

Capybara ride: evidence of whole aquatic plant dispersal

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Abstract: The functioning of diverse ecosystems relies on the dispersal processes facilitated by animals, known as zoochory. This ecological process is the only way in which some aquatic species can move between aquatic systems through the terrestrial matrix. Despite its paramount importance, the dispersal mechanisms involving certain vectors, such as mammals, have remained relatively poorly understood. Based on observation of capybaras *Hydrochoerus hydrochaeris* emerging from a wetland with various aquatic plant species attached to their fur, we hypothesized that these mammals play a crucial role in dispersing aquatic plants. We conducted a controlled experiment and confirmed that capybaras disperse two species of duckweed, *Lemna valdiviana* and *Wolffia columbiana*, through both endozoochory and epizoochory. The discovery of entire plant dispersal is noteworthy because it is not dependent on the season and does not rely on the production of specific reproductive diaspores. This study presents pioneering documentation of capybaras capacity to disperse entire plants through their gastrointestinal passage and offers further evidence of their role in epizoochory within neotropical wetlands.

Keywords: endozoochory; epizoochory; aquatic macrophytes; plant dispersal; wetlands.

Passeio de capivara: evidência de dispersão de plantas aquáticas inteiras

Resumo: O funcionamento de diversos ecossistemas depende de processos de dispersão facilitados pelos animais, conhecidos como zoocoria. Este processo ecológico é a única forma pela qual algumas espécies aquáticas podem se mover entre sistemas aquáticos, através da matriz terrestre. Apesar da sua importância, os mecanismos de dispersão envolvendo certos vetores, como os mamíferos, permanecem relativamente pouco compreendidos. Com base na observação de capivaras *Hydrochoerus hydrochaeris* emergindo de uma área úmida com diversas espécies de plantas aquáticas aderidas à sua pelagem, levantamos a hipótese de que esses mamíferos desempenham um papel crucial na dispersão de plantas aquáticas. Conduzimos um experimento controlado e confirmamos que capivaras dispersam duas espécies de lentilha-d'água *Lemna valdiviana* Fil. e *Wolffia columbiana* Karsten, ambas através de endozoocoria e epizoocoria. A descoberta da dispersão de plantas inteiras é notável porque não depende da estação do ano e da produção de diásporos reprodutivos específicos. Este estudo apresenta uma documentação pioneira da capacidade das capivaras de dispersar plantas inteiras através do seu trato gastrointestinal e oferece evidências adicionais de seu papel na epizoocoria em áreas úmidas Neotropicais.

Palavras-chave: endozoocoria; epizoocoria; macrófitas aquáticas; dispersão de plantas; zonas úmidas.

Introduction

The colonization of aquatic organisms in isolated wetlands has been debated since the time of the naturalists (Darwin 1859, Brown and Lomolino 2006, Green et al. 2023). Understanding the role of animals in the dispersal of aquatic organisms (zoochory) is crucial for comprehending the distribution of plant species across the landscape (Green et al. 2023). In this sense zoochory has proven to be essential for the dispersal of seeds (Figuerola et al. 2003, Flaherty et al. 2018, Silva et al. 2020, Lee et al. 2022) and whole plants (Coughlan et al. 2017, Silva et al. 2018, Paolacci et al. 2023). During a field expedition at the Taim Ecological Station (ESEC Taim; 32°32'51.76" S, 52°32'37.66" W), a Ramsar site in southern Brazil (Figure 1a), we observed a group of free-ranging capybaras emerging from a wetland while carrying various species of aquatic plants attached in their furs. We hypothesized that this species participates in the dispersal of aquatic plants between wetlands, and therefore contributes to their patterns of geographic distribution. The capybara, *Hydrochoerus hydrochaeris* Linnaeus, is the world's largest rodent (Mones and Ojasti 1986). Capybaras inhabit wetlands and are widely distributed in the South America, ranging from southern Panamá to Buenos Aires, in Argentina (Mones and Ojasti 1986). Categorized

as semiaquatic mammals, they have webbed hind feet and are being commonly found in aquatic habitats (Mones and Ojasti 1986, Silva 2014). These large herbivores live in groups and 80% of their food comprises aquatic plants (Borges and Colares 2007, Garcias and Bager 2009). The main goal of this study was to experimentally recognize the potential of capybaras to disperse aquatic plants in wetlands.

Materials and Methods

The dispersal of entire aquatic plants by capybaras was examined at a zoological park in southern Brazil (Parque Zoológico da Fundação Zoobotânica do Rio Grande do Sul – PZFZB, 29°47'47.99" S, 51°10'10.21" W). The model used was a male capybara of 35 kg and two years of age, born and raised in captivity. The capybara was housed in an enclosure that measured 18 m². It had a floor made of concrete and sand and free access to a 3 m² artificial pool (Figure 1b). The capybara diet at the park comprised fruits, vegetables, and sugarcane, and drinking water was always provided *ad libitum* during the experiment.

To conduct the experiment, we installed a 0.415 m × 0.315 m × 0.16 m container on the floor of the enclosure. Subsequently, we filled the container with clean water and included four species of floating aquatic plants (*Azolla filiculoides* Lam, *Salvinia minima* Bak, *Lemna valdiviana* Fil., and *Wolffia columbiana* Karsten) until they covered the water surface, totaling 0.13 m² (see Figure 1b). The selected aquatic plants naturally occur in Zoo's lakes and are widely distributed in southern Brazil (Rolon and Maltchik 2006) and the world, except for *S. minima* an endemic plant to Brazil (Pena et al. 2020). The aquatic plants were made available to the capybara for 26 hours and 30 minutes, during which the capybara could interact *ad libitum* (Figure 1c-d).

The percentage of aquatic plants added to the container matched the natural proportion found in the zoo's lake. The lake showed its entire surface covered by the plants, with *W. columbiana* and *L. valdiviana* being visually more abundant. The specific percentage of aquatic plants offered to the capybara is shown in the results section. The number of aquatic plants added to the container was estimated by counting all individuals in 12 random samples using an 8.55 cm² sampler. Counts of individuals were performed using a Zeiss Stemi 2000-C stereomicroscope. The mean and standard error were calculated for each species of aquatic plant based on these 12 samples. The values were extrapolated to estimate the population in the container. Before the experiment, no aquatic plants were detected in the enclosure.

We analyzed the dispersal of intact aquatic plants by capybaras through the digestive tract (endozoochory) and via fur over short distances (epizoochory). For endozoochory, we collected all fecal samples produced during 48 hours after the provision of aquatic plants (Figure 1e). During this period, a total of eight fecal samples were collected, taken to the laboratory, and washed under running tap water using stacked sieves with mesh sizes of 2 mm, 1 mm, 500 μ m, and 250 μ m. The retained aquatic plants were examined under a Zeiss Stemi 2000-C stereomicroscope and incubated separately in Petri dishes with filtered water from Zoo lake. The aquatic plants were kept in a greenhouse to assess their viability for 21 days. Throughout this period, the temperature ranged from 13°C to 29°C. Mortality and emergence of new aquatic plants were recorded every seven days during the incubation period. Epizoochorous dispersal was verified by observing the presence of aquatic plants in the pool area of the enclosure after 24 hours of the experiment. The number of plants carried to the pool was estimated by counting all individuals in 12 random samples using a 79.75 cm² sampler.

Results

A total of 97,611 \pm 11,459 individuals of *W. columbiana*, 24,960 \pm 2,008 of *L. valdiviana*, 497 \pm 195 of *S. minima*, and 395 \pm 64 of *A. foliculoides* were offered to the capybara, distributed in the following percentages: 79.1% *W. columbiana*, 20.2% *L. valdiviana*, 0.4% *S. minima*, and 0.3% *A. foliculoides*. Out of the eight collected fecal samples, three contained apparently viable aquatic plants (Figure 1e, f & h). We identified these samples as A1, A2, and A3, respectively (Table 1). In sample A1, an individual of *W. columbiana* and one of *L. valdiviana* were recorded. In sample A2, 28 individuals of *W. columbiana*, 18 individuals of *L. valdiviana*. In total, we recorded 55 aquatic plants, comprising 30 individuals of *W. columbiana*, 22 of *L. valdiviana*, and 3 of *A. filiculoides*. No individuals of the species *S. minima* were observed in fecal samples.

During the seventh day of incubation, there was no emergence of new aquatic plants. However, it was observed that 19 individuals of W. columbiana, seven of L. valdiviana, three of A. filiculoides in sample A2, and three individuals of L. valdiviana in sample A3, had died (see Table 1). On the 14th day of incubation, six new plant individuals were observed in the experiment: five individuals of L. valdiviana in sample A2 and one individual of W. columbiana in sample A3 (Table 1). On the 21st day of incubation, 24 new plant individuals were observed: one individual of W. columbiana in sample A1, 18 individuals of L. valdiviana and one of W. columbiana in sample A2, and four individuals of W. columbiana in sample A3 (Table 1). After 21 days of incubation, 53 aquatic plants remained alive (Table 1), confirming the dispersal of intact aquatic plants through the digestive tract of capybaras. Regarding epizoochorous dispersal, approximately $12,400 \pm 3,365$ W. columbiana and $5,017 \pm 911$ L. valdiviana plants were found in the enclosure's pool 24 hours after the experiment began. All the aquatic plants present in the pool were viable, without tissue damage, and capable of continuing their development. Of the total plants available for ingestion by the capybara or attachment to its fur, 0.03% of W. columbiana, 0.09% of L. valdiviana, and 0.76% of A. filiculoides were recovered from the fecal samples (endozoochory). Additionally, 13% of W. columbiana and 20% of L. valdiviana were found in the pool after 24 hours (epizoochory).

Discussion

We demonstrate for the first time that capybaras can disperse intact aquatic plants through their digestive tract. The dispersal of whole aquatic plants through endozoochory has been previously documented to water birds (Silva et al., 2018; Paolacci et al., 2023) and recently to *Myocastor coypus*, another semiaquatic rodent (Hoffmann et al. 2024). The understanding of how two small macrophyte species survive passage through the digestive tract of a large herbivore remains an open question for future research. The small size of these aquatic plants might



Figure 1. Capybaras in their natural habitat, the capybara of this study in its enclosure, and the aquatic plants that survived gut passage. (a) Epizoochorous evidence by indigenous capybaras at Estação Ecológica do Taim; (b) capybara in its enclosure, container with aquatic plants and the enclosure's pool in the beginning of the experiment; (c) capybara interacting with the aquatic plants; (d) capybara with aquatic plants attached in its fur; (e) screening of feces sample, in the detail on the right, three *L. valdiviana* retained in the sieve; (f) *L. valdiviana* of A2 sample after the passage through the capybara gut; (g) *L. valdiviana* of A2 sample after its passage through the capybara gut; (i) *W. columbiana* of A2 sample after its passage through the capybara gut; (i) *W. columbiana* of A2 sample after its passage through the capybara gut.

Samples	Plants species	Initial number apparently viable	Day 7			Day 14			Day 21		
			New plants	Dead plants	Live plants	New plants	Dead plants	Live plants	New plants	Dead plants	Live plants
A1	W. columbiana	1	0	0	1	0	0	1	1	0	2
	L. valdiviana	1	0	0	1	0	0	1	0	0	1
A2	W. columbiana	28	0	19	9	0	0	9	1	0	10
	L. valdiviana	18	0	7	11	5	0	16	18	0	34
	A. filiculoides	3	0	3	0	0	0	0	0	0	0
A3	L. valdiviana	3	0	3	0	0	0	0	0	0	0
	W. columbiana	1	0	0	1	1	0	2	4	0	6
Total plants		55			23			29			53

Table 1. Asexual reproduction of *Wolffia columbiana*, *Lemna valdiviana*, and *Azolla filiculoides* recovered from three capybara droppings, showing changes in the cumulative number of live and dead plants after 7, 14, and 21 days.

have facilitated their passage through the gut. Smaller seeds are known to pass through the digestive tract of wild ducks more quickly and in greater numbers (Soons et al. 2008). Additionally, the small size of the plants could enhance survival during mastication, and when ingested with parts of other plants, they might minimize the mechanical impact on the digestive tract. We also observed the potential dispersal of two aquatic macrophyte species, *W. columbiana*, and *L. valdiviana*, via capybara fur.

The opportunity presented by this study allowed us to quantify the dispersal of aquatic plants over short distances, similar to a study done with waterbirds (Coughlan et al. 2017). Compared to endozoochory, epizoochory led to a higher percentage of plants being carried by the capybara. The efficiency of plant dispersal between wetlands may decrease as the distances increase, since capybaras tend to shake themselves after exiting the water. However, dispersal between distant wetlands is not ruled out, as step-by-step dispersal between nearby wetlands is likely (Coughlan et al. 2017).

The dispersal of intact aquatic plants over long distances is rare due to desiccation and death of leaves (Landolt 1998, Coughlan et al. 2017). Ridley (1930), however, cultivated individuals of the aquatic macrophyte L. minor previously attached to bird feathers for 12 and 22 hours and demonstrated the ability of these aquatic plants to recover from the stress of being removed from the water. In a similar fashion, our findings suggest that, under specific conditions of humidity and protection against the wind, the capybara's fur may provide adequate protection against desiccation, enabling aquatic plants to reach new habitats. In addition, species of Lemnaceae have a great capacity for vegetative propagation, and under ideal circumstances, the number of aquatic plants can increase twofold within a day, and a solitary plant can give rise to a community of more than a million individuals in only 30 days (Landolt 1998). It has been found that, the dispersal of intact plants contributes to the increase in biomass and the establishment of new species in new habitats (van der Pijl 1982), and in addition to that the zoochory of asexual propagules facilitates the colonization of wetland areas, even outside the seed production period (Silva et al. 2018).

Capybara herds exhibit a home range of about 10 ha, with a daily average displacement of around 1 kilometer (Azcarate 1980).

Extensive home ranges can facilitate the dispersal of plants over long distances (Pellerin et al. 2016). Capybaras are social animals that live in family groups of 5-14 adult individuals (Herrera 2012b, Moreira et al. 2013), but they can also live in groups of up to 100 individuals (Garcia and Bager 2009). These groups typically consist of a dominant male, a few subordinate males, and several females (Moreira et al. 2013). Many males are found as peripheral elements to the group, and generally, young individuals disperse themselves (Moreira et al. 2013). Large herds of capybaras can transport a higher number of plants compared to solitary individuals, as the number of plants in their fur or guts is multiplied by the number of individuals in the group. This can lead to increased plant dispersal rates and potentially increase the local abundance of certain species. Despite this, family groups are more sedentary, while solitary individuals of both sexes have less restricted home ranges and can cover distances of up to 5 km (Herrera 1992b, Moreira et al. 2013). In this way solitary individuals are more likely to disperse to locations outside of the family groups territories enabling the dispersal of aquatic plants over long distances (Bartel and Orrock 2022). Another factor that might enhance the chances of colonization by capybara-dispersed aquatic plants is their behavior of depositing feces directly into the water (Piccinini et al. 1971), a favorable substrate for the plants to develop. This is an indication that capybaras could play a significant role in the dispersal of aquatic plants in southern Brazil, a region characterized by numerous small and isolated wetlands (Maltchik et al. 2003).

We propose that the widespread distribution of the studied macrophyte species (Rolon and Maltchik 2006, Rolon et al. 2004) might be a consequence of their substantial dispersal through capybaras (Hoffmann et al. 2024) and aquatic birds (Silva et al. 2018). Compared with aquatic birds, capybaras possess a larger body area and thus will play a prominent role in the local dispersal of aquatic plants via epizoochory. Additionally, capybaras can spread aquatic plants to new habitats through gut passage. In this sense, capybaras play a crucial role in the dispersal processes across continental wetlands, significantly influencing the distribution of species in these environments.

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Author Contributions

Pedro Hoffmann: substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Andressa Adolfo: substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Cristina Stenert: substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to critical revision, adding intellectual content.

Giliandro G. Silva: substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to critical revision, adding intellectual content.

Leonardo Maltchik: substantial contribution in the concept and design of the study; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare no conflict of interest regarding this publication. The authors have no relevant financial or non-financial interests to disclose.

Ethics

The experimental procedures were approved by the animal ethics committee of the Federal University of Rio Grande - FURG (CEUA Pq021/2022) and supervised by the Zoo veterinarian.

Data Availability

The data collected and generated during this study are available on SciELO Data at https://doi.org/10.48331/scielodata.UAK9VD. This dataset includes the count data used in the analyses. The authors confirm that all data necessary for reproducing the study findings are available in the designated dataset.

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