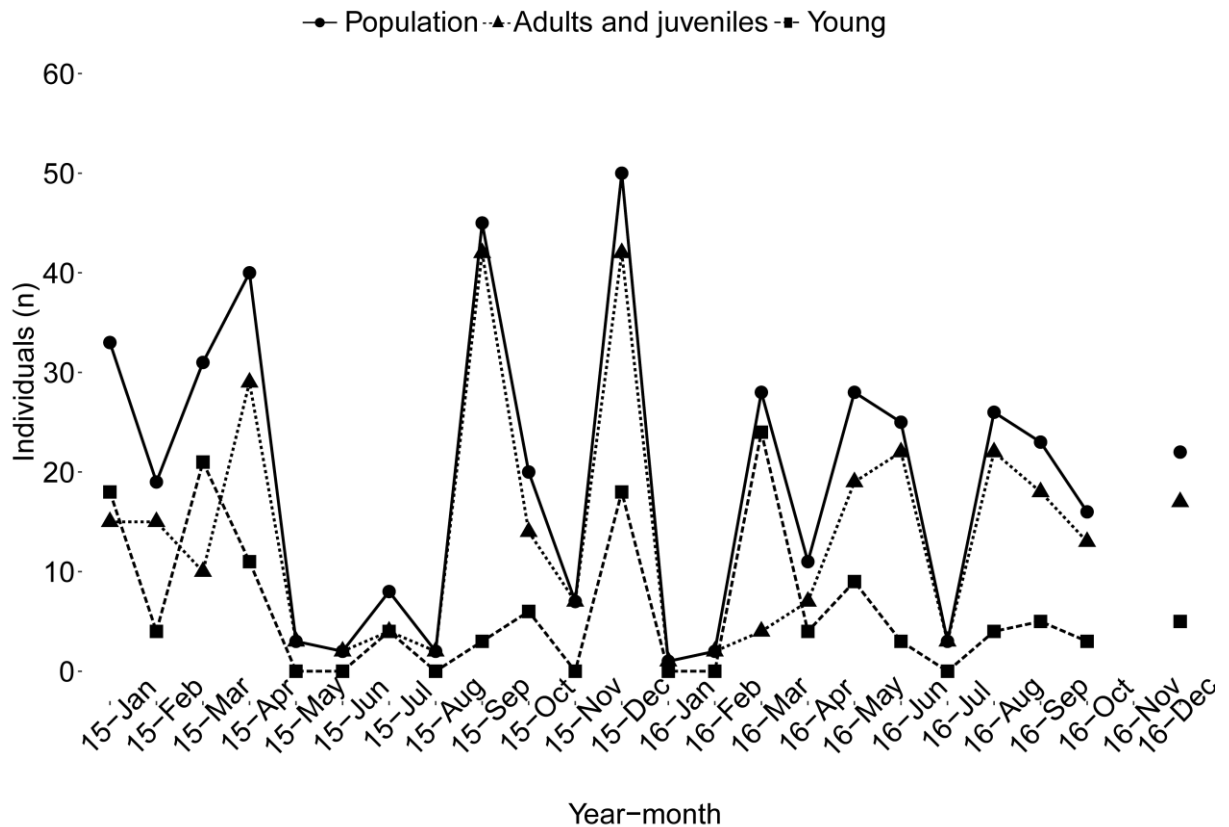


Figure 6. Population fluctuation of capybaras monitored in Pirassununga – Group Risca Faca, from January/2015 to December/2016.

The group CEPTOX, in Pirassununga, changed the fluctuation pattern along our two-year monitoring (Figure 7). It showed a large variation in the number of individuals counted from January/2015 until August/2015, followed by a stabilization in the number of individuals until the end of our monitoring. From January/2015 until August/2015 counts varied from zero to 30 individuals. The peak in the number of individuals occurred in August/2015 when it was also observed an increment of young individuals. However, the maximum number of young individuals was observed in April/2015 ($n = 10$ individuals). From September/2015 until the end of monitoring, population stabilized around 14 individuals. We observed young individuals through this whole period.

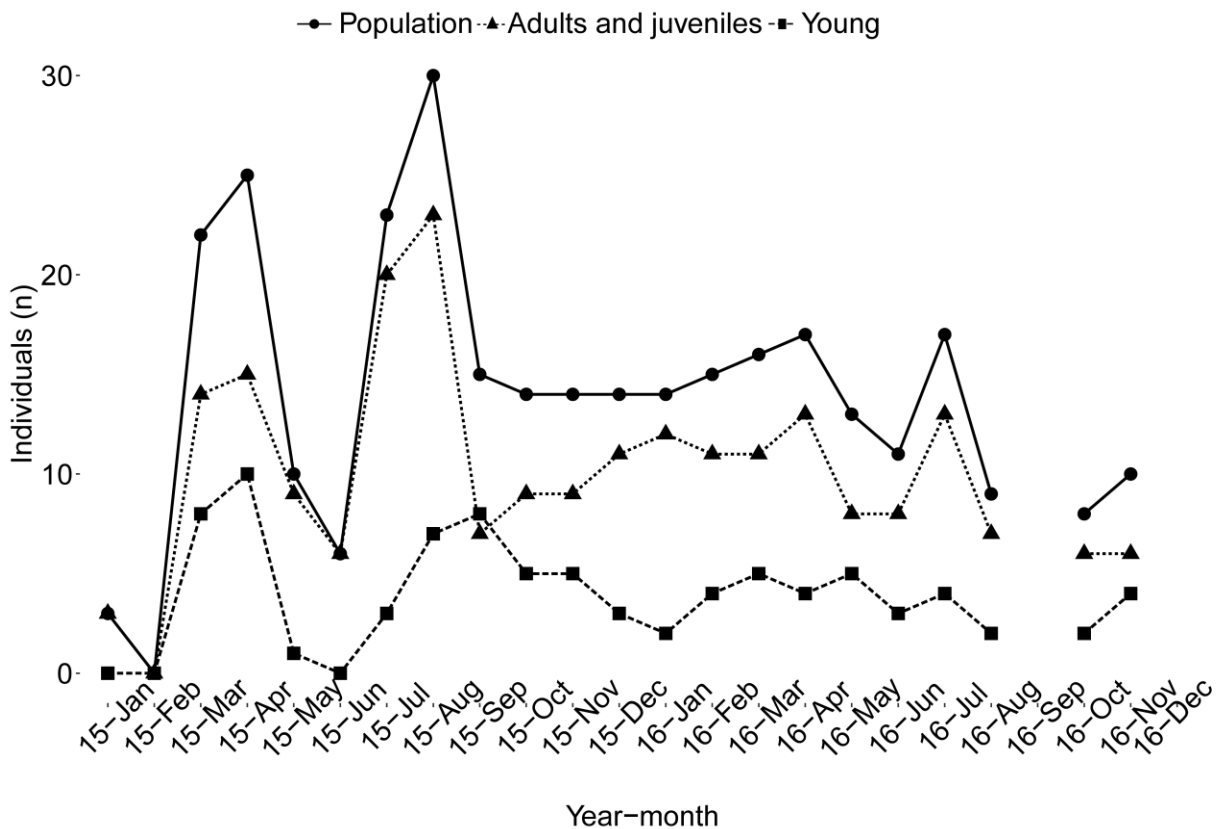


Figure 7. Population fluctuation of capybaras monitored in Pirassununga – Group CEPTOX, from January/2015 to November/2016.

The group USPRP, in Ribeirão Preto, increased from the beginning of our monitoring until its maximum in March/2017 ($n = 23$ individuals), then we noted a tendency of decrease (Figure 8). This group was stable from January/2015 until November/2015 (ranged from 10 individuals to 14 individuals). During this period, the maximum number of young occurred in May and, from August until November there was any birth detection. There was a decrease in the number of individuals from December/2015 until May/2016 (ranged from 7 to 9 individuals). We observed population growth from October/2016 until March/2017, with continuous increment of young individuals, especially from January to March ($n = 12$ young individuals). Population remained stable until July/2018, when it started to decrease again.

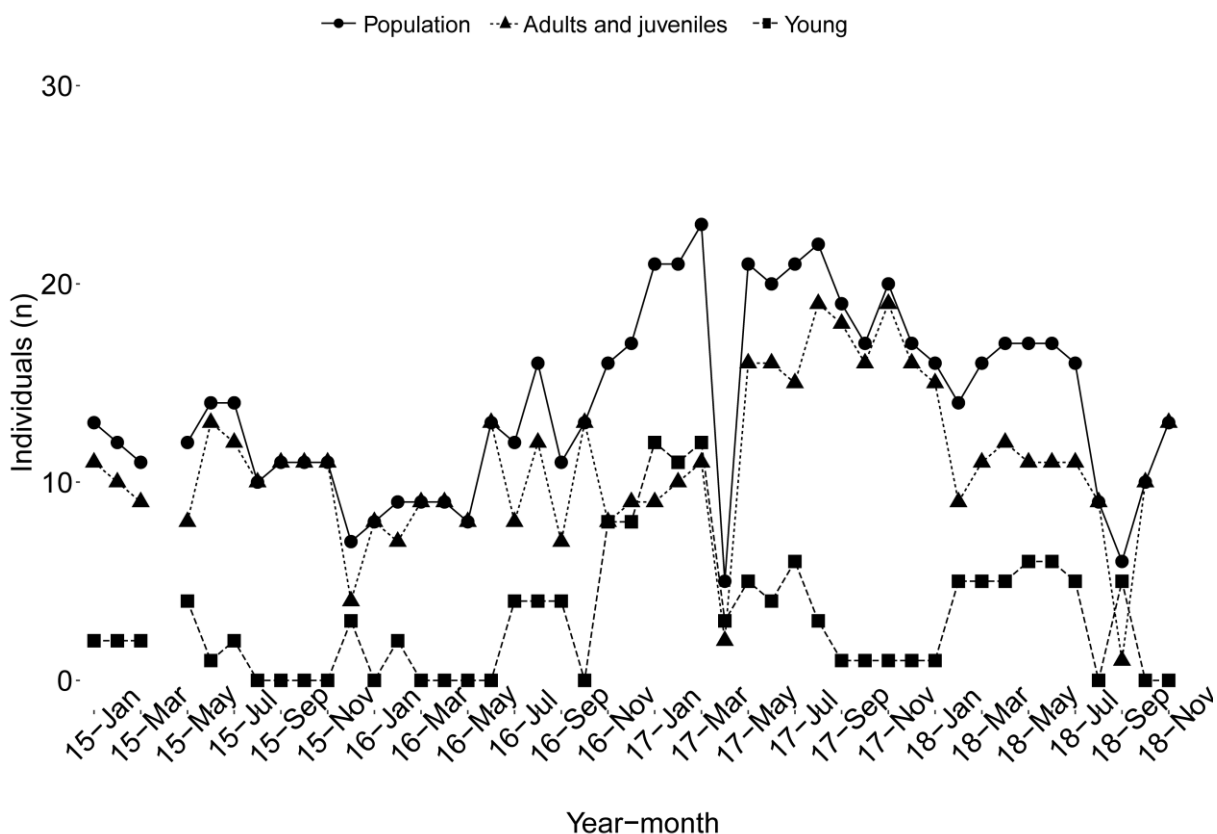


Figure 8. Population fluctuation of capybaras monitored in Ribeirão Preto – Group USPRB, from January/2015 to December/2018.

In general, it was observed similarities between capybara groups regarding annual fluctuations. All groups showed a decrease in the number of individuals around the months of May and June, followed by an increase around the months of July, August and/or September (Figures 9 and 10). In all BSF-endemic areas (Figure 9), we detected young individuals along the whole year with an increase in July and/or August. In Americana (Group Carioba) and Araras (Group UFScar) there was also increased number of young in January. In Piracicaba (Group Aeroporto), we observed two periods of young increment, which was in March/April and July/August. Population reached its maximum in October and minimum in May (Figure 9A). In Americana (Group Carioba), it was observed young throughout the whole year but periods of increased births occurred in January, April, August and December. We observed the maximum number of individuals in January and the smallest numbers of individuals in June and October (Figure 9B). In Araras (Group UFSCar), the maximum number of individuals counted was in July and, the smallest numbers of individuals was in June and September (Figure 9C). We observed periods of young increment from November until February and in July.

In BSF-non endemic areas, the peak of young happened later, after September (Figure 10). We observed that the groups Captação, Risca Faca e CEPTOX, both located in Pirassununga, fluctuated in a very similar pattern, showing two periods of group size increase: one around March/April and another around July, August and/or September, when it was also observed young increment. In both groups, population decreased in May and June. The group Risca Faca showed the maximum number of individuals counted in December and the minimum in July. We observed increment in the number of individuals in March and December (Figure 10A). The group Captação showed its maximum number of individuals and young in September. The minimums occurred in May and June (Figure 10B). While the group CEPTOX reached its maximums in April and July, and minimums in January/February and June. The increment of young happened in March, April and September (Figure 10C). The group USPRP) showed a very particular annual fluctuation. This group remained very similar throughout the whole year, showing soft decreases in April and October. It was observed few numbers of young during whole year. In this group, the peak of young occurred in December (Figure 10D).

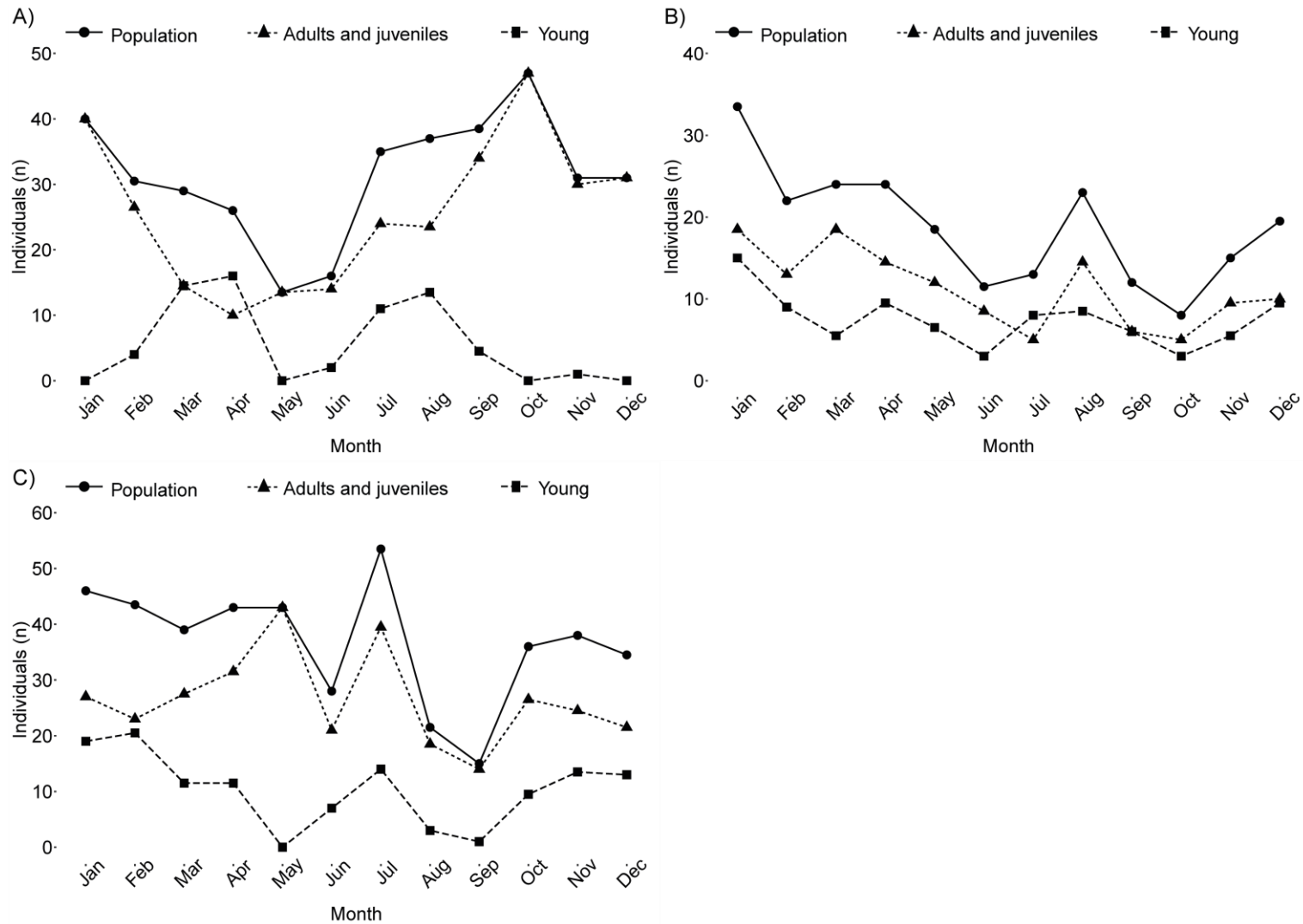


Figure 9. Annual population fluctuation of groups of capybaras monitored from January/2015 to December/2016 in BSF-endemic areas. A) Piracicaba – Group Aeroporto, B) Americana – Group Carioba and C) Araras – Group UFSCar.

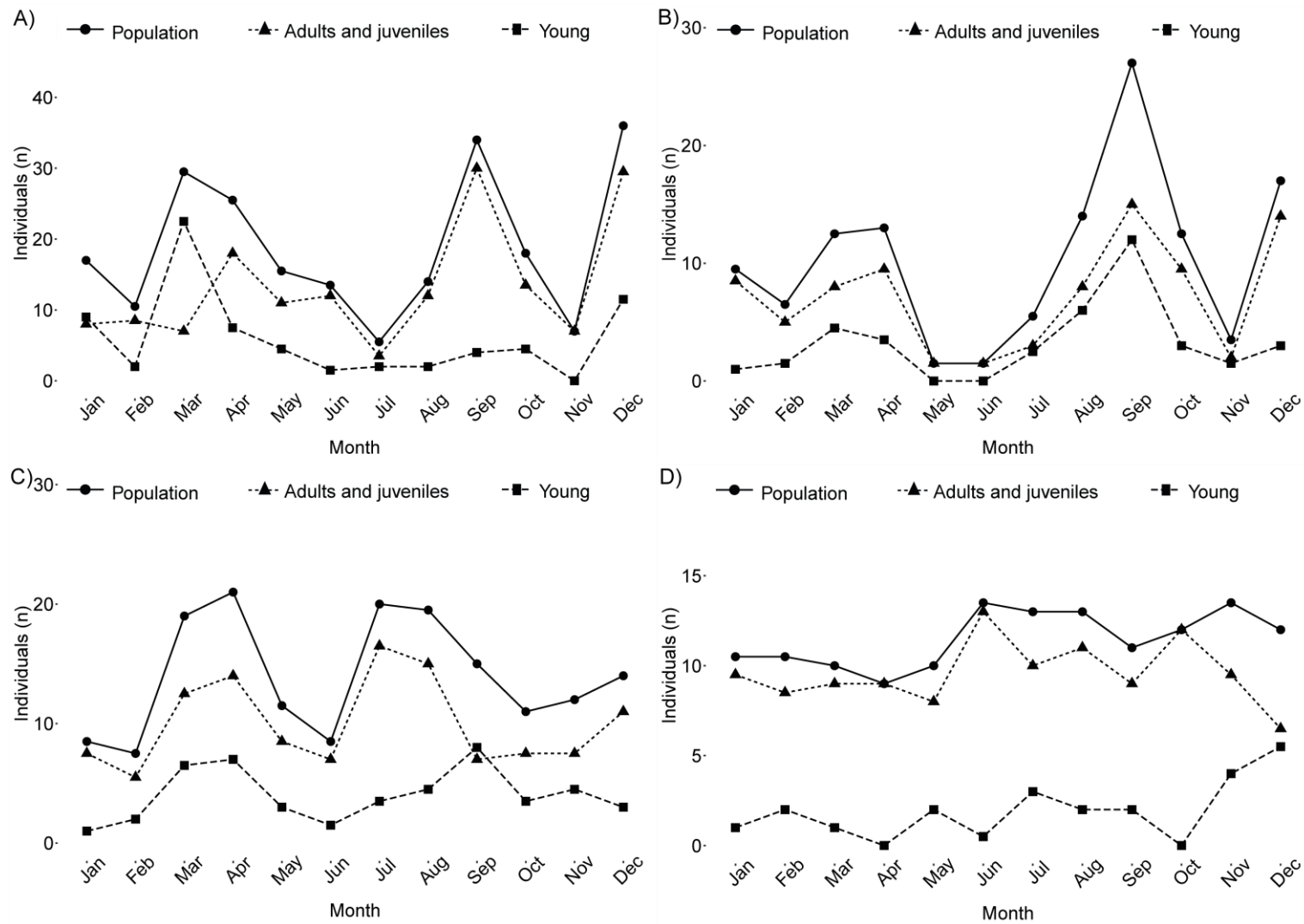


Figure 10. Annual population fluctuation of groups of capybaras monitored from January/2015 to December/2016 in BSF-endemic areas. A) Pirassununga – Group Risca Faca, B) Pirassununga – Group Captação, C) Pirassununga – Group CEPTOX and D) Ribeirão Preto – Group USPRP.

5.3. Capybara abundancy and density

We found a large variation in abundance indexes (Figure 11A) across months as well as in ecological densities in HMLs (Figure 11B, Table 3). As a general description of capybara groups in HMLS, we estimated an abundance index of 20.79 ± 14.31 individuals (range from 1 to 59), of which 15.21 ± 11.54 were adults and juveniles (range from 1 to 59) and 5.64 ± 6.72 were young (range from 0 to 31). For ecological densities, we estimated an average of 65.88 ± 57.15 individuals/km² (range from 1.56 to 222.73) of which 47.74 ± 42.51 were adults and juveniles/km² (range from 1.56 to 140.91) and 18.24 ± 23.27 were young/km² (range from 0 to 90.91).

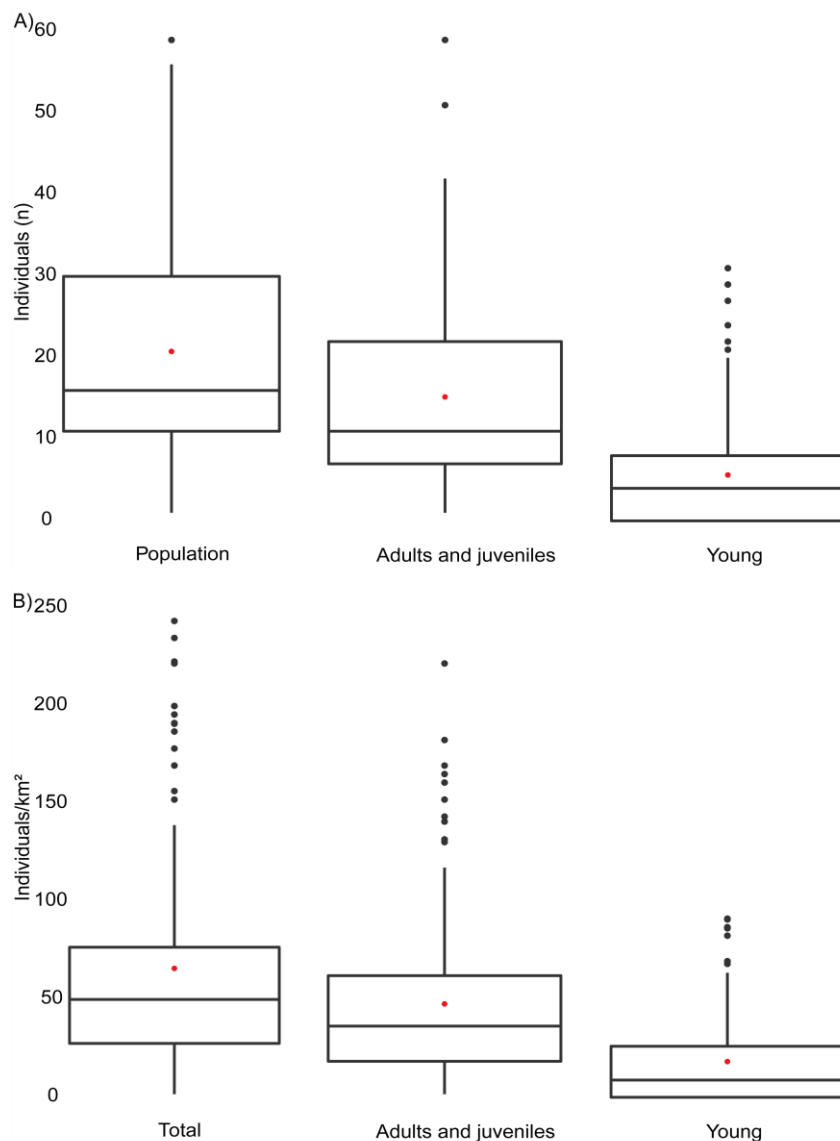


Figure 11. Boxplots of A) abundance index per age of capybara in HMLs and B) ecological densities per age of capybara in HMLs.

Table 3. Abundance indexes and ecological densities of capybara groups in human-modified landscapes, classified as BSF-endemic and non-endemic areas.

BSF-status (E – Endemic, NE – non- endemic)	Study Area	Capybara Group	Abundance Index (mean \pm SD individuals)			Ecological density (mean \pm SD individuals/km ²)		
			Population	Adults and Juveniles	Young	Population	Adults and Juveniles	Young
E	Piracicaba	Aeroporto	30.83 \pm 12.83	25.04 \pm 12.70	5.78 \pm 10.39	55.05 \pm 23.09	44.72 \pm 22.69	10.33 \pm 18.56
E	Americana	Carioba	18.67 \pm 13.14	11.25 \pm 8.34	7.42 \pm 5.71	88.85 \pm 59.74	51.14 \pm 37.89	33.71 \pm 25.95
E	Araras	UFSCAR	36.35 \pm 14.56	26.43 \pm 12.52	9.91 \pm 7.43	158.03 \pm 63.29	114.93 \pm 54.44	43.10 \pm 32.29
MEAN			28.47 \pm 15.31	20.77 \pm 13.15	7.70 \pm 8.11	99.1 \pm 67.17	69.99 \pm 50.97	29.11 \pm 29.28
NE	Pirassununga	1- Captação	11.18 \pm 7.62	7.88 \pm 5.15	3.29 \pm 3.33	26.61 \pm 18.14	18.77 \pm 12.25	7.84 \pm 7.93
NE	Pirassununga	2-Risca Faca	19.35 \pm 14.66	13.61 \pm 11.92	6.17 \pm 7.28	30.23 \pm 22.91	21.26 \pm 18.63	9.65 \pm 11.38
NE	Pirassununga	3- CEPTOX	14.57 \pm 6.43	10.52 \pm 4.77	4.05 \pm 3.33	27.49 \pm 12.13	19.86 \pm 9.00	7.64 \pm 4.94
NE	Ribeirão Preto	USPRP	11.61 \pm 2.68	9.61 \pm 2.27	2.00 \pm 2.62	64.49 \pm 14.86	53.38 \pm 12.62	11.11 \pm 13.50
MEAN			14.38 \pm 9.54	10.58 \pm 7.34	3.97 \pm 4.68	38.2 \pm 23.71	29.20 \pm 20.16	9.18 \pm 10.14
GENERAL MEAN			20.79 \pm 14.31	15.21 \pm 11.54	5.64 \pm 6.72	65.88 \pm 57.15	47.74 \pm 42.51	18.24 \pm 23.27

Considering population abundance indexes per capybara group, we found a variation from 11.18 ± 7.62 individuals to 36.35 ± 14.56 individuals (Table 3). We found the largest abundance index for all ages in the group UFSCar, located in Araras (Figure 12), followed by the group Aeroporto, in Piracicaba. Although the group Carioba, in Americana, showed smaller abundance indexes than the group Aeroporto, it showed, on average, a greater abundance index of young. In these three groups, it was observed a larger variation in abundance indexes across months than it was observed in the other four groups. The smallest population abundance index was recorded in the group Captação, located in Pirassununga. Abundance indexes of this group was very similar with the other groups located in the same municipality and with the group USPRP, in Ribeirão Preto.

Similar results were found for ecological density estimation per capybara group. Population ecological densities per group varied from 26.61 ± 18.14 individuals/km² to 158.03 ± 63.29 individuals/km². The group UFSCar showed the greatest density for all age classes (Figure 13). The group Carioba, in Americana, showed greater densities in all age classes than the group Aeroporto in Piracicaba, differently from the results of abundance indexes. All groups in Pirassununga showed the smallest ecological densities which were very similar between each other, except by the density of young in the group Captação, which was greater than the other two. Differently from results on abundance index, the group USPRP, in Ribeirão Preto, were among the greatest records, showing ecological densities even greater than the group Aeroporto.

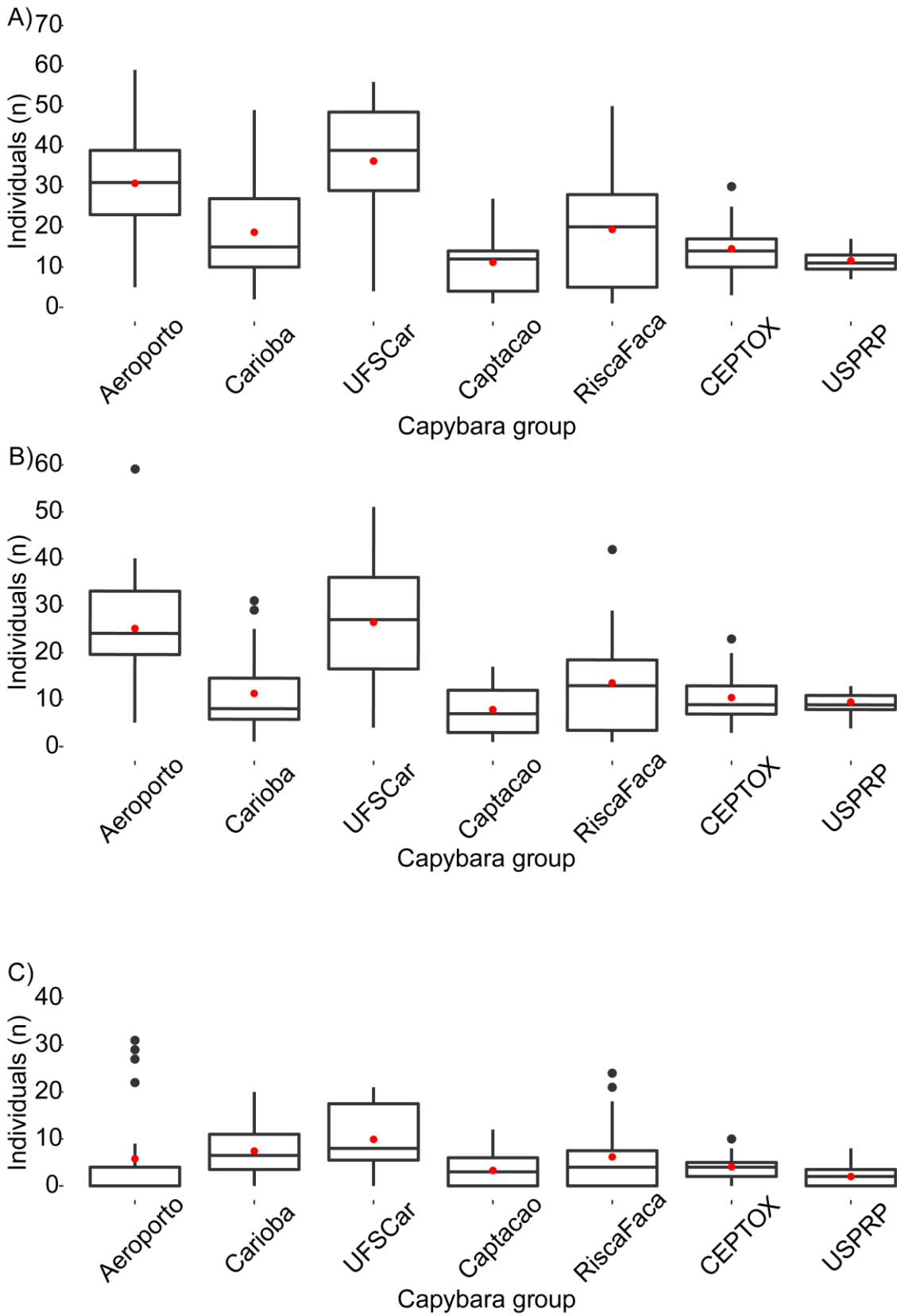


Figure 12. Boxplots of abundance indexes per capybara group. A) Population, B) adults and juveniles and C) young.

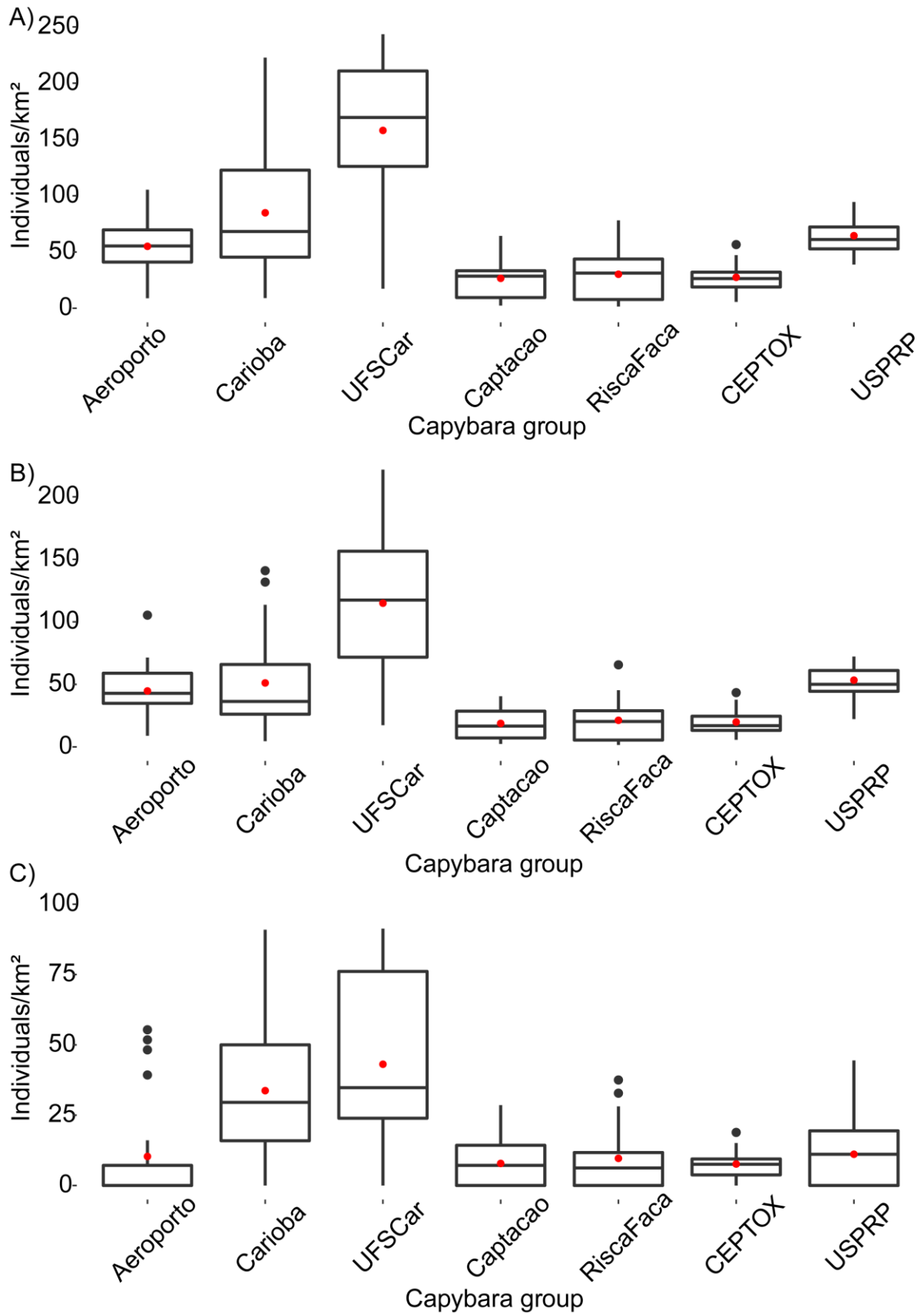


Figure 13. Boxplots of ecological densities per capybara group. A) Population, B) Adults and juveniles and C) Young.

Our results indicate significantly greater abundance indexes of capybaras in all ages in BFS-endemic areas (Figure 14A, Table 3). We estimated an overall abundance index of 24 ± 14 individuals (range from 2 to 54) in groups where BSF is present, of which 18 ± 12 were adults and juveniles (range from 1 to 50) and 7 ± 7 were young (range from 0 to 24). On the other hand, in BSF-non-endemic groups, the estimated abundance indexes were on average 12 ± 8 (range from 1 to 50) individuals, 9 ± 6 being adults and juveniles (range from 1 to 42) and 3 ± 4 young (range from 0 to 18, *P*-values are <0.001 ; <0.001 and, $=0.003$, respectively).

Similar results were found with ecological densities being greater in all ages in BFS-endemic areas (Figure 14B, Table 3). We found an average density of 85 ± 62 individuals/km² (range from 5 to 233) in these areas, 60 ± 57 are adults and juveniles/km² (range from 5 to 198) and 25 ± 26 are young/km² (range from 0 to 91). While in non-endemic ones, the ecological densities found were 33 ± 21 individuals/km² (range from 2 to 72), 26 ± 18 adults and juveniles/km² (range from 2 to 72), and 8 ± 9 young/km² (range from 0 to 91, *P*-values are all <0.001).

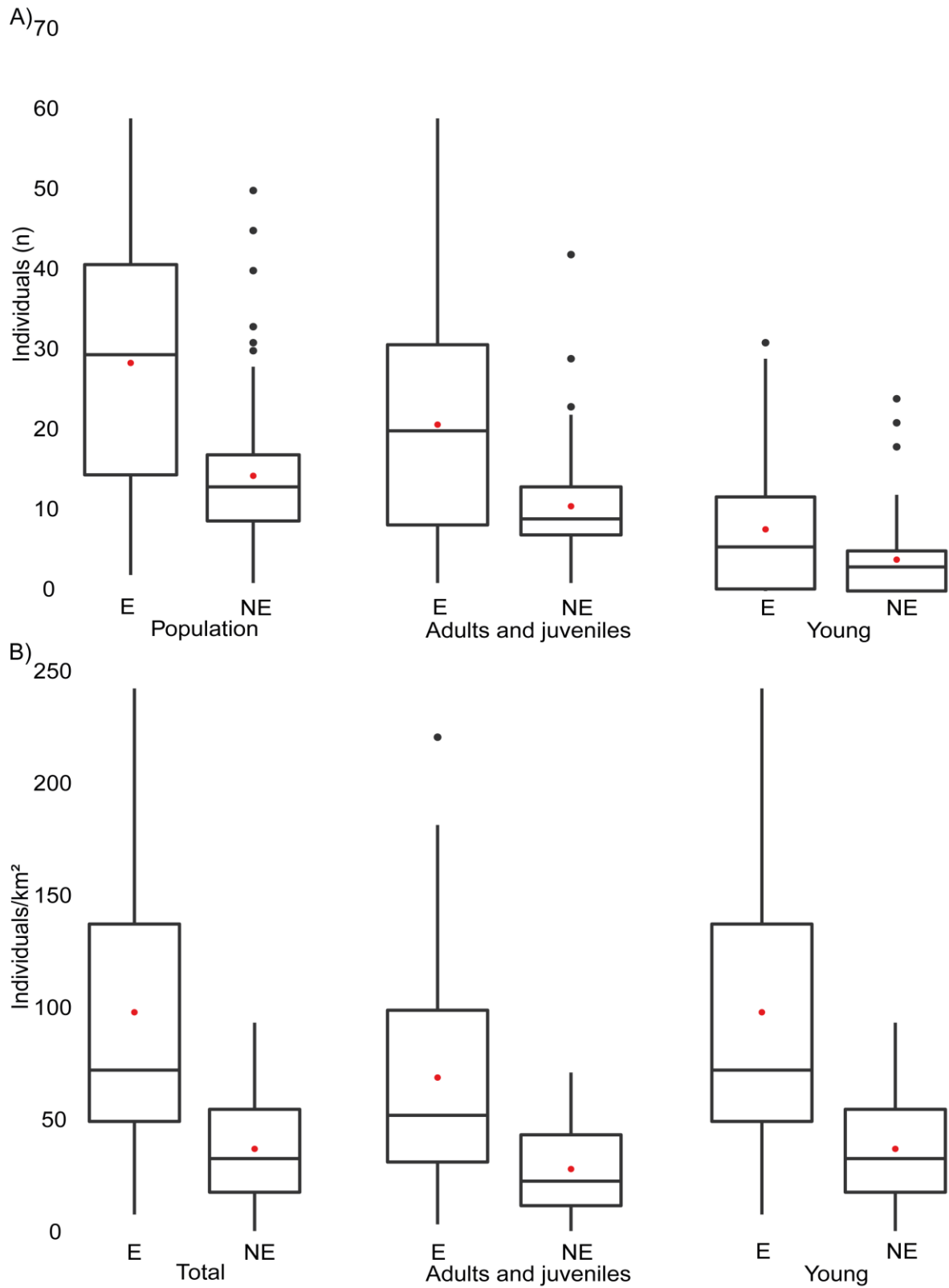


Figure 14. Boxplots of A) abundance indexes per age of capybaras in BSF-endemic (E) and non-endemic (NE) areas and B) ecological density per age of capybaras in BSF-endemic (E) and non-endemic (NE) areas.

6. DISCUSSION

We found remarkable results in capybara populations among our surveyed areas. Our results demonstrated that: (1) each capybara group showed a particular pattern of population fluctuation in HMLs; (2) the period of increased birth occurred previously in endemic areas, around July and August, while it occurred after September in non-endemic areas; (3) endemic areas showed greater abundance indexes and ecological densities of capybaras for all ages.

In natural habitats, capybara population fluctuates according to seasonal variation of limiting resources, such as water and food (MOREIRA et al., 2013c); however, in HMLs these vital resources show weak seasonality. On the contrary, there is a high availability and predictability in both time and space of supplemental food from agriculture crops and pasture, and, water from artificial water bodies (FERRAZ et al., 2007, 2003; VERDADE et al., 2012; VERDADE; FERRAZ, 2006). Our surveyed HMLs are characterized by high land use heterogeneity, being classified as agroecosystems (MELO et al., 2013). In addition, HMLs are susceptible to a series of anthropogenic influence, such as human facilities and transportation construction, logging, people movement and work, etc., which may explain we found very distinctive fluctuations among our monitored capybara groups and not a single common fluctuation pattern for all groups. For example, in Piracicaba, a ring road was built approximately 500 m in a straight line from the group home range during our population-monitoring period, which possibly affected group's movement and behavior. In Americana, our study area is located in a sewage treatment station, where we frequently observed movement of people and trucks, and, the area often had the grasses mowed. In Araras, the access to supplemental food in crops or pasture depended on operating condition of fences. Briefly, the heterogeneity of HMLs and specific anthropogenic modifications of each study area resulted in very particular capybara population fluctuations. Because of this, we considered each capybara group living in HMLs as a single ecological unit, which has to be specifically monitored when there is a management goal.

In general, we could detected young individuals throughout the whole year, which may be possible for this all-year fertile species (HERRERA, 1998; OJASTI, 1973). In natural habitats, capybaras increase birth when there is a positive balance between food availability and risk of infant mortality (MOREIRA et al., 2013c). In Brazilian Pantanal, the natural habitat for capybaras in Brazil, the peak in reproduction happens only once a year, at the end of rainy season (ALHO; CAMPOS; GONÇALVES, 1987; SCHALLER; CRAWSHAW,

1981). Our data revealed more than one period of increase of young individuals counted during the year and differences in timing among different groups. Low seasonality of vital resources in HMLs in addition to low predation risk makes reproduction to be low costly through the whole year. Differences in timing in each group may be resulted of a combination of specific types and management of food resources and other anthropogenic influences, which has to be deeply investigated in each situation.

Our findings indicate increased numbers of young individuals in July and/or August in BSF-endemic areas. In many BSF-endemic areas, capybaras act as amplifying hosts of *R. rickettsii* for ticks, playing a major role in BSF epidemiology (LABRUNA, 2013). Although there is transovarial transmission of *R. rickettsii* in a few *A. sculptum* ticks, this bacterium is partially pathogenic to ticks, causing higher mortality and lower reproductive performance among infected ticks. These statements support the low *R. rickettsii* infection rates (<1%) in *A. sculptum* populations, indicating that the bacterium requires amplifying hosts for its maintenance in tick populations (SOUZA et al., 2009). Amplifying hosts are vertebrates that once primarily infected develop bacteremia for some days or weeks, when ticks feeding on them acquire *R. rickettsii* infection and establish new cohorts of infected ticks within the tick population (LABRUNA, 2013). One of the requirements to be an efficient amplifying host is the continuous introduction of individuals susceptible to *R. rickettsii* infection; i.e., young individuals generated by high reproduction rates (LABRUNA, 2009). This condition points out the importance of young capybaras for BSF occurrence. The peak of capybara birth in these months indicates a higher availability of young capybaras during the second semester of the year, when there is a predominance of nymphs of *A. sculptum* (BARBIERI et al., 2019). Thus, this combination of simultaneously “peaks” of susceptible capybaras and *A. sculptum* nymphs should be important for the establishment and maintenance of *R. rickettsii* among *A. sculptum* populations. In fact, laboratory studies have demonstrated higher transovarial transmission rates of *R. rickettsii* in *A. sculptum* ticks when the *R. rickettsii*-acquisition feeding occurs during the nymphal stage (SOARES et al., 2012, GERARDI et al., 2019).

As expected, we found significant differences in population abundance indexes and densities between capybara groups in BSF-endemic and non-endemic areas. The results found in this study corroborate with the hypothesis that BSF-endemic areas show higher abundances and densities of capybaras than non-endemic areas. As previously described by LUZ et al., (2019), BSF-endemic areas also show significant higher burdens of *A. sculptum*. This positive correlation between the number of capybaras and ticks was supported by Nunes et al., (2019), which also detected *R. rickettsii* circulation only after the increment of both tick and capybara

populations. Given the importance of young for BSF maintenance, Polo, Labruna and Ferreira (2018) found a positive correlation between birth rates and ticks infection. Although we did not estimate birth rates for BSF-endemic capybara groups, our results indicate a larger number of young capybara per km² in BSF-endemic areas, which suggest that among these groups young capybaras play a significant role in *R. rickettsii* amplification.

The increment of ticks is caused by high densities of hosts, in this case capybaras, and suitable environmental conditions. Besides this higher availability of hosts for ticks in BSF-endemic areas, environmental conditions found in capybara habitats in HMLs, which is consisted preferentially of forests (DIAS et al., 2020), also promote tick reproduction and survival (BARBIERI et al., 2019; SZABÓ; PINTER; LABRUNA, 2013). Therefore, the combination of ecological aspects of capybaras in HMLs, such as habitat selection (DIAS et al., 2020), reduced home ranges and low displacement (LOPES et al., 2021) in addition to the observed greater group sizes and densities in BSF-endemic areas in this study is crucial to *A. sculptum* thriving, and subsequently, the prevalence of *R. rickettsii* and BSF transmission to humans.

In general, HMLs the state of São Paulo offer perfect conditions for capybara thriving. The anthropogenic land transformations occurred in the state in the last century create extensive areas of agricultural crops (DEAN, 2000; DURIGAN; RATTER, 2006), especially sugar cane, which nowadays occupies more than 25% of the state territory (SOUZA et al., 2020). It is already well known that capybaras feed from these high energetic agricultural resources which is directly related with the species high abundances and densities (BARRETO; QUINTANA, 2013; BOVO et al., 2016; FELIX et al., 2014; FERRAZ et al., 2003; MAGIOLI et al., 2019; ROCHA et al., 2017). Although both BSF-endemic and non-endemic areas investigated in this study are classified as HMLs, we did not investigate differences in resource availability between them, despite we know capybara groups eventually accessed sugar cane crops in Araras and Piracicaba municipalities (BSF-endemic areas). In BSF-non-endemic areas, they accessed less energetic food full-time during our population monitoring, such as pasture grasses in Pirassununga and scarce grass resources inside Permanent Preservation Area (PPA) in Ribeirão Preto. Differences in carrying capability could be a reasonable explanation for differences in capybara group sizes and densities across BSF-endemic and non-endemic areas. Indeed, further studies should be conducted to investigate the reasons why BSF-endemic areas sustain greater abundances and densities of capybaras.

During our four-year experience with capybara counting in HMLs we overcame some challenges. Logistics and other difficulties are common in monitoring surveys (WITMER, 2005). In our study, we dealt with missed counts due to team losses, difficulties of transportation and study area accesses and, adverse weather condition. We also dealt with many counts that capybara group was not found at the usual stationary sampling point, resulting in counts equal to zero, which were caused by land-use practices, such as logging, livestock grazing, people working, etc.. We noted external/anthropogenic interferences often influencing our research. Because of this, we had the strategy of analyzing our data selecting counts where we visualized maximum number of individuals per month, aiming to minimizing detection errors. In addition, we excluded counts equal to zero as an option to deal with zero inflation (DÉNES; SILVEIRA; BEISSINGER, 2015), which does not correspond to real population state. Based on our field experience and knowledge about capybara behavior, we recommend this protocol for further studies.

7. CONCLUSION

Capybara groups in HMLs does not show a single pattern of population fluctuation. Each capybara group was characterized by singular population fluctuation.

The increment of young during the second half of the year in BSF-endemic areas occurred earlier (July and August) than in non-endemic areas (September and December).

Capybara groups presented significantly greater abundance and ecological density indexes in BSF-endemic than in non-endemic areas.

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APPENDIX

Number of counts made per month and per year in each of the capybara groups monitored from 2015 to 2018.

BSF-status	Study area	Capybara group name	Year	Number of counts per month												Number of counts per year
				J	F	M	A	M	J	J	A	S	O	N	D	
E	Piracicaba	Aeroporto	2015	0	1	2	2	2	2	3	2	2	2	2	2	22
			2016	1	3	2	2	2	2	3	2	2	2	2	2	25
			2017	1	3	2	2	2	3	2	2	2	2	2	3	26
			2018	1	3	2	2	1	1	1	0	1	1	0	2	15
Total			3	10	8	8	7	8	9	6	7	7	6	9	88	
E	Americana	Carioba	2015	1	2	2	3	2	2	2	2	2	3	2	1	24
			2016	2	2	1	2	2	2	2	2	2	1	3	2	23
			2017	1	2	2	2	2	2	2	2	2	2	2	2	23
			2018	3	2	2	2	2	2	2	3	2	1	2	1	24
Total			7	8	7	9	8	8	8	9	8	7	9	6	94	
E	Araras	UFSCar	2015	0	1	2	2	2	2	2	2	2	2	2	2	21
			2016	2	2	2	2	2	2	2	2	2	1	2	1	22
			2017	2	2	2	3	2	1	2	2	2	2	2	1	23
			2018	1	2	2	2	2	2	2	2	2	2	2	2	23
Total			5	7	8	9	8	7	8	8	8	7	8	6	89	
NE	Pirassununga	1-Captação	2015	1	2	2	2	2	2	1	3	2	2	2	23	
			2016	2	2	2	3	2	2	2	0	0	1	1	0	17
Total			3	4	4	5	4	4	3	3	2	3	3	2	40	

NE	Pirassununga	2-Risca Faca	2015	1	2	2	2	2	2	1	2	2	1	3	1	21
			2016	2	3	2	2	2	3	1	2	2	2	2	0	1
Total				3	5	4	4	4	5	2	4	4	3	3	2	43
NE	Pirassununga	3-CEPTOX	2015	1	2	2	2	2	1	1	1	2	2	2	2	20
			2016	2	2	2	2	3	2	2	1	0	1	1	0	18
Total				3	4	4	4	5	3	3	2	2	3	3	2	38
NE	Ribeirão Preto	USPRP	2015	3	2	1	0	1	1	2	2	1	2	2	2	19
			2016	1	2	2	2	2	2	2	2	2	2	2	2	23
			2017	2	2	3	1	1	1	2	2	3	1	2	2	22
			2018	2	3	2	2	2	2	2	2	2	1	2	2	0
Total				8	9	8	5	6	6	8	8	7	7	8	6	86
SUM				32	47	43	44	42	41	41	40	38	37	40	33	478