Oecologia Australis
27(1):58–72, 2023
https://doi.org/10.4257/oeco.2023.2701.04

GROUP DYNAMICS OF CAPYBARAS IN A HUMAN-MODIFIED LANDSCAPE IN SOUTHEASTERN BRAZIL

Marcelo Bahia Labruna[1], Beatriz Lopes[2], Hector Ribeiro Benatti[1,3], Hermes Ribeiro Luz[1,4], Francisco Borges Costa[1,5], Sebastián Muñoz-Leal[1,6], Laís Silva Mariscal[1], Peter Leimgruber[7] & Katia Maria Paschoaletto Micchi de Barros Ferraz[2]*

[1] Universidade de São Paulo, Faculdade de Medicina Veterinária e Zootecnia, Av. Prof. Dr. Orlando Marques de Paiva, 87, CEP: 05508-270, São Paulo, SP, Brasil.

[2] Universidade de São Paulo, Escola Superior de Agricultura “Luiz de Queiroz”, Departamento de Ciências Florestais, Av. Pádua Dias, 11, CEP:13418-900, Piracicaba, SP, Brasil.

[3] University of Massachusetts Medical School, Horae Gene Therapy Center, 368 Plantation St, Worcester, MA 01605, United States

[4] Universidade Federal do Maranhão, Programa de Pós-graduação em Saúde e Ambiente (PPGSA), Programa de Pós-Graduação em Biodiversidade e Conservação (PPGBC), Ponto Focal Maranhão, Av. dos Portugueses, 1966, CEP: 65080-805, São Luís, MA, Brasil.

[5] Universidade Estadual do Maranhão, Faculdade de Medicina Veterinária, Av. Lourenço Vieira da Silva, 1000, CEP: 65055-310, São Luís, MA, Brasil.

[6] Universidad de Concepción, Facultad de Ciencias Veterinarias, Departamento de Ciencia Animal, Av. Vicente Méndez, 595, Chillán, Ñuble, Chile.

[7] Smithsonian Conservation Biology Institute, Conservation Ecology Center, 1500 Remount Road, 22630, Front Royal, VA, United States.

E-mails: labruna@usp.br (*corresponding author); beatriz2.lopes@usp.br; hector.benatti@gmail.com; hermesluz@globomail.com; franc.borgesma@gmail.com; seba.munozleal@gmail.com; lais.smbaba@gmail.com; LeimgruberP@si.edu; katia.ferraz@usp.br

---

Abstract: Previous studies monitoring free-ranging capybaras with GPS collars showed no evidence of capybara dispersion or the formation of new groups. These phenomena may have gone unnoticed due to the low number of collared capybaras in previous studies. Aiming to fill this lacuna, this study monitored the group dynamics of capybaras in a human-modified landscape in Pirassununga municipality, state of São Paulo, southeastern Brazil. To this aim, we documented group formation, number of individuals, and dispersion events of capybara groups from 2015 to 2020. We evaluated the presence of established groups and formation of new groups throughout the study period, when we monitored 12 adult female capybaras with GPS-collars and regularly counted the number of individuals per group. We found that an initial group of 33 - 45 capybaras split itself into two groups from 2016 to 2017, and then into three groups from 2019 to 2020, each one with at least 30 individuals. This is the first study reporting group dynamics in capybaras with the use of GPS-collars. Long-term studies are needed to assess the factors that are driving the formation and division of groups, and motivating dispersion events.

Keywords: *Hydrochoerus hydrochaeris*; Rodentia; capybara groups; dispersal; GPS collar

---

INTRODUCTION

The capybara, *Hydrochoerus hydrochaeris* Linnaeus, 1766 (Rodentia: Hydrochoeridae), is the largest extant rodent of the world, weighing on average ≈50-60 Kg, with established populations in all South American countries, except for Chile (Ferraz *et al.* 2005, Moreira *et al.* 2013a). Capybaras are semiaquatic grazers that live in social groups of typically 10 to 40 individuals (range: 4 – 100), composed by adults (males and females; female-biased in larger groups) and young (Moreira *et al.* 2013b). Capybaras live always close to water bodies because they use the water for body thermoregulation, mating, and to escape from predators (Moreira *et al.* 2013a). Although there is generally an annual peak in births, individuals of all age classes can be found in capybara groups throughout the year (Herrera *et al.* 2011, Moreira *et al.* 2013c). These groups tend to be stable, with a dominant male that, along with females and subordinate males, defends territories against intruding males (Herrera & Macdonald 1994, Honeycutt 2013). When main resources (water bodies and food) are more abundant and homogeneous in time and space, density increases and is associated with larger groups and more male-biased dispersal (Herrera *et al.* 2011, Campos-Krauer *et al.* 2014, Serra-Medeiros *et al.* 2021).

Previous studies have indicated a male-biased dispersal of capybaras that is generally characterized by a young male moving away from its group accompanied by a number of subadult females; i.e. group dispersal (Herrera 1992). The decision to disperse might be dictated, at least in part, by a lack of resources in the capybaras' original territories (Herrera *et al.* 2011). Dispersal patterns of capybaras seem to be related to the spatial distribution of water bodies, a key territory component (Herrera *et al.* 2011).

In the state of São Paulo, southeastern Brazil, capybaras have been expanding their range due to an intensive process of landscape alteration owing to the expansion of agriculture and pasture in recent decades. This range expansion into human-modified landscapes (HMLs) is primarily determined by food availability and predator decline, resulting in much higher carrying capacity and lower mortality for capybaras than observed in natural wetlands (Ferraz *et al.* 2007, Bovo *et al.* 2016). Consequently, major conflicts between capybaras and humans have risen in southeastern Brazil, mainly related to crop damage (Ferraz *et al.* 2003), roadkill events (Huijser *et al.* 2013, Magioli *et al.* 2019, Da Silva *et al.* 2022), and the role of capybaras in the reemergence of Brazilian spotted fever, a deadly tick-borne bacterial disease that is transmitted to humans by a capybara-associated tick species (Labruna 2013, Luz *et al.* 2019).

Recent studies have reported habitat selection, home range and movement patterns of capybaras through the evaluation of tracked animals by GPS collars in HMLs and natural landscapes (Dias *et al.* 2020, Lopes *et al.* 2021, Serra-Medeiros *et al.* 2021). In these previous studies, only one to four individual capybaras were monitored with GPS collars in each of the capybara areas, and in all cases, there was solid group cohesion with no migration of capybaras to other areas or formation of new capybara groups. Thus, it is possible that an increase in the number of animals monitored with GPS collars in the same area may result in more comprehensive results, considering the possible dispersion and formation of new groups. Here, we monitored 12 individual capybaras with GPS collars in a single area during a five-year period in a HML in São Paulo state (Brazil), aiming to both monitor the dispersal pattern of a large group of capybaras and evaluate the stability of the group and formation of new groups over time.

MATERIALS AND METHODS

Ethic statements

This study has been approved by the Institutional Animal Care and Use Committee (IACUC) of the Faculty of Veterinary Medicine of the University of São Paulo (approval number 5948070314), in accordance with the regulations/guidelines of the Brazilian National Council of Animal Experimentation (CONCEA). Field captures of capybaras were authorized by the Brazilian Ministry of the Environment (permit SISBIO Nos. 43259–6).

Study area

The study was carried out at the University of São Paulo, Pirassununga Campus (Pirassununga municipality; 21º 56' S; 47º 27' W), state of São

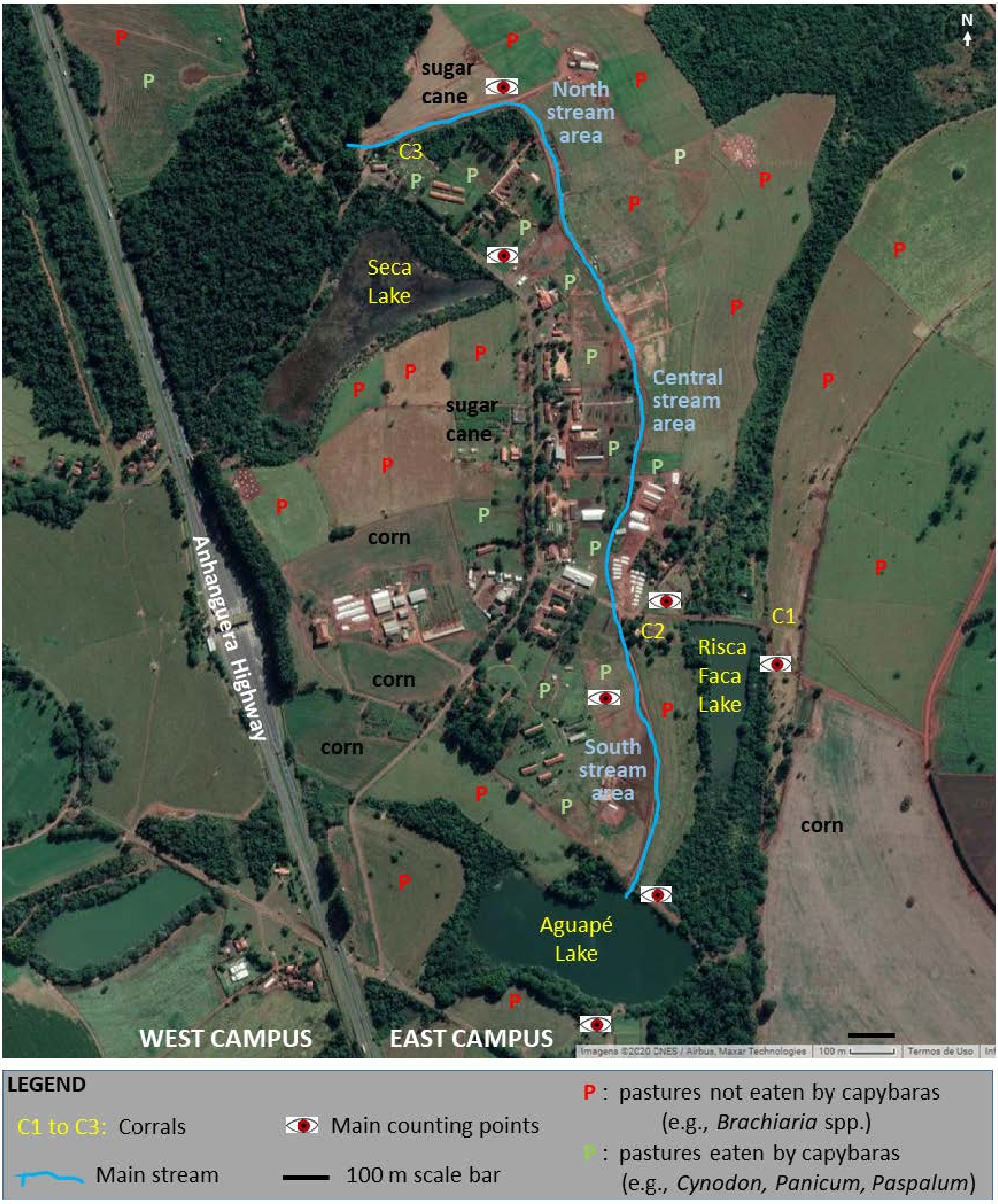

Figure 1. General view of the study area, at the East Campus of the University of São Paulo (Pirassununga, SP, Brazil). Satellite image retrieved from Google Earth in October 2020.

Paulo (SP), southeastern Brazil, from 2015 to 2020. The area is a HML composed by artificial pastures for livestock interspersed by corn and sugar cane crops and degraded riparian forests along artificial lakes and connected streams. The Campus is divided into East Campus (where the current study was performed) and West Campus, which are separated by the Anhanguera Highway (Figure 1). At the beginning of the study in 2015, only one large group of capybaras existed on East

Campus. This group inhabited the Risca Faca Lake area.

Capybara groups and counting

From January 2015 to December 2018, the study area (East Campus) was regularly inspected for the presence of capybara groups. For this purpose, at least once each month and mostly during the evening, the entire area was surveyed by vehicle, and the presence of capybara groups was recorded. Once a large group (>10 capybaras grazing or/and resting together) was detected, it was monitored by directly counting all individuals. This was conducted regularly, each two or four weeks, until December 2018, and then opportunistically at irregular intervals (every two or three months) during 2019 and 2020. Animal counts were performed during the last two hours of sunlight and the first two hours of sunset, which usually coincided with the period that animals started foraging in open areas, making them more detectable, as reported in previous studies (Verdade & Ferraz 2006). Direct counts were taken from a vehicle at strategic locations (Figure 1), areas where capybaras tended to aggregate in large numbers during dusk. While counting discriminated between young, juvenile, and adult capybaras, for the present study we only considered the total number of animals and the counts with highest numbers of each year.

Capybara capture and collaring

During 2015-2019, capybaras were captured in the study area by using 16 to 20 m^2–corrals baited with sugar cane and green corn. Corrals were settled within the capybaras' living area, close to their daytime resting places. Corrals were set up only a few days before the capture of individuals, remaining closed most of the time, minimizing the chances of interference from animal movements throughout the study. We collared 12 adult female capybaras using Lotek Iridium TrackM2D GPS collars (Lotek Wireless, Haymarket, Ontario, Canada) by adopting the same previously described procedures (Dias *et al.* 2020, Lopes *et al.* 2021). Briefly, once closed in the corral, the capybara was physically restrained by a net catcher and anesthetized with an intramuscular injection of a combination of ketamine (10 mg/kg) and xylazine (0.2 mg/kg). Under anesthesia, animals were weighed with an electronic balance (Pesola model PCS0300, Hatton Rock, UK), identified with a subcutaneous microchip (Alflex model P/N 860005-001, Capalaba, Australia) applied in the interscapular region, and collared with a GPS collar. All collared capybaras were adult females, usually among the heaviest of the group. This procedure was adopted because adult females have a decreased chance of mortality when compared to adult males, are thought to be philopatric in social groups, and the largest females are usually dominant, providing the best representation of group movement (Dias *et al.* 2020).

A total of 12 different capybaras were collared in this study (Table 1); one individual was captured in corral C1, two individuals in corral C2, and nine individuals in corral C3 (Figure 1). We programmed GPS collars to collect position every one or two hours. The only exceptions were the first two captured capybaras (animals CAP-1 and CAP-2), which were part of other studies (Dias *et al.* 2020, Lopes *et al.* 2021) in which the GPS collar was programmed to collect position every one hour for the first 30-40 days, and every four hours and 17 minutes thereafter. Collars were programmed to send GPS positions via satellite every time six consecutive positions were collected. For each collared capybara, all GPS positions were downloaded from the next day after capture/collaring to the last day the collar was still active. To avoid incorporating geolocations with large spatial errors, only GPS positions with a Dilution of Precision (DOP) < 5 were considered for analyses (Jung *et al.* 2018). The periods of collar activities were variable among collars (range: 12 – 329 days) due to the following reasons: the capybara removed the collar, the collar got damaged, or the capybara died (Table 1).

Data analysis

We combined field observations to infer group size, and GPS location visualization to infer space use and groups' dynamics. To assess group size, we selected the counts with highest number of animals of each year and only considered the total number of animals, independently of age. Results of space use are presented by showing the density of GPS locations over Google Tile Layer. Maps were built in ArcGis 10.3 software (ESRI 2010). To map

Table 1. Data for the 12 capybaras (CAP-1 – CAP-12) from different groups (A – C) that were captured in corrals (C1 – C3) and collared with a GPS collar in East Campus of the University of São Paulo at Pirassununga municipality, Brazil, during 2015 – 2020.

Animal	Corral	Body mass (Kg)	Group	No. other capybaras in the corral #	GPS collar data				Reason for end of collar data
					Start date	End date	No. Days	No. GPS positions	
CAP-1	C1	96.8	A	3F, 1M$^{\alpha}$	02 Oct 2015	05 Dec 2015	64	885	Collar removed
CAP-2	C2	77.4	A	0	08 Jun 2016	23 Apr 2017	319	1,806	Collar got damaged
CAP-3	C3	74.2	B	1M, 3Y	27 Oct 2017	11 Jan 2018	76	604	Collar got damaged
CAP-4	C3	72.8	B	1F	28 Jun 2018	17 Sep 2018	81	874	Collar removed
CAP-5	C2	74.5	A	3F, 3Y, 1M$^{\alpha}$	27 Jul 2018	30 Dec 2018	156	1,355	Collar got damaged
CAP-6	C3	107.0	B	0	24 Oct 2018	27 Nov 2018	34	369	Collar removed
CAP-7	C3	81.6	B	1F	14 Jan 2019	21 Feb 2019	38	1,222	Collar removed
CAP-8*	C3	73.0	B	1F	14 Jan 2019	08 Apr 2019	84	2,788	Animal moved out
CAP-9	C3	81.5	B	1F, 2Y	20 Jun 2019	25 Aug 2019	66	2,222	Capybara death
CAP-10	C3	79.0	B	3F, 2Y	08 Oct 2019	20 Oct 2019	12	268	Collar removed
CAP-11	C3	72.2	B, C	3F	09 Oct 2019	02 Sep 2020	329	7,470	Collar removed
CAP-12	C3	72.0	B	2M	24 Oct 2019	30 May 2020	219	4,134	Collar got damaged

refers to the number of additional capybaras (F: adult females; M: adult males; Y: young) that were captured in the corral together with the adult female that was collared; M$^{\alpha}$ refers presumably to an alpha dominant male, due to the presence of its prominent supranasal gland and large body size.

*this capybara moved out the study area at 08 April 2019.

the density of GPS locations, we firstly projected a grid of 50 m cell size (Create Fishnet tool) and then calculated the number of points per cell of 2,500 m² (Spatial Join tool). Finally, we classified GPS location density into five or six classes depending on the number of points and assigned a different color to each class.

RESULTS

When the study started in January 2015, only one large capybara group (>10 individuals) was identified in the study area. This group was designated as GA and was counted around the Risca Faca Lake area until the end of the study (Figures 1, 2). From 2016 to 2020, a second capybara group (GB) was counted in the north stream area. No capybara group had established at the Seca Lake area until 2020, when a third group (GC) assumed this area. The median and maximum numbers of counted capybaras in these three large groups according to year are illustrated in Figure 2. In addition, much smaller groups of capybaras (only 1 to 5 individuals at most) were observed in the Aguapé Lake area throughout the study.

A total of 12 different female capybaras (CAP-1 to CAP-12) were collared during 2015 - 2019 (Table 1). These animals weighed from 72.0 to 107.0 Kg (mean: 80.2 Kg) and were monitored for variable periods ranging from 12 to 329 days (mean: 127.9 days). Of these, six capybaras lost their collars before the end of the study. This

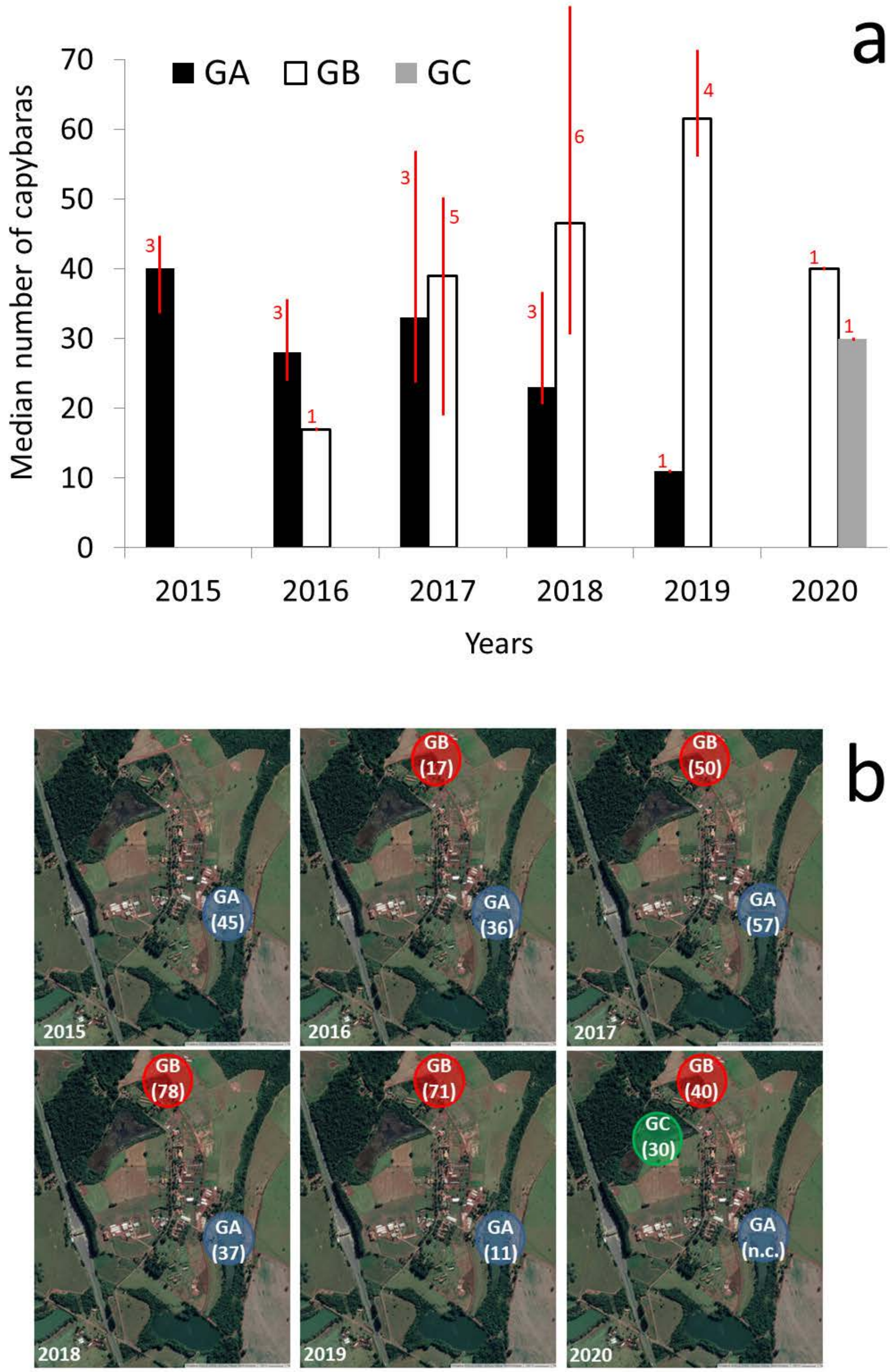

Figure 2. Median (a) and Maximum (b) numbers of capybaras counted per year (2015 to 2020) in each large group on East Campus, Pirassununga municipality, state of São Paulo, Brazil. GA group lived in the Risca Faca Lake area; GB group lived in the north stream area, and GC group lived in the Seca Lake area. GA group was not counted (n.c.) in 2020, but the group was visualized in this area during 2020. Red bars in A represent the range (maximum and minimum); number in bar is the number of counts in each year, considering only the counts when we had the opportunity to view the group together in an open area before their separation after sunset.

condition happened because capybaras do not have the neck region as constricted as it is in other mammal species, in relation to the head. Collars malfunctioned, were damaged, and stopped working in four additional capybaras. These were removed during a subsequent recapture. Finally, one capybara died while collared (death reasons not determined), and another one (CAP-8) dispersed out of the study area. The dispersion of CAP-8 will be reported separately in another manuscript.

The first capybara group capture was on 01 October 2015, when we collared the first female from the GA group (Risca Faca Lake area), designated as CAP-1. This adult female was captured in the C1 corral together with three other adult females and an adult male, presumably an alpha dominant male, due to the presence of its prominent supranasal gland and body mass (67.6 Kg). Unfortunately, this male did not recover from anesthesia and died after our procedures. His death might have affected capybara social structure and movements, as we discuss below. Based on GPS collar data, CAP-1 female lived mostly around the Risca Faca Lake and the central stream area (Figure 3a). However, a few points were registered in the northern stream area, where in December 2015 the collar was recovered in the environment, possibly due to active removal of the collar by CAP-1 female. Interestingly, until October 2015, no capybara was ever seen in the northern stream area. The presence of CAP-1 female in the north stream at the end of 2015 coincided with the visualization of a capybara group in this area for the first time in 2016; this new capybara group was designated as GB, with a maximal count of 17 individuals during 2016 (Figure 2).

Only one capybara was collared in 2016. This adult female, designated as CAP-2, was captured alone in the C2 corral. Based on GPS collar data, CAP-2 female lived around the Risca Faca Lake; however, it also frequently bordered the northeastern side of the Aguapé Lake (Figure 3b). CAP-2 female was captured alone in the corral, and every time this animal was observed during our regular inspections, it was also alone. When this animal was recaptured for collar removal, it was also alone.

During the subsequent years (2017 – 2019), the GA group continued to be counted in the Risca Faca Lake area (maximal counts from 11 to 57 individuals), where one female (CAP-5) was collared in 2018, showing that GA group remained established in the Risca Faca Lake area (Figure 4a). Concomitantly, three capybaras (CAP-3, CAP-4, CAP-6) from the newly established GB group were collared in the north stream area (Figures 3c, 3d, 4b), where maximal count numbers varied from 50 to 71 individuals. These three collared capybaras sent most of their GPS locations from the north stream area, in accordance with the establishment of GB group in this area. This pattern was corroborated by the six capybaras from GB group (CAP-7, CAP-8, CAP-9, CAP-10, CAP-11, CAP-12) that were collared during 2019 (Figures 4c, 4d, 5a, 5b, 5c, 5d). Noteworthy, at least five of these GB-collared capybaras yielded a minority of GPS positions from the Seca Lake area, where an established group had not been observed previously. Then, the establishment of a third large group (designated as GC) in the Seca Lake area in 2020, originated from GB group, was corroborated by CAP-11, which lived at both north stream and Seca Lake areas from its capture in October 2019 to 09 March 2020; however, from 10 March till the end of observations on 02 September 2020, CAP-11 lived exclusively at the Seca Lake and central stream areas, and did not visit the north stream area anymore (Figure 6).

During this second period (since 10 March 2020), CAP-11 used to stay during the day at the southeastern border of Seca Lake, where it was observed several times during the day with a group of nearly 30 individuals. Since no capybara group was previous seen to reside during the day in this specific area before 2020, these results indicate that CAP-11 was part of a third large group (GC), which derived from GB. This statement is corroborated by the fact that during 2018 and 2019, GB counts reached as much as 78 animals in the north stream area, whereas in 2020, GB counts did not surpass 40 animals (Figure 2).

DISCUSSION

The present study was performed in a HML composed by permanent water bodies, presenting abundant and diverse food items similarly to other HMLs in southeastern Brazil (Verdade & Ferraz 2006, Bovo *et al.* 2016, Lopes *et al.* 2021). During

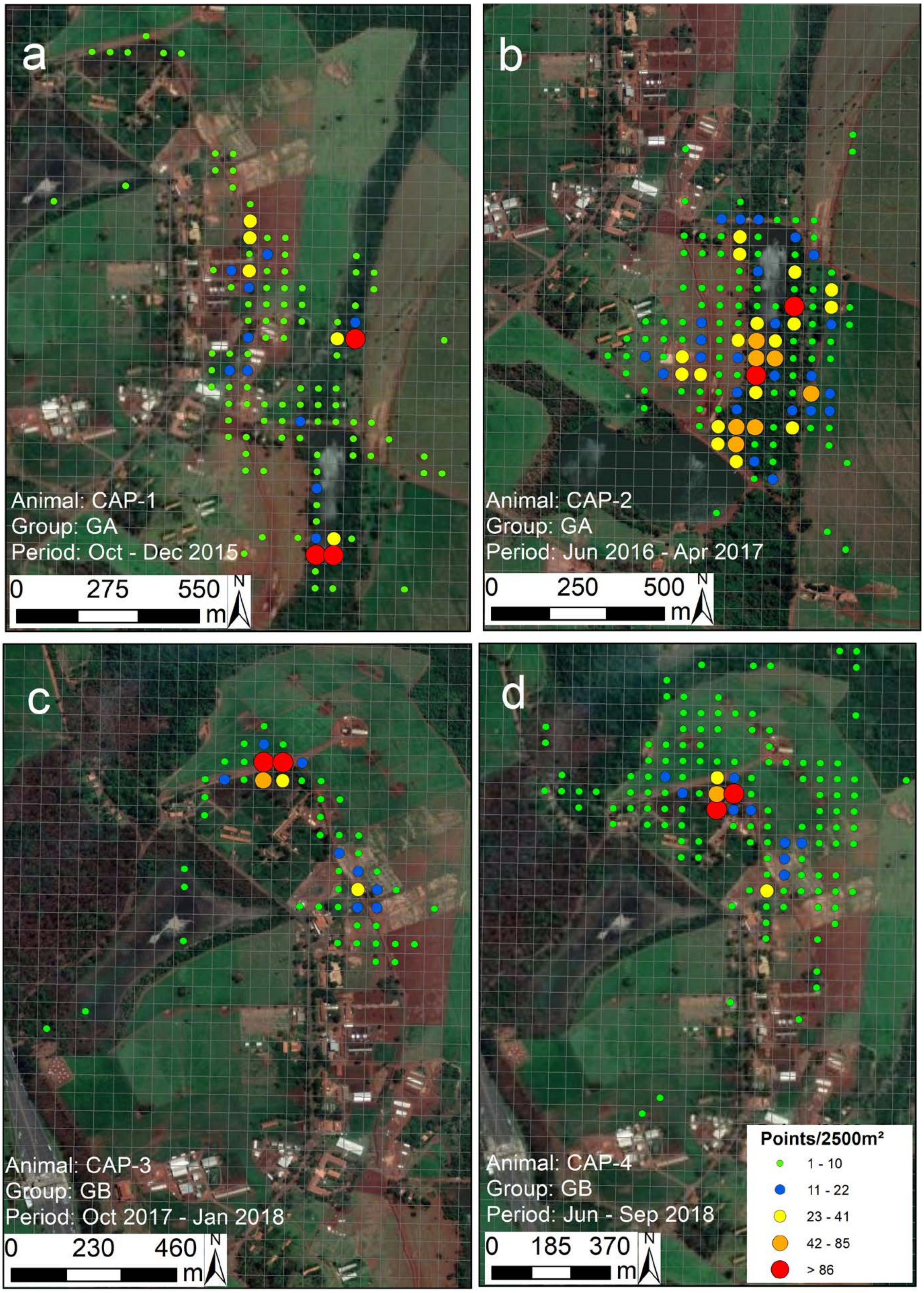

Figure 3. Positions sent by GPS collars for capybaras CAP-1 (a), CAP-2 (b), CAP-3 (c) and CAP-4 (d), corresponding to the dates (period) shown at the bottom of each figure. Capybara groups were designated as GA (mostly resident at the Risca Faca Lake area) or GB (mostly resident at the north stream area). Positions are represented by color circles in green (1 to 10 positions accumulated in the same place spot), blue (11 to 22 positions accumulated in the same place spot), yellow (23 to 41 accumulated in the same spot), orange (42 to 85 positions accumulated in the same place spot) and red (86 or more positions accumulated in the same place spot). Satellite image source: Google Tile Layers, 2020.

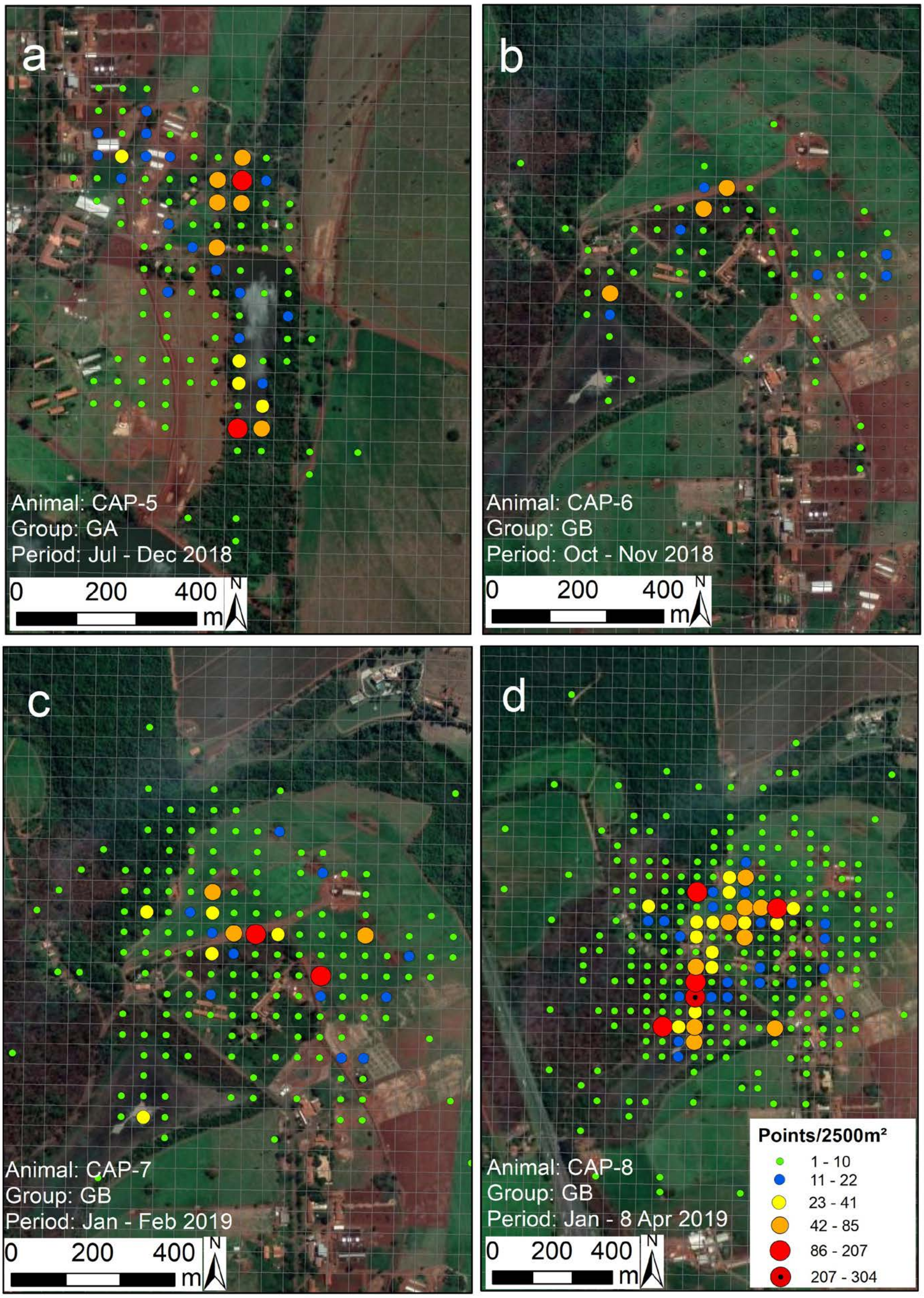

Figure 4. Positions sent by GPS collars for capybaras CAP-5 (a), CAP-6 (b), CAP-7 (c) and CAP-8 (d), corresponding to the dates (period) shown at the bottom of each figure. Capybara groups were designated as GA (mostly resident at the Risca Faca Lake area) or GB (mostly resident at the north stream area). Positions are represented by color circles in green (1 to 10 positions accumulated in the same place spot), blue (11 to 22 positions accumulated in the same place spot), yellow (23 to 41 accumulated in the same spot), orange (42 to 85 positions accumulated in the same place spot), red (86 or more positions accumulated in the same place spot) and red with black dot (207 to 304 positions accumulated in the same place spot). Satellite image source: Google Tile Layers, 2020.

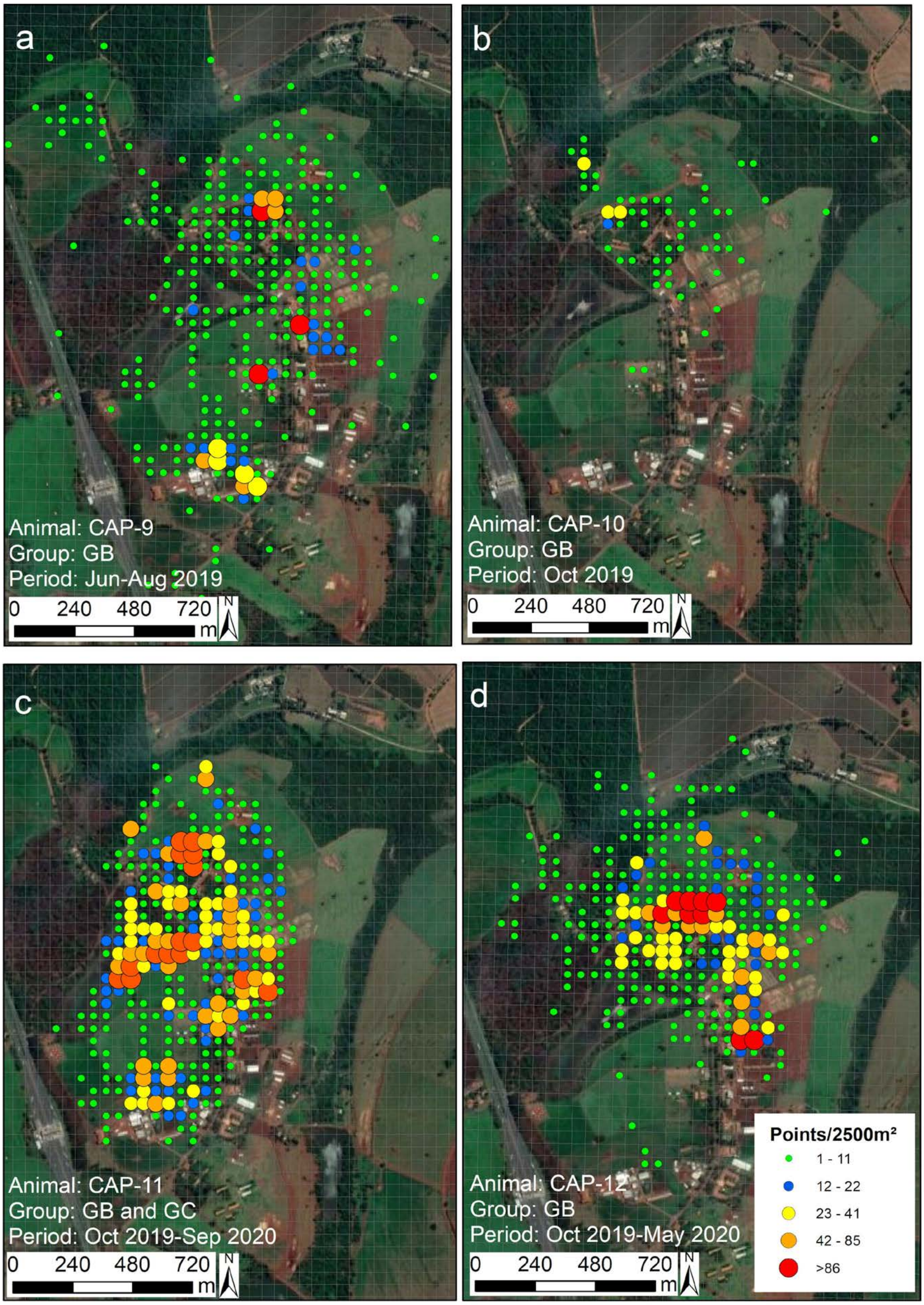

Figure 5. Positions sent by GPS collars for capybaras CAP-9 (a), CAP-10 (b), CAP-11 (c) and CAP-12 (d), corresponding to the dates (period) shown at the bottom of each figure. Capybara groups were designated as GB (mostly resident at the north stream area) or GC (mostly resident at the Seca Lake area). Positions are represented by color circles in green (1 to 10 positions accumulated in the same place spot), blue (11 to 22 positions accumulated in the same place spot), yellow (23 to 41 accumulated in the same spot), orange (42 to 85 positions accumulated in the same place spot) and red (86 or more positions accumulated in the same place spot). Satellite image source: Google Tile Layers, 2020.

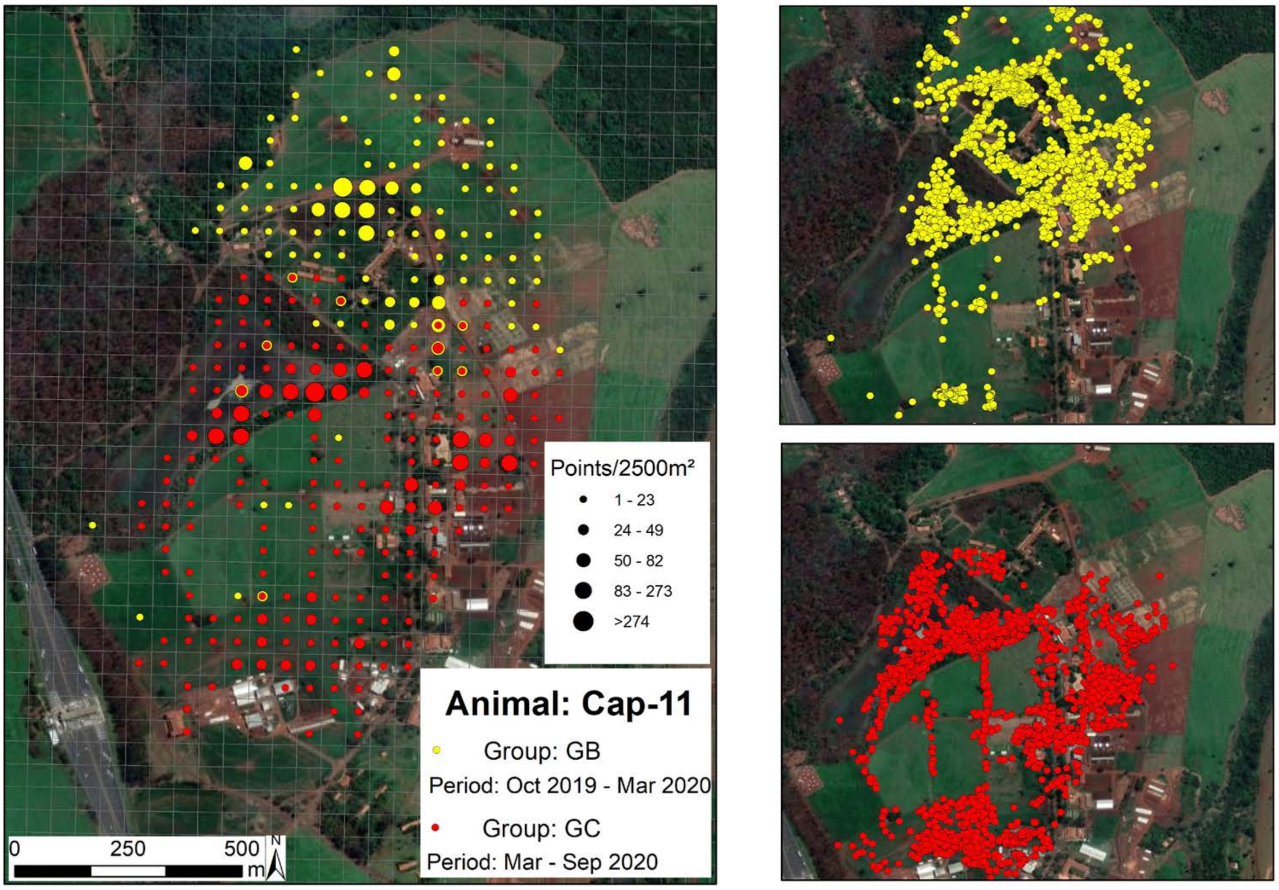

Figure 6. Positions sent by a GPS collar fitted to capybara CAP-11 from 09 October 2019 to 02 September 2020. Yellow circles represent individual positions from October 2019 to 09 March 2020, which were mostly at the north stream area (GB group). Red circles represent individual positions from 10 March to 02 September 2020, which were mostly at the Seca Lake area (GC group). Satellite image source: Google Tile Layers, 2020.

the years of the present study, the capybara population in a HML was composed of unstable social groups and varied significantly year-by-year (Figure 2). New groups were formed, apparently derived from GA, especially after the loss of the presumed dominant alpha male that died during the capture of CAP-1 in October 2015. It has been suggested that elimination of large males from social groups – e.g., by poaching – could lead to changes in group size and dispersal patterns, and drastic disruption of the group (Herrera *et al*. 2011). Interestingly, we found two carcasses of adult capybaras in the Risca Faca Lake area in May 2017; the two animals had been illegally hunted for food (carcasses contained only the head, feet, and skin), and one of them was identified as the CAP-1 female (it removed the collar in December 2015) through microchip identification (M.B.L. and H.R.L., unpublished data). Therefore, it is possible that the elimination of an alpha male from GA, plus other adult capybaras by poaching, could have contributed to the dispersion of this group during 2015-2020 into the north stream and Seca Lake areas, where capybaras had never been observed before. In fact, one of us (M.B.L.) has worked with horses and ticks in the Seca Lake and northern stream areas since 1997, and confirmed that before 2015, capybaras were never reported to inhabit those areas.

Competition for water and food resources under a social system involving group living and territoriality are considered important causes of capybara dispersal (Herrera 1992). Interesting, there were no substantial modifications in the landscape of East Campus, considering the availability of water and food resources during the present study or few years before; i.e., no change in the number of water bodies or any significant change in the overall availability of pastures or annual crops. While the Campus administration tried to protect a few crops by fencing, these procedures never worked for more than a few months, since the capybaras were highly effective in destroying such barriers for food. Furthermore, there were no noteworthy changes in the intensity and magnitude of human presence on campus from 2015 until the onset in Brazil of the Covid-19 pandemic in April 2020. Considering that before 2015 capybaras were never seen in the north stream and Seca Lake areas, we presume that the initial colonization of this area by GA group during late 2015 might have triggered a significant increase in the reproduction rate, because of the 'discovery' of new resources [water and food; i.e., sugar cane and pastures in the north stream area (Figure 1) were regularly visited by collared-GB capybaras during 2017 – 2018, as shown in Figures 2c, 2d]. Therefore, an increase of the capybara population in the next year resulted in the split of GA into two groups: GA restricted to the Risca Faca Lake area and central stream, and GB restricted to the north stream area. This statement is supported by the overall number of counted capybaras: 33-45 individuals for GA in 2015; 23-36 for GA, and 17 for GB in 2016; 23-57 for GA, and 19-50 for GB in 2017 (Figure 2). During 2018-2019, GB group, while mainly restricted to the north stream area, started to use occasionally the Seca Lake area. Again, the 'discovery' of a new water resource might have triggered the split of GB group into two groups: GB restricted to the north stream area, and GC restricted to the Seca Lake area. This statement is supported by CAP-11 GPS data, which from March 2020 onwards, stayed exclusively in the Seca Lake area with a group of nearly 30 individuals; before March 2020, most of the GPS locations of CAP-11 were in the north stream area (Figure 6).

CAP-2 female was captured alone in the Risca Faca Lake area (Table 1), and was solitary every time this animal was observed during our regular inspections, as well as during its recapture for collar removal. These observations suggest that CAP-2 female was a floater or a satellite animal to GA group. Interestingly, the designation of floater or satellite capybara is most commonly used for adult males, although a few solitary females have also been recorded in the Brazilian Pantanal (Alho & Rondon 1987) and in the Venezuelan Llanos (Herrera 2013). In addition, during 2017 we also captured a solitary adult male (body mass: 68.5 Kg; developed supranasal gland) at two different occasions in C2 corral, Risca Faca Lake area (data not shown), suggesting that this male was also a satellite individual. The condition of solitary adult capybara (satellite or floater) was reported to be more common in the presence of large groups of capybaras (Alho & Rondon 1987, Herrera 2013), which is in agreement with the GA group of the present study.

In contrast to CAP-2, the remaining collared capybaras were captured with other animals (Table 1), and in most of the cases, we observed additional capybaras in close proximity of the corral during the capture, suggesting that they belonged to the same group. The only exception was CAP-6 female, which was captured alone (Table 1). However, this female gave birth the day after capture, as we had the opportunity to observe her with her young through direct observation in the field (data not shown). This suggests that the night the CAP-6 female was captured, she was in the process of searching for a birthing site isolated from her main group, as has been observed for this species under natural conditions (Ojasti 1973).

The present study, conducted in a HML in southeastern Brazil, showed that an initial group of 33 - 45 capybaras split itself into two groups from 2016 to 2017, and then into three groups from 2019 to 2020, each one with at least 30 individuals. This is the first study reporting group dynamics in capybaras with the use of GPS-collars. Long-term studies are needed to assess the factors that are driving the formation and division of groups, and motivating dispersion events. Undoubtedly, the availability of food (crops, cultivated pastures) and water are factors that could favor the reproduction and the rate of increase of capybara populations. In HMLs, this availability has generated a series of conflicts related to crop damage (Ferraz *et al.* 2003), roadkill events (Huijser *et al.* 2013, Magioli *et al.* 2019, Da Silva *et al.* 2022) and the reemergence of Brazilian spotted fever in southeastern Brazil (Labruna 2013). In the latter case, recent mathematical model-based studies, based on the current scenario of the HMLs in the state of São Paulo, proposed that the sustained infection of capybara ticks (*Amblyomma sculptum* Berlese, 1888) with the bacterium *Rickettsia rickettsii* (the agent of Brazilian spotted fever) depends on high reproduction rates of capybaras (Polo *et al.* 2017), and that the propagation velocity of the disease increases as the capybara-carrying capacity becomes greater (Polo *et al.* 2018). Therefore, public health policies should include the adoption of measures that reduce the capybaras' access to areas with food and water resources not yet settled by capybaras. In a more applied way, capybaras population control programs should be implemented in areas with growth potential (Polo *et al.* 2017), as has been done in the state of São Paulo recently, through male vasectomy and female sterilization in areas with high risk of Brazilian spotted fever (Passos Nunes *et al.* 2020).

ACKNOWLEDGMENTS

This study has been supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grant #2013/18046-7). MBL and KMPMBF were funded by Conselho Nacional de Pesquisa e Desenvolvimento Científico e Tecnológico (CNPq) research grants (#301641/2019-6 and #308632/2018-4, respectively).

REFERENCES

Alho, C. J. R., & Rondon, N. L. 1987. Habitats, population densities, and social structure of capybara (*Hydrochaeris hydrochaeris*, Rodentia) in the Pantanal, Brazil. Revista Brasileira de Zoologia, 4(2), 139–149. DOI: 10.1590/S0101-81751987000200006

Bovo, A. A. D. A., Ferraz, K. M. P. M. B., Verdade, L. M., & Moreira, J. R. 2016. Capybaras (*Hyrochoerus hydrochaeris*) in anthropogenic environments: challenges and conflicts. In: C. Gheler-Costa, M. C. Lyra-Jorge & L. M. Verdade (Eds.), Biodiversity in agricultural landscapes of southeastern Brazil. pp. 178–189. Berlin: De Gruyter.

Campos-Krauer, J. M., Wisely, S. M., Benitez, I. K., Robles, V., & Golightly, R. T. 2014. Home range and habitat use of capybara in newly invaded pastureland in the Dry Chaco region of Paraguay. Therya, 5(1), 61–79. DOI: 10.12933/therya-14-177

Da Silva, A. C. F. B., De Menezes, J. F. S., & Santos, L. G. R. O. 2022. Roadkill risk for capybaras in an urban environment. Landscape and Urban Planning, 222, 104398. DOI: 10.1016/j.landurbplan.2022.104398

Dias, T. C., Stabach, J. A., Huang, Q., Labruna, M. B., Leimgruber, P., Ferraz, K. M. P. M. B., Lopes, B., Luz, H. R., Costa, F. B., Benatti, H. R., Correa, L. R., Nievas, A. M., Monticelli, P. F., Piovezan, U., Szabó, M. P. J., Aguiar, D. M., Brites-Neto, J., Port-Carvalho, M., & Rocha, V. J. 2020. Habitat selection in natural and human-modified landscapes by capybaras (*Hydrochoerus hydrochaeris*), an important host for *Amblyomma sculptum* ticks. PloS One, 15(8), e0229277. DOI: 10.1371/journal.pone.0229277

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands.

Ferraz, K. M. P. M. B., Lechevalier, M. A., Do Couto, H. T. Z., & Verdade, L. M. 2003. Damage caused by capybaras in a corn field. Scientia Agricola, 60(1), 191–194. DOI: 10.1590/S0103-90162003000100029

Ferraz, K. M. P. M. B., Bonach, K., & Verdade, L.M. 2005. Relationship between body mass and body length in capybaras (*Hydrochoerus hydrochaeris*). Biota Neotropica, 5(1), 197–200. DOI: 10.1590/S1676-06032005000100020

Ferraz, K. M. P. M. B., Ferraz, S. F. B., Moreira, J. R., Couto, H. T. Z., & Verdade, L. M. 2007. Capybara (*Hydrochoerus hydrochaeris*) distribution in agroecosystems: a cross-scale habitat analysis. Journal of Biogeography, 34(2), 223–230. DOI: 10.1111/j.1365-2699.2006.01568.x

Herrera, E. A. 1992. Growth and dispersal of capybaras (*Hydrochaeris hydrochaeris*) in the Llanos of Venezuela. Journal of Zoology, 228(2), 307–316. DOI: 10.1111/j.1469-7998.1992.tb04610.x

Herrera, E. A. 2013. Capybara social behavior and use of space: patterns and processes. In: J. R. Moreira, K. M. P. M. B. Ferraz, E. A. Herrera & D. W. Macdonald (Eds.), Capybara - Biology, use and conservation of an exceptional neotropical species. pp. 195–207. New York: Springer.

Herrera, E. A., & Macdonald, D. W. 1987. Group stability and the structure of a capybara population. Symposia of the Zoological Society of London, 58(1), 115–130.

Herrera, E. A., & Macdonald, D. W. 1994. Social significance of scent marking in capybaras.

Journal of Mammalogy, 75(2), 410–415. DOI: 10.2307/1382561

Herrera, E. A., Salas, V., Congdon, E. R., Corriale, M. J., & Tang-Martínez, Z. 2011. Capybara social structure and dispersal patterns: variations on a theme. Journal of Mammalogy, 92(1), 12–20. DOI: 10.1644/09-MAMM-S-420.1

Honeycutt, R. L. 2013. Phylogenetics of Caviomorph Rodents and Genetic Perspectives on the Evolution of Sociality and Mating Systems in the Caviidae. In: J. R. Moreira, K. M. P. M. B. Ferraz, E. A. Herrera & D. W. Macdonald (Eds.), Capybara - Biology, use and conservation of an exceptional neotropical species. pp. 61–81. New York: Springer

Huijser, M. P., Abra, F. D., & Duffield, J. W. 2013. Mammal road mortality and cost–benefit analyses of mitigation measures aimed at reducing collisions with capybara (*Hydrochoerus hydrochaeris*) in São Paulo state, Brazil. Oecologia Australis, 17(1), 129–146. DOI: 10.4257/oeco.2013.1701.11

Jung, T. S., Hegel, T. M., Bentzen, T. W., Egli, K., Jessup, L., Kienzler, M., Kuba, K., Kukka, P. M., Russell, K., Suitor, M. P., & Tatsumi, K. 2018. Accuracy and performance of low-feature GPS collars deployed on bison *Bison bison* and caribou *Rangifer tarandus*. Wildlife Biology, 2018(1), wlb.0040. DOI: 10.2981/wlb.00404

Labruna, M. B. 2013. Brazilian spotted fever: the role of capybaras. In: J. R. Moreira, K. M. P. M. B. Ferraz, E. A. Herrera & D. W. Macdonald (Eds.), Capybara - Biology, use and conservation of an exceptional neotropical species. pp. 371–383. New York: Springer

Lopes, B., McEvoy, J. F., Morato, R. G., Luz, H. R., Costa, F. B., Benatti, H. R., Dias, T. C., Rocha, V. J., Nascimento, V. R., Piovezan, U., Monticelli, P. F., Nievas, A. M., Pacheco, R. C., Moro, M. E. G., Brasil, J., Leimgruber, P., Labruna, M. B., & Ferraz, K. M. P. M. B. 2021. Human-modified landscapes alter home range and movement patterns of capybaras. Journal of Mammalogy, 102(1), 319–332. DOI: 10.1093/jmammal/gyaa144

Luz, H. R., Costa, F. B., Benatti, H. R., Ramos, V. N., Serpa, M. C. A., Martins, T. F., Acosta, I. C. L., Ramirez, D. G., Muñoz-Leal, S., Ramirez-Hernandez, A., Binder, L. C., Carvalho, M. P., Rocha, V., Dias, T. C., Simeoni, C. L., Brites-Neto, J., Brasil, J., Nievas, A. M., Monticelli, P. F., Moro, M. E. G., Lopes, B., Aguiar, D. M., Pacheco, R. C., Souza, C. E., Piovezan, U., Juliano, R., Ferraz, K. M. P. M. B., Szabó, M. P. J., & Labruna, M. B. 2019. Epidemiology of capybara-associated Brazilian spotted fever. PLoS Neglected Tropical Diseases, 13(9), 1–24. DOI: 10.1371/journal.pntd.0007734

Magioli, M., Bovo, A. A. A., Huijser, M. P., Abra, F. D., Miotto, R. A., Andrade, V. H. V. P., Nascimento, A. M., Martins, M. Z. A., & Ferraz, K. M. P. M. B. 2019. Short and narrow roads cause substantial impacts on wildlife. Oecologia Australis, 23(1), 99–111. DOI: 10.4257/oeco.2019.2301.09

Moreira, J. R., Moreira, J. R., Alvarez, M. R., Tarifa, T., Pacheco, V., Taber, A., Tirira, D. G., Herrera, E. A., Ferraz, K. M. P. M. B., Aldana-Domínguez, J., & Macdonald, D.W. 2013a. Taxonomy, Natural History and Distribution of the Capybara. In: J. R. Moreira, K. M. P. M. B. Ferraz, E. A. Herrera & D. W. Macdonald (Eds.), Capybara - Biology, use and conservation of an exceptional neotropical species. pp. 3–37. New York: Springer.

Moreira, J. R., Ferraz, K. M. P. M. B., Herrera, E. A., & Macdonald, D. W. 2013b. Capybara: Biology, Use and Conservation of an Exceptional Neotropical Species. New York: Springer. p. 419.

Moreira, J. R., Wiederhecker, H., Ferraz, K. M. P. M. B., Aldana-Domínguez, J., Verdade, L. M., & Macdonald, D. W. 2013c. Capybara Demographic Traits In: J. R. Moreira, K. M. P. M. B. Ferraz, E. A. Herrera & D. W. Macdonald (Eds.), Capybara - Biology, use and conservation of an exceptional neotropical species. pp. 147–167. New York: Springer.

Ojasti, J. 1973. Estudio biológico del chigüire o capibara. Fondo Nacional de Investigaciones Agropecuarias. Caracas: Editorial Sucre. p. 273.

Passos Nunes, F. B., Nunes A. Z., Nunes M. P., Labruna M. B., & Pizzutto, C. S. 2020. Reproductive control of capybaras through sterilization in areas at risk of transmission of Brazilian spotted fever. Ciência Rural, 50(9), e20200053. DOI: 10.1590/0103-8478cr2020053

Polo, G., Mera Acosta, C., Labruna M. B., & Ferreira, F. 2017. Transmission dynamics and control of *Rickettsia rickettsii* in populations of

Hydrochoerus hydrochaeris and *Amblyomma sculptum*. PLoS Neglected Tropical Diseases, 11(6), e0005613. DOI: 10.1371/journal.pntd.0005613

Polo, G., Mera Acosta, C., Labruna, M. B., Ferreira, F., & Brockmann, D. 2018. Hosts mobility and spatial spread of *Rickettsia rickettsii*. PLoS Computational Biology, 14(12), e1006636. DOI: 10.1371/journal.pcbi.1006636

Serra-Medeiros, S., Ortega, Z., Antunes, P. C., Miraglia Herrera, H., & Oliveira-Santos, L. G. R. 2021. Space use and activity of capybaras in an urban area. Journal of Mammalogy, 102(3), 814–825. DOI: 10.1093/jmammal/gyab005

Verdade, L. M., & Ferraz, K. M. P. M. B. 2006. Capybaras in an anthropogenic habitat in Southeastern Brazil. Brazilian Journal of Biology, 66(1b), 371–378. DOI: 10.1590/S1519-69842006000200019

Submitted: 02 March 2022
Accepted: 22 September 2022
Published online: 10 October 2022
Associated Editor: João Pedro Souza-Alves