2020

Temperature effects on moose (Alces alces) activity patterns in Isle Royale National Park

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Undergraduate Thesis
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Missoula, MT

May 2020

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Isabella Evavold, B.S., Spring 2020

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ABSTRACT

Moose (*Alces alces*) in Isle Royale National Park impact the ecosystem by browsing tree species and serving as the primary food source for wolves. As a heat-sensitive species, moose are susceptible to the impacts of climate change in the southern extent of their range which includes Isle Royale. Understanding how temperature impacts moose behavior is valuable and can be used to predict how moose may respond to changing temperature in the future. GPS enabled radio-collars with three-axis accelerometers were used to collect one year of temperature and activity data from 6 cow moose in Isle Royale National Park. The data was used to test the relationship between moose activity cycles and temperature using linear regression. Results show that moose activity patterns do change based on temperature. The relationship between temperature and moose behavior can be used to estimate moose browsing impact which determines food availability over time. Understanding the relationship between temperature and moose activity can be used to predict change in moose behavior in response to climate change, which would disrupt the successional progression of vegetation communities and alter the greater Isle Royale ecosystem in the future.

Acknowledgements

The data used for this project was collected as part of a collaborative collaring effort by Michigan Technological University, the National Park Service, University of Minnesota College of Veterinary Medicine, and the Grand Portage Band of Lake Superior Chippewa. Data access was approved by the National Park Service through research permit number ISRO-2019-SCI-0022.

Additional thanks to Dr. Sarah Hoy and Dr. John Vucetich from Michigan Technological University for providing this opportunity and helping with the development of the research question. I would also like to thank my senior thesis committee at the University of Montana including my advisor, Dr. Paul Lukacs, Dr. Mark Hebblewhite, and Dr. Jedidiah Brodie.

INTRODUCTION

Herbivory from large ungulates such as moose (*Alces alces*) can have significant impacts on vegetation and the larger ecosystem. Moose browsing can impact the cycling of nutrients such as nitrogen, which influences forest structure and tree species distribution, as well as the abundance of browse species like balsam fir (Murray et al. 2013, Vucetich 2003). In places such as Isle Royale National Park, where moose are the only large herbivore, these effects of browsing can have a profound impact on browse species and the ecosystem as a whole.

The impact moose have on ecosystems is likely to change in the future as temperatures increase under climate change. As a heat-sensitive species, moose are especially susceptible to changes in temperature (van Beest et al. 2012). Changes in moose activity due to temperature could impact moose herbivory on forage species. For Isle Royale specifically, where the average annual moose population growth rate has been 19% for the past eight years, understanding moose impact on balsam fir and other browse species can help predict the abundance of browse in the future (Hoy et al. 2019). In addition, the amount of browse available influences moose demography, so any changes in the future may have a significant impact on moose and the greater ecosystem (Hoy et al. 2019).

One method to monitor and measure impacts of moose herbivory in a changing climate is through the use of accelerometers. Accelerometers measure average levels of movement for up to three axes, including forward-backward, right-left, and up-down movements, which can be used to determine behavior (Brown et al. 2013). Accelerometer data can be used to find patterns in moose behavior, which can provide important insights into levels of herbivory and possible impacts on the larger ecosystem (Street et al. 2015). In addition, collars can include both accelerometers and temperature sensors, which can be used to test the relationship between temperature and activity for the collared species (Brown et al. 2013).

Based on temperature sensor and accelerometer data from moose in Isle Royale National Park, the correlation between number of moose active cycles per 24 hours and mean temperature per day was analyzed to see how increasing temperatures impact moose activity. The specific research question that was addressed was: Is there any association between temperature and moose activity pattern?

HYPOTHESES AND PREDICTIONS

Previous studies have found that moose reduce their activity levels as temperature increases (Renecker and Hudson 1986, Street et al. 2015). Based on these findings, the first hypothesis is that moose activity cycles are driven by temperature. I predicted that the number of active cycles will be negatively correlated to temperature (Figure 1).

Moose have also been shown to change behavior at certain temperature thresholds. Several studies have found that moose reduce travel and show signs of heat stress between 14-24° C in summer (Ditmer et al. 2017, Renecker and Hudson 1986, vanBeest et al. 2012). The second hypothesis is that moose activity cycles remain constant until the temperature reaches a heat threshold. The prediction is that cycles remain constant up until 14-24° C, after which the number of active cycles decreases as temperature continues to rise (Figure 1).

Both low and high temperatures can impact moose behavior. In addition to reducing activity when temperatures are above a certain temperature threshold, moose have also been known to reduce activity during winter when temperatures are coldest. In one study, the lowest level of activity occurred in winter (Cederlund 1989) while another study by the same author found that moose have the lowest number of active cycles in late winter, with only two to three occurring in 24-hours (Cederlund et al. 1989). A study on roe deer also found that fewer active periods occur in winter compared to spring and summer (Krop-Benesch et al. 2013). The same study suggests that this change is due to temperature, since roe deer were more active at midday when temperatures were warmer. As an ungulate, moose may react in a similar way to temperature. Based on these responses, cold temperatures may cause moose to reduce their activity. Therefore, the third hypothesis is that the number of active cycles decreases at extreme low and high temperatures. The subsequent prediction is that as temperatures increase, the number of active cycles per 24 hours increases up to a certain level before decreasing after the same heat threshold in hypothesis two (Figure 1). The fourth and final hypothesis is the null hypothesis. Under this hypothesis, none of the previous hypotheses are supported or there is no correlation between temperature and the number of activity cycles per 24 hours.

METHODS

Study Area

Isle Royale National Park in Michigan is an island archipelago located in the northwestern part of Lake Superior, 15 miles from the nearest shoreline. The park consists of about 535 square kilometers of land split between one large island and 450 smaller islands (National Park Service). In addition, 99% of Isle Royale is protected as a Wilderness Area. Because of the island's designation as a National Park and Wilderness, no hunting or timber harvest is allowed.

Isle Royale is home to 19 mammal species, including wolves and moose (National Park Service). Both wolves and moose are relatively recent additions to Isle Royale. The arrival of moose is estimated to have occurred in the early 20th century while the arrival of wolves occurred in the late 1940's (Wolves and Moose of Isle Royale). The dynamics between wolves, moose, and the greater Isle Royale ecosystem have been studied for the last 61 years as part of the Wolves and Moose of Isle Royale predator-prey study.

At the west end of Isle Royale, the landscape is dominated by a dense northern hardwood forest with interspersed conifers (Hoy et al.2019). The coasts and east end of Isle Royale are dominated by boreal forest, primarily of balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and mountain ash (*Sorbus decora*) (National Park Service). In winter, the primary species moose browse include balsam fir and northern white cedar (*Thuja occidentalis*). In summer, the primary browse species change to deciduous trees and shrubs like trembling aspen and paper birch (Sell 2007).

The climate of Isle Royale is largely driven by Lake Superior and the island's central location in North America. Mean temperature on the island is 3.9° C and average yearly precipitation is 734 mm (Fisichelli et al. 2013). Lake Superior waters cause Isle Royale to experience cooler summer and warmer winter temperatures compared to inland regions on the Minnesota and Ontario, Canada mainland (Fisichelli et al. 2013). In the Midwest, climate trends are expected to change in the future. From 1950 to 2010, the Midwest has seen an increase in air temperature of more than 0.83° C with warming occurring more rapidly during night and winter (Pryor et al. 2014). This warming trend is also present on Isle Royale, which has experienced a long-term warming trend for average winter temperature since the wolf-moose study began in 1959 (Hoy et al. 2017).

Moose GPS Collaring

On February 13, 2019, 20 moose on Isle Royale were collared with Global Positioning System (GPS)-enable radio collars (Vertex Plus 7 Collars, VECTRONIC Aerospace) as part of a larger, collaborative study including Michigan Technological University, the National Park Service, University of Minnesota School of Veterinary Medicine, and the Grand Portage Band of Lake Superior Chippewa. Each collar included a three-axis accelerometer, which measured forward-backward, up-down, and left-right movement, and an ambient temperature sensor. Movement and temperature data were retrieved from 19 out of 20 of the collars in February 11, 2020 resulting in an entire year of accelerometer and temperature sensor data. The loss of data from one of the collars was due to the collar malfunctioning before data could be collected. Since the data was housed at Michigan Technological University, restrictions due to the COVID-19 pandemic limited access to only six of the 19 moose data sets. The data that was able to be analyzed was from moose 12, 13, 15, 17, and 19.

Data Analysis

The accelerometer data from the collars was averaged every five minutes for each of the three axes. For every five-minute accelerometer average, ambient temperature was also recorded by the collars. The number of peaks in activity per day were counted for each moose, using movement readings from the x-axis. The x-axis, which measures forward-backward motion, was used since it has been found to be most closely correlated with resting, foraging, and other locomotor activities (Krop-Benesch et al. 2013). Krop-Benesch et al. used the x-axis to analyze long-term roe deer activity from GPS collars with two-axis accelerometers in Germany. The mean temperature per day was calculated using the temperature readings that accompanied every 5-minute activity average.

Linear regression was then performed for each moose using the log-transformed number of active periods per 24 hours and mean temperature per day to see if the number of active periods was correlated with temperature. Finally, a linear mixed-effects model was created for all combined moose data. The model accounted for variation across individual moose with a random effect for moose identity.

RESULTS

The mean number of active peaks per 24 hours for all six moose was 15.329. The maximum number of active peaks was 45 and the minimum number of active peaks was 0. For the study period, the mean daily temperature was 21.896° C. The minimum temperature was -10.017° C and the maximum temperature was 29.816° C (Figure 2).

There was a slight negative correlation between temperature and log number of active peaks per day. The average slope for the linear regression on each individual moose was -0.008 (SE = 0.002). The exponentiated average slope for the six linear regressions is 0.992, or for every one degree increase in temperature there is a decrease in activity bouts per day of about one. Individual linear regression slopes ranged from -0.008 to 0.014 (Table 1).

The mixed-effects model supported the negative correlation between temperature and the number of active peaks per day. For the combined data, the slope for the mixed-effects model was -0.006 (SE = 0.001, Figure 4). The exponentiated slope of the mixed-effects model was 0.994. This means that for every one degree increase in temperature, there was a decrease in the number of active bouts per day of about one based on the mixed-effects model. The standard deviation of the random effect, Moose ID, was 0.062.

Overall, there was a slightly negative correlation between log active peaks per day and mean temperature per day. Both the average slope of the six linear regressions and the slope of the mixed-effects model were slightly negative, despite two out of six moose having slightly positive linear regression slopes. The standard error was small for most of the linear regressions and the mixed-effects model, which means that the linear regressions and the mixed-effects model were representative of the slight negative trend in the data.

DISCUSSION

The results support hypothesis one, that there is a correlation between temperature and activity peaks, and that the correlation is negative. While both hypothesis two and three included a decrease in activity after a heat threshold, neither of these hypotheses were linear like hypothesis one so they don't reflect the results. This finding aligns with and supports the literature that moose do change behavior as temperature increases. On Isle Royale specifically, this finding may have future implications for moose behavior and survival.

Moose are a heat-sensitive species that are known to change behavior between 14 and 24° C (Ditmer et al. 2017, Renecker and Hudson 1986, vanBeest et al. 2012). They are also experiencing declines in most of their southern range (Ditmer et al. 2017). Increasing average temperatures in southern regions of moose range and the subsequent decrease in moose activity could be a factor in moose population declines. If increasing temperatures reduce the amount of time moose are active, the amount of time available to forage could be reduced. Without enough time to adequately forage, moose body condition could decrease, possibly reducing fecundity and increasing susceptibility to predation, disease, and ectoparasites like winter ticks (Samuel 2007). In Minnesota, moose population growth rate was found to be negatively correlated with mean summer temperature (Murray et al. 2006). Despite Isle Royale's location in the southern extent of moose range, the island has not yet experienced moose population declines like those occurring in nearby Minnesota. However, there is evidence that moose lifespans and skull sizes are decreasing as winter temperatures are increasing (Hoy et al. 2017). Since temperatures are expected to increase in the future, Isle Royale could start to see changes in moose survival like in Minnesota.

Future changes in moose behavior and population size due to increasing temperature could also change herbivory patterns, which would impact the greater ecosystem. On Isle Royale, temperature changes could have far-reaching impacts on species like balsam fir, the primary winter browse species of moose, and wolves, the primary predators of moose (Vucetich 2003). A more complete understanding of how temperature determines moose behavior could be used to form detailed predictions of how moose on Isle Royale could be impacted in the future. Using the same temperature and activity data, research could be continued to provide a better understanding of how moose on Isle Royale are responding to temperature.

One way to expand research using this data is to incorporate all three axes, rather than just the x-axis. Adding two more axes to the analyses could provide a more detailed record of moose behavior. A study by Löttker et al. used accelerometer data from two axes rather than one, to determine more specific behavior such as resting, feeding/slow locomotion, and fast locomotion of captive elk in Germany (Löttker et al. 2009). In addition, non-linear models could be used and compared to the linear regression and mixed-effects model used in the analyses to see which fit the data best. Factors such as daylight and seasonality could be incorporated into models since they may be additional factors that influence moose activity. Finally, the sample size could be increased to include all 19 moose and multiple years of activity and temperature data as it becomes available.

The accuracy of movement and temperature data could be tested, since accelerometer and temperature sensor measurements likely include error. To test that the accelerometers are recording activity correctly, in-field observations of the collared moose could be used to verify accelerometer readings. A study in Alaska by Ditmer et al. performed in-person observations of moose behavior on collared, captive moose that had accelerometers. Then, they used that data to validate wild moose accelerometer readings and more accurately categorize resting, foraging, and travelling behaviors (Ditmer et al. 2017). In addition, temperature recorded by collar sensors can be offset from the actual ambient temperature by 6.6° to 8.0° C (Ericsson et al. 2015). The temperatures recorded by the six collars on Isle Royale ranged between -10° C to 22° C despite temperatures falling well below -10° C during the 2019 winter study (Hoy et al. 2019). This indicates there may be a temperature offset for the collar temperature sensors. Comparing temperature readings with nearby weather stations could test whether the temperature readings are accurate and make any adjustments if there is an offset. Combined, broadening the analysis and testing for error of the temperature and accelerometer data would ensure the results accurately reflect moose responses to temperature.

In conclusion, accelerometers offer an opportunity to monitor animal activity year-round in remote areas like Isle Royale. Accelerometer data can then be used to test relationships between factors like temperature and predict how activity may change in the future. For moose on Isle Royale, the negative correlation between temperature and activity can be used to estimate the impact of herbivory on the ecosystem under climate change. Overall, accelerometer data provides an opportunity to better understand how the environment impacts moose activity and, in turn, how that activity impacts the environment. In combination with other research findings from Isle Royale National Park, the results of this research are another step toward building a comprehensive understanding of herbivory on an isolated island.

Figure 1. Prediction graphs for each of the three hypotheses. Hypothesis one prediction (blue) is that the number of active cycles per 24 hours is negatively correlated with temperature. Hypothesis two prediction (green) is that the number of active cycles stays constant before decreasing after the heat threshold of about 14-24° C. Hypothesis three prediction (orange) shows that activity cycles initially increase as temperatures increases, before levelling out and decreasing at the heat stress threshold of about 14-24° C.

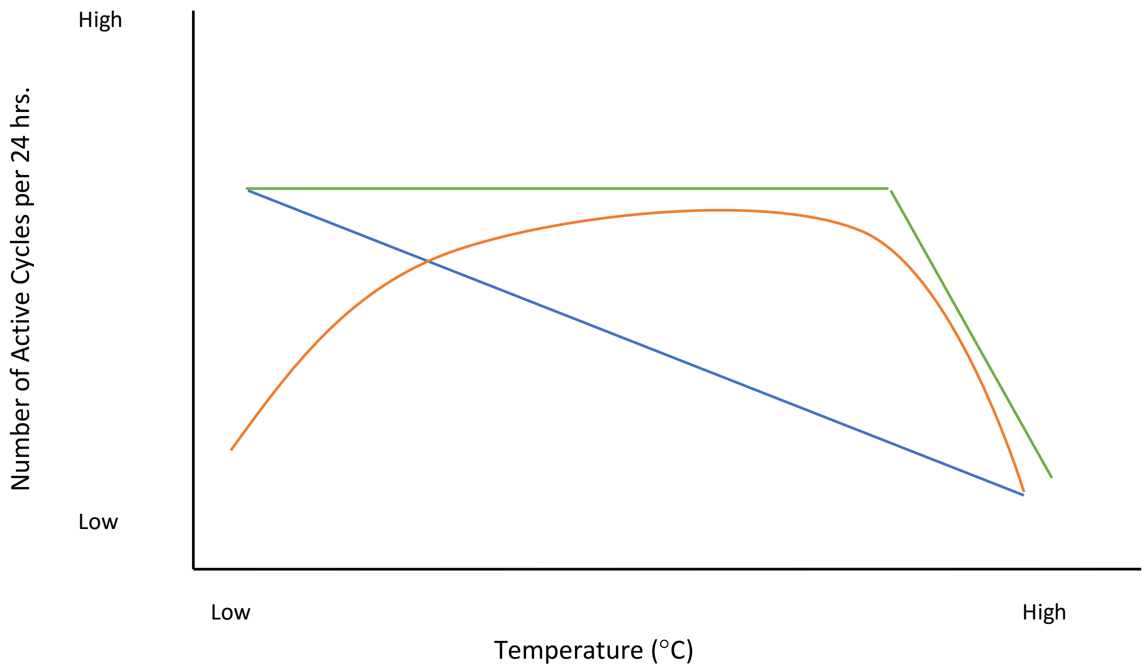


Table 1. Slope and standard error for each linear regression.

Moose ID	Linear Regression Slope	Standard Error
Moose 12	-0.008	0.002
Moose 13	-0.014	0.002
Moose 15	-0.008	0.002
Moose 17	0.001	0.003
Moose 18	-0.008	0.003
Moose 19	0.001	0.003
Average	-0.008	0.002

Figure 2. Boxplot showing the mean daily temperatures for all moose datasets. The mean temperature was 12.922° C with a minimum of -10.017° C and a maximum of 29.816° C.

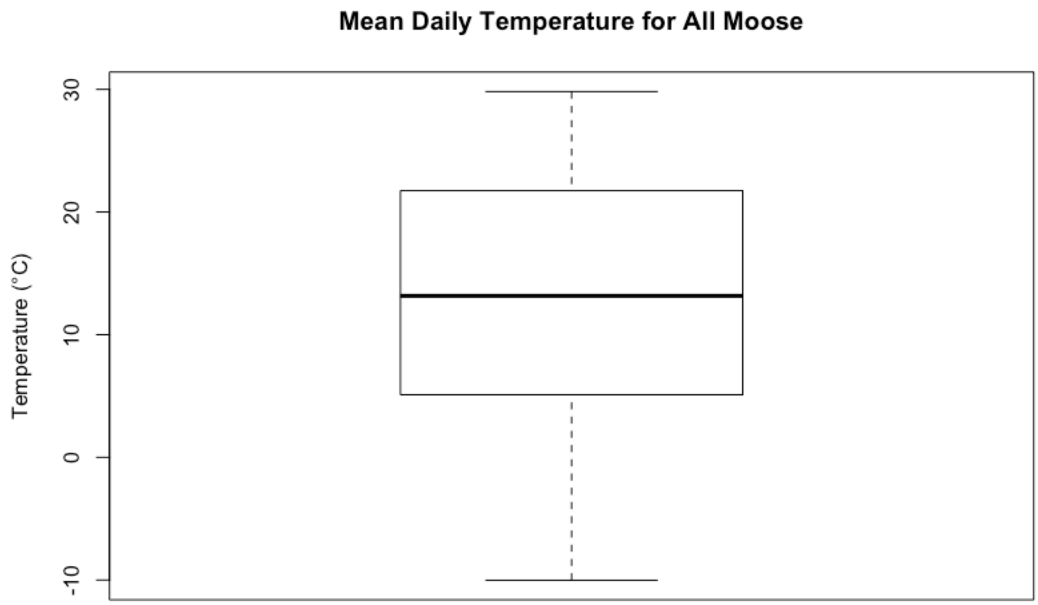


Figure 3. Log active peaks by mean temperature for each of the six moose. The red line is the linear regression for mean temperature per day and log active peaks per day.

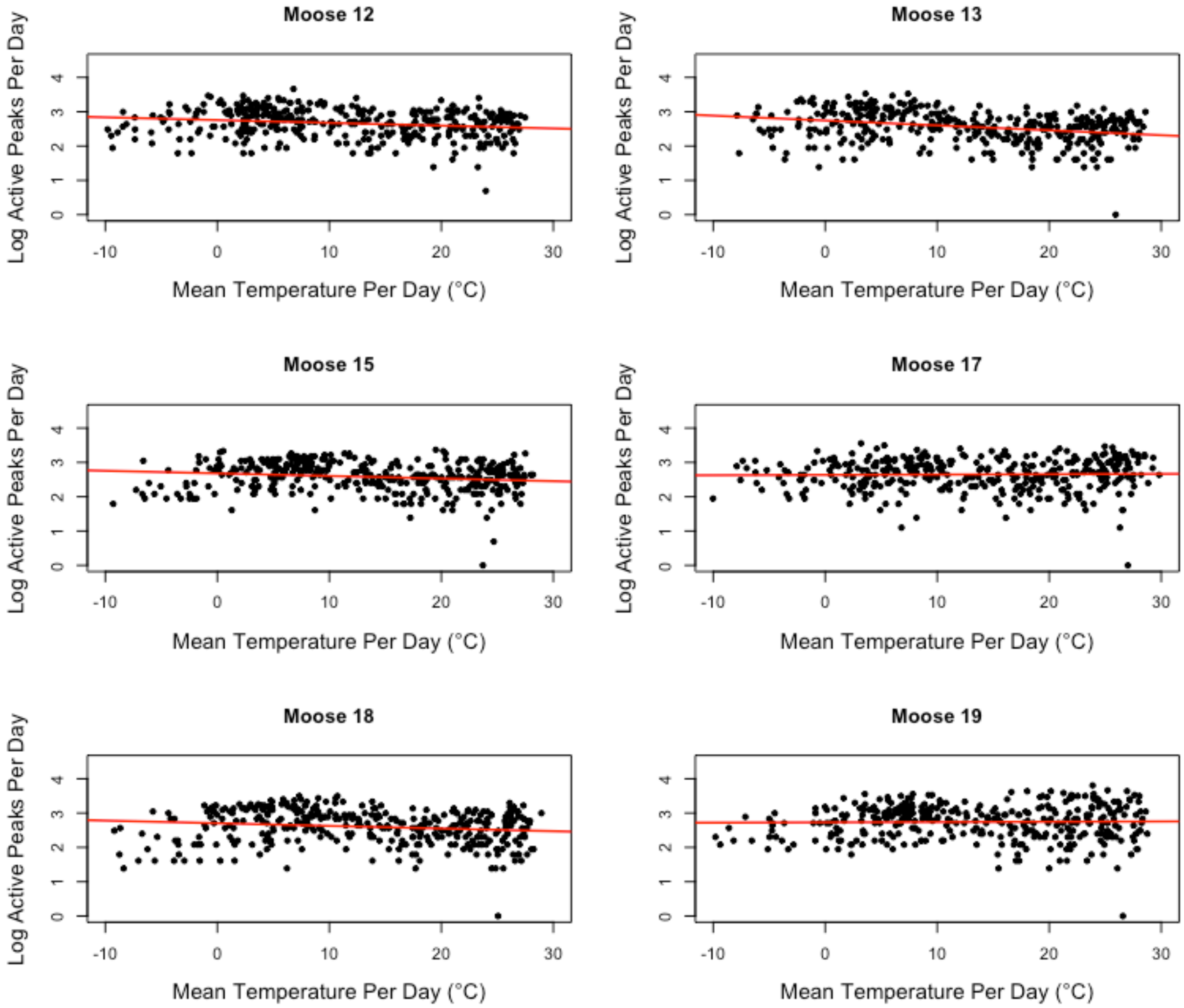
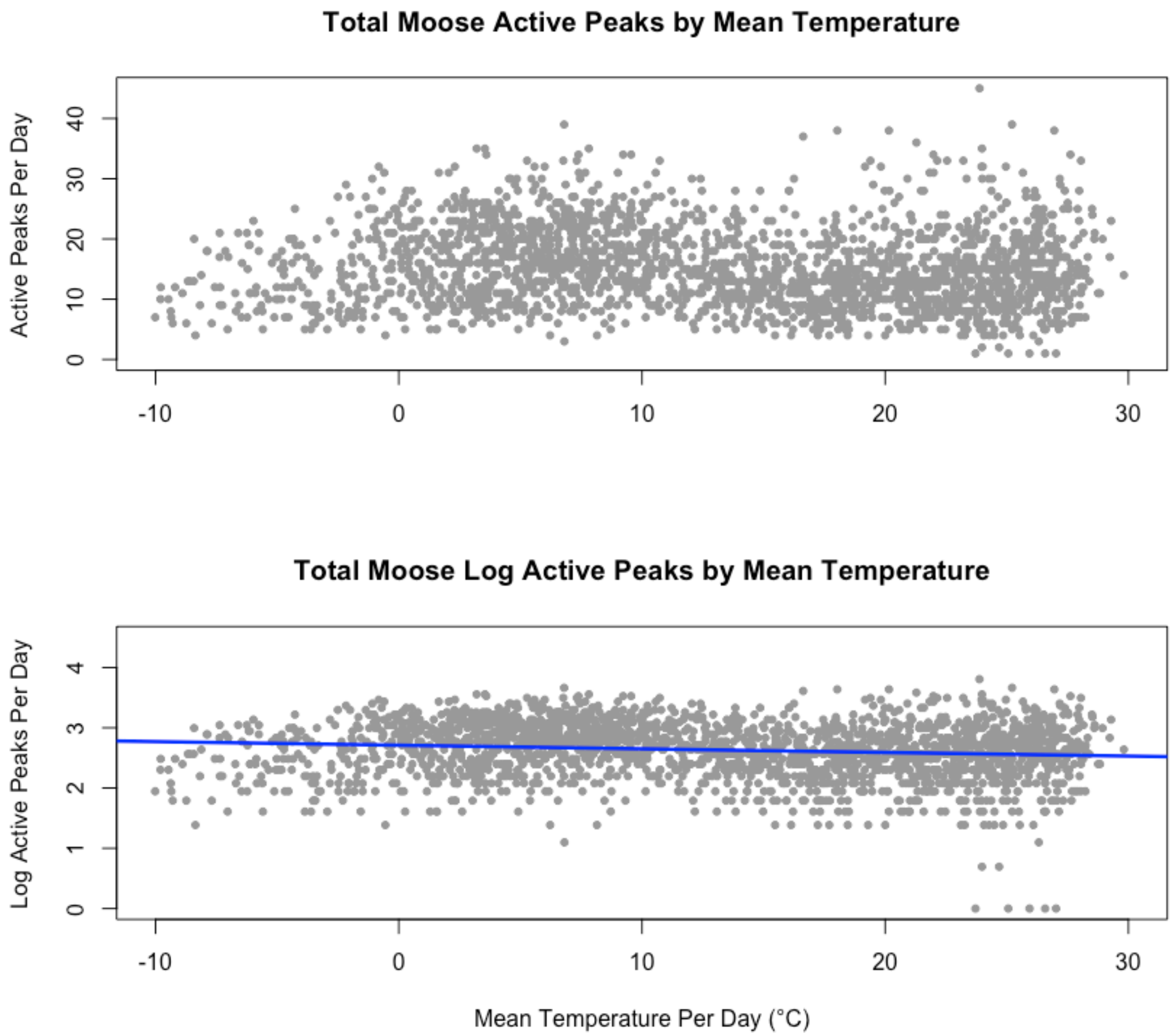


Figure 4. Active peaks by mean temperature for all moose (top) and log active peaks by mean temperature for all moose (bottom). The blue line represents the linear mixed-effects model for the log active peaks, with a slope of -0.006 and an intercept of 2.712. The five outliers are shown to represent the complete spread of the data but were not included in the analyses.



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