TIME ALLOCATED TO VIGILANCE: DOES ANTIPREDATOR BEHAVIOR DECREASE IN COLDER TEMPERATURES?

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A CAUTION TO THE READER

ASBTRACT

This thesis was designed to assess the effect an organism's environment has on its behavior. Specifically, the effect of air temperature on vigilance behavior was examined during the winter of 2016-2017. This study was completed by observing foraging woodpeckers remotely over high definition webcams as well as by hand filming. The study took place in Ithaca, New York as well as Waterloo, Ontario where filming was completed by a hand camera. Once the film was obtained, it was reviewed and vigilance rates were determined. These were obtained by measuring how many times an individual engaged in side to side head movement that was distinctly different from foraging and then dividing that by the total number of seconds spent at the feeder to get a rate of vigilance per second. This was then compared with air temperature and a linear regression was then completed to assess correlation. The results of this study were inconclusive. Due to conflicting results, one cannot say conclusively which hypothesis is correct. Alternatively, this study does lay a strong foundation for future work as well as for using webcams as wildlife monitoring technology. Moving forward in this field of study, a more controlled habitat such as an aviary would allow for more accurate measurement as there were many variables that could not be controlled in this study,

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INTRODUCTION AND OBJECTIVE

Optimal foraging theory states that all animals will feed in an optimal way (or as close to optimal as possible) to maximize their nutritional gains and minimize their nutritional losses (Pyke 1984). This topic, although well studied, is fundamental to understanding the behavior of birds especially in the cold and harsh winter environment of the boreal forest of northwestern Ontario. The optimal decision rule or more simply, an organism's best foraging strategy, will change as the conditions of its environment manipulates it. This will come into play in this study as environmental changes should be frequent and should alter normal foraging behavior.

In addition to optimal foraging theory, social foraging theory, the theory that animals will forage more efficiently in groups, plays a key part in this study (Giraldeau and Caraco 2000). It will not be directly measured in this study but a thorough understanding of the subject is critical. This is in part due to the reduced vigilance behavior that occurs in birds foraging in groups. One of the study animals, the downy woodpecker (*Picoides pubescens),* can be especially prone to this type of sampling error as it is a well-known social forager and is often found in both heterospecific and homospecific foraging groups,. This characteristic must also be considered.

Woodpeckers make for an ideal study subject because they are common, easily studied and their large (compared to body size) bill makes side to side head cocking (used to measure vigilance behavior) very observable. Downy, hairy and red-bellied woodpeckers, the three species used in this study (pictured at end of section) are predated on by predatory mammals such as weasels, cats and foxes as well as other birds such as accipiters and owls. During the winter in the study area, the primary predators will be cats, foxes, accipiters and the occasional owl. Although no predators were seen during filming, it is safe to assume that there were many around during the several weeks of filming.

The literature on this topic is very limited with only a handful of papers discussing how temperature relates to vigilance behavior. In the literature review, these studies will be discussed as well as the concepts of optimal foraging theory, social foraging and bird behavior in response to weather events. These topics will shed light on the background theory of this research and will allow for a clearer understanding of the results.

The null hypothesis is that there is no significant (alpha = 0.05) correlation between vigilance behavior (as measured by head cocking movement versus regular feeding movement) with average daily air temperature. The alternate hypothesis is that vigilance behavior while foraging will correlate with air temperature. This will be tested by measuring vigilance behavior at feeding stations and filming the birds while determining how many times they stop foraging and look for predators. This study will take place in Ithaca, New York (referred to as Sapsucker Woods Field Site) as well as in Waterloo, Ontario (referred to as Waterloo field site). If the null hypothesis is rejected then the alternative hypothesis that air temperature affects vigilance behavior will assumed. This realization would be of importance because it is an understudied aspect of foraging theory and could provide insight into the winter survival of birds as well as test the merits of this new methodology.

Figure 1. Downy Woodpecker (Left), Hairy Woodpecker (Middle), Red-Bellied Woodpecker (Right) Images retrieved from https://www.allaboutbirds.org/search/?q=woodpecker.

LITERATURE REVIEW

FORAGING

Optimal Thermal Regime

One of the most important aspects of this study is obviously the importance of the how temperature effects the behavior of organisms. This is strongly displayed when discussing optimal thermal regime. The optimal thermal regime is simply the range of temperature in which an organism can forage optimally (Kingma *et al* 2011). As an organism reaches a temperature that is either too high or too low they will not be able to forage optimally.

One critical aspect of optimal thermal regimes is the thermoneutral zone. The thermoneautral zone is defined by kingma *et al* as the range of ambient temperatures without a regulatory changes in metabolic heat production or evaporative heat loss of any organism. In simper terms, this is the range of temperatures that do not affect the behavior of an organism. This zone is affected by many things such as insulation qualities (fur, feathers, fat, clothing etc), body size, shelter and metabolism (Kingma *et al* 2011). Interestingly, an organisms location greatly effects their thermoneautral zone as tropical species and arctic species are effected very differently by changes in temperature. This was examined in 1950 by Scholander *et al* and it was found that large arctic mammals had incredibly large thermoneautral zones with little to no change in metabolism at temperatures as low as negative 40 degrees Celsius and as high as positive 30 degrees (Scholander *et al* 1950). Small arctic mammals and arctic birds also had increased resilience to metabolic changes but not nearly as much as the large arctic mammals. In the tropics, even a few degrees of temperature change can drastically impact an organisms metabolism. It was shown that even if the air temperature decreased 10 degrees Celsius it would greatly impact their metabolism (Scholander *et al* 1950). In the locations of this study, these effects should be somewhere in between these two extremes but as birds are still small organisms and have relatively high metabolisms there should be a strong correlation between their need for foraging and their air temperature.

Trade-offs

All organisms spend a large portion of their lives searching for the necessities of life: food, water, and shelter. During foraging, organisms are faced with a critical trade-off: stay hidden and remain relatively safe; or venture into the open and risk being predated upon. This trade-off was studied in great detail by Lima (1985) who found that organisms must ultimately leave shelter at many points throughout their lives in order to forage and breed. Lima (1985) outlined two different methods of foraging by the black-capped chickadee. The first, is characterized as feeding at a maximum rate while in the open in order to minimize total time spent exposed to predators; the second is gathering food and then retreating back to safety before consuming it to minimize exposure to predators. The effectiveness of these strategies depends on the total distance from the food source to the cover, as the farther the distance, the less food is consumed if the chickadee is flying back and forth between cover and food. In this study, when the feeder was close to nearby cover they carried the seeds from the feeder to the cover (Lima 1985). Conversely when the feeder was farther away they stayed at the feeder and ate more rapidly. This topic relates to the study because it provides a basic understanding of the trade-off between foraging and vigilance that is the essence of this research project.

Optimal Foraging Theory

Optimal foraging is the central theory of this study and plays a crucial part in understanding foraging. The most important part of this theory relevant to this thesis is the optimal decision rule (Sinervo 2006). This rule states that an animal makes decisions that will maximize its currency (whatever it is trying to obtain) under the given environmental constraints. This is what initially created optimal foraging theory (OFT).

Animals will forage in ways that are most beneficial to them and will maximize their gains while minimizing their losses. In this study, it is expected that in order for woodpeckers to forage optimally and efficiently on the coldest days they are going to sacrifice vigilance behavior for greater foraging intensity in order to maintain their metabolism.

Another key part of optimal foraging theory is the prey-size threshold which states that organisms will not forage on prey objects that take too long for them to capture and eat (Sinervo 2006). A study by Richardson and Verbeek (1986) examined how crows were constrained by size of potential clams as well as energy required to open the clams by dropping them from short flights. Of course, if there was not an abundance of clams this would not be a concern but in this scenario the crows can afford to be somewhat picky. The crows in this scenario choose clams that are as large as they can get without running into processing constraints. This threshold is shown in the study where it was seen that as clams approach 30 mm in size the rate of energy gains quickly declines to almost 0 at greater than 35mm (Sinervo 2006). But if the crows are too picky they waste too much time searching for food and not enough time consuming the clams. The optimal foraging rule for these crows is to accept all clams above 28.5 mm because clams at 28.55 mm have the highest energy gain. Although the largest clams (>35mm) represent a very small energy gain they are relatively rare and most clams will represent high energy gains and some will be optimal (Sinervo 2006). A similar study done by Meire and Ervynck (1986) was completed on oystercatchers and the results were essentially duplicated (Sinervo 2006). Also in this study, it was shown that foraging technique was taught by parents to their young so that their individual foraging strategy was passed down. These strategies were split into three categories: dorsal hammerers, ventral hammerers, and stabbers. Each strategy worked better for different types and sizes of mussels and were all profitable.

The final aspect of optimal foraging theory that will be discussed in this literature review is marginal value theory which specifies when an organism should leave a patch that it is foraging in. Although this does not directly apply to this study it would be negligent to completely ignore as it plays a very important role in optimal foraging theory. The example given in the Sinervo text is European starlings foraging in a study done by Kacelnik (1984). In this study starlings fly from their nest to foraging sites and then back to the nest to feed the young before foraging again. This is referred to as a round trip. Starlings are capable of holding several larvae in their bills at one time but as they hold more, their foraging becomes less efficient. So when should they stop? In the Kacelnik (1984) study an artificial feeder was used and the feeder provided fewer and fewer meal worms over time to simulate a depleting feeding site. The feeder was moved to determine whether or not starlings would adjust their larvae load with distance and it was shown that they in fact did. This means that starlings will leave a trip with less larvae when the trip is short but when the round trip time is longer they will leave with significantly more larvae. This shows marginal value theory at work because the starlings leave when it is no longer optimal for them to be there.

Understanding these fundamental aspects of optimal foraging theory provides the groundwork for looking at how vigilance behavior can play a role in foraging. If the crows for example were facing a risk of predation, they would not be able to so efficiently harvest clams. Vigilance behavior is in fact a constraint on foraging as the constant risk of predation requires birds to forage and be on the lookout for predators at the same time. It is because of this constant need to be on the lookout for predators that birds forage together which is what will be discussed in the next section.

Social Foraging

Social foraging is the theory that birds forage together in order to maximize individual gains due to the decreased risk of predation and increased chances of finding food. One of the study animals for this thesis, the downy woodpecker is a well-known social forager and understanding this tendency is important to understanding how downy woodpeckers forage. The other two woodpecker species do not engage in social foraging as much as the downy but all birds benefit from social foraging to at least some degree. The downy woodpeckers' proclivity towards social foraging was examined by Kimberly Sullivan in 1984 in a study entitled "the advantages of social foraging in downy woodpeckers" (Sullivan 1984). In this study woodpeckers were observed both when foraging alone and when foraging in multi-species flocks. When foraging alone, woodpeckers showed high levels of vigilance as measured by head cocking rates, and low feeding rates. This is due to the higher rate of predation when foraging alone which was seen by Page and Whitacre (1975) on raptors predating shorebirds. When foraging in multi-species groups woodpeckers were less vigilant and had higher feeding rates. The reason for this was cited as "downy woodpeckers spend less time on vigilance, they devote more time to foraging, thereby increasing their foraging efficiency" (Sullivan 1984). Social foraging is not a direct part of this study but it is important to note it because if woodpeckers are foraging with other birds then the vigilance rates will be lower than foraging alone, potentially skewing the data

VIGILANCE

Measurement

Vigilance behavior is the primary behavior being measured in this study and as such, a proper method of measuring it must be determined. There are many ways of doing this but the most effective method is to use side to side head movement and erect posture distinctly different from feeding. This is based on the literature by Sullivan (1986), Pravosudov and Grubb (1995), Fernández-Juricic *et al.* (2011) and Watson *et al.* (2007). In Sullivan (1986) and Pravosudov and Grubb (1995), head cocking movement was used to measure vigilance whereas Watson *et al.* (2007) vigilance was defined as being in the upright posture with neck outstretched, scanning the surroundings. Fernandez-Juricic *et al.* (2011) measured vigilance simply with scanning behavior. For this thesis, head cocking behavior was selected as the best method of accurately assessing vigilance behavior. This was because it provides an easily observed motion as opposed to general scanning behavior. Typically, vigilance behavior was measured as head cocks (or scans) per time unit resulting in an easily interpreted relative measure of vigilance.

Air Temperature and Vigilance

The literature on this topic is limited but there are several studies that have examined it with varying results. Ward and Low (1997) examined crows' vigilance behavior in urban areas and used many different variables including air temperature but found that it was not a major factor effecting vigilance behavior. Beveridge and Deag (1987) also examined sex, temperature and companions on looking-up and feeding in single and mixed species flocks of house sparrows (*Passer domesticus*), chaffinches (*Fringilla coelebs*), and starlings (*Sturnus vulgaris*) in 1987. Their results showed that looking up behavior (vigilance) in house sparrows and starlings increased with temperature due to reproductive reasons (searching for and defending a mate). On the other hand chaffinches scan more at lower temperatures in order to find other birds foraging in better locations. This study was done with flocks of birds, in a warm environment and not done in the winter so the results should differ from the hypothesis of our study.

In a slightly more comparable study, vigilance behavior was compared directly to air temperature by Pravosudov and Grubb by using tufted titmice in the deciduous forests of Ohio and it was found that temperature had a negative correlation with vigilance behavior due to the increased need for energy gains at low temperatures. It is important to note the range in temperature in this study was a low of -23 Celsius to a high of +14 degrees Celsius and it took place from December to February. An additional study was done by Conde and Vidal in 2007 looking at vigilance behavior in godwits and it was found that air temperature as well as presence of a predator (black-headed gull) were the two greatest factors effecting vigilance behavior. Interestingly, this study also found that the head movement associated with vigilance behavior may also be used for thermoregulation in godwits. This study was done in the summer during the warmest times of the year in Spain.

METHODS

Vigilance behavior was measured as side to side head movement which is distinctly different from routine foraging behavior. In order to assure that this is properly measured the woodpeckers will be filmed and the number of head cocks per second will then be determined. The filming was done primarily over high definition webcams as well as a few observations filmed by hand with high quality cameras. Temperature values will be obtained with online temperature information. Temperatures will be averaged out for 12 hours previous to time of observation. This was done in order to get a more accurate measurement of the conditions that the birds are facing. The birds were told apart by a series of indicators: location, band, sex, physical characteristics and species. The two birds from the Waterloo feeders were differentiated by sex and were the only regularly occurring woodpeckers in the area. The Sapsucker Woods woodpeckers were told apart by species and gender but there were also several that were banded and several that were not. Additionally, some birds had particular physical characteristics such as an eye infection (bird not used due to this). Once the birds were identified and their behavior was observed, a vigilance rate must be determined. This was done by determining the number of vigilance movements per second. The results were graphed with temperature on a standard scatterplot and a regression analysis was completed. In order to determine the significance of these scatterplots the P value was compared with the alpha (0.05). The results of the regression, the equation of the regression line and the associated p value are all included on the graph.

RESULTS

Six of eight birds showed that their vigilance rates increased along with temperature as demonstrated by a positive trend line (Figure 2-5). But upon closer inspection , the data is not strongly correlated. Additionally, the p values for all birds with the exception of the female downy from Waterloo (DOWO-F-W) were below the desired value of 0.05 indicating that the findings are not significant. These values can be seen on the below graphs. The birds were also grouped together in figure 5 which resulted in another insignificant p value and low R^2 value but interestingly, when all birds were combined it was significantly closer to being significant than most.

Additionally, the data was also compared by species and by sex. There was little difference between sex with values of only 0.057 vigilance movements per second for males and 0.055 vigilance movements per second for females. Furthermore, there was some difference between species. Downy woodpeckers, were the least vigilant species with an average vigilance rate of 0.044 vigilance movements per seconds, this was followed by hairy woodpeckers with a rate of 0.061 vigilance movements per seconds and lastly, by red-bellied woodpeckers who had a foraging rate of 0.08 vigilance movements per seconds. In the following discussion section, the possible implications of these findings will be discussed as well as a section on interesting and distinct behaviors observed.

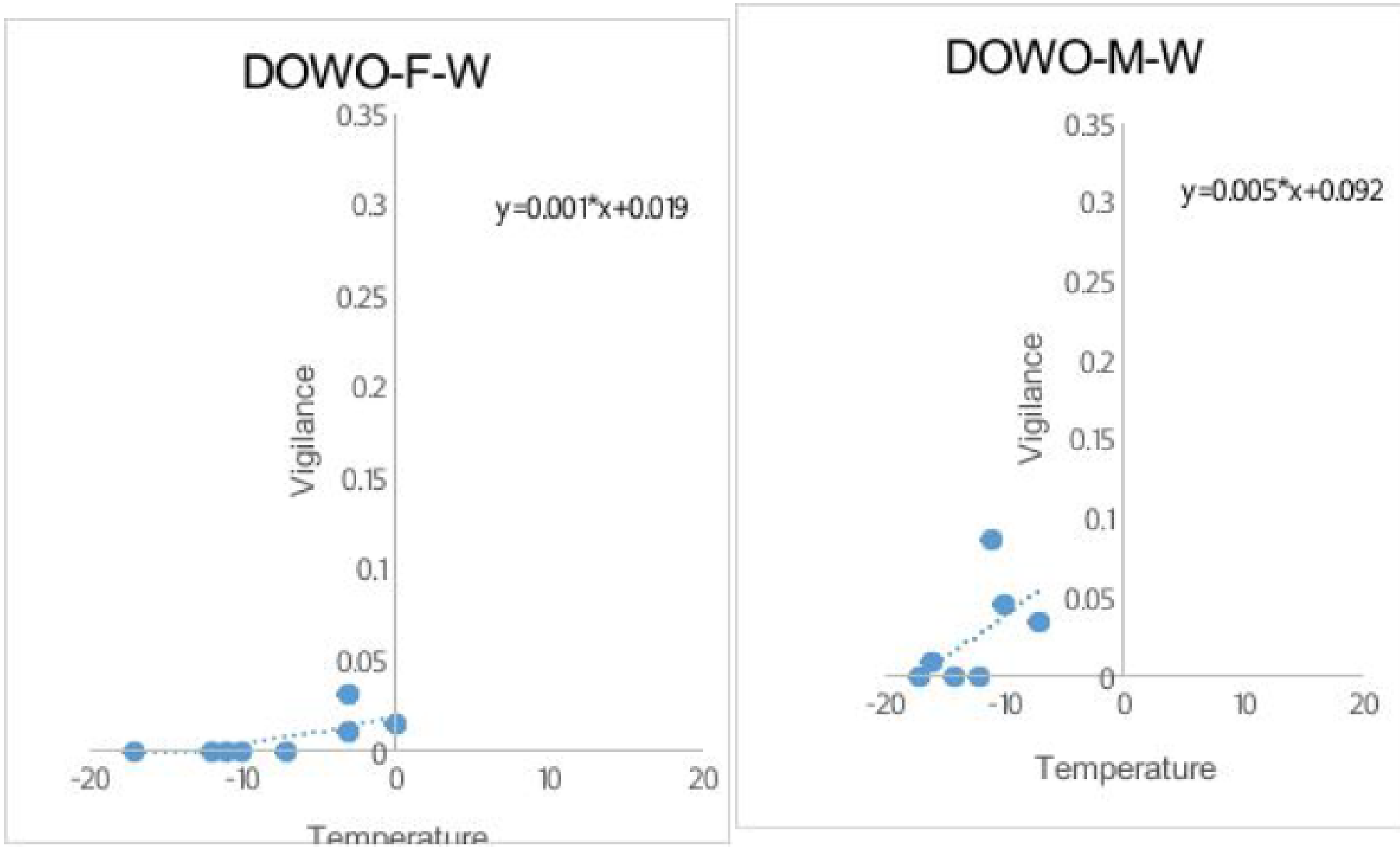

Figure 2. Air Temperature Compared to Vigilance Rates of Downy Woodpeckers From Waterloo Field Site

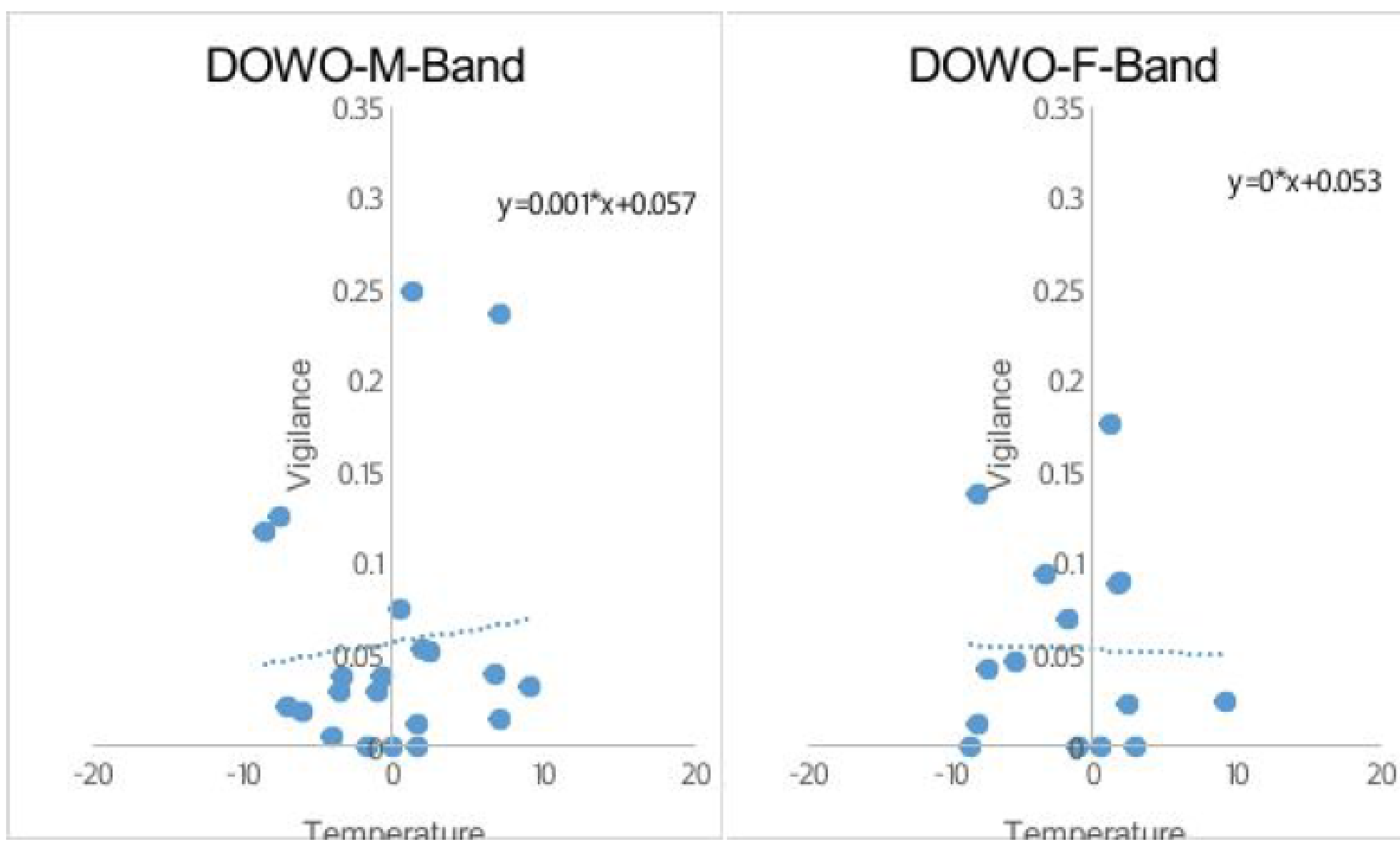

Figure 3. Vigilance Rates Compared With Temperatures of Downy Woodpeckers From Sapsucker Woods Field Site

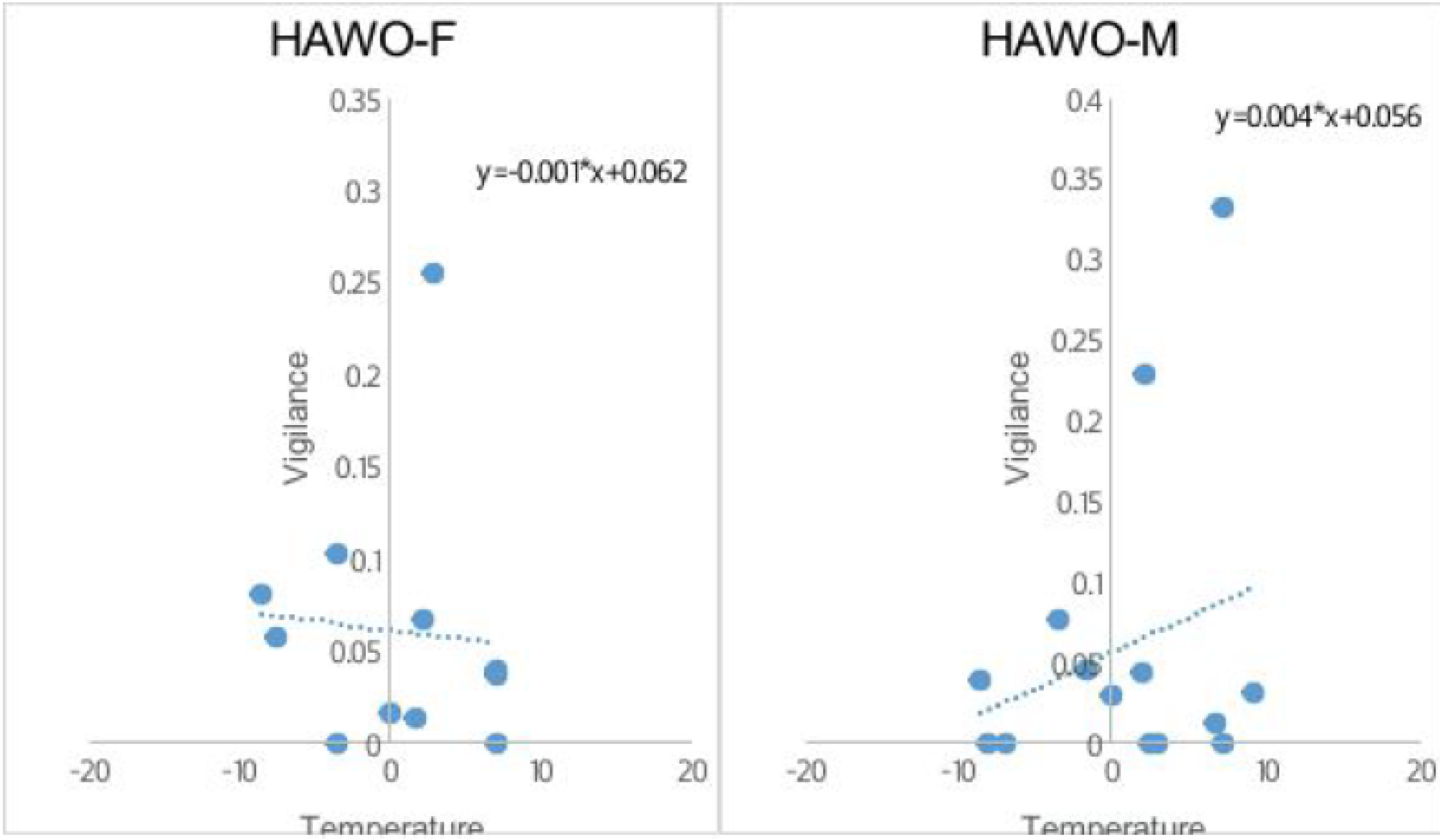

Figure 4. Vigilance Rates Compared With Temperatures of Hairy Woodpeckers From Sapsucker Woods Field Site

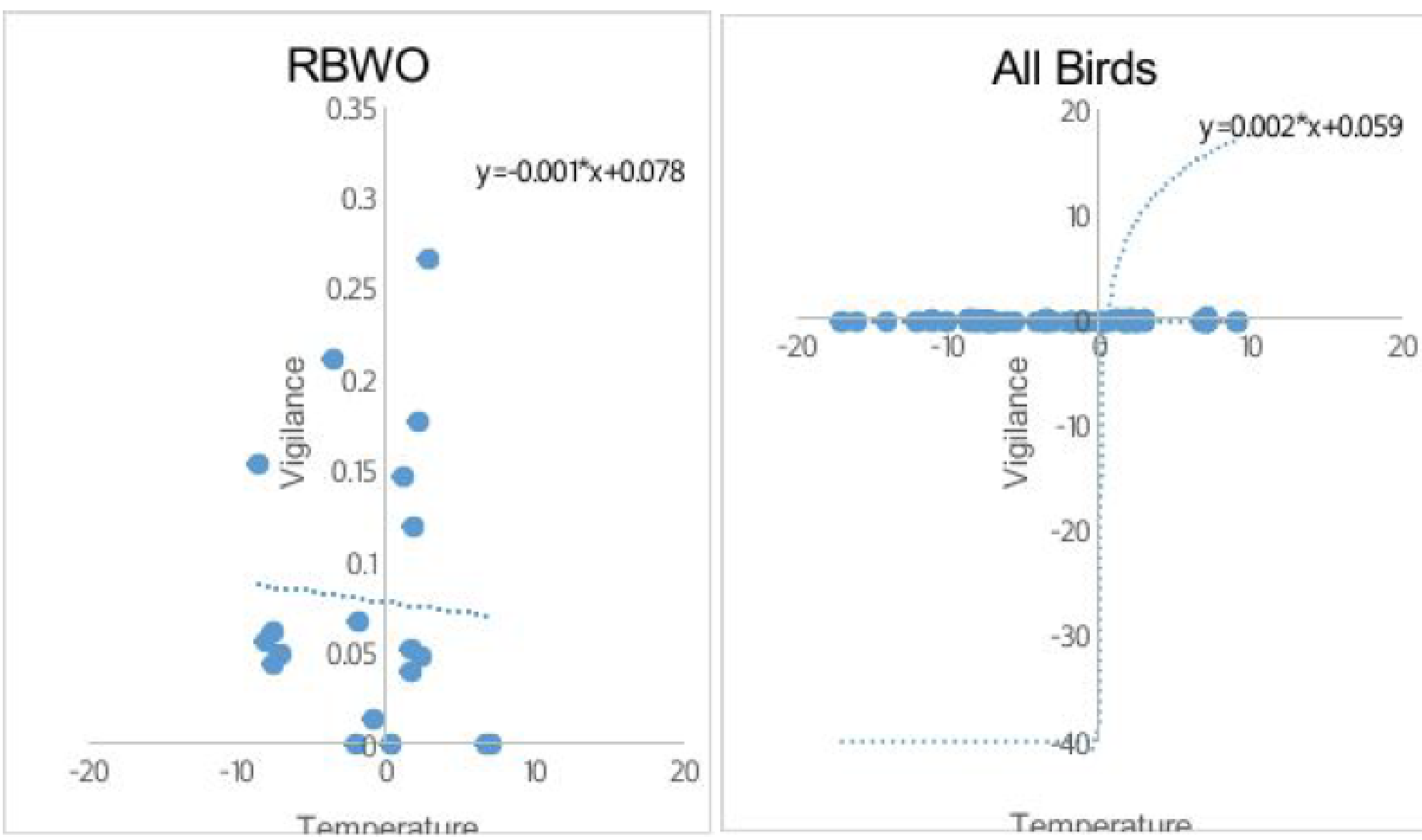

Figure 5. Air Temperature Compared to Vigilance Rates of Red-Bellied Woodpeckers (Combined) From Sapsucker Woods Field Site and All Birds Together

DISCUSSION

The results of this study ultimately proved to be inconclusive. As a whole, the linear regression showed that there was not significant correlation between air temperature and vigilance. Although there was one bird (DOWO-F-W) that showed a strong correlation (both high R^2 and significant P value), the rest of the birds did not; with very low r squared values and insignificant p values. One of the major problems with the study was that there were too many uncontrolled variables. There could have been unknown predators present, wind could have played a large factor in foraging behavior and social foraging could have skewed the results. If this study were to be repeated, the birds would be in a controlled environment like an aviary where the variables would be more easily controlled. Perhaps adding a fake predator periodically and looking at the birds associated vigilance behavior would add another important level to the study. In addition to this, the sample size may have been too small. Initially, there were 11 individual birds in the studies but three were removed as outliers. One had a visible eye deformity, one only showed up to the feeder once and another from the Algonquin park feeder did not have high enough video resolution to determine an accurate measure of vigilance.

Although the primary purpose of this study was not to determine the differences of foraging rate between species and sex, the results will none the less still be discussed here. When comparing the foraging rates between the two sexes, there was only a 0.002 difference between males and females. This is to be expected as there is similar pressures for both genders during the winter, but perhaps this would be different during the breeding season. Additionally, the different woodpecker species were also compared, which produced the most interesting results of the study. The downy woodpecker had the lowest vigilance rate of any of the species examined. This is potentially due to their small body size and increased nutritional needs when faced with cold temperatures. When species body size increased from downy to hairy and lastly to red-bellied, vigilance actually increased. This was unexpected as some might believe that a small body size would result in a large amount time being spent vigilant. Other possible explanations for this are that the downy woodpecker practiced social foraging more than the others which has been well documented in the literature. It could have also simply been a coincidence but nonetheless, it is an interesting observation that could lead to future study on the relationship between body size and vigilance of birds. When all birds were examined together, the correlation was marginally stronger, but was still not significant enough to draw any conclusions.

Outside of the actual study itself, there were many interesting behaviors observed which are worth discussing. Firstly, certain individual birds foraged differently than others of the same species. For example, the female hairy woodpecker from the Sapsucker Woods field site foraged on the feeding tray beneath the feeder far more frequently than any other bird. Conversely, the male hairy almost always flew directly onto the suet feeder as did most of the downy woodpeckers. The male and female red-bellied woodpecker also behaved very differently from each other. The male red-bellied woodpecker was the most aggressive bird in the study frequently chasing other birds off the feeder whereas the female was fairly docile and typically only foraged when no other birds were present which resulted in it appearing very few times. The downy woodpeckers proclivity towards social foraging was also seen in this study, frequently foraging with other birds on the same feeder as them as well as being surrounded by other birds on the platform. One of the most interesting aspects of observing large amounts of bird foraging was seeing theory in motion. The most obvious example of this was prey handling time. Typically, birds would forage for a period of time but when a particularly large morsel of food was found, the birds almost invariably left the feeder. This was mostly done by hairy and red-bellied woodpeckers which can take larger food items than the downy woodpeckers. These observations, if quantified would also provide interesting research questions moving forward.

CONCLUSION

Although the results of this study were not conclusive, we believe that there was still valuable knowledge and experience gained from this study. The results did not conclusively ratify the hypothesis but they also did not completely disprove it. Many of the birds did follow the expected trend so there is certainly merit for future study on the topic. If more variables were controlled for and there was a larger study group, the relationship between foraging behavior and air temperature could become more clearly illuminated.

Additionally, the validity of using high quality webcams to observe avian behavior was also examined and proven to be quite effective. The only major shortcoming of the webcams is their narrow field of view. This could be alleviated by setting up an array of webcams or using more expensive 360 degree view cameras. This would allow for predators to be viewed and subsequent study observations marked as having a predator present. Furthermore, webcams provide relatively low levels of intrusion into organism's lives and are fairly cost effective. We believe that a combination of bird feeders and webcams provide not only a cost effective method of observing wildlife but also an accurate method. As technology allows for more and more accurate observation of wildlife, studies such as this pave the way for future studies done by remote cameras.

The inconclusive results, are nonetheless still results and show that there is potential for further studies on this topic and perhaps a reader will find that the methodology and recommendations from this study will assist them in setting up their own study.

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