RESEARCH ARTICLE

Movement patterns of the rodent *Trinomys dimidiatus* in Atlantic Forest

Gabriel Cupolillo[1] | Júlia Lins Luz[2] | Camila dos Santos de Barros[3] | Rui Cerqueira[3,4]

[1]Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

[2]Piper 3D – Pesquisa, Educação e Consultoria Ambiental, Rio de Janeiro, Brazil

[3]Programa de Pós-Graduação em Ecologia, Laboratório de Vertebrados, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

[4]Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

Correspondence
Gabriel Cupolillo, Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, Cidade Universitária, Ilha do Fundão, CEP: 21941-971, Rio de Janeiro, RJ, Brazil.
Email: gcdeazeredo002@gmail.com

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Ministério do Meio Ambiente

Abstract

Animal movements of wild species are in theory related to individual and species' traits such as sex and reproductive condition, and temporal variation in resource availability or population density. Understanding how individuals move within an area throughout life, how frequent exploratory and dispersive movement are in the population and which individual traits and environmental conditions influence movement are of great importance for understanding how animals respond to environmental changes. Using capture-mark-recapture data of *Trinomys dimidiatus* gathered for 8 years in a montane Atlantic Forest area, we describe movement patterns by comparing two distance metrics (ORL—Observed Range Length and SDT—Mean Successive Distance/Time); we also evaluate the influences of sex on these distance metrics and residence time and number of captures on ORL. Additionally, model selection was used to evaluate the role of individual traits and environmental factors on *T. dimidiatus'* movements. We recorded 44 individuals (60.27%) with restricted movement pattern and 29 individuals (39.73%) with broad movement pattern within our grid. Broad movement pattern was observed in individuals with both long and short residence time. Males presented larger distance metrics and movements than females. Individuals with greater residence time presented larger ORL, mainly males. Heavier individuals of both sexes presented larger movements than lighter ones, especially males. Males presented shorter movements in periods of increased rainfall, but females' movements did not respond to rainfall variations. Overall, body mass was more important than rainfall in determining movements. The results here show that *T. dimidiatus* may present different movement patterns, including exploratory or dispersive movements to a new core area. Also, we highlight the importance of individual traits and environmental factors and reinforce sexual differences in individuals' movements and lifetime use of space.

KEYWORDS
body mass, dispersal, movement, rainfall, sex differences

INTRODUCTION

Animal movement is defined as the spatial change of an organism's location in a specific time interval (Nathan et al., 2008). The frequency and the way animals move can influence or be influenced by populational and community patterns, for example, negatively density-dependent dispersal leading to stability of metapopulations, population isolation forcing longer movements (Baguette et al., 2013; Bowler & Benton, 2005) and temporary modification in community composition due to large periodic movements (Gentile & Cerqueira, 1995) or occasional intra-guild predation leading

to area abandonment (Moura et al., 2009). Thereafter, information about movements and habitat utilization patterns may give clues about how animals respond to environmental changes in landscape configuration (Berger-Tal et al., 2011; Sutherland, 1998).

To understand animal movements, the concept of home range area is helpful. This is the area where animals daily perform frequent movements in search of resources, shelter and mates (Burt, 1943). Movements outside this area are considered exploratory movements (Burt, 1943). Yet, for animals that do not encounter their requirements in a single area, and thus need to change home range location from time to time, or also animals which frequently use common trails to escape from predators, exploratory movements and home range definitions are debatable (Powell & Mitchell, 2012). Beyond estimating home range area, studying movements per se, such as how individual and environmental variables affect movements, may give valuable information to understand how individuals use space through time.

Movements may also be useful to describe the mating system, when considering sex differences in movements. For polygynous species of small mammals, males usually perform larger movements than females, covering larger areas searching for reproductive mates. Such behaviour has been described for some rodent species (Adler, 2011; Attuquayefio et al., 1986; Bergallo & Magnusson, 2004; Fleming, 1971; Wolff & Cicirello, 1990). Monogamous species do not present sex difference in home range and movement length while polygynous ones do so (Bergallo & Magnusson, 2004).

Body mass can also determine movements, as it can represent body fat and may indicate energy reserve (Godsall et al., 2013; McCue, 2010). Larger movements are expected in heavier animals when considering body mass as indicative of energy reserve. However, females could use this energy reserve for gestation and lactation (Gittleman & Thompson, 1988) and thus this pattern may not apply to all females (e.g. Almeida et al., 2013; Bergallo & Magnusson, 2004), despite long movements for dispersal of newly pregnant females has been reported (Wolff & Cicirello, 1990). When considering age, juveniles can move large distances independent of sex and body mass, known as juvenile dispersal (Bowler & Benton, 2005; Le Galliard et al., 2011).

As energy reserve is peremptory for movement length, the availability of food resources is also a determinant factor for movements. Common food resource of small mammals such as fruits and soil arthropods, have a positive relationship with rainfall (Bergallo & Magnusson, 1999; Cerqueira, 2004; Cerqueira & Lara, 1991; Leiner & Silva, 2007a). Thus, movements could be larger during dry seasons as animals need to move larger areas to find food, as described for neotropical marsupials (Ferreira et al., 2017; Leiner & Silva, 2007b; Loretto & Vieira, 2005), or shorter when food availability is high, as described for temperate rodents, since individuals find enough food items in a smaller area (Jonsson et al., 2002; Ostfeld, 1986; Taitt & Krebs, 1981). Besides, shorter movements are expected with greater population density given the ease of finding mates or to avoid agonistic interactions (Adler et al., 1997; Casula et al., 2019; Wolff & Cicirello, 1990). Effects of food availability and population density may further interact since areas with large food resources availability may have increased population densities (Adler et al., 1997; Dugatkin, 2009; Galindo-Leal & Krebs, 1998; Mello et al., 2015; Taitt & Krebs, 1981; Wolff & Cicirello, 1990), leading to unexpected patterns.

Here we describe the movement patterns of individuals from a population of the poorly studied Neotropical rodent *Trinomys dimidiatus* (Rodentia; Echimyidae) in the Atlantic Forest. We used a long-term

capture-mark-recapture (CMR) dataset of small mammals in Brazil to test the relationship between movements and individual traits and environmental factors. We verified the influence of sex and individual residence time on distance metrics. Also, to understand possible drivers of movements, we analysed the distance between capture points in relation to sex, reproductive condition (reproductively active or not), body mass, rainfall and population size. Our hypothesis is that (I) movement length is different between sexes, with males of this echimyid species presenting larger movements than females, a pattern frequently observed on polygynous mating systems, common in echimyids; (II) movement length is different between reproductively active individuals and those not, with larger movements for reproductively active individuals, as they cover larger areas searching for mates, particularly males; (III) movement length is positively related to body mass for both sexes, reflecting energy availability, but this relationship is stronger for males; (IV) movement length is negatively related to rainfall for both sexes, given less food availability with less rainfall and (V) movement length is negatively related to population density for both sexes, probably in response to the ease to find reproductive mates within the area.

METHODS

The study was conducted from May 2012 to March 2020 at the Rancho Frio site (22°27′29″ S, 43°00′14″ W), 1250 m.a.m.s.l. in Serra dos Órgãos National Park (PARNASO; Teresópolis, Rio de Janeiro, Brazil). PARNASO is at the mountain chain of Serra do Mar, the largest patch of extant Atlantic Forest in the state. The vegetation is classified as dense montane rain forest (IBGE, 1992). One of the most common fructiferous plant species in the area is *Euterpe edulis* (Arecaceae; Matos et al., 2007). Another species commonly observed in the area, *Guapira opposita* (Matos et al., 2007), have high fructification indices during rainy season (Lorenzi, 1998). Mean annual rainfall for the studied years was 2835.29 ($\pm$444.32) mm, with more rainfall between October and April although occurring year-round. Data were collected in 48 five-night trapping sessions every 2 months. The trapping grid was ca 3 ha (90 trap stations spaced 20 m apart; Figure 1). Each station had four traps: two traps, one Tomahawk (40.64 × 12.70 × 12.70 cm) and one Sherman trap (7.64 × 9.53 × 30.48 cm), were placed on the ground, one Sherman trap placed in the understory (1.5–2.0 m high) and another in the canopy high (6–20 m high). All traps on the ground were baited with a mixture of banana, peanut butter, oatmeal and bacon and a piece of red meat and bacon; traps in the understory and canopy were baited with slices of banana (see details in Loretto & Vieira, 2023). Each animal captured received two unique numbered ear tags. We recorded the sex and reproductive condition (reproductive females: perforate vagina, pregnant or lactating; reproductive males: visible scrotum; Cademartori et al., 2005; McCravy & Rose, 1992). For each animal in each trapping session, we measured body length, tail length and body mass. Individuals were considered adults if body mass was greater than the lighter reproductive individual of each sex in the population (male: 80 g; female: 90 g). Individuals were released at the same point of capture. These data are part of a long-term study of the Laboratório de Vertebrados—UFRJ. Animals were not anaesthetised to minimize physiological stress. Trapping and handling followed the guidelines sanctioned by the American Society of Mammalogists (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). This study was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade/Ministério do Meio Ambiente (Authorization number 33746-10).
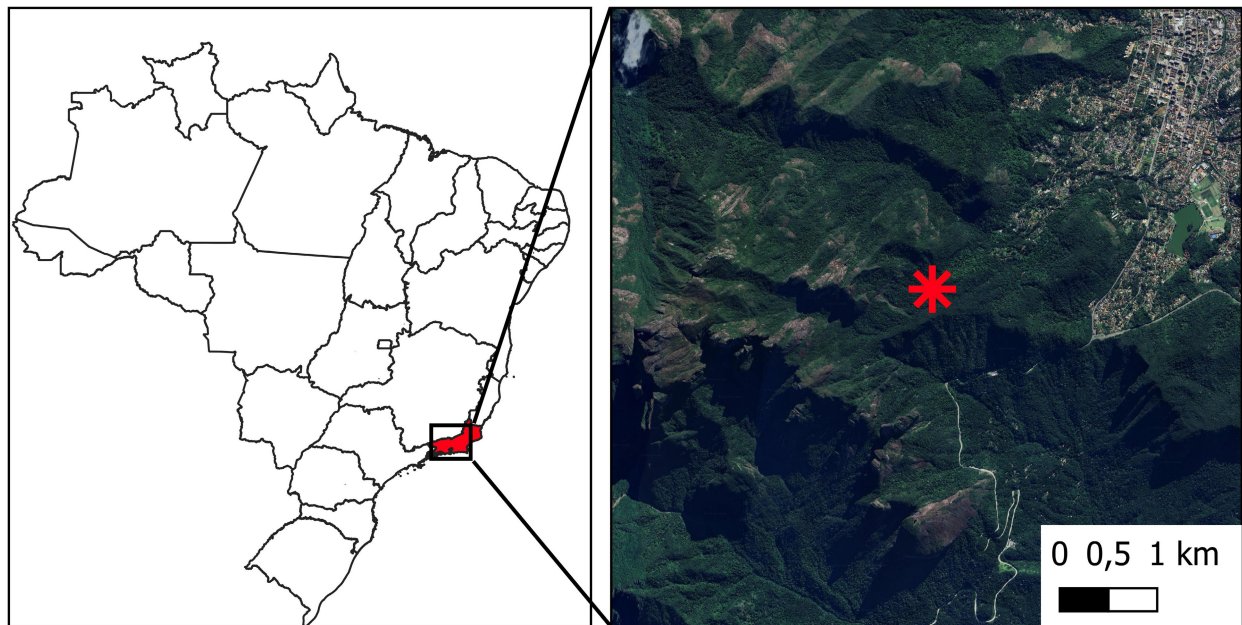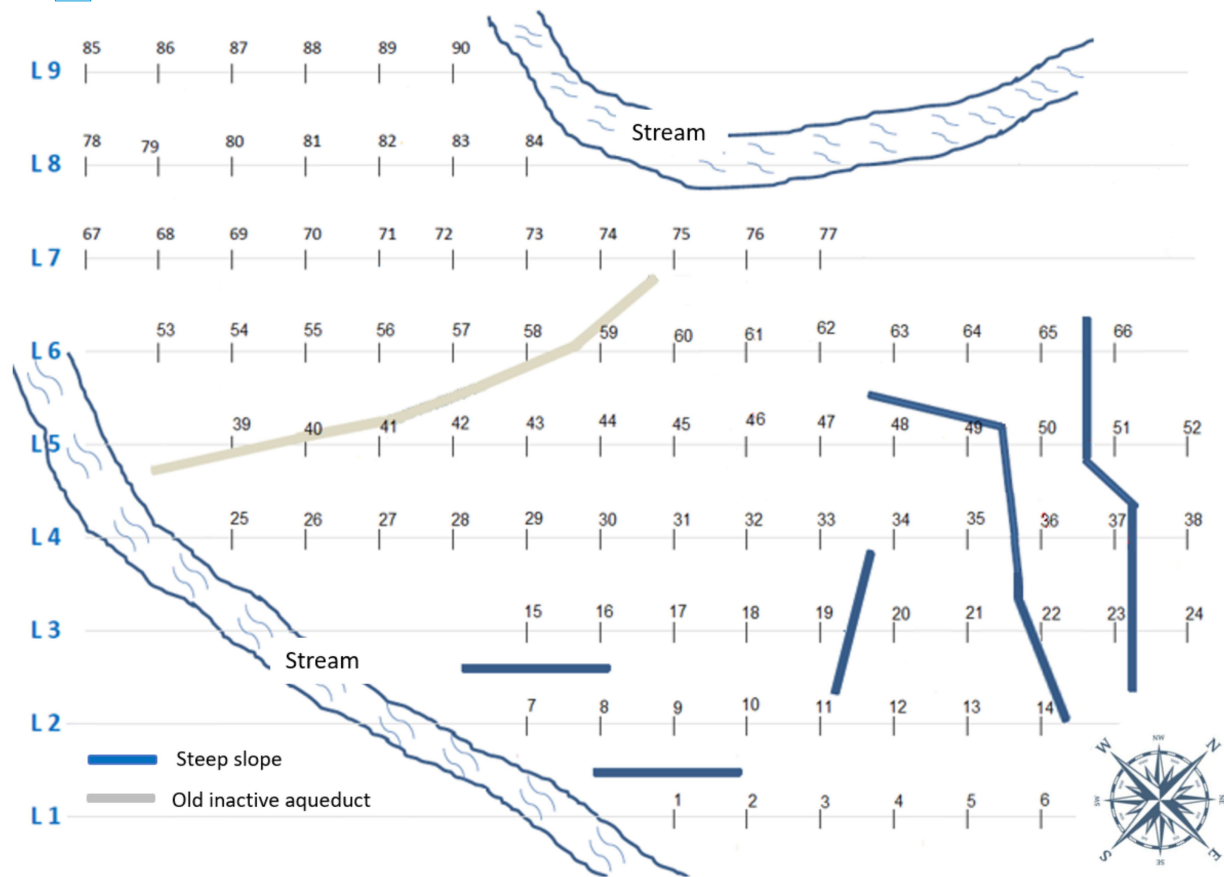
FIGURE 1   Rancho Frio trapping grid of ~3 ha with 90 trapping stations 20 m apart of each other distributed in nine lines between two streams and located at Serra dos Órgãos National Park at the municipality of Teresópolis (bottom right), Rio de Janeiro State (bottom left).

The focal species is *T. dimidiatus*, an echimyid rodent endemic to the Atlantic Forest largely distributed in Rio de Janeiro State and the northern coast of São Paulo State, Brazil (Attias et al., 2009; Pessôa et al., 2005). Adult body dimensions are 86–234 mm (head and body length) and 80–375 g

(body mass; Cupolillo, 2023). It is solitary, nocturnal and terrestrial. Results from a laboratory experiment (R. Cerqueira, unpublished data, 2012) following the protocol established in Finotti and Cerqueira (2018) revealed a preference for the consumption of fruits, seeds and roots. Ecological studies of *T. dimidiatus* are scarce and all available and relevant information of this species within our knowledge have been included.

CMR within a trapping grid is a largely used method to study small mammals' populations (e.g. Barros et al., 2007; Bergallo, 1994; Bovendorp et al., 2020; Cerqueira et al., 1993; Ferreira et al., 2016), resulting in a large amount of available data. Trapping grids are not the primary method for movement ecology studies, however, the large data available offers a unique opportunity to study movement patterns while considering the method's limitations. We used two distance metrics for studying animal movements using CMR data: mean distance between successive capture points (Stickel, 1954), with an adjustment to standardize the time interval considering only the distances between two trapping sessions consecutive in time, which we call SDT (mean successive distance/time), and observed range length—maximum distance possible between all captures of that individual (ORL—Stickel, 1954). To guarantee data independence, we only considered the first capture of an individual in each trapping session, so that captures and trapping sessions have interchangeable meanings throughout the text. Given that SDT is a mean, only individuals captured in at least three trapping sessions were considered in the study.

The ease in calculating those distance metrics, the possibility of including individuals with a minimum of three captures (hence increasing the sample size), and their correlation with each other and with home range estimates, favour the use of those indices when studying home ranges (Püttker et al., 2006, 2012). Those metrics however indicate different lengths of the space used. Since they are supposed to represent the same home range, that difference may be a problem, but it represents a great opportunity for describing how individual's movements are distributed in space and time (e.g. a large distance moved by an individual can be reached through a unique large movement in a short period or by different short movements, using different parts of the habitat in a larger time interval). ORL and SDT can describe two-time intervals related to different ranges of behaviours: the mean range of distances between successive capture points (SDT) represents movements in a short-time interval, here 2 months, and may represent frequent behaviours such as searching for food and partners, while the largest distance between capture points (ORL) represents the individual's range during the whole residence time (time between the first and the last capture) and may be achieved both through frequent behaviours or through exploratory or dispersive ones.

We defined two patterns of movements (restricted and broad) based on the combinations of SDT, ORL and the points of capture. Using the locations of captures in the grid (e.g. Figure 2) we define a nucleus of nearby captures of each individual, which we called the core area of movements. Each individual could have one or more core areas. Using the two metrics, we considered three classes (restricted, exploratory and migratory) within the two types of movement pattern (restricted and broad). We named individuals with restricted movement pattern those that present the largest movement range (ORL) not different from the distances moved in short time interval (SDT; Figure 2a). We named individuals with broad movements those individuals that presented ORL differently from SDT. Then, we classified broad movement pattern in exploratory movements outside the core area (Figure 2b) or dispersive movements changing the location of the core area, which may be a gradual (Figure 2c) or an abrupt change (Figure 2d). All restricted movement patterns presented a single core area
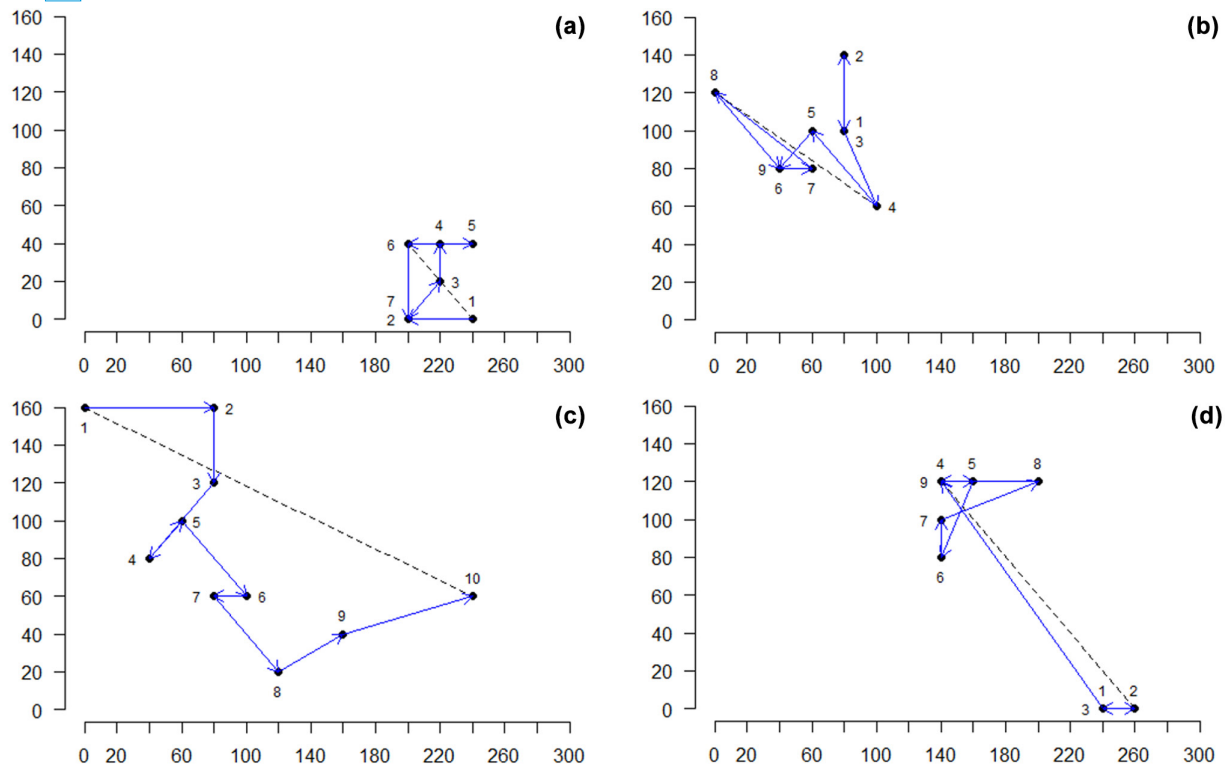
FIGURE 2 Representation of different types of movement with capture-mark-recapture data in a hypothetical grid. We represented the captures as numbers and arrows help to indicate the movement direction in a hypothetical grid (*x* and *y* axes represent two perpendicular directions) with capture points every 20 meters. (a) Restricted movement: The individual maintains a single core area. (b) Exploratory movements: The individual maintains a single core area and performs exploratory movements. (c, d) Dispersive movement: (c) The individual presents more than one core area throughout life with a gradual change in their location. (d) The individual presents more than one core area throughout life with an abrupt change in location. These hypothetical data represent individual captures (black dots), sequence of captures (numbers), individuals' route between two consecutive trapping sessions (grey arrows) the and maximum range (ORL) of an individual (black dashed lines).

while broad ones can have one or more core areas, based on the location of capture points. We give examples of these movement patterns in a hypothetical grid in Figure 2.

To observe core areas and describe movement patterns, we constructed maps with a sequence of captures similar to those presented in Figure 2. We calculated SDT and ORL for each individual and defined a threshold value of ORL as the 97.5th percentile of SDT for each sex to decide when to consider a broad movement pattern instead of a restricted movement pattern. This threshold value was qualitatively chosen based on inflection points on the probability density function of SDT. Values beyond this threshold value have a low probability of occurring and represent the frequent behaviours represented by SDT, such as the search for food and partners (Tucker et al., 2018, 2023). Therefore, when comparing SDT to ORL, any ORL value larger than the threshold value has little probability (<0.025) of being a value related to frequent behaviours and the individual either presents exploratory movements or shifts the location of its core area in time (check Figure 2 for examples). Shifts of core area location were visually defined following examples in Figure 2. We used a generalized linear model following a Poisson error distribution to evaluate possible sex differences in distance metrics.

Additionally, we did a model selection with Generalized Linear Models (GLM) following a Poisson error distribution to evaluate any influence of sex, number of captures and residence time (i.e. number of months between first and last captures of an individual) on ORL; additive and interactive

TABLE 1 Result of the model selection for maximum possible distance between all captures (ORL) as a function of sex, residence time and number of captures for *Trinomys dimidiatus* in the Serra dos Órgãos National Park (Rio de Janeiro, Brazil).

Model	ΔAICc	df	Weight
Sex + residence time + sex:residence time	**0.0**	**4**	0.935
Sex + residence time	5.3	3	0.065
Sex + captures + sex:captures	85.3	4	<0.001
Sex + captures	119.4	3	<0.001
Residence time	217.5	2	<0.001
Captures	344.0	2	<0.001
Sex	719.9	2	<0.001
Null	954.5	1	<0.001

Note: It presents the delta of AICc values (ΔAICc), degrees of freedom (df) and AICc weight for all models. Most plausible model (ΔAICc <2) is bolded.

combinations of these variables were also considered. Number of captures is correlated with residence time ($r = 0.78$, $p < 0.01$) thus these two variables were not included in the same model (Table 1).

To evaluate possible influences of individual traits (sex, reproductive condition and body mass), population size and environmental factors (rainfall) in animal movements, we did a GLM model selection following a Poisson error distribution, considering the effects of additive and interactive combinations between variables (Table 2) on the distance moved between successive captures. We only considered interactions of up to three variables, given the overloaded complexity of models with four or more variable interactions. Here we do not use the mean value, that is SDT, but the actual distance between consecutive capture points in distinct, 2 months apart, trapping sessions. As one movement represents two captures, we considered the reproductive condition and population size recorded at the first capture, the body mass of the second capture and the amount of rainfall accumulated in the month before the second capture. Population size of each trapping session was estimated using Minimum Number Known Alive (MNKA; Krebs, 1966). Body mass was correlated with population size (Pearson's correlation coefficient $= -0.19$; $p < 0.01$) and reproductive condition (generalized linear model estimate for reproductive individuals $= 12.70$; $p = 0.02$), thus these variables were not considered in the same model. We also used a *t*-test to see if there was a sexual dimorphism on body mass to dissociate the effects of body mass per se from sex effects on movements.

We assessed the plausibility of candidate models using Akaike's Information Criterion corrected for small samples (AICc; Burnham & Anderson, 2002; Williams et al., 2002). AICc values of each model were subtracted from the AICc value of the most plausible model (ΔAICc), and models were considered equally plausible with ΔAICc ≤2 (Burnham & Anderson, 2002). All analyses were run in R environment 4.0.2 (R Core Team, 2020).

RESULTS

We captured 287 *T. dimidiatus* individuals, but only 73 (25.44%, 36 females and 37 males), were present on three or more trapping sessions; all 73 were adults. Total mean of trapping sessions was 5.37 (±3.21). Males were captured in a mean (±standard deviation) of 5.43 (±3.17) trapping sessions, ranging from three to 19, while females were captured

TABLE 2 Result of the model selection for distance moved between successive captures as a function of sex, reproductive condition (RC), body mass (BM), rainfall (RF) and population size (PS) for *Trinomys dimidiatus* in the Serra dos Órgãos National Park (Rio de Janeiro, Brazil).

Model	ΔAICc	df	Weight
Sex + BM + RF + sex:BM + sex:RF + BM:RF + sex:BM:RF	0.0	8	1
Sex + BM + RF + sex:BM + sex:RF + BM:RF	36.9	7	<0.001
Sex + BM + sex:BM	50.3	4	<0.001
Sex + BM + RF	56.9	4	<0.001
Sex + BM	57.6	3	<0.001
Sex + PS + RC + sex:PS + sex:RC + PS:RC + sex:PS:RC	112.0	8	<0.001
Sex + PS + RC + sex:PS + sex:RC + PS:RC	119.6	7	<0.001
Sex + RF + RC + sex:RF + sex:RC + RF:RC + sex:RF:RC	139.0	8	<0.001
Sex + RF + RC + sex:RF + sex:RC + RF:RC	156.1	7	<0.001
RF + PS + RC + RF:PS + RF:RC + PS:RC + RF:PS:RC	159.6	8	<0.001
Sex + PS + RC	168.8	4	<0.001
Sex + RC + sex:RC	172.0	4	<0.001
BM + RF + BM:RF	174.3	4	<0.001
PS + BM + RF	180.2	4	<0.001
Sex + RF + RC	181.5	4	<0.001
Sex + RC	185.0	3	<0.001
BM + RF	190.1	3	<0.001
BM	191.2	2	<0.001
RF + PS + RC + RF:PS + RF:RC + PS:RC	203.1	7	<0.001
PS + RC + PS:RC	304.1	4	<0.001
RF + PS + RC	335.9	4	<0.001
PS + RC	341.0	3	<0.001
RF + RC + RF:RC	351.7	4	<0.001
Sex + RF + PS + sex:RF + sex:PS + RF:PS + sex:RF:PS	359.7	8	<0.001
RF + RC	361.1	3	<0.001
RC	364.2	2	<0.001
Sex + RF + PS + sex:RF + sex:PS + RF:PS	395.2	7	<0.001
Sex + PS + sex:PS	486.2	4	<0.001
Sex + RF + PS	493.0	4	<0.001
Sex + PS	493.7	3	<0.001
Sex + RF + sex:RF	504.2	4	<0.001
Sex + RF	508.3	3	<0.001
Sex	508.4	2	<0.001
RF + PS + RF:PS	529.4	4	<0.001
RF + PS	638.0	3	<0.001
PS	639.6	2	<0.001
RF	659.6	2	<0.001
Null	660.1	1	<0.001

Note: It presents the delta of AICc values (ΔAICc), degrees of freedom (df) and AICc weight for all models. Most plausible model (ΔAICc <2) is bolded.

in 5.31 ($\pm$3.29) trapping sessions, ranging from three to 18. Mean SDT was 37.07 ($\pm$20.31) m considering both sexes, 41.34 ($\pm$21.19) m for males and 32.12 ($\pm$18.34) m for females. Mean ORL was 79.59 ($\pm$50.24) m considering both sexes, 95.03 ($\pm$59.50) m for males and 63.11 ($\pm$32.89) m for females. Males had significantly larger distance metrics than females ($p < 0.001$).
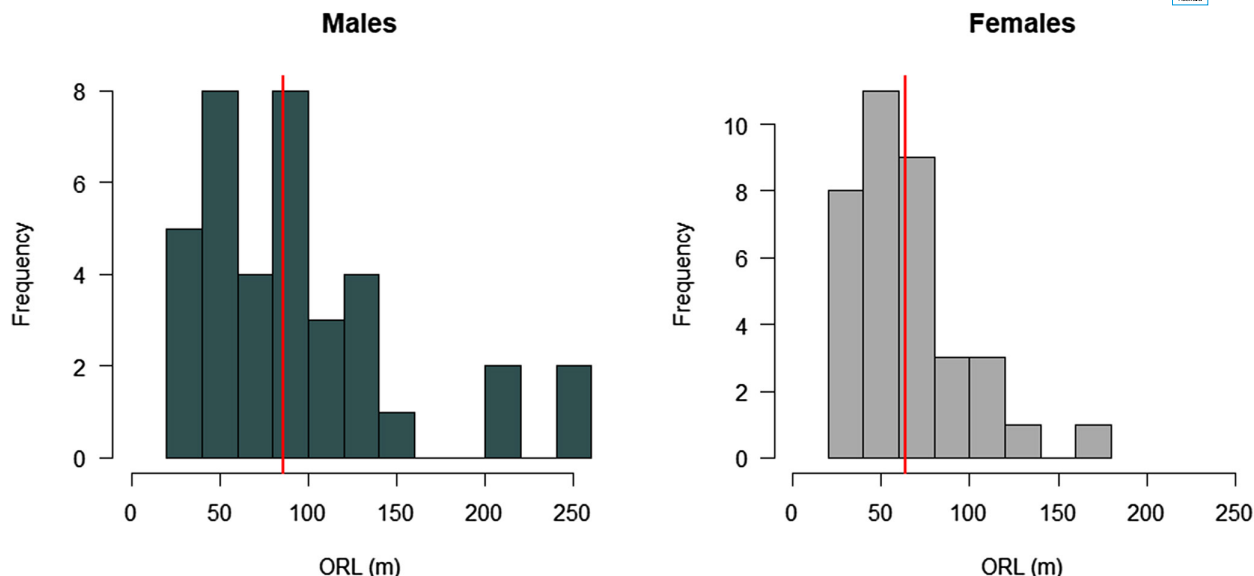
FIGURE 3 Histogram showing the frequency of individuals with each class of values for Observed Range Length for females (light grey) and males (dark grey) of *Trinomys dimidiatus* in the Serra dos Órgãos National Park (Rio de Janeiro, Brazil). The dashed line corresponds to the threshold value of mean successive distance/time's 97.5th percentile calculated for each sex (females: 63.78 m; males: 85.94 m).

The defined threshold value of SDT for defining a broad movement pattern was 63.78 m for females and 85.94 m for males. For males, 15 individuals (41.67%) presented broad movements (Figure 3), of which two changed core area location. For females, 14 individuals (38.89%) presented broad movements (Figure 3), with five of them changing core area location. No individuals made more than one change in the location of its core area and all individuals but one female changed the core area location abruptly.

Residence time and sex best explained ORL variation (Table 1). Both sexes presented larger ORL with greater residence time but this increase was stronger in males (Table 1; Figure 4). Though it is clear that longer residence time led to larger ORL and that a broad movement pattern is partially dependent on a large ORL it is possible to observe a broad movement pattern in some individuals with shorter residence times (Figure 4).

The analysis of the influence of sex, reproductive condition, body mass, rainfall and population size on the distance between successive captures indicated that reproductive condition and population size had a negligible influence, but sex, body mass and rainfall interact to explain the distance moved (Table 2). For both sexes heavier animals moved larger distances than lighter ones; body mass effect on distance moved is stronger in males than females (Figure 5). Males moved shorter distances with increased rainfall, but females' movements were not influenced by it (Figure 5).

Mean ($\pm$ standard deviation) body mass was 218.47 ($\pm$36.97) g for males and 217.57 ($\pm$42.27) g for females. Result from the *t*-test for sexual dimorphism on mean body mass was not significant ($t_{189.92}=-0.17279$; $p=0.863$).

DISCUSSION

Here we showed that there are different movement patterns among individuals of *T. dimidiatus*, sex being of great importance. We found evidence to support our hypothesis of difference in movements between sexes since males present larger distance metrics and movements (i.e. distances between two successive trapping sessions) than females. Also,
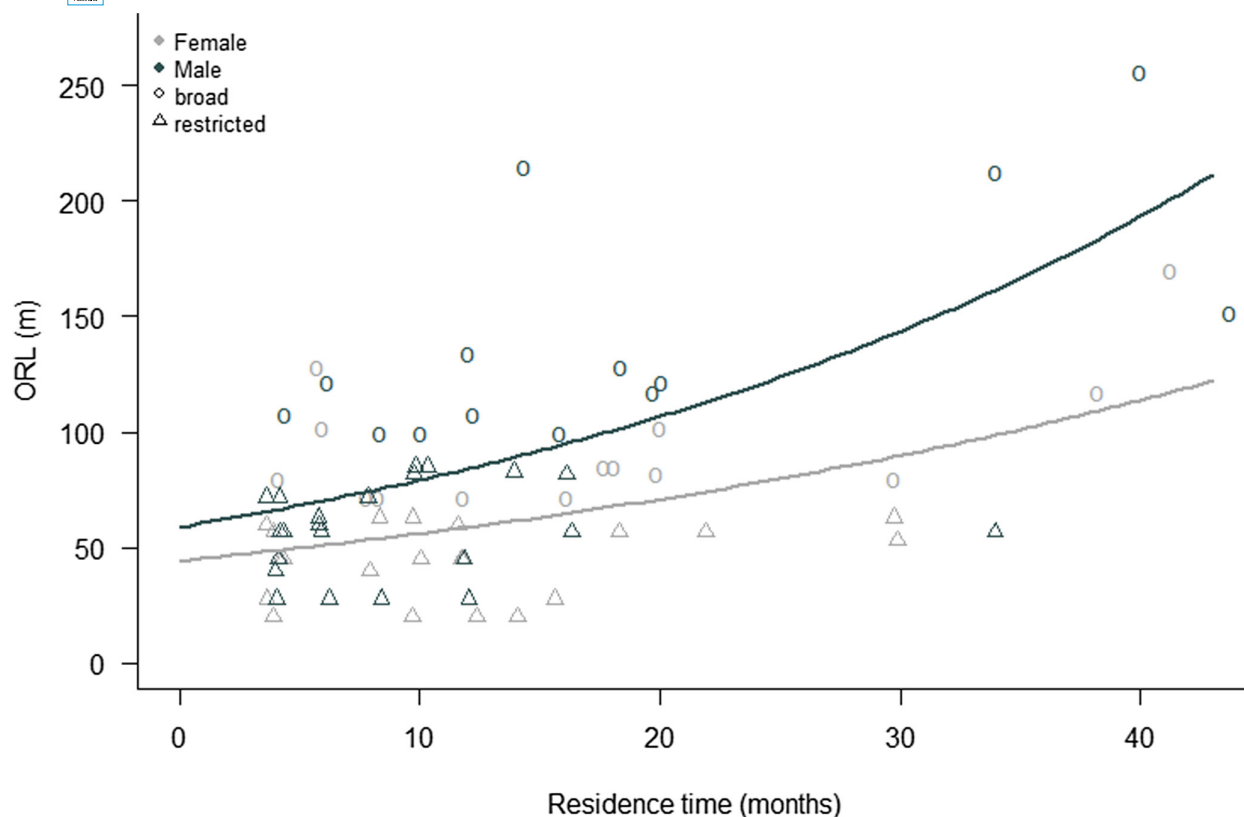
FIGURE 4 Relationship between maximum possible distance between all captures (ORL, calculated in meters) and the total number of months that males (dark grey) and females (light grey) of *Trinomys dimidiatus* were present in the study area in the Serra dos Órgãos National Park (Rio de Janeiro, Brazil). Lines represent the generalized linear regression for each sex. Shapes represent the pattern of movement of each individual.

as hypothesized, body mass has a positive relationship with movement length, being stronger for males, and rainfall has a negative relationship with movement length, but only for males. Population size and reproductive activity, however, had no effect on movement length. Therefore, we observe that individual traits (sex and body mass) and an environmental factor (rainfall) have important effects on the movements of the studied population.

We considered that the applied method allowed us to achieve a reliable estimate of all types of movement patterns during individuals' lifetime. Although the description of movement patterns is based on a simple statistical metric, the study is based on a long-time sampling period (8 years; 48 trapping sessions), individuals have a relatively large mean number of captures and the size of the sampling grid is greater than the home range of *T. dimidiatus*' congeneric species (i.e. *T. iheringi*; ~1 ha; Bergallo, 1995).

We observed a slightly smaller frequency of broad (0.40) than restricted movement pattern (0.60). For the congeneric, *Trinomys* [*Proechimys iheringi*] *eliasi* (Pessôa & Reis, 1993) there was a frequency of 0.91 of restricted movement pattern against 0.09 of broad movement pattern at a *restinga* site (Cerqueira, 2000; Gentile & Cerqueira, 1995). The greater frequency of broad movement pattern here compared to previous works may occur due to differences in methodology, by considering differences between sexes in the definition of a broad movement pattern threshold value. Also, rodents' movements in habitats with patchier food resources, such as sand dunes, are larger (Attuquayefio et al., 1986; Corp et al., 1997). Therefore, it is expected that the frequency of broad movements would be greater in the patchy habitat studied by Gentile and Cerqueira (1995)
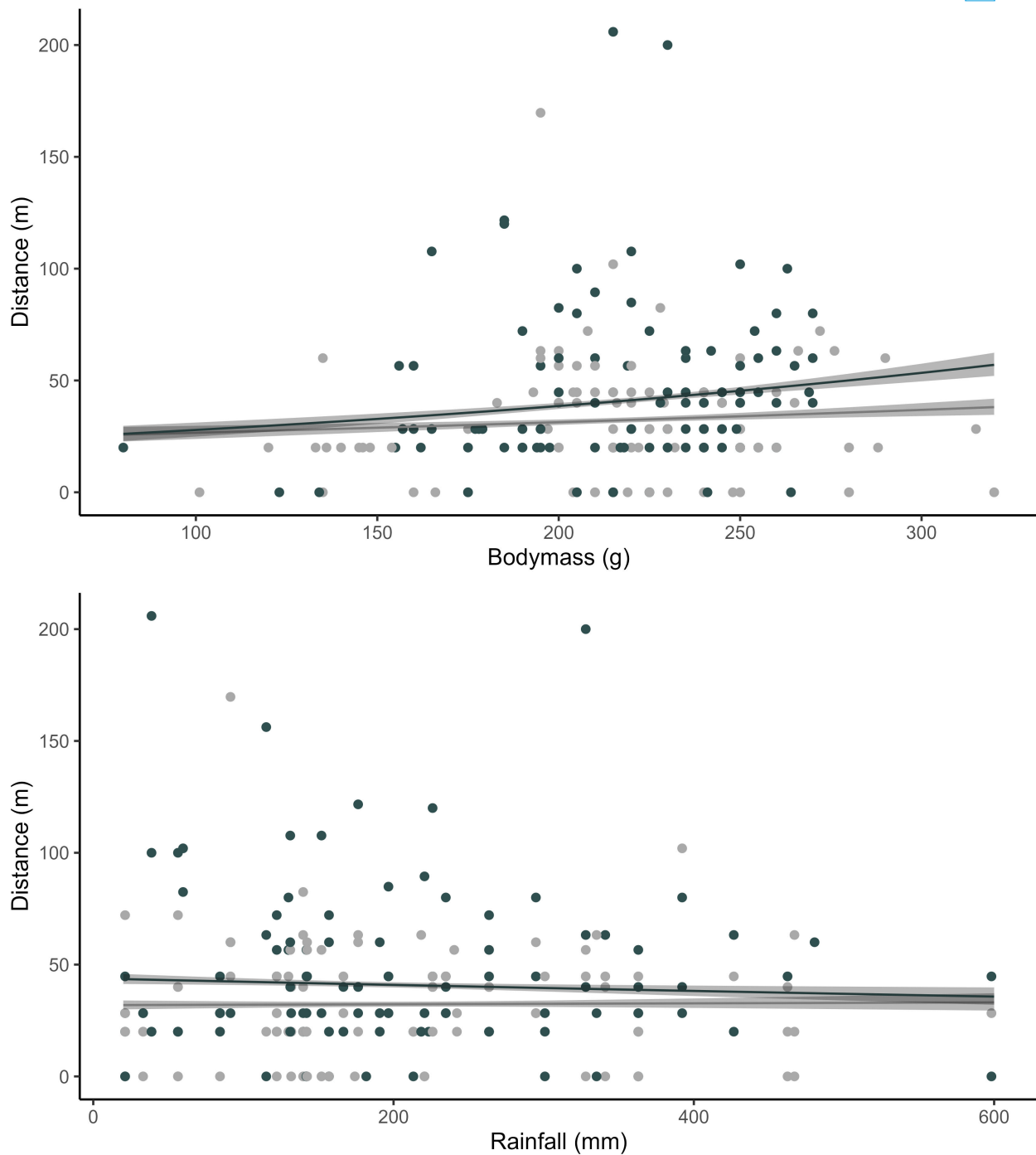
FIGURE 5   Distance moved between consecutive trapping sessions as a function of body mass (top) and rainfall (down) for *Trinomys dimidiatus* in the Serra dos Órgãos National Park (Rio de Janeiro, Brazil). Dark blue dots and lines indicate males and light blue indicates females. Lines are the representation of the best model for the variables presented. Grey shadowed areas represent the confidence interval (95%) for each curve.

compared to those observed in our study, but the restriction of the sampling area to a trapping grid may have prevented the observation of such large movements, as some of them may have occurred outside this area.

Confinement of the sampling area to a trapping grid may have led to an underestimation of the frequency of broad movement patterns in our study as well, mainly for males' changes in core area location. Although low, the greater frequency of changing the core area location on females is probably related to males of mammal species frequently dispersing to

more distant areas compared to females (Bowler & Benton, 2005), thus some males' movements of changing core area location may have occurred outside the grid. Indeed, the four individuals with extremely large ORL (>200 m) are males, while the other individuals, males or females, did not present ORL larger than 170 m. Those rare long-distance movements are a common observation in movement studies (e.g. Byrne et al., 2014; Saitoh, 1995; Schneider et al., 2003; Slip & Shine, 1988; Spirito et al., 2020; Wells et al., 2008) and are often considered as temporarily or definitive dispersive movements. Also, agonistic behaviours towards males are more frequent in *Trinomys setosus* and may indicate a male-biased dispersal in the genus *Trinomys* (Cantano et al., 2023). All individuals that changed core area location did it only once and most changes occurred during the initial captures and then the individuals kept being captured in the new core area. Therefore, some observed core area changes could be the result of the recruitment of adult individuals into the population still looking for a definitive core area.

Variation in ORL was better explained by an interaction of sex and residence time, although we found a positive relationship between ORL and the number of captures as well as other studies (e.g. Püttker et al., 2012). Number of captures can sometimes obscure residence time, as a consequence of multiple captures in the same sampling occasion or two captures with a large interval in between them. Thus, our result is not a merely geometric correlation between variables, as indicated in other studies for the relationship between the number of captures and ORL (Püttker et al., 2012), but actually that some individuals may expand the area they explore throughout life. In this sense, most broad movement patterns were performed by individuals with long residence times; however, we recorded broad movement pattern for some individuals with shorter residence times as well. Therefore, exploratory or dispersive movements (i.e. broad movement pattern) are not strictly dependent on a long residence time (i.e. the time an individual is record in the studied population from the first to the last capture) but other factors may also influence the occurrence of those behaviours, such as nest floods and presence of a predator (Bowler & Benton, 2005; Madsen & Shine, 1996).

Larger movements for males of Echimyid species are frequently observed when compared to females (Adler et al., 1997; Adler, 2011; Almeida et al., 2013; Endries & Adler, 2005). The observation of larger distances moved between trapping sessions as well as greater distance metrics (SDT and ORL) for males is possibly a result of the species likely polygynous mating system, although no specific study described *T. dimidiatus*' mating system (Adler, 2011). It is noteworthy however, that different approaches, such as genetic and spatial distribution, may indicate distinct mating systems in small mammals, like promiscuous ones (Ferrando et al., 2023; McEachern et al., 2009); thus, more studies are needed to better understand *T. dimidiatus*' mating system.

The most plausible model for movements (i.e. distances between two successive trapping sessions) indicates the importance of body mass, rainfall and sex. Following the expectation that body mass may indicate a greater energy availability, enabling individuals to move larger distances, we recorded larger movements between trapping sessions in heavier animals, especially for males (Bowler & Benton, 2005; Godsall et al., 2013). Another echimyid species, *Trichomys fosteri*, has presented a sex-dependent body mass effect on movements (Antunes et al., 2020). The authors associate the observed difference in movements to a sexual dimorphism in body mass, where males have greater body mass than females, which is not observed in our data. Here, the different effects of body mass for each sex could be explained by a polygynous mating system, which is frequently observed in

echimyids (Adler, 2011, but see McEachern et al., 2009), so males, especially large ones, move larger distances because of their energy reserve but also to find more partners. Another interpretation could be that part of the accumulated energy in heavier females is allocated to reproduction efforts, such as defending newborns from aggression or defending areas with greater resource availability, as observed for other rodents (Cantano et al., 2023; Godsall et al., 2013; Ostfeld, 1986; Wolff, 1993).

The results from rainfall effect on movements indicate that, as hypothesized, during periods with more rainfall, and thus expected greater food availability, individuals tended to move shorter distances, however, contrary to expected, this was only observed for males. Negative effects of rainfall on movement length may occur through changes in food availability, with shorter movement length when food items abundance is high (Ostfeld, 1986; Taitt & Krebs, 1981). Also, as individuals' migration to areas with greater food availability may occur and increase population size, shorter movements may be expected as individuals seek to avoid negative interactions (Bogdziewicz et al., 2016; Casula et al., 2019; Dugatkin, 2009; Efford et al., 2016). As population size was not among the best models the decrease in movement length observed among males with increased rainfall seems to be, as expected, a response to the ease of finding food items during these periods (Bergallo & Magnusson, 1999; Leiner & Silva, 2007a). Still, it is important to better understand the relationship between food availability and rainfall in the study area. For females on the other hand, the absence of a clear relationship between rainfall and movement length may be a result of a protective behaviour towards newborns, since infanticide has already been observed in rodents (Opperbeck et al., 2012; Wolff, 1993; Ylönen et al., 1997). In rodent species where infanticide is common, females tend to increase vigilant behaviour and reduce movements to near the nest when confronting strange reproductive males that may offer some risk to newborns (Breedveld et al., 2019). Therefore, given that tropical rodents may reproduce throughout the year (Bergallo & Magnusson, 1999), females of *T. dimidiatus* may keep movements close to the nest regardless of rainfall amount and food item availability to avoid males' aggressions towards newborns. Although aggressions to newborns have already been observed in *T. setosus* (Cantano et al., 2023), group formation, burrow sharing and social behaviours have been also recorded for both *T. setosus* and *T. yonenagae* (Cantano et al., 2023; Santos & Lacey, 2010). Thus, the occurrence of infanticide and its effects on *T. dimidiatus* females' movements must be further investigated.

We found that *T. dimidiatus* presents both restricted and broad movement patterns and uses the space differently between time scales, with some individuals presenting more than one core area throughout life. We also found that males tend to present larger movements than females, which could indicate a polygynous mating system in *T. dimidiatus*, but this hypothesis still needs to be tested in different environments and by different methods. The influence of body mass and rainfall also differ for each sex, indicating possible behavioural sex differences. Results found here increase the knowledge on the movement ecology of a poorly known species and are an inception to unravel the effects that individual traits and environmental factors may have on this species' movements.

AUTHOR CONTRIBUTIONS

Gabriel Cupolillo: Conceptualization (equal); data curation (lead); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (lead). **Júlia Lins Luz:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); methodology (equal); supervision (equal); writing – original draft (equal). **Camila dos Santos de

CONFLICT OF INTEREST STATEMENT
There is no conflict of interest concerning the manuscript's contents.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in github at https://github.com/GCupolillo/Trinomys-dimidiatus-movements.

ORCID
Gabriel Cupolillo https://orcid.org/0000-0003-0243-4665
Júlia Lins Luz https://orcid.org/0000-0003-4515-7442

REFERENCES
Adler, G.H. (2011) Spacing patterns and social mating systems of echimyid rodents. *Journal of Mammalogy*, 92, 31–38.

Adler, G.H., Endries, M. & Piotter, S. (1997) Spacing patterns within populations of a tropical forest rodent, *Proechimys semispinosus*, on five Panamanian islands. *Journal of Zoology*, 240, 43–53.

Almeida, A.J., Freitas, M.M.F. & Talamoni, S.A. (2013) Use of space by the neotropical caviomorph rodent *Thrichomys apereoides* (Rodentia: Echimyidae). *Zoologia*, 30, 35–42.

Antunes, P., Oliveira-Santos, L.G.R., Santos, T.M.R., Menezes, J.F.S., Tomas, W.M., Forester, J.D. et al. (2020) Mating system of *Thrichomys fosteri* in the Brazilian Pantanal: spatial patterns indicate promiscuity. *Mammalian Biology*, 100, 365–375.

Attias, N., Raíces, D.S., Pessôa, F.S., Albuquerque, H., Jordão-Nogueira, T., Modesto, T.C. et al. (2009) Potential distribution and new records of *Trinomys* species (Rodentia: Echimyidae) in the state of Rio de Janeiro. *Zoologia*, 26, 305–315.

Attuquayefio, D.K., Gormanand, M.L. & Wolton, R.J. (1986) Home range sizes in the wood mouse *Apodemus sylvaticus*: habitat, sex and seasonal difference. *Journal of Zoology*, 210, 45–53.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, 88, 310–326.

Barros, C.S., Crouzeilles, R. & Fernandez, F.A.S. (2007) Reproduction of the opossums *Micoureus paraguayanus* and *Philander frenata* in a fragmented Atlantic Forest landscape in Brazil: is seasonal reproduction a general rule for neotropical marsupials? *Mammalian Biology*, 73, 463–467.

Bergallo, H.G. (1994) Ecology of a small mammal community in an Atlantic Forest area in southeastern Brazil. *Studies on Neotropical Fauna and Environment*, 29, 197–217.

Bergallo, H.G. (1995) Comparative life-history characteristics of two species of rodents, *Proechimys iheringi* and *Oryzomys intermedius* in an Atlantic Forest of Brazil. *Mammalia*, 59, 51–64.

Bergallo, H.G. & Magnusson, W.E. (1999) Effects of climate and food availability on four rodent species in southeastern Brazil. *Journal of Mammalogy*, 80, 472–486.

Bergallo, H.G. & Magnusson, W.E. (2004) Factors affecting the use of space by two rodent species in Brazilian Atlantic Forest. *Mammalia*, 68, 121–132.

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P. & Saltz, D. (2011) Integrating animal behavior and conservation biology: a conceptual framework. *Behavioral Ecology*, 22, 236–239.

Bogdziewicz, M., Zwolak, R., Redosh, L., Rychlik, L. & Crone, E.E. (2016) Negative effects of density on space use of small mammals differ with the phase of the masting-induced population cycle. *Ecology and Evolution*, 6, 8423–8430.

Bovendorp, R.S., Heming, N.M. & Percequillo, A.R. (2020) Bottom-up effect: a rodent outbreak following the bamboo blooming in a neotropical rainforest. *Mammal Research*, 65, 535–543.

Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80, 205–225.

Breedveld, M.C., Folkertsma, R. & Eccard, J.A. (2019) Rodent mothers increase vigilance behaviour when facing infanticide. *Scientific Reports*, 9, 12054.

Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimode inference: a pratical. In: *Information-theoretic approach*, 2nd edition. Fort Collins, CO: Springer.

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24, 346–352.

Byrne, A.W., Quinn, J.L., O'Keeffe, J.J., Green, S., Paddy Sleeman, D., Wayne Martin, S. et al. (2014) Large-scale movements in European badgers: has the tail of the movement kernel been underestimated? *Journal of Animal Ecology*, 83, 991–1001.

Cademartori, C.V., Fabián, M.E. & Manegheti, J.O. (2005) Biologia reprodutiva de Delomys dorsalis (Hensel, 1872) – Rodentia, Sigmodontinae – em área de floresta ombrófila mista, Rio Grande do Sul, Brasil. *Mastozoología Neotropical*, 12, 133–144.

Cantano, L.M.R., Luchesi, L.C., Takata, J.T. & Monticelli, P.F. (2023) Behavioral repertoire of the Brazilian spiny-rats, *Trinomys setosus* and *Clyomys laticeps*: different levels of sociality. *Brazilian Journal of Biology*, 83, e241164.

Casula, P., Luiselli, L. & Amori, G. (2019) Which population density affects home ranges ofco-occurring rodents? *Basic and Applied Ecology*, 34, 46–54.

Cerqueira, R. (2000) Biogeografia das restingas: um ensaio. In: Esteves, F.A. & Lacerda, L.D. (Eds.) *Ecologia de restingas e lagoas costeiras*. Rio de Janeiro: NUPEM/UFRJ, pp. 65–75.

Cerqueira, R. (2004) Fatores ambientais e a reprodução de marsupiais e roedores no leste do Brasil. *Arquivos do Museu Nacional*, 63, 29–39.

Cerqueira, R., Gentile, R., Fernandez, F.A.S. & D'Andrea, P.S. (1993) A five year population study in an assemblage of small mammals in southeastern Brazil. *Mammalia*, 57, 507–517.

Cerqueira, R. & Lara, M. (1991) Rainfall and reproduction of cricetid rodents in northeastern Brazil. In: Bobcek, B., Perzanovski, K.K. & Regelin, W.L. (Eds.) *Global trends in wildlife management*, vol. I. Krakow: Swiat Press, pp. 545–549.

Corp, N., Gorman, M.L. & Speakman, J.R. (1997) Ranging behaviour and time budgets of male wood mice *Apodemus sylvaticus* in different habitats and seasons. *Oecologia*, 109, 242–250.

Cupolillo, G. (2023) *Implicações da história de vida na dinâmica populacional de pequenos mamíferos não-voadores*. Master thesis. Universidade Federal do Rio de Janeiro, 101 p.

Dugatkin, L.A. (2009) *Principles of animal behaviour*, 2ª edition. W.W. Norton & Company: New York, p. 642.

Efford, M.G., Dawson, D.K., Jhala, Y.V. & Qureshi, Q. (2016) Density-dependent home-range size revealed by spatially explicit capture–recapture. *Ecography*, 39, 676–688.

Endries, M.J., & Adler, G.H. (2005) Spacing patterns of a tropical forest rodent, the spiny rat (Proechimys semispinosus), in Panama. *Journal of Zoology*, 265, 147–155.

Ferrando, C.P.R., Oshima, J.E.F., Lacey, E.A. & Leiner, N.O. (2023) Spatial and social organization of the burrowing rodent *Clyomys laticeps* (Thomas, 1909). *Journal of Mammalogy*, 104, 591–602.

Ferreira, M.S., Delpupo, G.G.V., Vieira, M.V. & Cerqueira, R. (2017) Climate-driven variation in space use by the neotropical marsupial *Metachirus nudicaudatus*. *Oecologia Australis*, 21, 450–454.

Ferreira, M.S., Kajin, M., Cerqueira, R. & Vieira, M.M. (2016) Marsupial population dynamics in a tropical rainforest: intraspecific competition and nonlinear effect of rainfall. *Journal of Mammalogy*, 97, 121–127.

Finotti, R. & Cerqueira, R. (2018) Preferência alimentar pesquisada em laboratório e sua aplicação ao estudo da ecologia de pequenos mamíferos: vantagens e críticas após trinta anos de aplicação do método. *Boletim da Sociedade Brasileira de Mastozoologia*, 81, 14–25.

Fleming, T.H. (1971) *Population ecology of three species of Neotropical rodents*. Miscellaneous publications. Museum of Zoology, University of Michigan, N°. 143, 77 p.

Galindo-Leal, C. & Krebs, C.J. (1998) Effects of food abundance on individuals and populations of the rock mouse (*Peromyscus difficilis*). *Journal of Mammalogy*, 79, 1131–1142.

Gentile, R. & Cerqueira, R. (1995) Movement patterns of species of small mammals in a Brazilian restinga. *Journal of Tropical Ecology*, 11, 671–677.

Gittleman, J.L. & Thompson, S.D. (1988) Energy allocation in mammalian reproduction. *American Zoologist*, 28, 863–875.

Godsall, B., Coulson, T. & Malo, A.F. (2013) From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent. *Journal of Animal Ecology*, 83, 126–135.

Instituto Brasileiro de Geografia e Estatística - IBGE (1992) Manual Técnico da Vegetação Brasileira. Série Manuais Técnicos Número 1. Departamento de Recursos Naturais e Estudos Ambientais, Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, Brasil. p. 92.

Jonsson, P., Hartikainen, T., Koskela, E. & Mappes, T. (2002) Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. *Evolutionary Ecology*, 16, 455–467.

Krebs, C.J. (1966) Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs*, 36, 239–273.

Le Galliard, J.-F., Rémy, A., Ims, R.A. & Lambin, X. (2011) Patterns and processes of dispersal behavior in arvicoline rodents. *Molecular Ecology*, 21, 505–523.

Leiner, N.O. & Silva, W.R. (2007a) Seasonal variation in the diet of the Brazilian slender opossum (*Marmosops paulensis*) in a montane Atlantic Forest area, southeastern Brazil. *Journal of Mammalogy*, 88, 158–164.

Leiner, N.O. & Silva, W.R. (2007b) Effects of resource availability on the use of space by the mouse opossum *Marmosops paulensis* (Didelphidae) in a montane Atlantic Forest area in southeastern Brazil. *Acta Theriologica*, 52, 197–204.

Lorenzi, H. (1998) *Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil*, 2nd edition. Nova Odessa: Editora Plantarum, p. 384.

Loretto, D. & Vieira, M.V. (2005) The effects of reproductive and climatic seasons on movements in the black-eared opossum (*Didelphis aurita* Wied-Neuwied, 1826). *Journal of Mammalogy*, 86, 287–293.

Loretto, D. & Vieira, M.V. (2023) A literature review and field test on the role of bait type on capture success of arboreal small mammals. *Oecologia Australis*, 27, 208–223.

Madsen, T. & Shine, R. (1996) Seasonal migration of predators and prey – a study of pythons and rats in tropical Australia. *Ecology*, 77, 149–156.

Matos, D.M.S., Terra, G., Pardo, C.S.R., Neri, A.C.A., Figueiredo, F.O.G., Paula, C.H.R. et al. (2007) Análise florística do componente arbóreo de florestas na região da Serra dos Órgãos, Teresópolis, RJ. In: Cronemberger, C. & Viveiros de Castro, E.B. (Eds.) *Ciência e Conservação na Serra dos Órgãos*. Brasília: IBAMA, pp. 69–81.

McCravy, K.W. & Rose, R.K. (1992) An analysis of external features as predictors of reproductive status in small mammals. *Journal of Mammalogy*, 73, 151–158.

McCue, M.D. (2010) Starvation physiology: reviewing the different strategies animals use to survive a common challenge. *Comparative Biochemistry and Physiology, Part A*, 156, 1–18.

McEachern, M.B., McElreath, R.L., Van Vuren, D.H. & Eadie, J.M. (2009) Another genetically promiscuous 'polygynous' mammal: mating system variation in *Neotoma fuscipes*. *Animal Behaviour*, 77, 449–455.

Mello, J.H.F., Moulton, T.P., Raíces, D.S.L. & Bergallo, H.G. (2015) Sobre ratos e jaqueiras: modelando a capacidade suporte de uma população do rato-de-espinho da Mata Atlântica *Trinomys dimidiatus* (Günther, 1877) – Rodentia, Echimyidae – em relação a diferentes abundâncias de jaqueiras (*Artocarpus heterophyllus* L.). *Brazilian Journal of Biology*, 75, 208–215.

Moura, M.C., Vieira, M.V. & Cerqueira, R. (2009) Occasional intraguild predation structuring small mammal assemblages: the marsupial *Didelphis aurita* in the Atlantic Forest of Brazil. *Austral Ecology*, 34, 481–489.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. et al. (2008) A movement ecology paradigm for unifying organismal movement reasearch. *PNAS*, 105, 19052–19059.

Opperbeck, A., Ylönen, H. & Klemme, I. (2012) Infanticide and population growth in the bank vole (*Myodes glareolus*): the effect of male turnover and density. *Ethology*, 118, 178–186.

Ostfeld, R.S. (1986) Territoriality and mating system of California voles. *Journal of Animal Ecology*, 55, 691–706.

Pessôa, L.M., Corrêa, M.M.O., Bitencourt, E. & Reis, S.F. (2005) Chromosomal characterization of taxa of the genus *Trinomys* Thomas, 1921 (Rodentia, Echimyidae) in the states of Rio de Janeiro and São Paulo. *Arquivos do Museu Nacional*, 63, 161–168.

Pessôa, L.M. & Reis, S.F. (1993) A new subspecies of *Proechimys iheringi* Thomas (Rodentia: Echimyidae) from the state of Rio de Janeiro, Brazil. *Mammalian Biology*, 58, 181–190.

Powell, R.A. & Mitchell, M.S. (2012) What is a home range. *Journal of Mammalogy*, 93, 948–958.

Püttker, T., Barros, C.S., Martins, T.K., Sommer, S. & Pardini, R. (2012) Suitability of distance metrics as indexes of home-range size in tropical rodent species. *Journal of Mammalogy*, 93, 115–123.

Püttker, T., Meyer-Lucht, Y., & Sommer, S. (2006) Movement distances of five rodent and two marsupial species in forest fragments of the coastal Atlantic rainforest, Brazil. *Ecotropica*, 12, 131–139.

R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Saitoh, T. (1995) Sexual differences in natal dispersal and philopatry of the grey-sided vole. *Researches on Population Ecology*, 37, 49–57.

Santos, J.W.A. & Lacey, E.A. (2010) Burrow sharing in the desert-adapted torch-tail spiny rat, *Trinomys yonenagae*. *Journal of Mammalogy*, 92, 3–11.

Schneider, C., Dover, J. & Fry, G.L.A. (2003) Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. *Ecological Entomology*, 28, 219–227.

Sikes, R.S. & the Animal Care and Use Committee of the American Society of Mammalogists. (2016) 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97, 663–688.

Slip, D.J. & Shine, R. (1988) Habitat use, movements and activity patterns of free-ranging Dyamond Pithons, *Morelia spilota spilota* (Sepentes: Boidae): a radiotelemetric study. *Australian Wildlife Research*, 15, 515–531.

Spirito, F., Rowland, M., Wisdom, M. & Tabeni, S. (2020) Tracking native small mammals to measure fine-scale space use in grazed and restored dry woodlands. *Global Ecology and Conservation*, 24, e01348.

Stickel, L.F. (1954) A comparison of certain methods of measuring ranges of small mammals. *Journal of Mammalogy*, 35, 1–15.

Sutherland, W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour*, 56, 801–809.

Taitt, M.J. & Krebs, C.J. (1981) The effect of extra food on small rodent populations: II. Voles (*Microtus townsendii*). *Journal of Animal Ecology*, 50, 125–137.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, S., Bracis, C., Brown, D., Bruyn, P. J. N., Cagnacci, F., …, Mueller, T. (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359, 466–469.

Tucker, M. A., Schipper, A. M., Adams, T. S. F., Attias, N., Avgar, T., Babic, N. L., Barker, K. J., Bastille-Rousseau, G., Behr, D. M., Belant, J. L., Beyer Jr., D. E., Blaum, N., Blount, J. D., Bockmühl, D., Boulhosa, R. L. P., Brown, M. B., Buuveibaatar, B., Cagnacci, F., Calabrese, J. M., Cerne, R., Chamaillé-Jammes, S., Chan, A. N., …, Mueller, T. (2023) Behavioral responses of terrestrial mammals to COVID-19 lockdowns. *Science* 380, 1059–1064.

Wells, K., Lakim, M.B. & Pfeiffer, M. (2008) Movement patterns of rats and treeshrews in bornean rainforest inferred from mark-recapture data. *Ecotropica*, 14, 113–120.

Williams, B.K., Nichols, J.D. & Conroy, N.J. (2002) *Analyses and management of animal populations: modeling, estimation and decision making*. London: Academic Press.

Wolff, J.O. (1993) Why are female small mammals territorial? *Oikos*, 68, 364–370.

Wolff, J.O. & Cicirello, D.M. (1990) Mobility versus territoriality: alternative reproductive strategies in white-footed mice. *Animal Behaviour*, 39, 1222–1224.

Ylönen, H., Koskela, E. & Mappes, T. (1997) Infanticide in the bank vole (*Clethrionomys glareolus*): occurrence and the effect of familiarity on female infanticide. *Annales Zoologici Fennici*, 35, 259–266.