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Prey choice of introduced species by the common vampire bat (*Desmodus rotundus*) on an Atlantic Forest land-bridge island

Fernando Gonçalves[1, 2, 9], Marcelo Magioli[3, 4, 5], Ricardo S. Bovendorp[1, 6], Katia M. P. M. B. Ferraz[3], Letícia Bulascoschi[1], Marcelo Z. Moreira[7], and Mauro Galetti[1, 8]

[1]*Instituto de Biociências, Departamento de Biodiversidade, Universidade Estadual Paulista, 13506-900 Rio Claro, São Paulo, Brazil*
[2]*Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, United Kingdom*
[3]*Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Escola Superior de Agricultura 'Luiz de Queiroz', Universidade de São Paulo, Av. Pádua Dias, 11, Agronomia, 13418-900, Piracicaba, São Paulo, Brazil*
[4]*Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros (CENAP), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Estrada Municipal Hisaichi Takebayashi, 8600, Bairro da Usina, 12952-011, Atibaia, São Paulo, Brazil*
[5]*Instituto Pró-Carnívoros, Av. Horácio Neto, 1030, Parque Edmundo Zanoni, 12945-010, Atibaia, São Paulo, Brazil*
[6]*Laboratório de Ecologia Aplicada à Conservação, Universidade Estadual de Santa Cruz, Rodovia Ilhéus-Itabuna, km16 /Salobrinho, 45662-900, Ilhéus, Bahia, Brazil*
[7]*Laboratório de Ecologia Isotópica, Centro de Energia Nuclear na Agricultura (CENA), Universidade de São Paulo, Av. Centenário, 303, São Dimas, 13416-903, Piracicaba, São Paulo, Brazil*
[8]*Department of Biology, University of Miami, Coral Gables, CP 33146, FL, USA*
[9]*Corresponding author: E-mail: fhm.goncalves@unesp.br*

The proliferation of native, alien, invasive and domestic species offers enough novel and abundant food resources for the common vampire bat, *Desmodus rotundus*, to potentially alter preferences for prey. By reference to a stable-isotope analysis for carbon and nitrogen, we report here on the choices of introduced mammal prey made by *D. rotundus* residing on Anchieta Island — a tropical land-bridge island from which domestic animals were removed and 100 individuals of 15 mammal species were introduced intentionally. Our analysis shows that the studied individuals of *D. rotundus* were more likely to prey upon species of open habitats (mean value of δ^{13}C = -14.8‰), that is, animals with high δ^{13}C values characterising the consumption of C_4 resources. The δ^{15}N values for *D. rotundus* were higher than expected, most likely similar to apex predator species (mean value of 8.2‰) and overlapped the isotopic niche with capybaras (*Hydrochoerus hydrochaeris*) on the island. Values were in turn distant from those noted for coatis, as well as other potential prey from a preserved area on the mainland (capybaras included), indicating that, from among all the potential mammalian prey species, the studied bats were feeding exclusively on capybaras, which also represent the species with the greatest mammalian biomass on the island. Previous information regarding the time of human occupation suggests that the domestic animals then present on Anchieta Island might have been the main prey of *D. rotundus* and responsible for maintaining a viable population. As capybaras were introduced only 36 years ago, this suggests a rapid shift in predation preference induced by anthropogenic disturbances that have allowed *D. rotundus* to exploit these rodents successfully. Records in the literature further show that common vampire bats were not captured in preserved areas of the mainland close to Anchieta Island, indicating that the rate of capture characterising *D. rotundus* is usually low in natural forested habitats where potential prey are scattered. As three individuals of the introduced population of capybaras were confirmed to have died from bat rabies virus (RABV) in 2020, we advocate periodic monitoring for bat rabies viruses in the *D. rotundus* population on Anchieta Island (as well as nearby areas), so that the magnitude of the outbreak may be determined and control strategies developed. Such actions are all the more important given that both the island and nearby areas are frequented by tourists. We highlight that the prey choice indicated here is context-dependent, and possibly influenced by the removal of domestic animals, as well as the explosive population growth achieved by the introduced capybaras, in combination with the predictability of their foraging behaviour.

Key words: Atlantic Forest, Brazil, stable isotopes, predation, feeding habit, diet analysis, Capybara, Anchieta Island

Introduction

The common vampire bat *Desmodus rotundus* (Geoffroy, 1810), an obligate blood-feeding species and the primary reservoir of rabies, has experienced changing availability of both wild and domestic prey (Greenhall *et al*., 1983; Galetti *et al*., 2016; Gnocchi and Srbek-Araujo, 2017; Zortéa *et al*., 2018) throughout its range from Mexico to northern Argentina. Common vampire bats usually occur in low densities in old-growth forest (Bernard, 2001; Bobrowiec *et al*., 2014; Gonçalves *et al*., 2017) where potential prey are sparse, and are at higher densities in fragments surrounded by pastures due to increased availability of livestock species (Delpietro *et al*., 1992; Bobrowiec, 2015). The high densities of livestock in the Neotropical region, combined with the introduction of native, alien and invasive species, has created novel, abundant and reliable sources of blood for *D. rotundus*, resulting in population growth and geographic range expansion (Delpietro *et al*., 1992; Lee *et al*., 2012; Bobrowiec *et al*., 2015; Galetti *et al*., 2016).

Detailed analyses of prey choice of *D. rotundus* in this anthropogenic scenario are fundamental to answer questions about trophic interactions, such as how predators and prey interact and how prey availability affects predator density and distribution (Sheppard and Harwood, 2005). In the past two decades, stable isotope analysis and molecular typing of DNA in vampire bat faeces have been used to demonstrate reliance on livestock when they are locally abundant (Voigt and Kelm, 2006; Bobrowiec *et al*., 2015) while studies with camera traps based on video footage have revealed behavioural aspects of feeding on wild species (Galetti *et al*., 2016; Gnocchi and Srbek-Araujo, 2017; Zortéa *et al*., 2018). However, prey choice by *D. rotundus* in regions with introduced species rather than livestock has yet to be investigated in spite of its critical importance due to risks to public health and consequences for the transmission of infectious diseases by altering demographic processes, animal interactions and host immunity (Schneider *et al*., 2009; Stoner-Duncan *et al*., 2014; Streicker and Allgeier, 2016).

Here, we report, based on analysis of stable carbon and nitrogen isotopes, the prey choice of *D. rotundus* on introduced mammals on a tropical island where 100 individuals of 15 mammal species were intentionally introduced 36 years ago. Our analysis shows that, between two suitable species classified as potential prey, the common vampire bat fed exclusively on capybaras (*Hydrochoerus hydrochaeris*), the species with the greatest mammalian biomass on the island. We highlight that this prey choice is context-dependent, and possibly influenced by the removal of domestic animals and the explosive population growth of introduced capybaras, combined with their predictable foraging behaviour.

Materials and Methods

Study Area

The study was carried out on Anchieta Island (23°27'S; 45°02'W), a 828-ha land-bridge island of the municipality of Ubatuba off the north coast of São Paulo State, Brazil (Fig. 1). The island is 500-meters away from the mainland, has a long history of human occupation and was once called Ilha dos Porcos (Pigs Island) in allusion to the large number of resident pigs (Guillaumon *et al*., 1989). In the beginning of the 20th century there was a prison on the island and, especially when the prison was active (1904–1955), cattle, pigs, dogs, cats, and domestic fowl were brought to the island (Galetti *et al*., 2009) in order to sustain its human community that reached over 1,000 residents of 420 families (Guillaumon *et al*., 1989). The prison and all infrastructures were expropriated and the island was transformed into a state park in 1977, with the removal of all domestic animals (Guillaumon *et al*., 1989).

In March 1983, the São Paulo Zoo Foundation introduced 100 individuals of 14 mammal species onto the island (Guillaumon *et al*., 1989), of which seven have not been recorded since and have probably been extirpated (Bovendorp and Galetti, 2007; Supplementary Table S1). Little is known about the mammalian fauna of the island prior to human occupation; however, it is probable that it was similar to that of the mainland given its proximity (500 m), with the exception of large predators (e.g., jaguars and pumas) and ungulates. Thirty-six years after the introduction, the island now harbours the highest density of terrestrial mammals (486 ind./km^2) in the entire Atlantic Forest bioregion (Bovendorp and Galetti, 2007). The vegetation on the island is composed with coastal plains where notable features include a stretch of *restinga* (a distinct type of coastal tropical and subtropical moist broadleaf forest), and large areas of disturbed vegetation dominated by ferns (*Gleichenia*) (Galetti *et al*., 2009).

We undertook two field expeditions, one in October 2017 and the other in November 2018, to capture and sample the predator-prey systems present on the island. We selected three accessible forest sites and three accessible open sites without prior knowledge of the presence of common vampire bats or their potential prey. Each habitat was sampled for three consecutive days during each field expedition such that each received the same sampling effort.

Capture and Sampling of Common Vampire Bats

We mist-netted bats for three consecutive nights during the two field expeditions. Netting was undertaken during the absence of moonlight using 2.6 × 12 m ground-level mist nets opened for six hours after dusk. The number of nets per night ranged from three to six but did not vary among habitats (open area and forest). The capture effort (net area multiplied by the number of hours nets were open) in each habitat was 310 m^{2}h. All captured bats were kept individually in cloth bags for 45–60 min, during which we collected hair from the postero-dorsal region for stable isotope analysis; the bats were then released at the site of capture.

Capture and Sampling of Potential Prey

According to literature records, common vampire bats feed exclusively on medium- and/or large-sized mammals (> 1 kg),

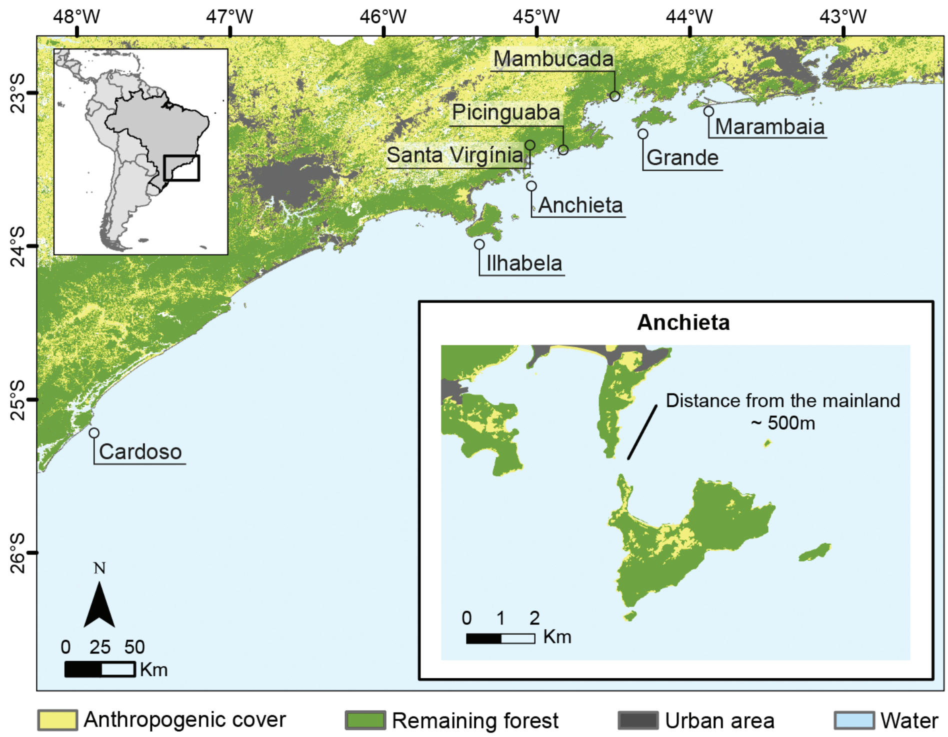

Fig. 1. Location of Anchieta Island, state of São Paulo, southeastern Brazil and its proximity with another islands and mainland sites

thus coatis (*Nasua nasua*) and capybaras (*H. hydrochaeris*) are the only suitable potential prey on the island. In order to capture and collect hair from coatis, we used 30 live traps in each sampling site (forest and open) during three consecutive nights simultaneously to the mist-netting for bats, which resulted in a capture effort of 360 trap-nights. For capybaras, we collected hair samples stuck in barbed-wire fences of all trails on Anchieta Island. To complement our sampling effort, hair samples from coatis and capybaras were collected opportunistically with tweezers. All capture, handling, and tagging techniques followed the guidelines of the International Society of Mammalogists (Sikes *et al.*, 2016).

To understand if common vampire bats of Anchieta Island use the nearby mainland to feed on wild animals, we used isotopic values obtained by Magioli *et al*. (2019) for five large-bodied mammals [white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), deer (*Mazama* sp.), lowland tapir (*Tapirus terrestris*) and capybara] from a protected area on the mainland (Núcleo Santa Virgínia, an administrative division of the Serra do Mar State Park). This area is inserted in the largest continuous remnant of the Atlantic Forest and is ca. 19 km (Fig. 1) straight-line-distance from Anchieta Island.

Common Vampire Bats Feeding on Potential Prey

We observed feeding by common vampire bats via ad libitum sampling (Martin and Bateson, 2007) during 17 nights (47 hours of observation, in October 2017 and November 2018 at the same six sites selected for sampling. Observations occurred between 6 pm and 5 am during specific shifts of two to five hours per night. Observers, equipped with red flashlights, were situated on high ground in order to observe the entire area. When capybaras were detected, the observers approached them slowly and observed if common vampire bats were feeding and, if so, recorded it (Supplementary Videos S1 and S2).

Data Analysis

We also compiled bat capture data, including capture effort, from the only two previous studies on the island (Aires, 1998; Colas-Rosas, 2009), in order to complement our species list and to estimate capture percentage. The capture percentage for *D. rotundus* on Anchieta Island was calculated by dividing the total number of bats mist-netted by effort (m^2h) and then multiplying by 100. We used data from Bovendorp and Galetti (2007) to estimate potential prey density on the island, and body mass data from Gonçalves *et al*. (2018) to estimate prey biomass.

Stable Isotopes Analysis

To analyse stable carbon and nitrogen isotopes, we cleaned the hair samples with water and 70% alcohol to remove any residue and dried them with absorbent paper. We then cut up the samples and stored them in thin capsules. Later, we used a CHN-1110 Elemental Analyser (Carlo Erba, Milan, Italy) to combust the material, and separated the resultant gases in a chromatographic column. Lastly, we inserted the gases in a coupled continuous flow isotope ratio mass spectrometer (Delta Plus, Thermo Scientific, Bremen, Germany) to obtain the isotopic composition of the samples. The isotopic values of carbon and nitrogen were expressed in delta notation ($\delta^{13}C$, $\delta^{15}N$) as parts per mil (‰) relative to V-PDB (Vienna-Pee Dee Belemnite) and atmospheric N_2 standards, respectively. Delta values were calculated based on standards using the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$$

where X represents the stable carbon or nitrogen isotopes (^{13}C or ^{15}N), and R the isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$).

We performed replicates for the same individual material for only 10% of the samples, but the precision of the analytic method for the 22 replicates of an internal standard for all batches was estimated as 0.09‰ for carbon and nitrogen. The samples were anchored to international scales by the use of international reference materials: NBS-19 and NBS-22 for carbon, and IAEA-N1 and IAEA-N2 for nitrogen.

Resource Use

To obtain information on resource use by *D. rotunduis* on Anchieta Island, we adapted the analytical approach used by Magioli *et al*. (2014, 2019). This analysis consists of using a simple mixed model that interpolates the stable carbon isotopic values of samples, accounting for specific fractionation factors, with the mean values of different vegetation types (C_3 and C_4 plant photosynthetic cycles), while also considering the minimum and maximum values obtained for all animal samples analysed. To estimate fractionation factors ($\Delta^{13}C$ and $\Delta^{15}N$), we used the 'SIDER' package (Healy *et al*., 2018), available in R 3.5.3 (R Core Team, 2019), which estimates species-specific fractionation factors from phylogenetic regression models, accounting for a database of fractionation values available for several species. We generated the $\Delta^{13}C$ value for *D. rotundus* on the island (2.1 ± 1.9‰) using the script available in Healy *et al*., (2018).

To determine the origin of food items consumed by potential preys (i.e., C_3 or C_4 plants) we calculated the carbon content of each sample ($\delta^{13}C$ values corrected by $\Delta^{13}C$ values) using the following equation: C_3 carbon incorporated =

$$= \frac{\delta^{13}C_{corrected}\text{ sample - }\delta^{13}C_{mean}\ C_4\text{ vegetation}}{\delta^{13}C_{mean}\ C_3\text{ vegetation - }\delta^{13}C_{mean}\ C_4\text{ vegetation}} \times 100$$

As a base for our model we used the mean $\delta^{13}C$ value of -32‰ to indicate C_3 plants, and -12‰ V-PDB to indicate C_4 plants. These values were obtained from the extreme $\delta^{13}C_{corrected}$ values of all animal samples analysed (predator and prey). After calculating the proportion of C_3/C_4, we classified samples into three groups: (1) C_3 group — species that preferentially consume C_3 items (> 70% of C_3 carbon; $\delta^{13}C$ = -32 to -26‰); (2) Mixed group — species that consume both C_3 and C_4 food items (from 30 to 70% of C_3 carbon; $\delta^{13}C$ = -25.9 to -18.1‰); and C_4 group — species that mainly consume C_4 items (< 30% of C_3 carbon; $\delta^{13}C$ = -18 to — 12‰). We also corrected the $\delta^{15}N$ values using the fractionation factor ($\Delta^{15}N$ = 3.4 ± 1.5‰) generated by the 'SIDER' package.

Isotopic Niches

To assess overlap of resource use by *D. rotundus* and its potential prey, we analysed isotopic niche widths using the 'SIBER' package (Jackson *et al*., 2011), available in R 3.5.3. This package calculates the standard ellipses area (SEA), using $\delta^{13}C_{corrected}$ and $\delta^{15}N_{corrected}$ values, that contains 95% of the data, independent of sample size, which allows isotopic niche widths to be compared between species. We used the corrected SEA (SEAc) to control for sample size differences.

Results

Capture of Common Vampire Bats and Potential Prey

We captured 187 individuals of 13 bat species on Anchieta Island, including 16 vampires (Supplementary Table S2), and collected fur of 17 capybaras and 10 coatis (Supplementary Table S3 and Supplementary Fig. S1). The capture percentage for *D. rotundus* was 0.12% (16 individuals/12,607 m^2h * 100) (Supplementary Table S2), while the mean density of both potential preys together was estimated as 60.9 individuals/km^2 (coati = 25.06 and capybara = 35.30) (Table 1). Capybaras had the greatest mean biomass (1,112 kg/km^2) on the island (Table 1). Due to the predictable foraging behaviour of capybaras in open areas, only the bat-capybara system was detected by observers. Common vampire bats fed on capybaras during 17 observations of 47 hours of sampling effort (Supplementary Table S4, and Supplementary Videos S1 and S2).

Prey Choice of the Common Vampire Bat

Common vampire bats on Anchieta Island were more likely to prey upon species of open habitats (mean value of -14.8‰), that is, animals with high $\delta^{13}C$ values due to the consumption of C_4 resources. The ^{15}N values for *D. rotundus* were higher than expected and most likely similar to apex predator species (mean value of 8.2‰) (Fig. 2, Supplementary Table S3). The coati largely depended on resources from forest remnants (C_3 resources), while capybaras presented a broad isotopic niche, using

Table 1. Population size, density, and biomass [mean followed by a range in parentheses; values obtained from Bovendorp and Galetti (2007) and Gonçalves *et al*. (2018)] of potential prey of *D. rotundus* on Anchieta Island, São Paulo State, southeastern Brazil, including the number of individuals of each species introduced in 1983

Potential prey species	Body mass (kg)	No. of animals introduced	Population size	Density (ind./km^2)	Biomass (kg)
Hydrochoerus hydrochaeris	31.50	7	272.51 (151–492)	35.30 (19.56–63.75)	1112.00 (616.14–2008.00)
Nasua nasua	3.88	13	163.96 (96–279)	25.06 (14.72–42.67)	97.23 (57.11–165.55)

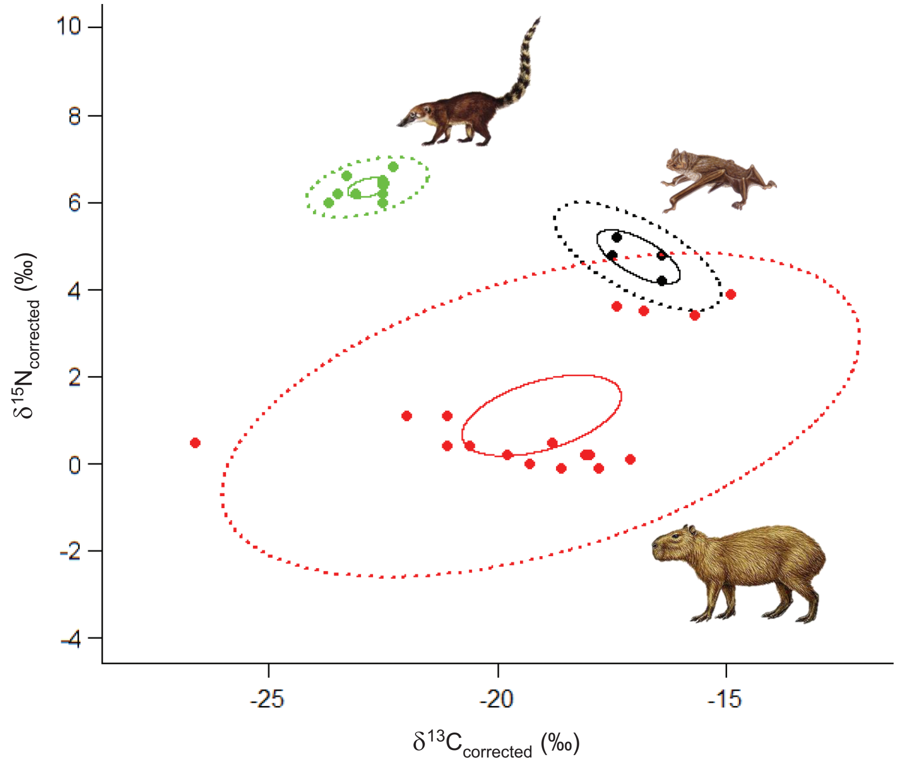

FIG. 2. Isotopic niches (standard ellipses area corrected — SEAc) and individual values ($\delta^{13}C$, $\delta^{15}N$) of common vampire bats (*D. rotundus*) (black) and its potential prey on Anchieta Island, state of São Paulo, southeastern Brazil. Isotopic values for *D. rotundus* were corrected using species-specific fractionation factors ($\Delta^{13}C$ = 2.1‰; $\Delta^{15}N$ = 3.4‰). Dashed lines = estimated standard ellipses using 95% of the data; solid lines = confidence intervals (95%) around the bivariate means; capybara (*H. hydrochaeris*) = red; coati (*N. nasua*) = green

resources from both open areas and forest remnants, but feeding mainly on C_4 plants (Fig. 2). The isotopic niche of *D. rotundus* overlapped that of the capybara, while it was distant from that of the coati (Fig. 2), and distinct from mean isotopic niche values of potential prey, including the capybara, on the mainland (Fig. 3).

DISCUSSION

The mean isotopic niche of the common vampire bat and capybara overlapped on Anchieta Island (Fig. 2), and differed from potential prey in the preserved area of the mainland (Fig. 3), indicating that capybaras of Anchieta Island are their main food source. Even with concentrated sampling effort, our results support previous studies that showed a choice by *D. rotundus* to feed on locally abundant and reliable prey (Voigt and Kelm, 2006; Bobrowiec *et al.*, 2015; Streicker and Allgeier, 2016; Zórtea *et al.*, 2018). Previous long-term isotopic studies analysing tissues with different isotopic turnover rates (e.g., blood, skin and hair from different individuals and assemblages), showed that the dietary preference of *D. rotundus* varies little over time and does not change over seasons (Voigt and Kelm, 2006; Voigt *et al.*, 2008; Streicker and Allgeier, 2016). This information was supported by direct observations, which showed that these bats can use memory and/or sensory cues to repeatedly feed on the same group of capybaras (Supplementary Videos S1 and S2).

Common vampire bats were not captured in studies in preserved areas of the mainland (Picinguaba, Mambucada and Santa Virgínia) that are near Anchieta Island (Supplementary Table S5, and Fig. 1). This evidence corroborates the hypothesis that the capture percentage for *D. rotundus* is usually low in natural forested habitats where potential prey are scattered, while it is high in areas with a high concentration of prey (Bobrowiec *et al.*, 2015). Furthermore, the number of individuals mistnested differed from nearby islands with a different history of human occupation (Supplementary Table S5 and Fig. 1) indicating that individuals of *D. rotundus* may respond to different types and intensities of anthropogenic disturbance (Streicker and Allgeier, 2016; Gonçalves *et al.*, 2017).

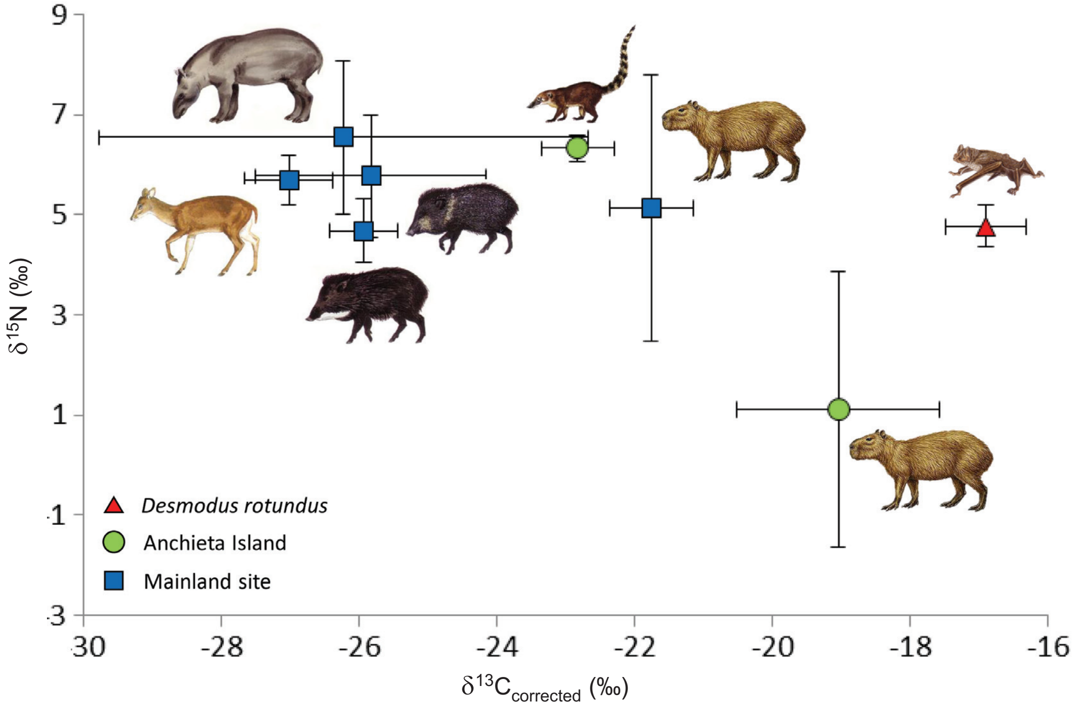

FIG. 3. Mean and standard deviation of δ^{13}C and δ^{15}N values of common vampire bats (*D. rotundus*; red triangle) and its potential prey on Anchieta Island (green circles) and Núcleo Santa Virgínia of the Serra do Mar State Park (mainland site; blue squares), state of São Paulo, southeastern Brazil. Isotopic values for *D. rotundus* were corrected using species-specific fractionation factors (Δ^{13}C = 2.1‰; Δ^{15}N = 3.4‰). Anchieta Island potential prey: capybara (*H. hydrochaeris*) and coati (*N. nasua*). Mainland site potential prey: white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), deer (*Mazama* sp.), lowland tapir (*Tapirus terrestris*) and capybara

The current native mammal fauna on Anchieta Island is quite impoverished due to its south-eastern isolated location and past human impacts (Bovendorp and Galetti, 2007; Souza *et al*., 2019; Supplementary Table S1). There have been no previous studies on the occurrence and/or diet of *D. rotundus* on the island since the beginning of the 20th century (Garbino, 2016; Muylaert *et al*., 2017). However, previous information on human occupation of the island (Guillaumon *et al.*, 1989), and records of common vampire bats on the mainland and nearby islands (Garbino, 2016), lead us to believe that the domestic animals once present on Anchieta Island (especially cattle, pigs and dogs) were the main prey of *D. rotundus* and responsible for maintaining a viable population there. When the island became a state park in 1977, all domestic animals were removed (Guillaumon *et al*., 1989), which forced the population of *D. rotundus* to leave or reach a very low density. After the mammal introductions in 1983, capybaras underwent explosive population growth due to the availability of food and the absence of predators and, consequently, became an abundant and reliable source of blood for the common vampire bats on the island. This new anthropogenic scenario allowed these bats to return to the island and/or the population density to increase. An alternative hypothesis is that *D. rotundus* never existed on the island, and that the new scenario created by the introductions allowed the species to colonize.

The extent to which common vampire bats can shift to new food sources is poorly understood, but the degree to which they exhibit dietary shifts and how these feeding strategies respond to human activity can be an indicator of community-level responses to environmental changes (Bolnick *et al*., 2003; Layman *et al*., 2007; Gonçalves *et al*., 2017). The common vampire bat needs to feed every night (Freitas *et al*., 2003), and prey that are dispersed or free to move are more difficult to attack (Delpietro, 1989). Capybaras present a more predictable and constant food source on Anchieta Island, as they feed on grasses in open areas during the night, and are larger than coatis, reinforcing our conclusion that capybaras are the most attractive and reliable food source for *D. rotundus* on the island.

The large biomass of capybaras on Anchieta Island and their predictable behaviour make them easy to find and more accessible than other potential prey for *D. rotundus*. The relatively recent introduction of capybaras to Anchieta Island only 36 years ago has allowed *D. rotundus* to successfully exploit them, and reflects a rapid prey shift due to anthropogenic disturbances. The shift from a livestock-based diet to one based on introduced species poses interesting questions for the health and behaviour of *D. rotundus*. Blood from translocated species might affect common vampire bats directly through differences in nutritional quality and exposure to new diseases, such as serologically confirmed leptospirosis in some individual bats from Anchieta Island (Aires, 1998). Additionally, three individuals of introduced capybaras were confirmed to have died from bat rabies virus (RABV — variant 3) in 2020 (P. S. Moreira, unpublished data). Therefore, we recommend that periodic monitoring be undertaken for bat rabies viruses (RABV) in *D. rotundus* populations on Anchieta Island and other nearby areas in order to quantify the magnitude of the outbreak and develop strategies for controlling viruses, especially considering that the island and nearby areas are frequently visited by tourists.

In summary, stable isotope analysis is a useful tool for studying prey choice because it integrates information across wide time spans (4–6 months prior to sampling) when quantified from tissues with slow turnover such as hair (Peterson and Fry, 1987; Voigt and Kelm, 2006). Our results indicate that, in the absence of livestock and domestic animals, the common vampire bats of Anchieta Island feed primarily on capybaras, which is consistent with bats having a preference for abundant species. The results are context-dependent and strongly influenced by: (1) the extirpation of domestic animals; (2) the high abundance of the prey species, capybara, which has the highest mean biomass on the island; and (3) the predictable foraging behaviour of capybaras in open areas.

Supplementary Information

Contents: Supplementary Tables: Table S1. Introduced species and current population size and density of mammals [adapted from (Bovendorp and Galetti, 2007)] on Anchieta Island, south-eastern Brazil, and their respective biomass [body mass according to Gonçalves *et al.* (2018)]; Table S2. Bat species recorded on Anchieta Island; Table S3. $\delta^{13}C$ and $\delta^{15}N$ values for *D. rotundus* and potential prey (*H. hydrochaeris* and *N. nasua*) on Anchieta Island, including the number of samples analyzed (N); Table S4. Number of events of *D. rotundus* feeding on capybaras (*H. hydrochaeris*) on Anchieta Island; Table S5. Number of individuals of *D. rotundus* captured on Anchieta Island and nearby Mainland areas, including capture effort, size of the study area, and if domestic or introduced animals were present. Supplementary Fig. S1. Capture and sampling of common vampire bats (*D. rotundus*) and potential prey: (1) capybaras (*H. hydrochaeris*) and (2) coati (*N. nasua*) on Anchieta Island, south-eastern Brazil. Supplementary Videos: Video S1 and S2: Common vampire bats (*D. rotundus*) feeding on capybaras on Anchieta Island, south-eastern Brazil. Supplementary Information is available on BioOne and GitHub (github.com/fhmgoncalves).

Acknowledgements

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