



Variability in the Daily Activity of the Nine-banded Armadillo across the Americas

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Introduction

The nine-banded armadillo (*Dasypus novemcinctus*, Cingulata, Dasypodidae) is one of the most unique mammalian species of the Western hemisphere. Though sometimes mistaken for a reptile, these placental mammals have bony plates across their back for protection against predators. They produce their offspring in an interesting manner; despite mating season being in mid-summer, the zygote doesn't implant itself until early winter. It is also one of the only mammals to regularly produce identical offspring consistently, with each zygote splitting into genetically indistinguishable quadruplets (Loughry et al. 1988). They also differ from certain trends most mammalian species follow. They have a low metabolic rate for their size and have a high thermal conductance as well (Boily 2002). They are deemed imperfect homeotherms as their ability to thermally regulate is so poor, and their body temperature depends much more on environmental factors than other endotherms (Boily 2002).

They play an important role in the ecosystem as well. They are primarily insectivores, but also eat plant matter, and thus can serve to control insect and pest populations while promoting seed dispersal (Rodrigues et al. 2019). Another major impact they have on the environment is their establishment of burrows, which are used by a number of other species as well. They offer shelter and warmth for species like opossums, squirrels, foxes, bobcats, and even some birds (DeGregorio, Veon, & Massey 2022). In addition, their actions can also negatively impact human development. They are often declared a nuisance in the United States due to their ability to cause tunnelling in lawns and gardens as well as destroying agricultural landscapes.

Although the main topic of this paper is not on the geographic range of the nine-banded armadillo, it

is an important point to discuss. At its simplest, it is the locales in which a species resides. It depends on the interplay between numerous variables. Abiotic factors, like climate, temperature, and altitude, can provide obstacles for a species' occupation (Holt 2003; Sexton et al. 2009). Biotic factors also play an important role; the presence or absence of food sources, predator threats, and competitors can limit the locations of specific species (Holt 2003; Sexton et al. 2009). Geographic availability is the final consideration, as a species must be able to reach and establish themselves in a location in order for them to occupy it. Ranges are not static concepts; as the above variables change, species' ranges can contract or expand (Sexton et al. 2009). Furthermore, the evolution of a species can change its range, despite the external variables remaining constant. The changes in a species range can, in turn, further alter those abiotic factors and create new symbiotic relationships between species. Helping identify species' ranges can be important in predicting ecological interactions, changes to the environment, and species at risk of endangerment (Gaston and Fuller 2009).

The nine-banded armadillo is unique as it has had massive geographic expansion. It originates in the northern parts of South America but has spread its occupation substantially further north than south. They have not colonized the southern reaches of South America but continue to push into the United States of America. McNab (1980) posits that this may be due to interspecific competition in the south that is absent in the north. This expansion demonstrates a remarkable plasticity on the nine-banded armadillo's part, as the Northern and Southern Temperature regions have a much different climate than their tropical origin (McNab 1980). There is some evidence that their northern expansion is slowing down, due to colder





temperatures and frozen precipitation, which provides a thermal stress and hinders foraging (DeGregorio & Deshwal 2025). In addition, their western range in the US has already shown some contraction, possibly due to increasing levels of aridity (Humphrey 1974).

The primary subject of this paper is temporal niches. Similar to spatial niches, temporal niches play a role in a species' fitness. Most higher order vertebrate species operate on a 24-hour circadian clock and are active at regular select intervals in a day. Typically, there are three categories of temporal niches: diurnal, nocturnal, or crepuscular. There are varying degrees of flexibility to which a species can change their temporal activity (Levy 2019). For example, Levy points out that some rattlesnake species are active at certain times depending on heat levels, regardless of the light levels at the time. However, many species are limited in their ability to change their niche by internal biological constraints, like retinal sensitivity (Levy 2019). The ability of a species to change the time of day in which they are active can provide a valuable ability to improve fitness. It can help to reduce interspecific competition or increase resource availability.

The large expansion in the nine-banded armadillo's range has introduced a number of different variables from their origin in the tropics. Temperature, land cover, and seasonal differences occur across their distribution. In the South American tropics, research typically describes them as nocturns. However, in the northernmost parts of their range, some research describes them as exhibiting more diurnal activity (DeGregorio 2021; Green 2016; McDonough). This is especially true in the wintertime, which is much more pronounced in the Temperate zones than in the Tropics. This is likely to avoid the frigid temperatures of the winter nights. Armadillos are well known to have very poor thermal regulation compared to other mammals, so their activity is highly temperature-dependent. This seems to be the most prominent variable in determining the temporal distribution of their daily activity. Another strong factor is human activity; developed areas tend to cause more nocturnal activity, most likely as an avoidance mechanism since mortality rates are high in these areas due to dog attacks and car accidents (DeGregorio 2023).

The plasticity of the nine-banded armadillo's temporal activity greatly determines the extent of its range and how it can respond to different factors. This study aims to investigate potential changes in armadillo activity across the latitudes of its range and relate those to variables that could be affecting them, such as temperature, land cover, or seasonality. As distance from the equator increases, a corresponding increase in diurnality is expected to occur due to the higher frequency of colder temperatures. When separated by season, this effect in the extratropical latitudes should be most pronounced in the winter and least pronounced in the summer. The seasonal differences in the tropics should be minimal, as temperature fluctuations are very small between seasons. Prior research has shown that temperature is the primary determinant of activity, so seasonal differences accounting for temperature should not be strong. Temperature should be the strongest determinant of activity and the differences between temperature groups should be prominent. In addition, the armadillo has been shown to prefer tree-covered areas, partially because it provides shade and thermal regulation on hot days. Accounting for temperature, it might be possible to see a slight increase in diurnality in treeoccupied areas relative to artificial surfaces or grassland when temperatures exceed a certain point.

Methods

Data Collection

The primary data for this study was sourced from Wildlife Insights, a public database of camera trap data from researchers and labs across the globe. Camera traps are a common tool used in ecology to determine location and timing of organismal activity. They are near-identical to hunting cameras and are often attached to trees or vertical surfaces to gain a view of a specific habitat or area. An organism's movement activates either the taking of one image, multiple images (a sequence), or a video.

Wildlife Insights was filtered such that only *Dasypus novemcinctus* (nine-banded armadillo) images and sequences were retrieved. All of the data was merged into a single dataset, and data cleaning and analysis was done in R; camera trap sequences were given a timestamp the same as the first image present in each sequence (i.e., a sequence with multiple images





ranging from 1:04:54-1:07:32, the time stamp for the observation would be 1:04:54). These images were then filtered to remove images within an hour of the previous observation from the same camera trap, to ensure each image was an independent observation; this is a common practice in the field of ecology, though the time difference may vary depending on the species and study site (Sollman 2018).

Each image was associated with the country and location (latitude/longitude) of its respective camera trap. Seasonality of each image was determined using meteorological season, which denotes each season as starting the first day of the month containing the respective solstice/equinox. The landcover of the camera trap was obtained using the FAO map of the dominant land cover type (2014). The location of each camera trap was mapped onto the landcover map in QGIS (Image 1). Using the Vector Geoprocessing tool Buffer, an area of radius 187.12 meters was drawn around each camera trap. This area is meant to approximate the home range of nine-banded armadillos (estimates vary depending on the study, so a roughly median value of 11 hectares was chosen) (Gammons, Mengak, & Conner 2009). Raster zonal statistics were then used to calculate the predominant

landcover type around each camera trap.

Temperature was gathered using the “ERA5 post-processed daily statistics on single levels from 1940 to present.” This dataset provides a raster file with values for each day in a year, at a resolution of 0.25° longitude and latitude. Each photo was related to the closest point in the ERA5 raster and the temperature was extracted for the given day of the photo.

Statistical Methods

For latitudinal analysis, the range of locations were split into seven slices. Each one is a range of 11.75°, except for the northernmost and southernmost slices, which extend to the most distant observation in their group (45° to 35.25°, 35.25° to 23.5°, 11.75° to 0°, 0° to -11.75°, -23.5° to -11.75°, -30° to -23.5°). The total number of latitudinal slices in the tropics are four, and there are three extratropical groups. These allowed for latitude to become a categorical variable to make statistical analysis more manageable. Kernel density estimates (R package overlap) were used in order to visualize the daily temporal activity of *Dasypus novemcinctus*. Watson-Williams tests of homogeneity of means were used to determine if distributions were significantly different (R package circular).

Results and Discussions

The data represented almost all of the North and South American countries [Image 1], except for those with insufficient observations to be included (Honduras, El Salvador, Nicaragua, Venezuela, Argentina, Chile, and Uruguay) as well as island nations without the species present. The number of camera traps and images per latitude group vary. For example, the group from 11.75° to 23.5° had the smallest sampling (n=258) while the other latitudes had an order of magnitude greater (n=1188-5786).

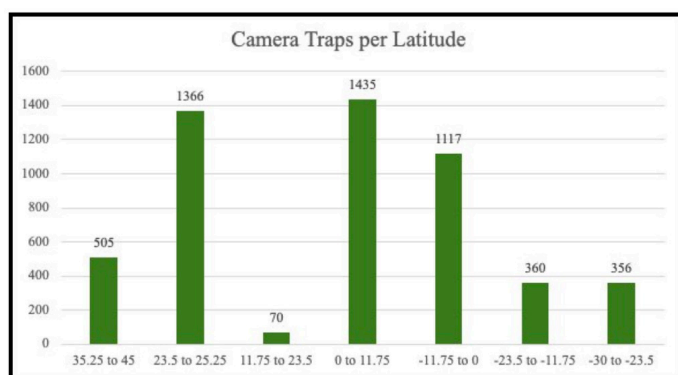


Figure 1. Number of Camera Traps per Latitude

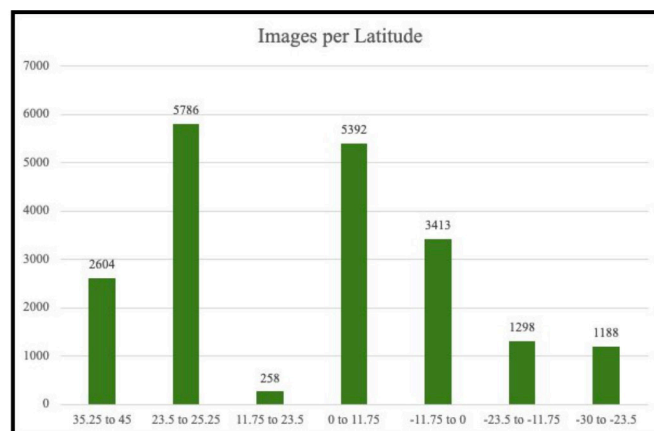


Figure 2. Number of Independent Images per Latitude



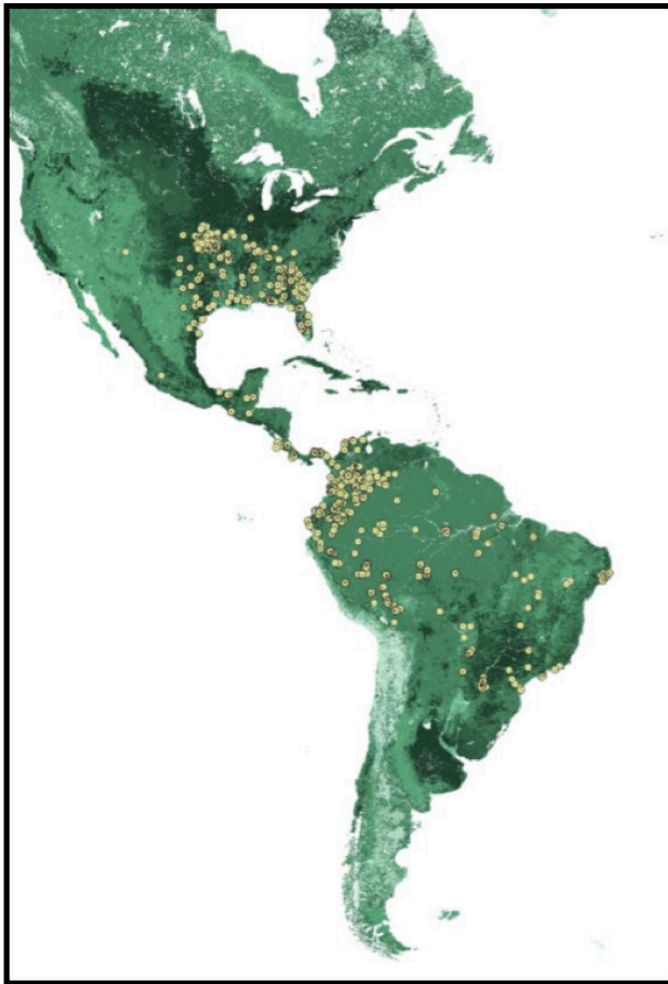


Image 1 Spatial Distribution of Camera Trap Deployments

The distribution of seasons in this dataset is not even across the latitudes [Figure 3]. The proportions within and between the latitudes differ, especially in regards to winter and fall. The two northernmost latitudinal groups have an abundance of fall sampling compared to the other seasons. This can be a limitation in comparing latitudes, especially in the extratropics where distributions vary significantly between seasons and oversampling can shift distributions.

All of the latitudes are predominantly tree-covered areas, with none being less than half of the sample [Figure 4]. The proportions of the others vary significantly. The most prominent across groups besides tree-covered were cropland, artificial surfaces, and grassland. For certain latitudes, these groups did not have sufficient sampling to produce a density plot,

and thus were left out. Others were included, but their samples were quite small such that random variation produces an unusual plot. Other categories, like waterbodies or shrubland, were left out of analysis entirely due to their consistent lack of sampling and inability to produce significant results.

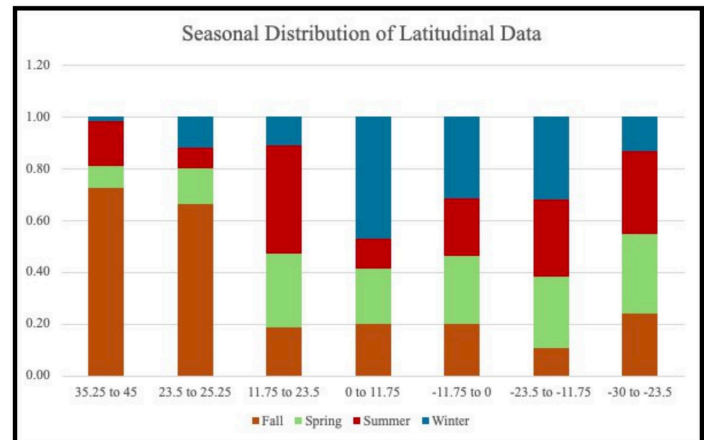


Figure 3. Seasonal Proportions in Each Latitude's Dataset

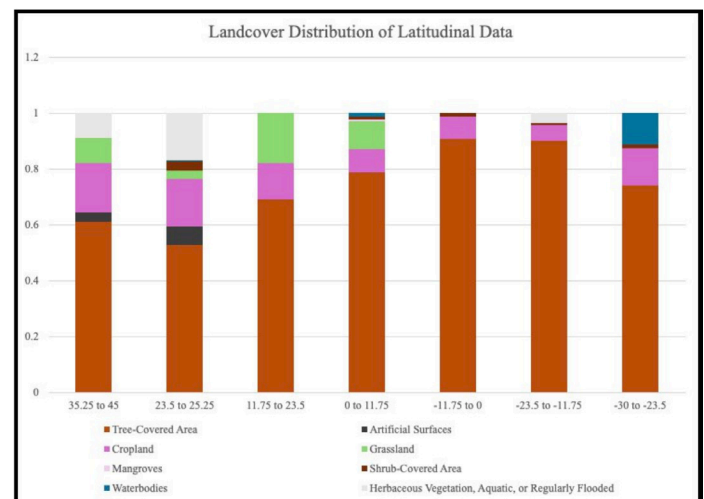


Figure 4. Landcover Proportions in Each Latitude's Dataset



Latitudinal Differences in Daily Activity

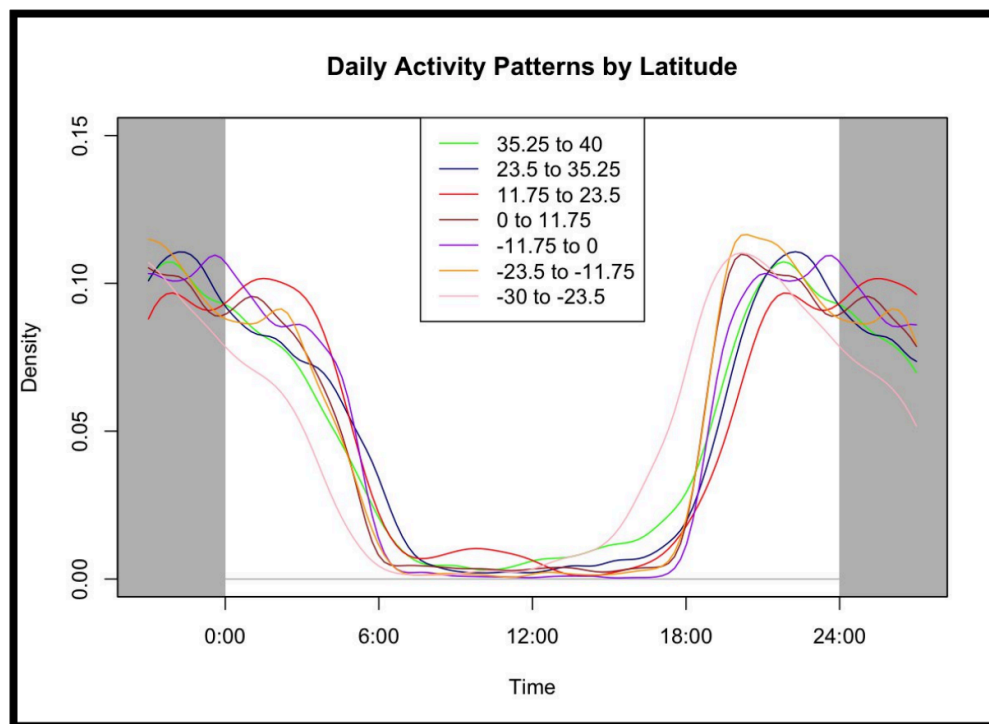
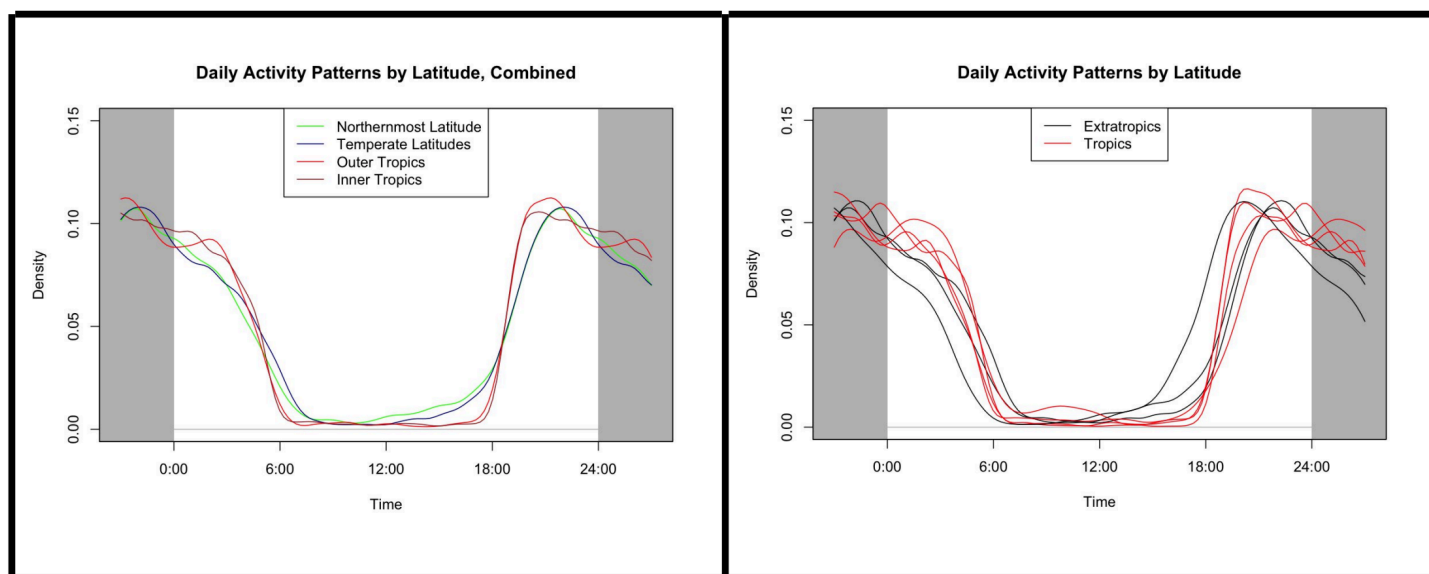


Figure 5. Daily Activity Patterns By Latitude



Figures 6 & 7. Daily Activity Patterns By Latitude Altered for Clarity





In general, the daily activity patterns of the nine-banded armadillo are the same across latitudes. They exhibit a nocturnal activity pattern with maximum activity between ~19:00 to ~22:00. Activity drops consistently from ~6:00 to ~7:00. During the day, activity is low, but between ~16:00 and ~18:00 activity begins to rise again until its peak. Variations between latitudes are small, with the Watson-Williams Test showing no consistent pattern in significant differences between density curves of extratropics vs. tropics (Appendix, [Table 1]).

The southernmost latitude shows the greatest difference from the others, reducing activity in the morning and increasing it in the evening before the others. There are other armadillos in this area, so it could be possible that the combination of extratropical seasonal differences combined with competition and niche partitioning could result in the effect seen, though I think this to be unlikely.

One qualitative observation is that the extratropical latitudes tend to drop from the peak of their activity earlier than do the tropics, but take longer to reach their low daily activity. This results in the trend observed above where in the early morning tropical activity exceeds extratropical activity, but they cross over due to the more rapid decrease of tropical activity in the morning. This is most visible in [Figure 7], due to the contrast.

One limitation is that the makeup of this data is not uniform; as can be seen in [Figure 3] in the next section, the distribution of the seasons is not even across each latitude due to some being oversampled. In addition, seasonality means different things in the tropics than it does in the extratropics; therefore, the northernmost latitude's density distribution is an average across all seasons, while the tropics is technically the same, but the seasonal differences are minute

Temperature and Seasonal Effects on Daily Activity

Seasonality seems to play a role in the daily activity of the nine-banded armadillo in the extratropics, but this difference disappears in the tropics (for significance, see Appendix, [Table 2]). The extratropics north of the equator (45° to 23.5°) showed more diurnal activity during the winters as well as a spring peak in the evening substantially higher than the other seasons. For example, in the northernmost latitude group, winter had a probability density of 0.34 compared to values of 0.13, 0.02, and 0.07 for fall, spring, and summer, respectively from 6:00 to 18:00. For the spring season, the increased activity in the evening compared to the morning was an unexpected find, but this could be due to precipitation generally occurring in the evening more than the morning. Rain could lower temperatures compared to the morning, and also simultaneously encourage insect activity in the soil while making foraging easier. These effects could account for the heightened evening activity in the spring.

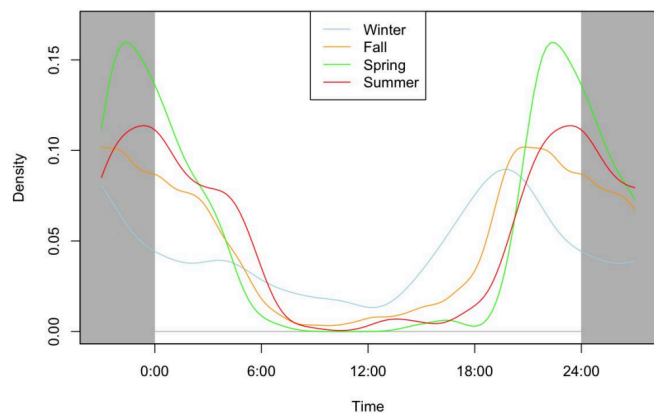
There was an observed seasonal difference in the latitudinal range from 23.5° to 11.75° , which was unexpected due to it being in the tropics, but the smaller sample size ($n=258$) may contribute to the differences seen. The rest of the tropical latitudes had very little difference between the seasons, as expected. Since the primary factor in armadillo activity has been shown to be temperature, the little seasonal difference in tropical areas is likely due to the slim temperature differences throughout the seasons.

Some mammals have seasonal variation due to factors other than temperature, including light levels and breeding seasons. To further determine if there is a seasonal effect separate from temperature, the extratropical latitudes were combined and separated by seasons. Each season only included the temperatures between 20° and 30°C , in order to ensure temperature's effect on the distribution was reduced. The plot is shown in [Figure 9].

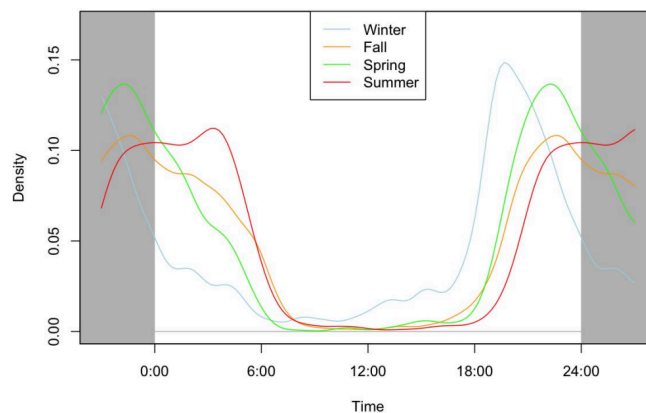




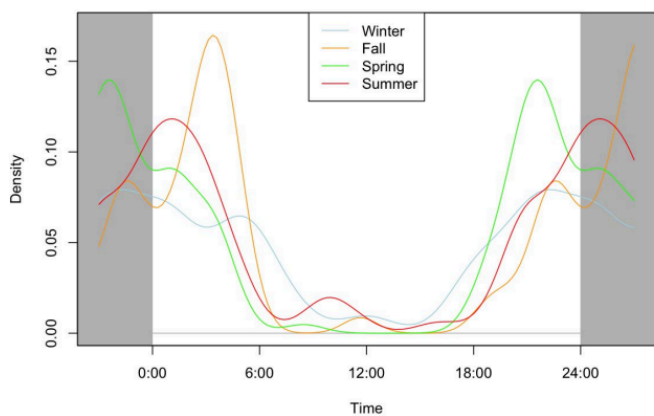
Daily Activity Patterns by Season, 35.25 to 45



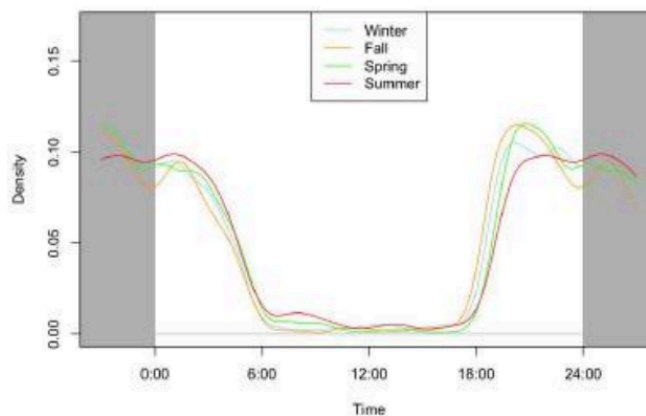
Daily Activity Patterns by Season, 23.5 to 35.25



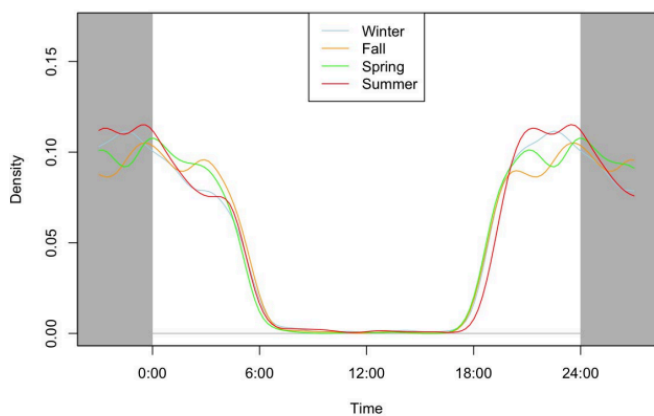
Daily Activity Patterns by Season, 11.75 to 23.5



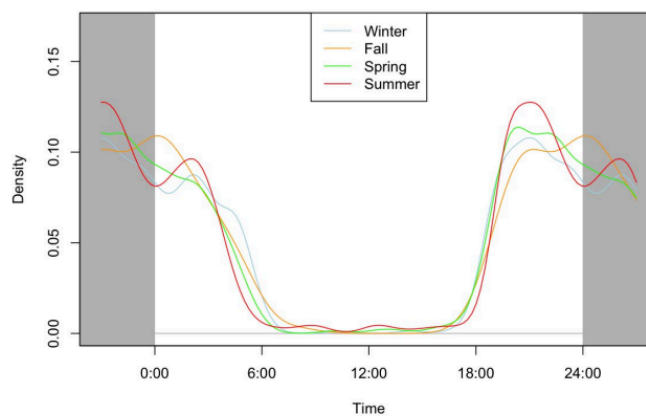
Daily Activity Patterns by Season, 0 to 11.75



Daily Activity Patterns by Season, -11.75 to 0



Daily Activity Patterns by Season, -23.5 to -11.75



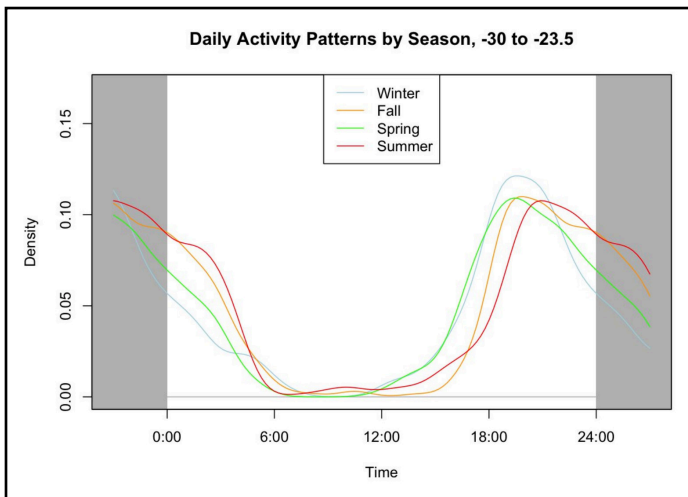


Figure 8 Seasonal Differences in Temporal Activity by Latitudinal Section

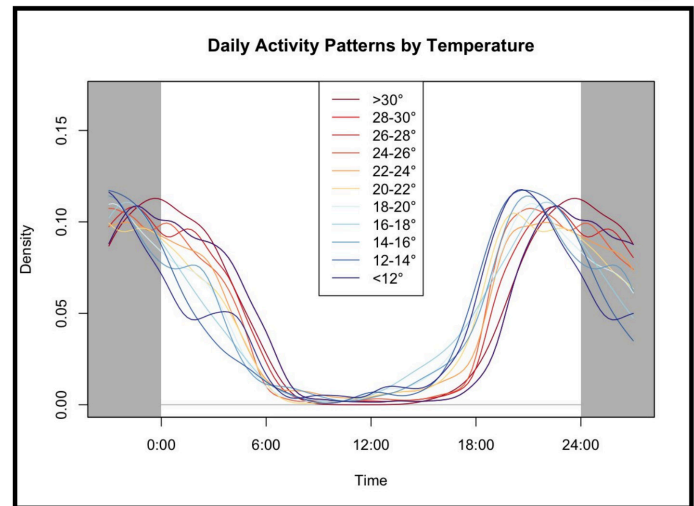


Figure 10 Temperature Differences on Temporal Activity

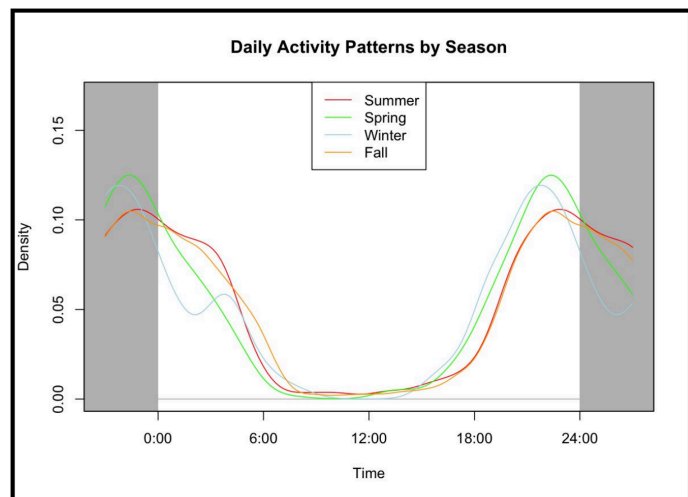


Figure 9 Seasonal Differences on Temporal Activity in the Extratropics, Accounting for Temperature

The variation seen previously in the extratropics mostly disappears in [Figure 6]. There remains some significant difference in the plots, variations in the temperature distributions between the seasons and smaller sample sizes that likely account for the small differences seen. [Figure 9] indicates that the majority of the seasonal differences in activity are due to temperature differences.

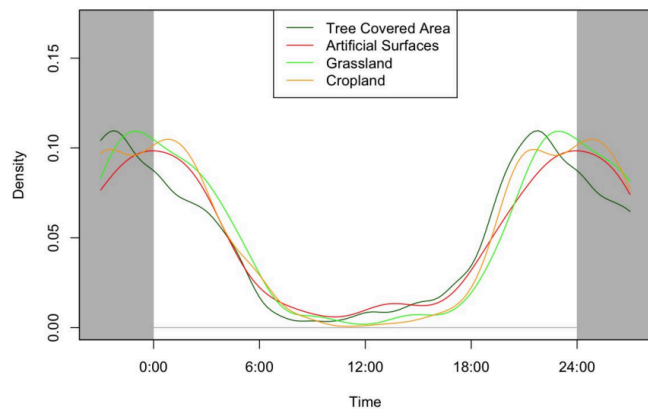
[Figure 10] seeks to establish how temperature differences affect activity patterns. It takes from a smaller sample, only the years 2018-2023. Due to the lack of an appropriate regression model in order, temperature was converted into a categorical variable; each line represents a range of 2°C , except for the warmest and coolest categories, which extend from 30° to 33.94° and 1.86° to 12° , respectively. The darkest red corresponds to the warmest temperature, and the darkest blue the coolest. [Figure 10] shows that warmer temperatures decrease activity in the morning and increase activity in the evening later than the cooler ones. The delayed activity in the evening is almost assuredly to avoid the hotter temperatures of the afternoon. In order to account for the delay in the evening, it is possible the armadillos prefer to stay active a little later in the morning. Thermal inertia means that the morning temperatures are relatively cooler than the evening ones of the same day, causing the shift in activity seen in [Figure 10].

The coolest temperatures match the winter observations from above, indicating higher diurnality. The diurnality exhibited is not a constant higher rate of activity from 6:00 to 18:00, but instead a minimum around 6:00 like the warmer temperature, and then a steady climb in activity until the peak around 20:00. This results in increased daytime activity in the afternoon, and an insignificant difference in the morning when compared to the warmer temperatures. The trend in [Figure 10] is consistent, with decreasing temperature categories shifting the plot steadily to the left.

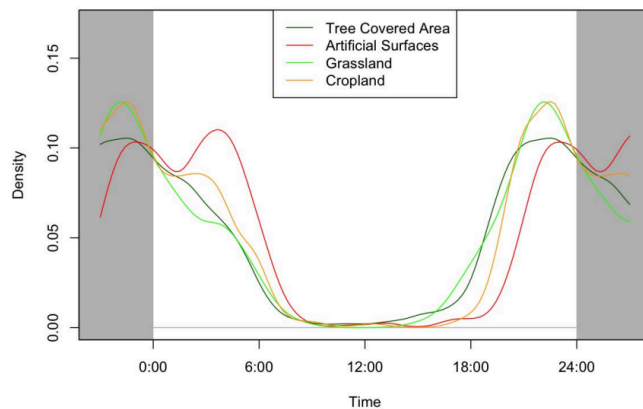


Landcover

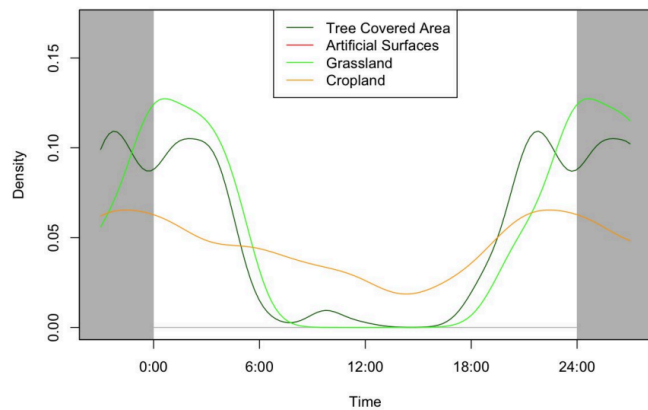
Daily Activity Patterns by Landcover, 35.25 to 45



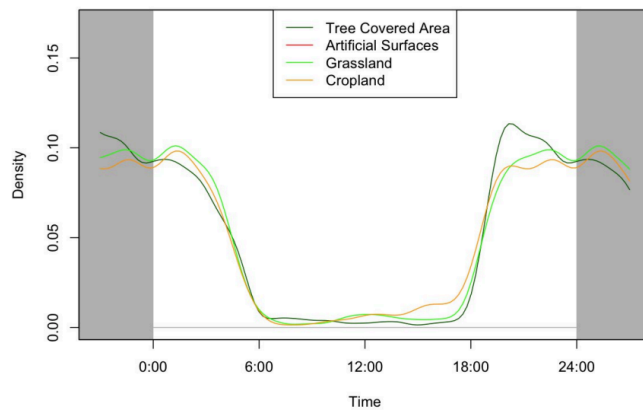
Daily Activity Patterns by Landcover, 23.5 to 35.25



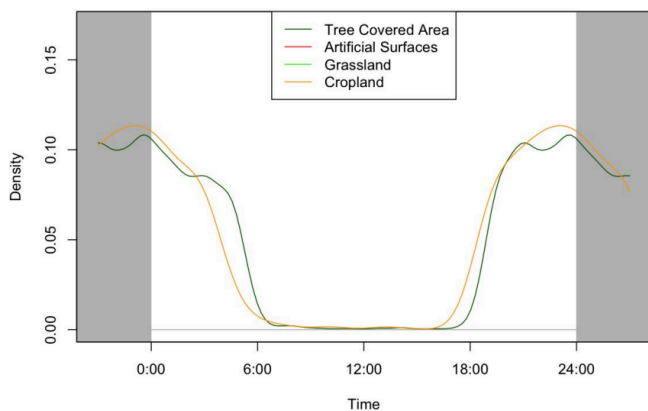
Daily Activity Patterns by Landcover, 11.75 to 23.5



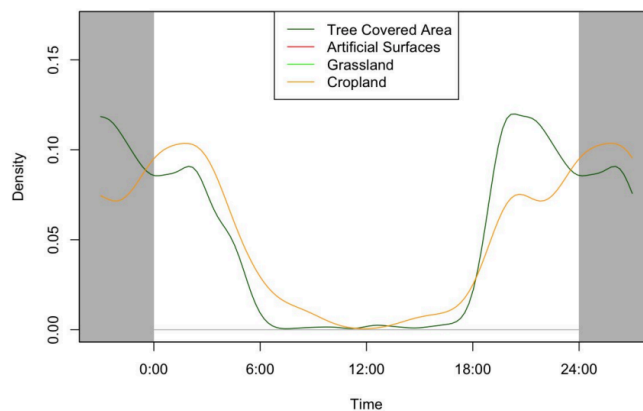
Daily Activity Patterns by Landcover, 0 to 11.75



Daily Activity Patterns by Landcover, -11.75 to 0



Daily Activity Patterns by Landcover, -23.5 to -11.75



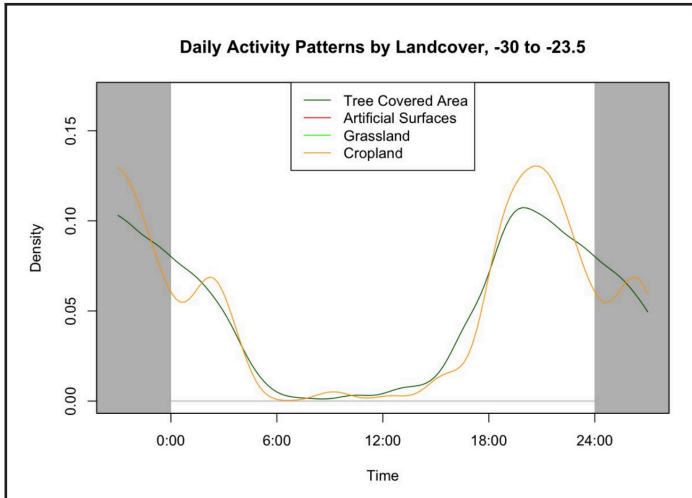


Figure 11 Landcover Differences in Temporal Activity by Latitudinal Section

Landcover does not seem to provide a great impact on the activity patterns of the ninebanded armadillo. The hypothesis that tree-covered areas have different distributions than the uncovered areas, like grasslands, was not supported. The shape of the distributions match consistently across landcover types. The variation seen in some of the plots, like from 11.75° to 23.5°, is most likely due to their small sample sizes rather than any significant difference occurring. The Appendix, [Table 3] shows the significance values for each latitude. To account for temperature variations between latitudes, another plot was generated with only temperatures between 26 ° and 30° were included.

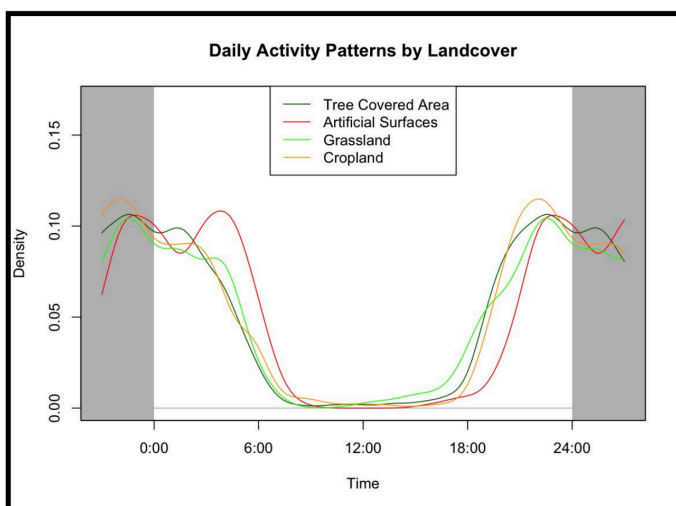


Figure 12 Landcover Differences on Temporal Activity, Accounting for Temperature

In [Figure 12], the tree-covered areas, grassland, and cropland all have near identical distributions. Artificial surfaces have the same shift as hotter temperatures did in [Figure 10]: a later decrease in activity in the morning and a later increase in the evening when compared to the other landcovers. Additionally, it was the only plot significantly different from any of the others ($p = 0.0005755$, 0.06591 , 0.0002631 , for tree-covered, grassland, and cropland, respectively). Since artificial surfaces typically have hotter temperatures than do the natural habitat or croplands in a given setting due to their darker material and higher absorptivity, this shift makes sense.

Conclusion

This study found that of the variables tested, temperature had the most significant effect on armadillo activity. As temperatures increase, the decrease in activity in the morning (~6:00) occurs later; furthermore, the increase in activity that happens in the evening also occurs later with hotter temperatures. This is likely due to a preference for the relatively cooler mornings than the evenings, due to the thermal inertia throughout the day. Cooler temperatures also had relatively more activity during the day, occurring after the drop in the morning and a steady increase during the day. This results in their diurnal activity happening more in the afternoon than in the late morning and midday.

Seasonal differences in activity did occur, but it was almost entirely due to temperature differences. Wintertime had the same shift that the cooler temperatures had compared to warmer seasons like summer. One unexpected find was that springtime in the extratropics tended to have relatively more activity in the evening than morning. It is possible that this is due to more precipitation occurring in the evening than the morning, creating better foraging environments and more reasonable temperatures.

Different landcover types did not cause significant variations in the activity patterns, with the exception of artificial surfaces. The heat island effect, well noted in urban areas, is the most likely cause for the shift, as the difference from the other landcover types was the same as that of hotter temperatures from the colder temperatures.



As the nine-banded armadillo migrates further northward, seasonal differences are expected to become more profound. The encountered temperatures will become increasingly colder, eventually reaching a point where no shift in activity patterns can offset fitness costs. The species may eventually become more completely diurnal in the wintertime if physiologically possible, but this research nor any others published have indicated this as a possibility. Their ability to counteract the frigid temperatures and precipitation of the northern United States will ultimately determine the upper limit of their range.

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Conflicts of Interest

The authors declare no conflicts of interest that would influence or appear to influence the results of this work.

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About The Author

Colin Wilson is an undergraduate majoring in Ecology, Evolution, and Organismal Biology from Louisville, KY. He is a member of the Jorge Lab, which specializes in Neotropical mammalian ecology. His research interests focus on the interactions between animals, plants, and fungi. Following graduation, he will be pursuing a Master's degree in Ecology and Conservation Biology at Texas A&M University. Outside of the lab, he enjoys reading, playing soccer, and spending time outdoors.

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