



Plasticity in the timing of activity in the Red-rumped Agouti, *Dasyprocta leporina* (Mammalia: Rodentia), in the Atlantic Forest of southeastern Brazil

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Abstract: Timing of activity is a consequence of adaptations to daily and seasonal changes in the environment and examining these patterns is important to better understand the temporal niches of the species. Here we examine temporal activity in the Red-rumped Agouti (*Dasyprocta leporina*) in two fragments of Atlantic Forest and those factors that influence the circadian rhythm in the study areas. Camera traps were used to gather data in two protected areas (one montane and other coastal) in the state of Espírito Santo, southeastern Brazil. A total of 49 photos were taken in the mountains and 152 in the coastal area. Activity patterns were diurnal and bimodal, and animals were active for 14–15 hours each day. Activity peaked in the morning soon after sunrise and then before and during dusk. Activity patterns were different in the two study areas ($W = 6.77$, $p = 0.034$). There was a longer peak in the morning in the coastal area, and a higher peak in the evening in the mountains, where activity starts later and becomes less intense earlier. The difference between activity patterns in the two locations suggests plasticity in agouti behavior. Because the two study areas are at about the same latitude, we suggest that the behavioral plasticity is due to different temperature regimes associated with a local effect of altitude and topography of the terrain on the incidence of solar rays inside the forest. The influence of other factors is also discussed. In addition to a better understanding of the temporal niche of the Red-rumped Agouti, the behavior patterns we describe here can be useful to optimize strategies for *D. leporina* conservation in southeastern Brazil once the species is more susceptible to poaching at times when animals are most active.

Keywords: *Dasyproctidae*, abiotic factors, activity patterns, circadian rhythm, photoperiod.

Plasticidade comportamental no horário de atividade de cutia, *Dasyprocta leporina* (Mammalia: Rodentia), na Mata Atlântica do sudeste do Brasil

Resumo: O horário de atividade reflete adaptações e respostas das espécies às variações diárias e sazonais do ambiente, sendo o entendimento destes padrões importante para uma melhor compreensão do nicho temporal das espécies. Este trabalho objetivou caracterizar o horário de atividade da cutia (*Dasyprocta leporina*) em dois remanescentes de Mata Atlântica e estabelecer os fatores que podem interferir no ritmo circadiano da espécie considerando peculiaridades das áreas amostradas. Foram analisados dados obtidos a partir de armadilhas fotográficas em duas áreas protegidas, sendo uma na região serrana e outra próximo à costa, ambas no estado do Espírito Santo, sudeste do Brasil. Foram obtidos 49 registros na região serrana e 152 registros na área costeira. A espécie apresentou padrão de atividade diurno e bimodal, mantendo-se ativa por 14-15 horas. Foi detectado um pico de atividade matutino, logo após o nascer do sol, e outro vespertino. O padrão de distribuição diária dos registros foi diferente entre as áreas amostradas ($W = 6,766$; $p = 0,034$), ressaltando que o pico de atividade matutino apresentou maior duração na área costeira, enquanto o pico vespertino foi proporcionalmente mais representativo na região serrana, onde as atividades se iniciam mais tarde e se tornam menos intensas mais cedo. Estas diferenças evidenciam a ocorrência de plasticidade comportamental em *D. leporina* no que se refere ao padrão de atividade local. Entretanto, a diferença entre as áreas estudadas não pode ser atribuída à latitude, uma vez que a distância entre as localidades é de menos de um grau. Sugere-se que a variação do horário de atividade de cutias nas áreas amostradas seja devido a diferenças na temperatura ambiente, associadas a variações locais decorrentes do efeito da altitude e da topografia do terreno na incidência de raios solares no interior da floresta. A influência de outros fatores também é discutida. Além do melhor entendimento do nicho temporal de cutias, os padrões comportamentais descritos no presente estudo podem ser úteis para otimizar estratégias de conservação de *D. leporina* no sudeste do Brasil considerando que a espécie é mais suscetível à caça quando os animais estão mais ativos.

Palavras-chave: *Dasyproctidae*, fatores abióticos, fotoperíodo, padrão de atividade, ritmo circadiano.

Introduction

Circadian rhythms are intervals of approximately 24 hours during which the vital biological processes that maintain organisms occur (Goldman 1999) and are part of the suite of adaptations of species to their environments. These rhythms are physiological and behavioral adjustments in response to changes in environmental conditions that are consequence of the day-night cycle (Beltran & Delibes 1994, Goldman 1999). Thus, patterns of sleep-vigilance, variable body temperature, hormone and enzyme secretions and regulation of cell cycles (among others) are consequences of circadian rhythms (Kronfeld-Schor & Dayan 2003, Pita et al. 2011). These patterns are due to as biological clocks that provide the organisms with the mechanisms to anticipate and prepare for daily changes that occur regularly in the environment (Goldman 1999).

Timing of activity is one of the expressions of the circadian rhythm and is part of a species' natural history and their manifestations have ecological and evolutionary significance (Kronfeld-Schor & Dayan 2003). This is due to the fact that patterns of activity are molded by selective forces (e.g., ecological interactions) and evolutionary constraints (e.g., functional and morphological constraints, genetic variability), that are the basis of time partitioning among species and that, in turn, may allow or not species coexistence (Kronfeld-Schor & Dayan 2003).

While daily activity patterns tend to be ubiquitous in terrestrial mammals, some plasticity is often found in response to environmental variations. Activity patterns may be influenced by abiotic factors, such as light (photoperiod), moon cycle, temperature, precipitation and latitude, and by biotic factors, such as food availability, interactions with competitors and risk of predation (e.g. Bronson 1988, Beltran & Delibes 1994, Goldman 1999, Kenagy et al. 2002, Kronfeld-Schor & Dayan 2003, Wagner et al. 2008, Pita et al. 2011, Suselbeek et al. 2014, Sassi et al. 2015). Thus, examining how organisms respond to daily and seasonal variation in the environment and plasticity in behaviors allows us to better understand patterns of community structure, species coexistence, resource partitioning and predator avoidance (Kronfeld-Schor & Dayan 2003).

Agoutis (genus *Dasyprocta* Illiger, 1811) are medium-sized terrestrial rodents whose diet mainly comprises fruits, seeds and roots (Oliveira & Bonvicino 2006). They often collect and bury fruits and seeds in holes they excavate, and thus store for later consumption. Because they do not always recover stored seeds and fruits, they are also important in seed dispersal (Galetti et al. 2006, Oliveira & Bonvicino 2006). Agoutis are threatened in some localities due to illegal hunting (Cullen Jr. et al. 2000), and their population decline results in reduced seed dispersal and negative consequences for plant species whose seeds are dispersed by agoutis (Galetti et al., 2006).

Here, we examine daily activity patterns of the Red-rumped Agouti, *Dasyprocta leporina* (Linnaeus, 1758), in two Atlantic Forest fragments in southeastern Brazil. Also, by comparing patterns in the two fragments, we infer factors that may generate plasticity in the timing of agouti activity patterns.

Material and Methods

1. Study area

The study took place in two protected areas in the state of Espírito Santo. One in the mountainous central-southern region of the state, the Santa Lúcia Biological Station (Estação Biológica de Santa Lúcia - EBSL, 19°57'-19°59' S and 40°31'-40°32' W), in the municipality of Santa Teresa. The other, in the northeastern coastal region of the state, the Vale Natural Reserve (Reserva Natural Vale - RNV, 19°06'-19°18' S and 39°45'-40°19' W), in the municipality of Linhares (Figure 1).

The EBSL comprises ca 440 ha and with adjacent private lands they form a forest fragment of 900 ha (Srbek-Araujo & Chiarello 2005). This fragment includes primary forest that is predominantly Ombrophilous Dense Forest (Thomaz & Monteiro 1997). It is a mountainous region and elevation varies from 550 to 950 m (Srbek-Araujo & Chiarello 2005). Annual temperature averages 19.9°C (Thomaz & Monteiro 1997), varying between an average minimum of 16.5°C and average maximum of 22.8°C (Álvares et al. 2013). Annual rainfall is 1,868 mm (Thomaz & Monteiro 1997). Climate, following Köppen's classification, is humid subtropical with temperate summer (Cfb, Álvares et al. 2013). A network of trails allows access to different areas in the reserve.

The RNV comprises 22,711 ha and is connected to the Sooretama Biological Reserve (Reserva Biológica de Sooretama; 27,859 ha) and two other smaller, private, protected areas (Reserva Particular do Patrimônio Natural – RPPN Recanto das Antas and RPPN Mutum-preto; Srbek-Araujo & Chiarello 2017). Together they form a remnant of natural habitat of ca 50,000 ha (Linhares-Sooretama Block) and comprise more than 10% of the remaining Atlantic Forest in the state (based on data available in FSOSMA & INPE 2017). Most of the RNV is dense lowland forest (Tabuleiro forest), classified as Perennial Seasonal Forest (Jesus & Rolim 2005). Here the topography is relative flat, varying from 28 to 65 m above sea level (Jesus & Rolim 2005). Average annual temperature is 24.3°C, with average minimum of 18.7°C and average maximum of 29.9°C (Kierulff et al. 2015). Annual rainfall is 1,214 mm and varies widely year to year (Kierulff et al. 2015). Climate here, following Köppen's classification, is tropical with a dry winter (Aw; Alvares et al. 2013). The RNV has a network of unpaved roads that permit access to various parts of the reserve.

2. Data collection

To record the activity of *D. leporina*, all data were gathered using camera traps (hereafter, simply 'camera'). Because animals have to be active to trigger photographs, we assumed that the capture is indicative of the activity of the species being photographed, then capture rate is proportional to the level of activity in each place (Srbek-Araujo & Chiarello 2013) as well as at each time of day (Rowcliffe et al. 2014). While the model of camera may differ in sampling efficiency (Srbek-Araujo & Chiarello 2007), we also assumed that difference will not affect the timing of the photographs obtained for the same species.

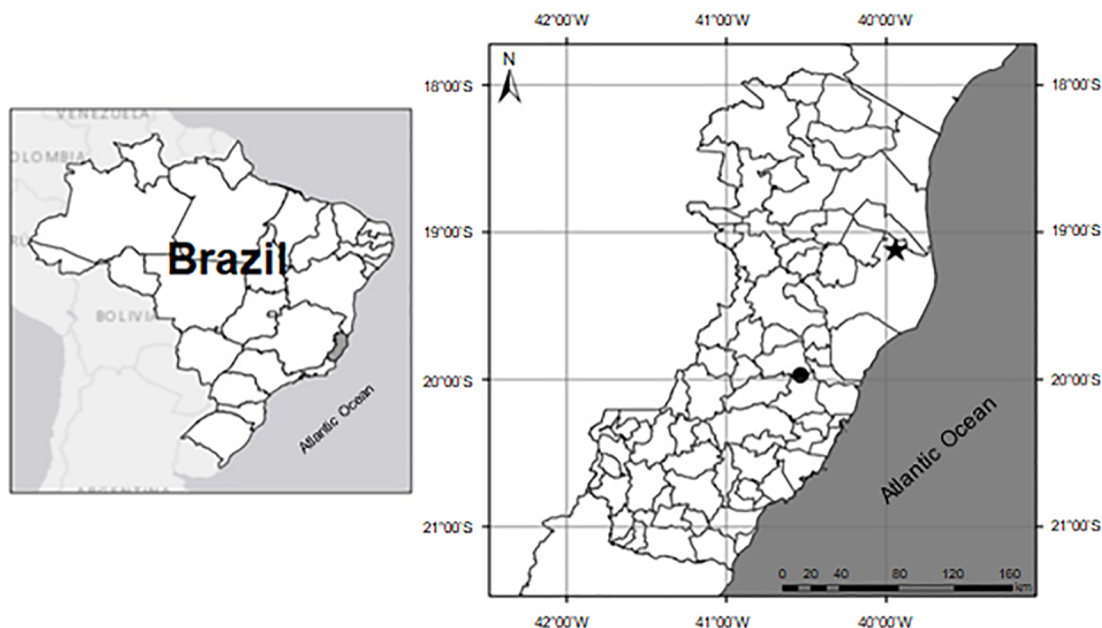


Figure 1. Map illustrating the locations of the study areas in southeastern Brazil, with a circle indicating Santa Lúcia Biological Station and a star indicating Vale Natural Reserve, in the state of Espírito Santo.

In the EBSL, cameras were in the field from February 2002 to January 2004 (~24 months). From February to November 2002 we used three Wildlife Pro Cameras (Forestry Suppliers Inc., USA), after which we used an additional three Deer Cam – Scouting Cameras (Non Typical Inc., USA) for a total of six cameras during that time interval. Cameras were setup on trails and over a total of 20 independent and widespread points within the EBSL. Cameras were moved monthly between sampling points.

In the RNV, cameras were installed from August 2007 to October 2008 (~14 months). At this time, we used 10 Tigrinus cameras (conventional model; Tigrinus Research Equipment, Brazil). Cameras were setup along trails 500 m from the nearest internal road. Cameras were placed in 10 independent and distant sampling points in different parts of the RNV and all 10 were sampled throughout the study period.

All cameras were set to function 24 hours/day, with an interval of 20 s between triggered events, and were loaded with 200 ISO 35 mm color negative films with 36 exposures. The cameras were set to stamp the date and the time of the record on each photo. Solar time was always used for the time of day. We checked cameras once each month for general maintenance and collecting records. We did not use bait and placed cameras about 45 cm above the ground attached to tree trunks. For details of camera protocol see Srбек-Araujo & Chiarello (2005, 2013).

3. Data analysis

To avoid double counting of photographs related to the same capture event and insure independence of records, at each sampling point we counted only the first capture of *D. leporina* when more than one record was obtained within 1 hour interval (= independent record). Thus, a new, independent observation was separated from the previous observation by at least one hour (following Srбек-Araujo & Chiarello 2013).

We summed independent records in hourly intervals to characterize the activity pattern at each reserve. We then calculated the percent of records obtained at each one-hour interval to highlight differences related to the pattern of records distribution, rather than differences resulting from the distinct number of records obtained per locality. We defined an activity peak as when the percentage of captures in any given hour was greater than half that of the hour with the greatest percent of captures.

To compare activity patterns between the two study areas, we used Mardia-Watson-Wheeler test (circular statistics). This test uses the exact time of each capture as an independent input for the analyzes. We used the program Oriana (version 4.0; Kovach Computing Services 2009), and alpha for tests was set at 0.05 (Zar 2010).

Results

In a total of 201 independent agouti captures, 49 were from EBSL and 152 from RNV. Animals were active during about 15 hours throughout the day and are clearly diurnal (Figure 2). The first capture was at 04:52 h and the last at 18:50 h (Table 1). Activity was bimodal, with the first activity peak in the morning, between 05:00 h and 08:00 h, and the second peak in the afternoon to dusk, from 14:00 h to 17:00 h (Table 1, Figure 2).

Agoutis had a total of about 14 hours of activity in the EBSL, most of which occurred during two peaks. The morning peak was at 06:00 h and the afternoon peak at 14:00 h–15:00 h (Table 1, Figure 2). No agoutis were captured here between 08:56 and 10:32 h (Figure 2). Agouti activity lasted 15 hours, also with two peaks, at RNV. The morning peak was between 05:00 h–08:00 h and the evening peak between 16:00 h–17:00 h (Table 1, Figure 2). In both areas, activity declined greatly

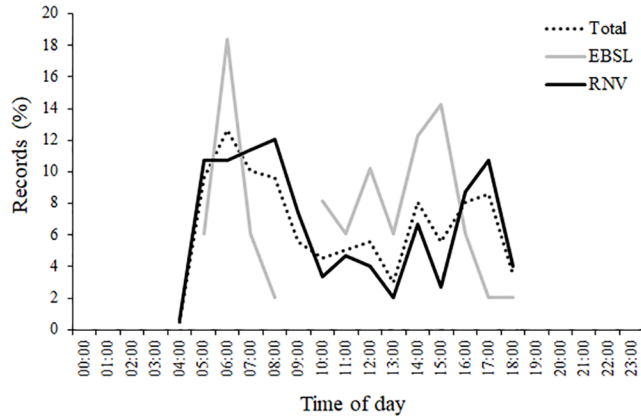


Figure 2. Hourly records of the Red-rumped Agouti (*Dasyprocta leporina*) indicating the percent of the total activity and that at the Santa Lúcia Biological Station (EBSL) and the Vale Natural Reserve (RNV) in southeastern Brazil.

Table 1. Timing of activity of the Red-rumped Agouti (*Dasyprocta leporina*) overall (Total) and by study area (Santa Lúcia Biological Station – EBSL, Vale Natural Reserve – RNV) in southeastern Brazil.

Event	Total	EBSL	RNV
First record	04:52	05:01	04:52
Last record	18:50	18:50	18:49
First peak activity - morning	05:00-08:00	06:00	05:00-08:00
Second peak activity - afternoon	14:00-17:00	14:00-15:00	16:00-17:00

after the morning peak and the afternoon peak was preceded by two small groupings of records (Figure 2). Agoutis were only captured three times at night (19:48 h, 20:06 h, 23:53 h) all in the RNV.

Agouti activity patterns differed between the two study areas ($W = 6.77$, $p = 0.034$). The morning peak was longer in the RNV, while the afternoon peak was higher in the EBSL, where activity starts later and becomes less intense earlier (Figures 2 and 3).

Discussion

The Red-rumped Agouti has a very clear diurnal and bimodal pattern of activity in both study areas. The two intervals with the most activity, after sunrise (morning) and then before and during dusk, are similar to the daily activity patterns of agoutis in different parts of the Americas (Oliveira & Bonvicino 2006, Lambert et al. 2009, Norris et al. 2010, Suselbeek et al. 2014, Cid et al. 2015, Ferregueti et al. 2018). This pattern differs from that observed in Ecuador (Blake et al. 2012) and Panama (Duquette et al. 2017), where the activity pattern was unimodal. While the general bimodal pattern of activity seems to be more common for the genus *Dasyprocta*, some plasticity in the timing of activity is evident, such as the differences between EBSL and RNV.

Latitude is one of the main abiotic factors that can influence the daily and seasonal activity in mammals because the incidence of light changes with latitude, changing light intensity and daylength (Bronson 1988), and altering the physiological response of the species due to variations in the duration of day and night (Goldman 1999, Wagner et al. 2008). In this study, the two study areas are less than one degree apart in latitude, and therefore latitude is unimportant as a factor to explain the difference of agouti activity patterns between EBSL and RNV.

We suggest that variation in patterns of agouti activity between the study areas may be a consequence of the variation in luminosity due to the differences in altitude (mountainous versus coastal) associated with topography (shady slopes versus flat plains) between the study areas. These factors result in differences in the incidence of light (solar rays) inside the forest. In this sense, we emphasize the EBSL is at a minimum of 500 m higher and has more complex topography than the RNV. The relief on the EBSL area is composed of slopes with accentuated soil declivity and small intermontane floodplains overlapping rivers and streams, being the reserve subdivided by a deep valley in the direction northwest to southwest in which runs the Timbuí river (Mendes & Padovan 2000).

Additionally, temperature also affects different aspects of the biology of the organisms, controlling physiological adjustments to those conditions, such as variation in metabolic rate, thermoregulation, and coat properties (e.g. Walsberg 1988, Kenagy et al. 2002, Sassi et al.

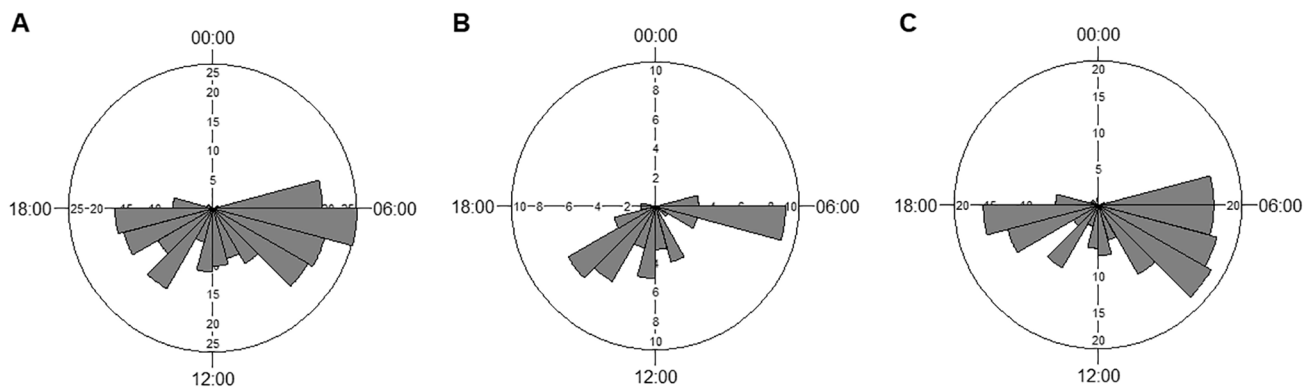


Figure 3. Rose diagrams showing activity patterns of the Red-rumped Agouti (*Dasyprocta leporina*) with the total (A), for the Santa Lúcia Biological Station (B) and for the Vale Natural Reserve (C) in southeastern Brazil.

2015), highlighting that behavior can also be influenced by variation in solar radiation (Hinze & Pillay 2006). Even though mammals thermoregulate, it is clear that climate regimes (mainly low or high external temperatures) have consequences for energetics and therefore can moderate the level of activity of both diurnal and nocturnal species (Beltran & Delibes 1994, Kenagy et al. 2002). The influence of temperature on agouti daily activity have already been proposed for Central American Agouti (*Dasyprocta punctata* Gray, 1842) in Panama (Lambert et al. 2009) and Azara's Agouti (*Dasyprocta azarae* Lichtenstein, 1823) in Brazilian Pantanal (Cid et al. 2015). In these areas, the agoutis may use behavioral strategies to reduce the exposure to heat during the hottest times of the day (Lambert et al. 2009), and the activity pattern change across the temperature gradient during the day (Cid et al. 2015). Nevertheless, the agoutis keep the daily activity range constant, with similar amount of time performing their activities regardless the temperature during the morning and in the afternoon (Cid et al. 2015). Thus, we suggest agouti activity patterns in study areas may also be influenced by differences in the ambient temperature, especially lower temperatures at the beginning and at the end of the day in EBSL, perhaps explaining why activity is different in the mountainous region with a milder climate compared to the hotter coastal region (more than 4°C greater on average at RNV, noting that the daily thermal amplitude may be even higher in mountainous regions). Behavioral plasticity in response to environmental heterogeneity was also recorded to the small rodent *Phyllotis xanthopygus* (Waterhouse, 1837), for which groups of individuals collected at different altitudinal sites showed different rate and pattern of activity under the influence of different experimental temperatures (Sassi et al. 2015).

In addition to the abiotic factors cited, environmental perturbations, such as habitat fragmentation, may also influence mammalian behavior (Norris et al. 2010). Comparing remnants in a forested landscape of the southern Brazilian Amazon, *D. leporina* had a more pronounced peak of activity earlier in the morning in larger fragments, while activity was distributed more evenly throughout the day in smaller fragments (Norris et al. 2010). The patterns we observed in both areas are similar to those reported in larger fragments (Norris et al. 2010), yet the peak before dusk was higher in our study. Also, the overall level of activity of *D. punctata* was inversely related to food availability in Panama (Suselbeek et al. 2014), which help to explain the fact that agoutis tend to be active for more time in forest fragments that have been isolated longer (Norris et al. 2010). The risk of predation is another biotic factor that affects the activity pattern, and *D. punctata* avoid periods of high exposure to predators (Lambert et al. 2009, Suselbeek et al. 2014). Despite the peculiarities among the studied reserves, the principal predators of agoutis, the ocelot *Leopardus pardalis* (Linnaeus, 1758) and puma *Puma concolor* (Linnaeus, 1771), are both present in EBSL and RNV. Therefore, we assume that the risk of predation may not be a factor that explains the differences in the activity pattern of the agouti between areas.

Red-rumped Agouti activity lasted more or less the duration of daylight (14–15 hours), similar to that of a previous study in the RNV (14 hours, Ferregueti et al. 2018). The Coiban Agouti (*Dasyprocta*

coibae Thomas, 1902) and *D. punctata* were active, respectively, 15 and 14 hours each day in Panama (Suselbeek et al. 2014, Duquette et al. 2017). The Black Agouti (*Dasyprocta fuliginosa* Wagler, 1832) was active for 13 h in Ecuador (Blake et al. 2012). In the Pantanal, *D. azarae* was active up to 17 hours each day (Cid et al. 2015). These data demonstrate that factors other than latitude (and hence photoperiod), as previously discussed, influence the agouti activity pattern also by considering broader geographic scales.

In a previous study in the RNV, *D. leporina* was not recorded during the hottest hours of the day, between 12:00 h and 13:30 h (more than 750 independent camera trap records; Ferregueti et al. 2018). In this study we found less activity between 10:00 h and 13:00 h in RNV, but there was always some activity. This pattern has also been observed elsewhere in agoutis (Norris et al. 2010, Blake et al. 2012, Suselbeek et al. 2014, Cid et al. 2015, Duquette et al. 2017). No agouti activity was observed during the 09:00 h interval in the EBSL (between 08:55 h and 10:18 h), but this can be attributed to the lower number of records obtained in this area, associated with the reduction of the activities of the species at this time, similar to that observed in RNV.

We only had three nocturnal captures of *D. leporina*, all in the RNV. Occasional nocturnal activity of *D. punctata* occur in periods of fruit abundance, even though foraging at night may have greater predation risk (Lambert et al. 2009). In our study, the nocturnal captures were in February (n = 1) and October (2), which are rainy months with greater food availability.

Red-rumped Agouti was active throughout the day, with a bimodal pattern of activity (morning and afternoon), and nocturnal activity was rare. These activity characteristics are similar to that recorded for agoutis in one or more localities. The study areas had somewhat different activity patterns, demonstrating plasticity on the part of the agouti that is probably due to differences in ambient temperature, associated with local effects of altitude and topography of the terrain on the incidence of light in the interior of the forest in the two locations. This shows behavioral plasticity in the activity pattern of *D. leporina* in the Atlantic Forest can be influenced by factors other than latitude. In addition to a better understanding of the temporal niche of the Red-rumped Agouti, our data can also be used to help to optimize strategies for *D. leporina* conservation in southeastern Brazil. We suggested the intensification of activities to combat agouti poaching at the times of the day when the species is most active and consequently more susceptible to hunting. This would be applied particularly to areas where agouti is one of the main hunting target species.

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Author Contributions

Ana Carolina Srbek-Araujo: Concept and design of the study, data collection, data analysis and interpretation, manuscript preparation.

Laura Martins Magalhães: data analysis and interpretation, manuscript preparation.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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